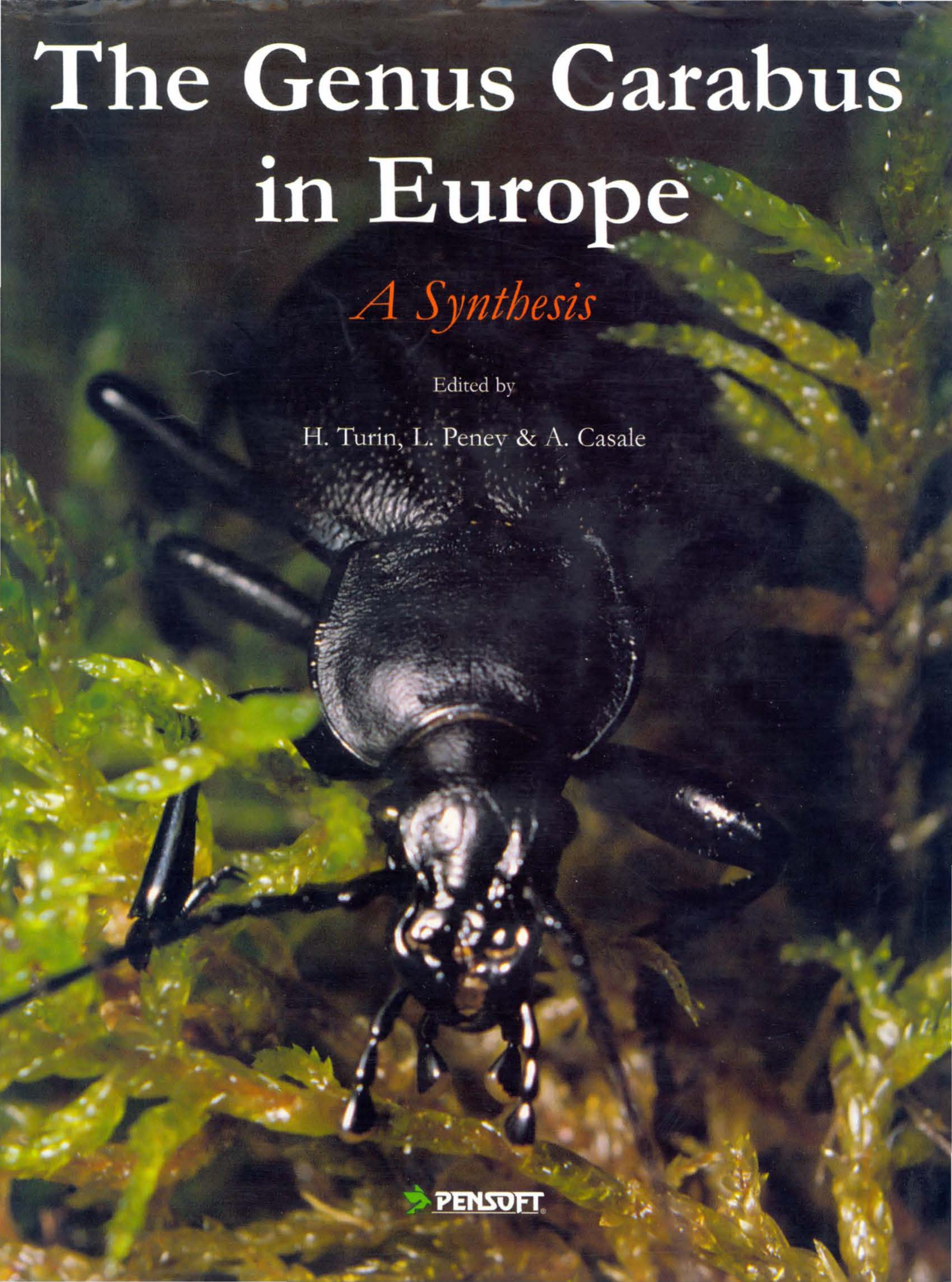
The Genus Carabus in Europe

A Synthesis

Edited by

H. Turin, L. Penev & A. Casale



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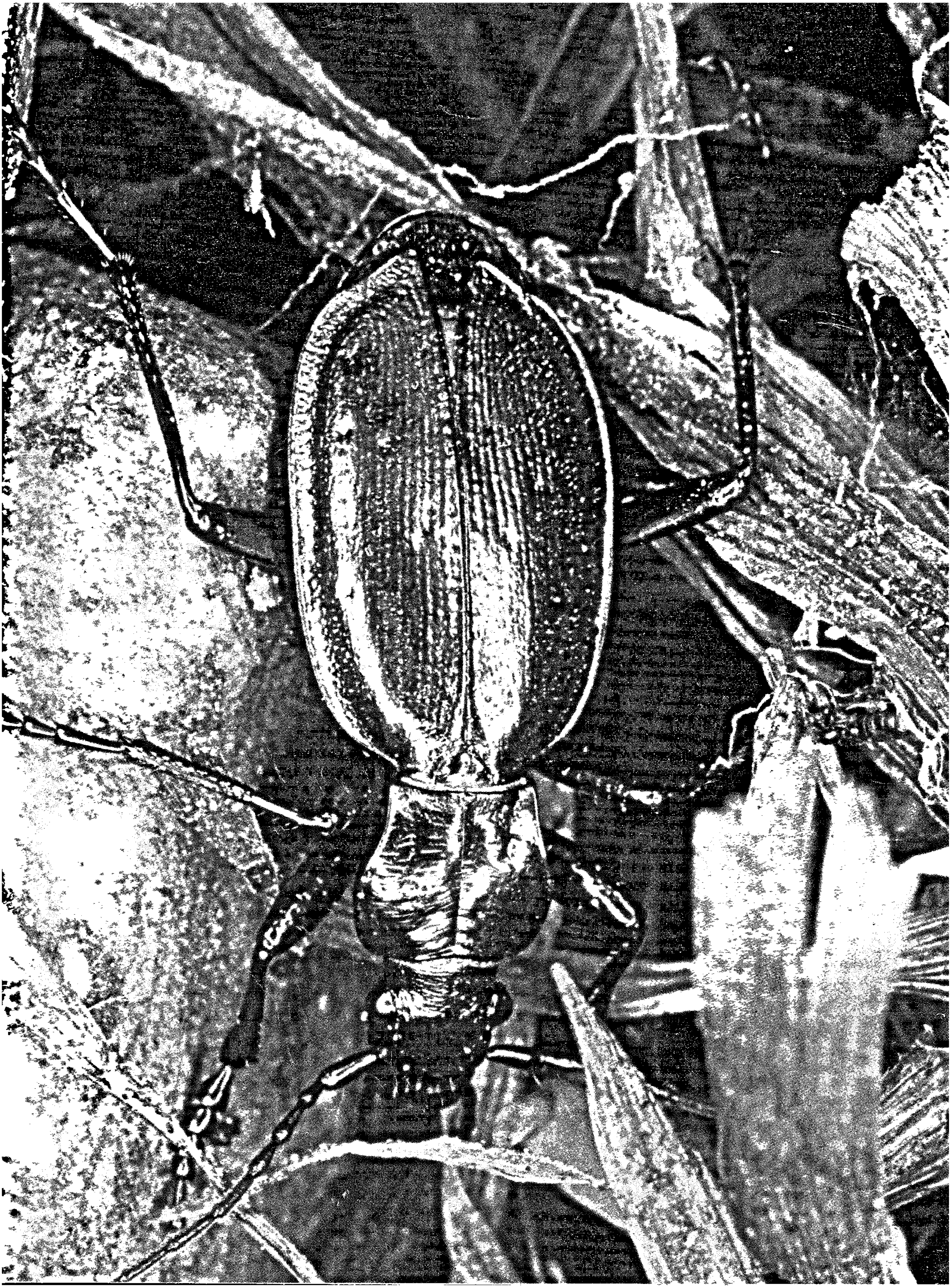

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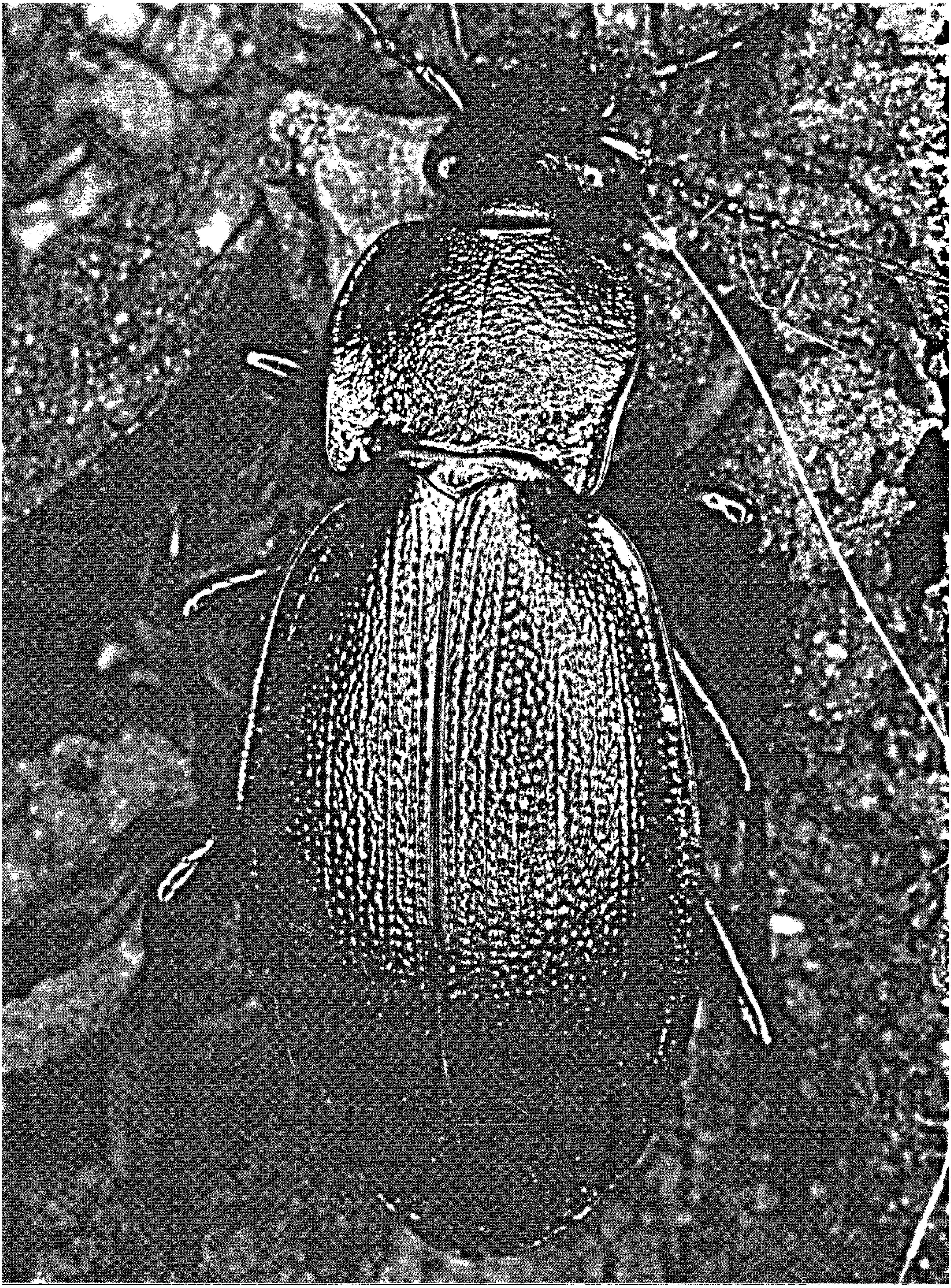
Dedicated to the memory of our colleague and friend
Professor Oleg Leonidovich Kryzhanovskij
(28.05.1918 – 15.06.1997)



Preface

G.E. Ball

'Carabus' – for the neophyte collector of insects, this word conjures images of large, showy beetles of magnificent colors and elegant forms. To the seasoned carabidologist, the name recalls memories of remote forests and high mountain slopes difficult of access, and the excitement of finding for the first time a rarely collected, or even undescribed, species. These beetles are creatures of wonder and because of their visceral attractiveness as well as marked diversity both specific and infraspecific, they figure prominently in private collections, as well as in the holdings of public museums of natural history.

Derived from the Greek noun *karabos*, meaning 'horned beetle', the Latin name *Carabus* was applied by Carolus Linnaeus, in the Systema Naturae, Editio Decima (1758), to one of 21 genera, assigned to the Order Coleoptera, in which he arranged the several hundred beetle species known to him. Evidently, the 'horned' part of the Greek name applied to the moderately long, slender antennae, characteristic of carabids, rather than to the unarticulated cuticular projections that are characteristic of many scarabaeids.

The 31 species of *Carabus* were arranged in two groups: *'Majores'*, or the big ones, and the *'Minores'*, or smaller ones. A uniform assemblage within the Coleoptera, the Linnaean *Carabus* formed a sound base for the Family Carabidae, established by Pierre Andre Latreille, in 1802, at the same time as he introduced the family category to animal classification, generally. The nine species of the '*Majores*' became, a decade later, in the accomplished hands of Franco Andrea Bonelli, the basis for the Simplicimani (later, tribe Carabini) in the family Carabidae, with the species of the *Minores* distributed among other suprageneric groups recognized by that astute systematist. The genus *Carabus*, essentially as we understand it now, was established in 1801, with recognition of *Calosoma*, a second genus for inclusion of part (two species) of the Linnaean *Majores*. To the remaining seven species, the name *Carabus* was restricted. Under the intense scrutiny of primarily European coleopterists, knowledge of *Carabus* diversity grew through the 19th and 20th centuries, as knowledge of biotic diversity expanded, generally.

A Holarctic genus of about 800 species grouped in 114 subgenera, *Carabus* is primarily Palaearctic in distribution, with only 11 species confined to the Nearctic Region. This book is about the 132 species that inhabit Europe. The Checklist, comprising Chapter 2, shows that this number of species is a distillate of more than 2000 specific and infraspecific taxa that have been named, in an effort to capture the divergence represented by this genus in the European area.

Although almost all of the European species of *Carabus* were known by the end of the 19th century, during the 20th century, some 1300 new names (infraspecific epithets, many invalid because they were proposed to represent infrasubspecific entities) were published, giving the impression that the genus was a playground for those suffering from an acute case of 'the *mihi* itch', *i. e.*, the desire to name taxa, primarily for self-gratification. Most of these names survive now as junior synonyms, best forgotten.

While the wheels of the taxonomic enterprise, during much of the 20th century, were spinning in the dust of arid infraspecific description that tended to obscure knowledge of species and that discouraged many able carabidologists from studying seriously the taxonomic aspects of this protean genus, other types of investigation of *Carabus* diversity and divergence were being conducted: nationally based regional treatments, primarily for identification of members of the local fauna; description and systematization of larvae; determination of karyotypes; phylogenetic analysis, using molecular as well as structural features; determination of habitats, life histories, food habits, and population dynamics; community composition and structure; and correlation of distribution patterns with past geological events to provide a temporal dimension for understanding diversity. Most recently, considerations of conservation have assumed considerable prominence. This book is about these multifarious aspects, placing this otherwise widely scattered information between two buckram covers, so that one can gain rapidly and easily an appreciation and understanding of this quintessential group of carabid beetles.

The act of compiling the vast array of information contained in this book would be a daunting task for a single individual. Analyzing the data would require much of the career of an able, determined systematic entomologist. But

◀◀ *C. **depressus lucens*** Schaum. Italy, Cottian Alps (C. Valcavera). Photo by A. Vigna Taglianti (front page).

◀ *C. **violaceus picenus*** A. & G.B. Villa. Italy, Latium (Rome). Photo by A. Vigna Taglianti.

these tasks were achieved within a few years because of a spirit of cooperation that drew together workers (three editors, 14 authors, and 38 additional contributors from over 20 European nations), each of whom contributed to the enterprise some unique aspect of *Carabus* lore. Indeed, cooperation is the method being used increasingly to achieve broadly conceived, complex tasks.

This particular cooperative venture seems to have grown out of the association of carabid specialists drawn together through the peripatetic European Carabidologists Meetings, the first of which, organized by Piet den Boer, and held at Wijster, in The Netherlands, in 1969, primarily to discuss the then rapidly expanding knowledge of ecological aspects of European carabids. The ending of the Cold War facilitated discourse and joint action between Eastern and Western European carabidologists.

As this volume shows, European carabidologists have brought knowledge of *Carabus* a considerable distance from what was known about the group in the 18th century. Hopefully knowledge of the genus is through the first stage of systematic endeavor (i.e., concentration on basic taxonomic description), so that investment of the taxonomic enterprise in naming yet more intraspecific variants based on features of adults, will be reduced, though the possibility of discovery of new species or subspecies must be acknowledged. Discovery of species known only as fossils may be expected, and they will require description. Further, stage one study of the immature stages will be important.

This book is primarily an endeavor in second stage systematics, being an extensive revision with a base in evolutionary theory, and an abundance of other information, much of which is based on ecological theory about species level divergence. It will provide the basis for third stage analyses, which involve formulation of more sophisticated phylogenetic hypotheses and their testing, in part with extensive use of molecular and genetic techniques, more detailed studies of ethology and ecological aspects, and studies of interactions with one another of sympatric species. Having effectively removed the European taxa of the genus *Carabus* from the hands of the describers, this synthetic treatment offers this genus to those seeking taxa for investigation of biological phenomena. We may hope that this offer is seized upon, and that the name *Carabus* becomes, as it should, as well known in biological circles as is the name *Drosophila*.

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Our late colleague and co-author
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He was responsible for the basis of the
key to the adults and gave many helpful advices
during the first stages of the project.
[3]

[The numbers refer to the numbers of the chapters]

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SPECIAL PART

GENERAL PART

Chapter 1 Introduction

H. Turin, L. Penev & A. Casale

1.1 Why Carabus?

Biologists working on birds, mammals or other vertebrates can look back on a relatively long tradition of biological, ecological and environmental research. For some groups basic knowledge was already available from recreational biology, such as bird watching or hunting, which in fact preceded professional faunistics, ecology and conservation biology. Many eighteenth and nineteenth-century vertebrate biologists were dedicated hunters who, when sent abroad by museums of natural history, often had strict orders to shoot everything they saw for incorporation into the collections. Also, entomologists focussed mainly on enrichments of collections, which can be considered a kind of hunting, and on taxonomy. A good example was Charles Darwin who started his biological career as a highly active beetle collector. Fortunately, in most cases the catches of entomological collectors have ended up in collections, carefully managed by scientific institutions, thus providing a historical 'database'. These collections contain specimens dating from the middle of the 19th century or earlier. The information on the labels allowed the faunistically and biogeographically interested coleopterists, like Breuning, Holdhaus, Horion, Jeannel and Lindroth, to produce the first distribution maps and draw their conclusions. Today, the value of historical data for analysing changes in species' distribution, especially with respect to environmental and conservation biology, is obvious and generally-recognised.

A severe minus for entomological studies in general is that, compared to vertebrate groups, the number of entomologists is low and the number of species yet to be described and studied is very high. Recent estimates mention between 10 and 30 million species worldwide (Erwin, 1982, 1991). As a result, just a few insect groups have a reputation of being well-studied. In first place of course the butterflies (Lepidoptera, Rhopalocera) not at least because of their undisputed beauty, but also dragonflies (Odonata) and hoverflies (Diptera, Syrphidae), mainly for the same reasons. For the general public, most beetles are considered less attractive and often incorrectly simply referred to as 'bugs'. Nevertheless, a small number of beetle families have been relatively well-studied, some for economic reasons, such as damage in agriculture, e.g. some Curculionidae (weevils) and Chrysomelidae (leaf beetles), others for their diverse and bizarre morphology or ecology, such as Lucanidae (stag beetles), Scarabaeidae (dung beetles) and Cerambycidae (longhorns).

Within the beetles, ground beetles have always had a special position. Biologists studying surface dwelling fauna frequently encounter carabids and many collect them, even if they are not the subject of their special interest. As a result, carabids are relatively well represented in collections and consequently well-founded studies can be realized. From the middle of the 20th century systematic and standardized pitfall trapping enabled ecological, life history and population biology studies. At present an enormous amount of literature, based on carabids, is available. A rapidly growing number of national or regional checklists, catalogues and atlases have provided a sound basis for faunistic studies. Since 1969, every three years there has been a meeting of European carabidologists with published proceedings. However, even for this 'well-studied' group, there are still enormous gaps in our basic knowledge. For most genera the distributions of the species and habitat preferences are insufficiently known, and often a relatively low number of larvae have been described, mainly because only very few specialists dedicated their research to just one group with sufficient thoroughness.

In this respect, the genus *Carabus* is a remarkable exception and perhaps the only large genus of all Coleoptera that can compete in popularity with butterflies. One of the most significant main features is the on average large size of the species. The smallest species are *C. cristoforii* and *C. nitens* with specimens of 12-13 mm and the biggest are representatives of the subgenus *Procerus* reaching up to over 50 mm. Many species are between 20 and 30 mm long, making them difficult to be overlooked in the field by hand-sampling collectors. Many *Carabus*-species are of fascinating beauty and therefore notable items for collections. This is illustrated in the big insect fairs where *Carabus* is represented in most beetle stands. As a result, a rich faunistic material is available for most species, at least for the European territory.

Moreover, a number of workers have developed methods to rear species, which has added a great deal of knowledge

◀ ***C. glabratus*** Paykull. France. Photo by Th. Heijerman.

to the biology of many species (i.e. Hůrka, 1973; Malausa, 1977; Sturani, 1962, 1963, 1964, 1969). Pitfall trapping and other methods such as radioactive labeling in order to follow specimens in the field and methods of molecular research have also significantly contributed to our knowledge.

In this work a comprehensive synthesis is presented for the genus *Carabus*, possibly serving as a model for other beetle groups. An inventory of the most important gaps in knowledge is also presented, with suggestions for future research, especially in the field of using *Carabus* spp. as indicators for environmental monitoring and other studies.

1.2. Some problems and 'solutions'

The first basis for a cooperation concerning a thorough study of *Carabus*, was found in combining the complementary and huge faunistic databases of Western Europe and the European part of the former Soviet Union respectively, built and owned by the first two editors. With these data we considered it possible to carry out a basic biogeographical analysis, if possible involving phylogeny, physical and ecological parameters (see Penev & Turin, 1994). From the beginning, it was clear that the project could only be successful if a number of specialists would contribute to the chapters such as Keys to adults and larvae, Ecology, Phylogeny, Conservation etc. We realized that this, almost inevitably, would introduce different, or even controversial, opinions within the framework of the book.

In *Carabus* classification, we faced rapid developments during the last decades. For Europe, this started with a detailed study of the Italian *Carabus* (Casale *et al.*, 1982) and the authoritative world list of Deuve (1991). This list was soon followed by a preliminary checklist and atlas for Europe (Turin *et al.*, 1993), a new version of the world list (Deuve, 1994) as well as a world list with distributional annotations by Březina (1994, 1999). Also studies of larvae played an important role (Arndt, 1985; Makarov, 1992). From these works, it became clear that absolute consensus with respect to classification and (sub)species level taxonomy, within the time schedule of the project, would be unrealistic. For instance the opinions of taxonomists working on larvae or adults, with different methods, such as anatomy, morphometric or molecular analysis, turned out to be quite different and sometimes in disagreement with each other. Therefore, we had to look for some pragmatic solutions.

1.3. Nomenclature in Checklist, Key to the adults and Species accounts

The taxonomic basis of the present book is a checklist, presenting all taxa and their synonymy, thus providing access to other sources.

The *Key to the adults* follows this checklist where possible with respect to classification, but it has been considered acceptable to choose practical solutions when combining the keys from Eastern and Western Europe into one European key. For practical reasons it was sometimes necessary to combine representatives from different subgenera into one key.

In the *Species accounts*, the checklist has also been followed. In fact the *Checklist* (Chapter 2), the *Key to the adults* (Chapter 3) and the *Species accounts* (Chapter 5) follow the same classification, nomenclature and numbering of subgenera and species, because these three chapters form the 'backbone' of the *Special Part* and also of the entire book.

1.4. Key to the larvae

The *Key to the larvae* follows it's own pattern because it is a scientific subject 'under construction'. About 43% of the larvae of the ca. 132 European species can be identified directly by the key (Chapter 4). An additional 31% can be identified by allopatric distribution. The key does not cover 26% of the larvae. Although much better than for most coleopterous genera, this made it unpractical or even impossible to apply the same strict rules concerning classification as to the systematic chapters.

1.5. General chapters

In the *General Part*, the Chapter 8 *Biogeography* follows the classification as proposed in the *Checklist*. For instance, when calculating the distribution of endemism, the taxonomic basis of the resulting figures should be clear. For the Chapter 7 *Phylogeny*, the 'under construction' status also rules. As molecular methods in taxonomy became more generally used, opinions evolve so rapidly that fresh results, as presented here, cannot be expected to match completely with the more traditionally based taxonomy. The chapters *Biology and Ecology* (Chapter 6) and *Conservation Biology* (Chapter 9) have a more thematic approach and are largely independent of taxonomy. Nevertheless, these chapters also strictly follow the same nomenclature.

1.6. Subspecies

To facilitate searching for information, subspecies have been treated in two places in this book in different ways, that is in the *Key to the adults* and in the *Species accounts*. In the *Key to the adults*, the subspecies have been presented with emphasis on their taxonomic features. Here the main goal was to provide as much information as possible in order to facilitate the identification of specimens from various places and habitats, with attention to the various forms. In the treatment of the subspecies in the *Species accounts* we omitted all taxonomic information, but the geographical information is often more detailed and extended. Also the presentation of the subspecies is considered a valuable addition to the maps and to the written distribution information arranged in 'political' units. Combining all information concerning subspecies in one treatment would be less clear and certainly less accessible.

The reader will appreciate that, following our intention to use only well-established subspecies, their number is reduced considerably. In the *Checklist*, a list is presented of all forms and synonyms found in the literature. The authors are well aware that certain choices may be questionable and that views may change rapidly, especially with respect to the increasing use of molecular techniques in taxonomy.

1.7. Mapping

A significant part of the work for this book concerned compiling the distribution maps in the *Species accounts* (Chapter 5). The provisional maps for Europe, that were first presented in Turin *et al.* (1993), generated a number of additions and corrections (mainly by Th. Deuve, M.L. Luff, J. Trautner, and F. Weber, *in litt.*), all of them valuable improvements. Moreover, a number of detailed new atlases were recently published, such as those for Northern Ireland (Anderson *et al.*, 2000), Britain (Luff, 1998), the Netherlands (Turin, 2000), France (Forel & Leplat, 1995; Coulon *et al.* 2000), Iberian Peninsula (Forel & Leplat, 1998) and former Yugoslavia (Pavicevic & Mesaros, 1999, released on cd-rom), as well as Red Lists, checklists and catalogues, e.g. for Bulgaria (Guéorguiev & Guéorguiev, 1995), Byelorussia (Alexandrovitch *et al.*, 1996), Canary Islands (Machado, 1992), Carinthia (Paill & Schnitter, 1999), Czechia & Slovakia (Pulpan & Hůrka, 1993), Flandria (Desender *et al.*, 1995), Germany (Trautner & Müller-Motzfeld, 1995; Trautner *et al.*, 1997), Iberian Peninsula (Zaballos & Jeanne, 1994), Italy (Vigna Taglianti, 1993), Moldova (Neculiseanu & Matalin, 2000), the former Soviet Union (Kryzhanovskij *et al.*, 1995), and for Anatolia (Casale & Vigna Taglianti, 1999). Using these sources many maps were improved significantly.

The European distribution maps should be considered primarily as an outline of the main area of distribution. To illustrate this approach one may look at the map of *Carabus granulatus*, one of the very few species that covers most of Europe and the distribution of which has been illustrated in many regional maps (fig 1.1a-p). This clearly illustrates the heterogeneity of geographical information and omissions. Gaps between the available maps have been filled, where possible, by information from checklists and catalogues (see above and section 5.1 *Explanation of the species accounts*), and sometimes by 'interpolation' from general, large-scale maps. Even if clear 'white' areas are present within the distribution area (see map of *Carabus granulatus* in Chapter 5, p. 178, and fig. 1.1s), we have often chosen to fill these areas, because the European maps intend in the first place to outline the total range. It must be realised that within an area of distribution there are nearly always significant gaps where a species has not been reported, for instance when it concerns a stenotopic forest species. By presenting this example of all available regional maps and the resulting map for Europe, we hope to illustrate that choices had to be made and that some of them were arbitrary. In this book, the disadvantages of the European maps have hopefully been counterbalanced by the presentation of additional (dotted) maps for the Russian Plain.

1.8. Ecological transects

In a separate section of Chapter 8 *Biogeography*, we present 100 transects that illustrate the distribution of *Carabus* species along ecological gradients, across Europe. Most of these transects can be considered as real 'local faunas' (Penev & Turin, 1994; Penev, 1997), especially those based on so called 'activity densities' derived from actual pitfall trapping, but others are more hypothetical faunas based on several faunistic publications. The latter describe a fauna situation that is not unrealistic, but not exactly recorded in one transect. These transects have been compiled from catalogues and maps, often in combination with data from pitfall trapping in the same area. Most transects were relatively small and may vary from a few hundred meters to a maximum length of 20-25 km.

In a few cases, separate transects have been combined, for instance forming a cross-section of a larger mountain chain. We illustrate this with three examples, representing a schematic *Carabus*-fauna of Western Germany (Westphalia: fig. I-1), the Urals (fig. I-2) and Central Italy (fig. I-3), together covering over 30 species. The figures clearly illustrate that, although overall species diversity in southern Europe (in this case the Mediterranean area) is higher than in northern areas, the diversity in certain localities in the north may be even higher than in the south due to certain local factors (i.e. higher habitat diversity), rather than to regional ones (isolation, small ranges etc.). Furthermore, in the *Species accounts*, we refer to the occurrence of the respective species in the ecological transects, as additional information on the species' habitat preferences.

1.9. About Europe

The rich *Carabus* fauna of the Caucasus has been excluded from the book for the reasons provided in Turin *et al.*

(1993). Also, the Canarian *Carabus* species have been excluded, because the Canary Islands belong geographically to Africa.

1.10. Acknowledgements

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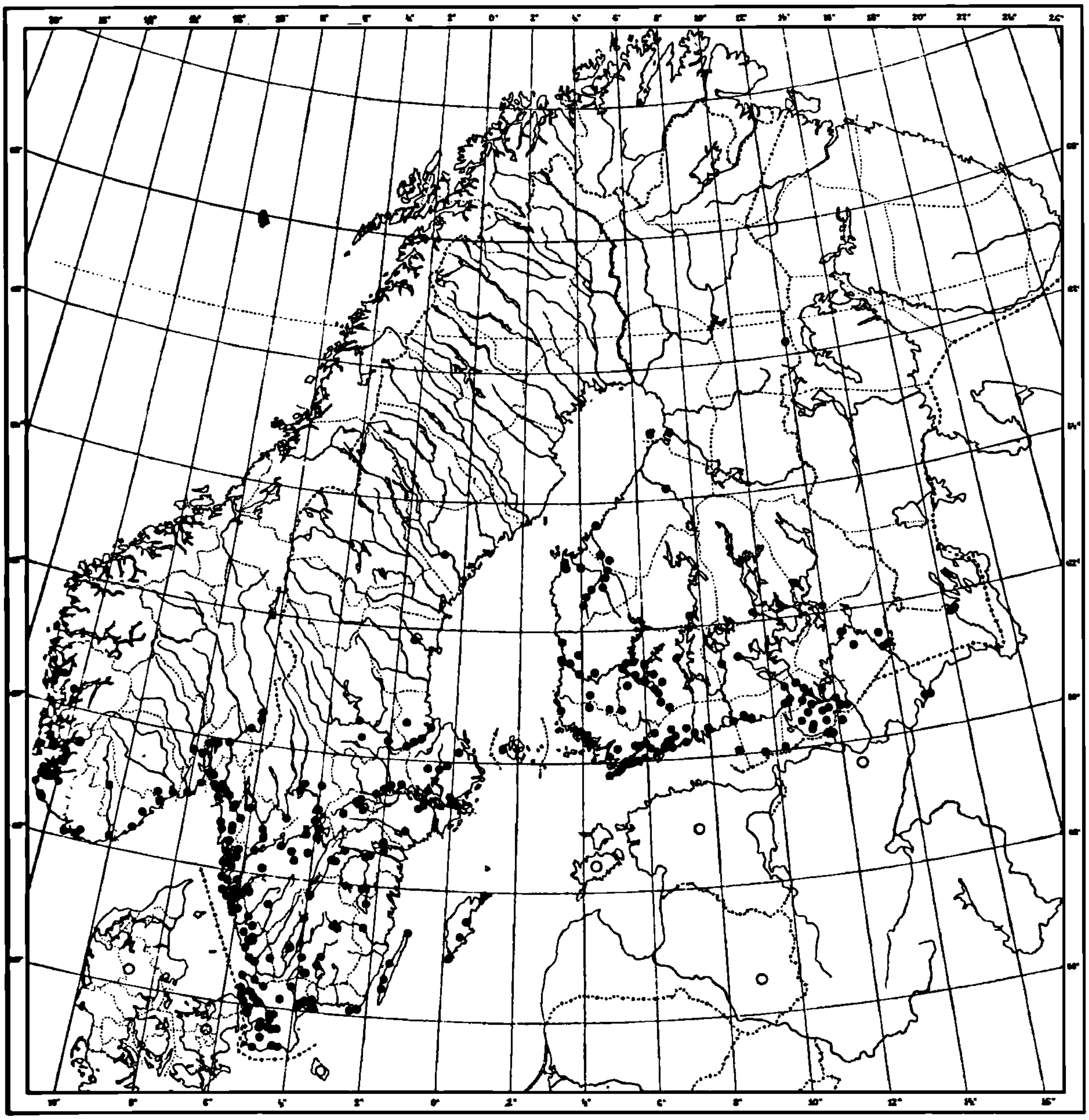
The authors were delighted to find the Board of the European Invertebrate Survey International willing to co-publish this book. We thank the series editors Peter van Helsdingen and Roy Kleukers for carefully reading all manuscripts, their valuable suggestions and practical help with numerous matters concerning the publication of the book. It is hoped that the series Fauna Europaea Evertebrata will soon be continued with further studies on equally interesting groups.

Fig. 1.1. Distribution maps of *Carabus granulatus* L. (from literature).

a-p: regional maps: **a.** Fennoscandia (Lindroth, 1945); **b.** Denmark (Bangsholt, 1983, from the "old" European map, as published in Turin *et al.*, 1977); **c.** Northern Ireland (Anderson, 2000); **d.** Britain (Luff, 1998); **e.** The Netherlands (Turin, 2000); **f.** Belgium and Luxembourg (Desender, 1986); **g.** Eastern Germany (Arndt, 1989); **h.** Estonia (Haberman, 1968); **i.** Czechoslovakia (Niedl, 1957); **j.** Austria (Mandl, 1955); **k.** Russian Plain (Penev, this volume); **l.** Former Yugoslavia (Pavicevic & Mesaros, 1999); **m.** Italy and adjacent territory (Vigna *et al.*, 2000); **n.** Switzerland (Marggi, 1992); **o.** France (Forel & Leplat, 1995); **p.** Iberian Peninsula (Forel & Leplat, 1998).

q-s: compilations: **q.** Original map made by Breuning (1937); **r.** Outline by Panin (1955) obviously directly taken from Breuning's map; **s.** Area map for Europe, compiled from above mentioned regional atlases, catalogues and checklists see text).



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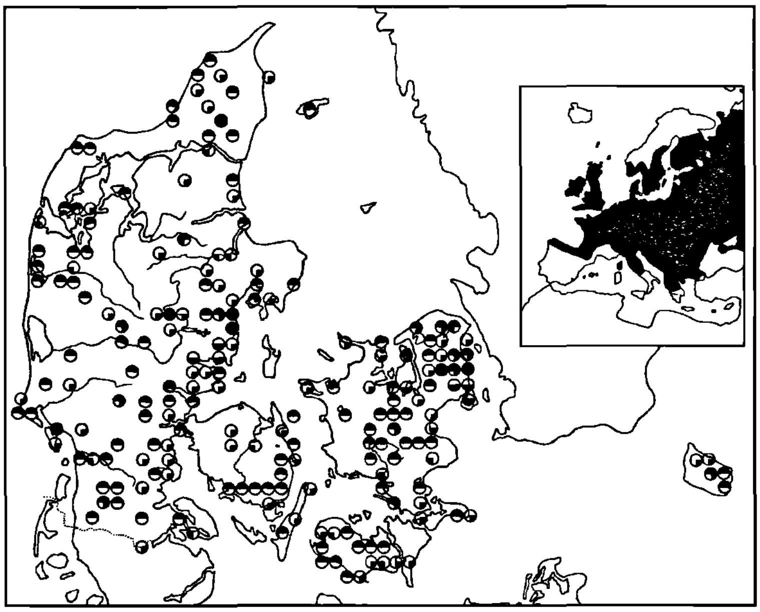

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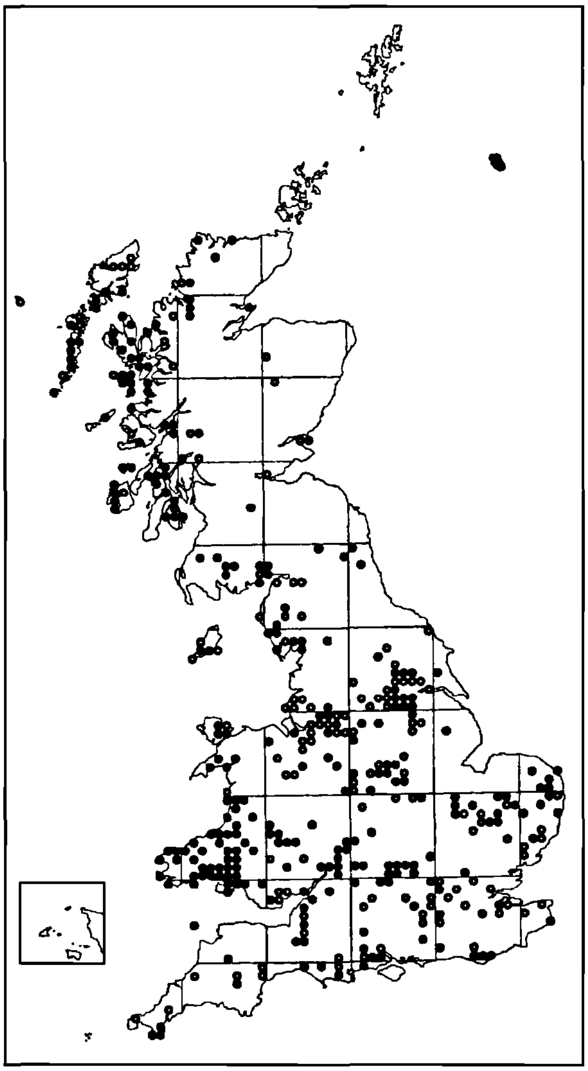

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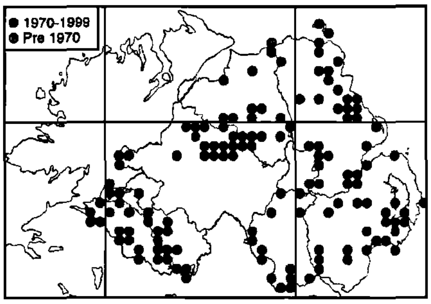

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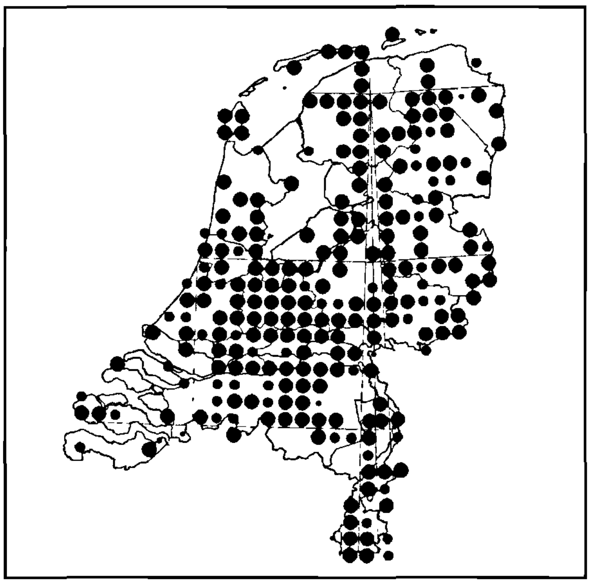

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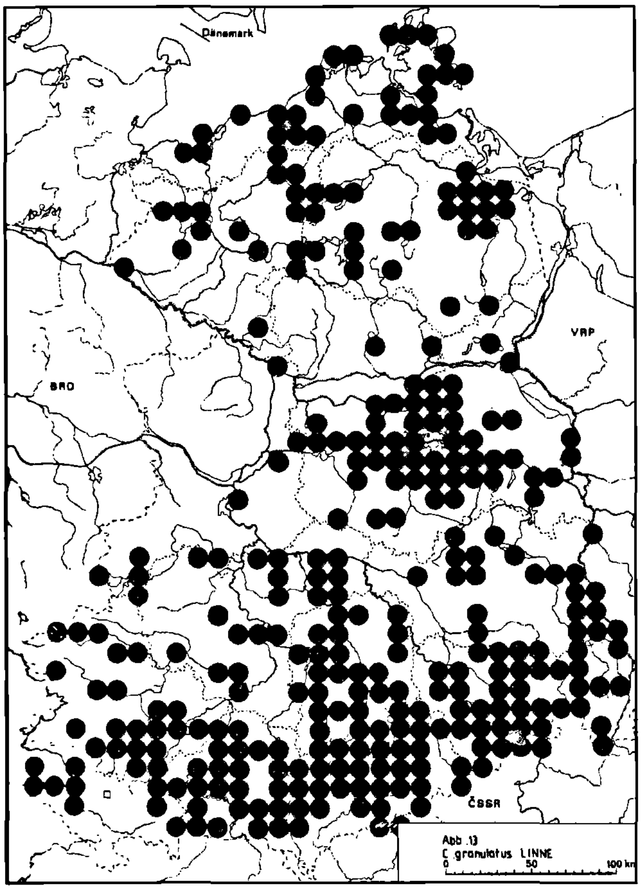

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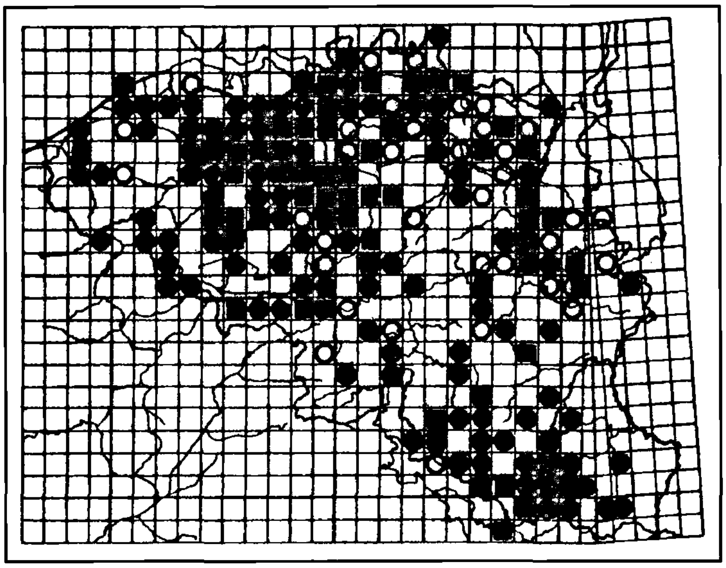

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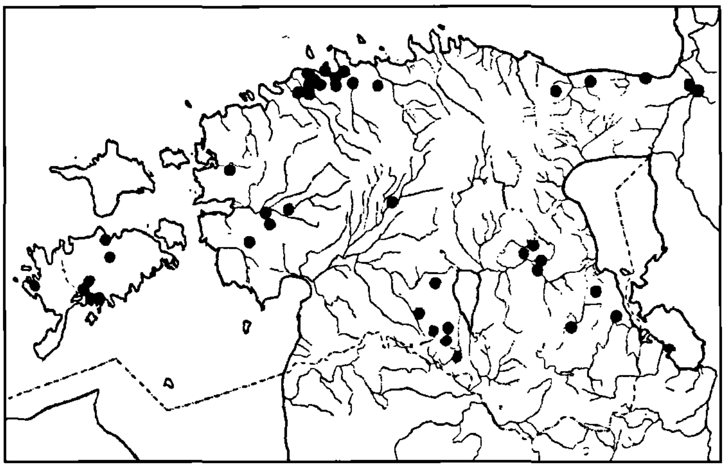

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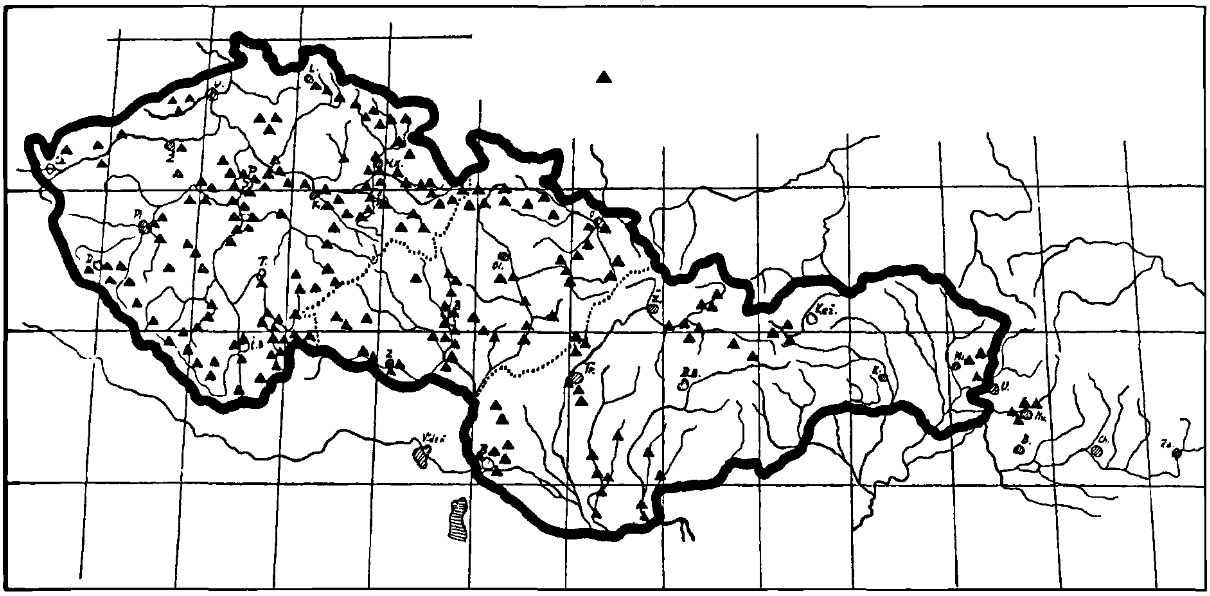

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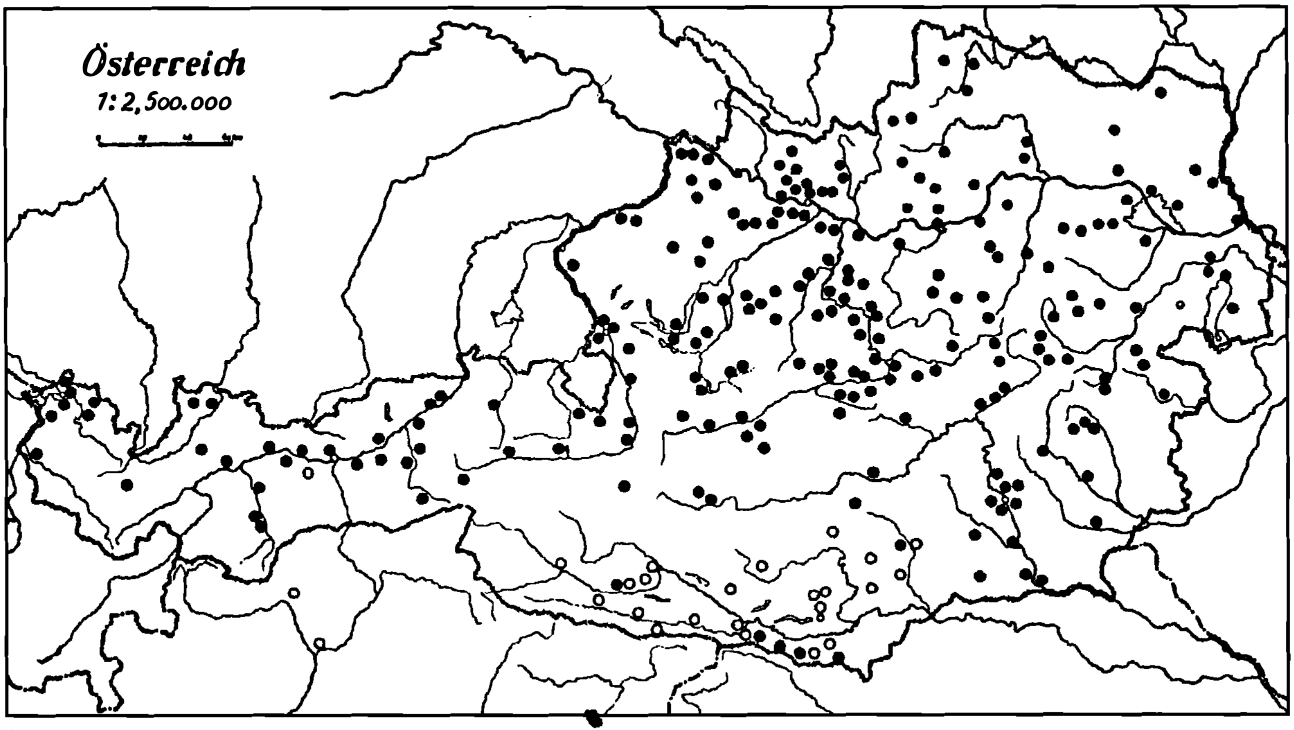

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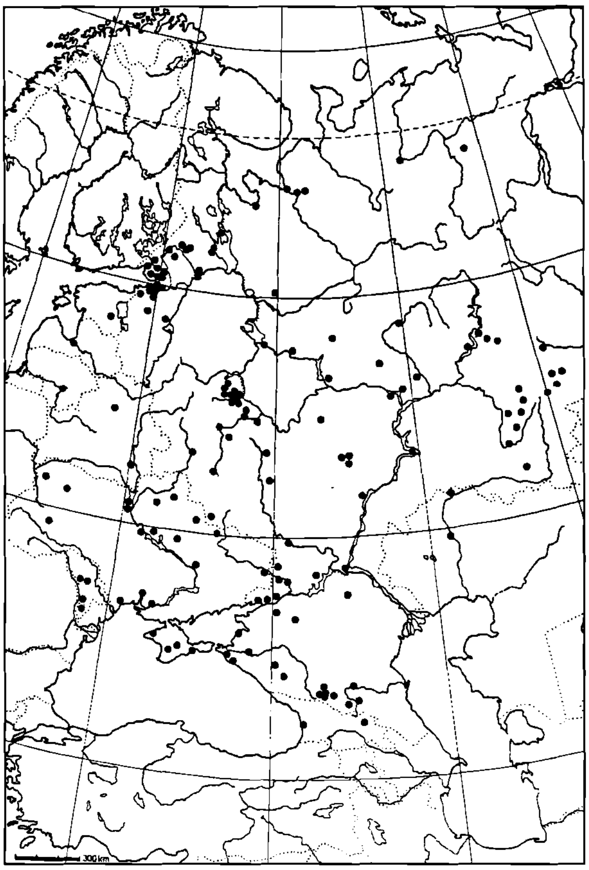

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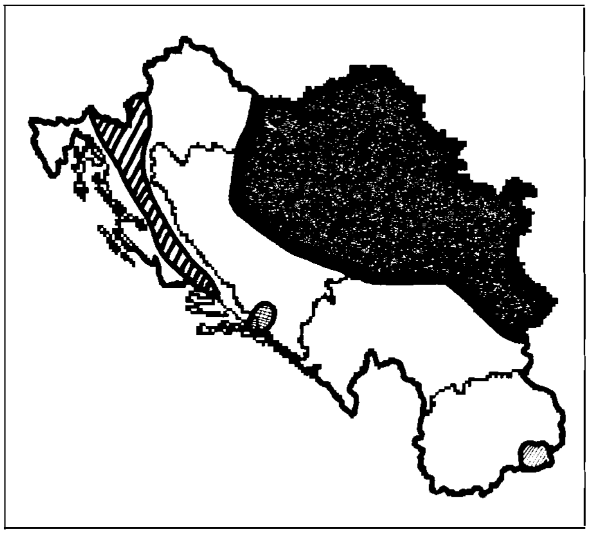

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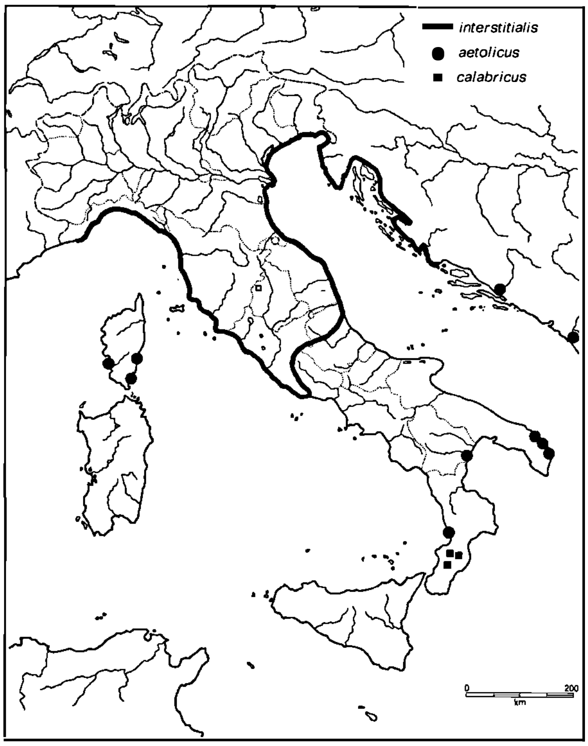
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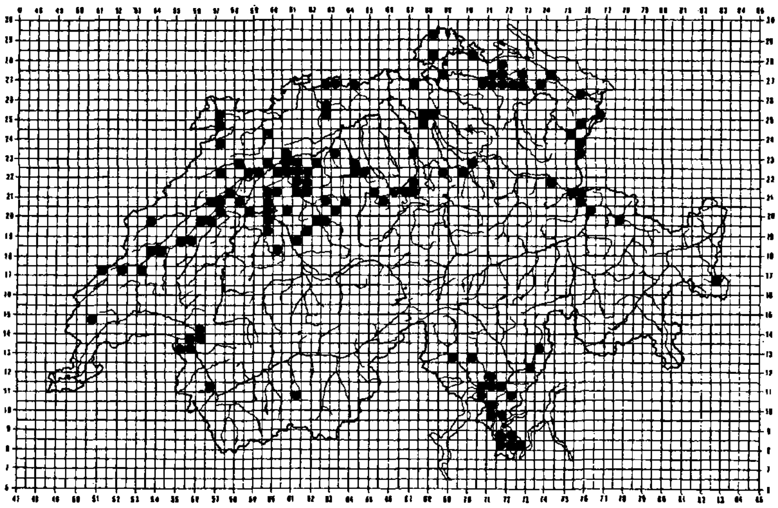

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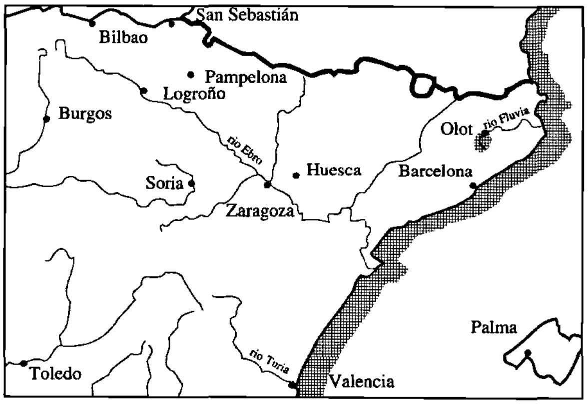
San Sebastián
Bilbao
Pampelona
Logroño
Burgos
rio Ebro
Olot
rio Fluvia
Huesca
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Soria
Zaragoza
Palma
rio Turia
Toledo
Valencia

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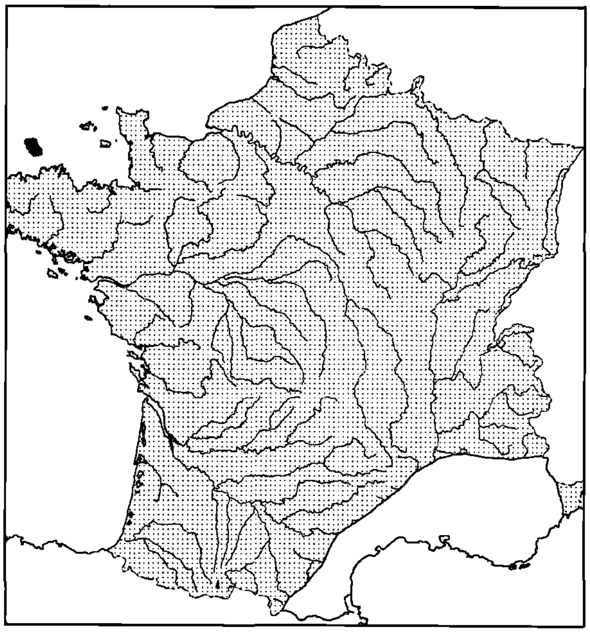

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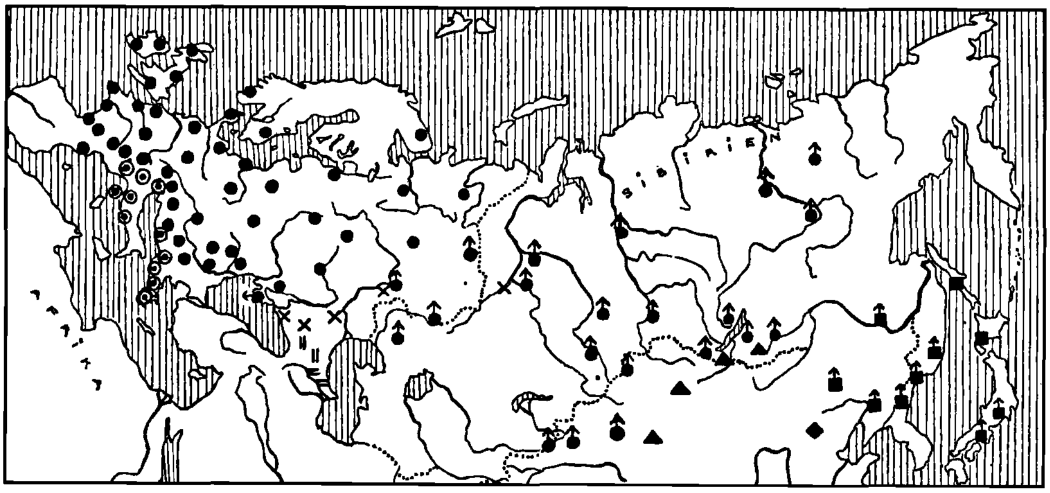

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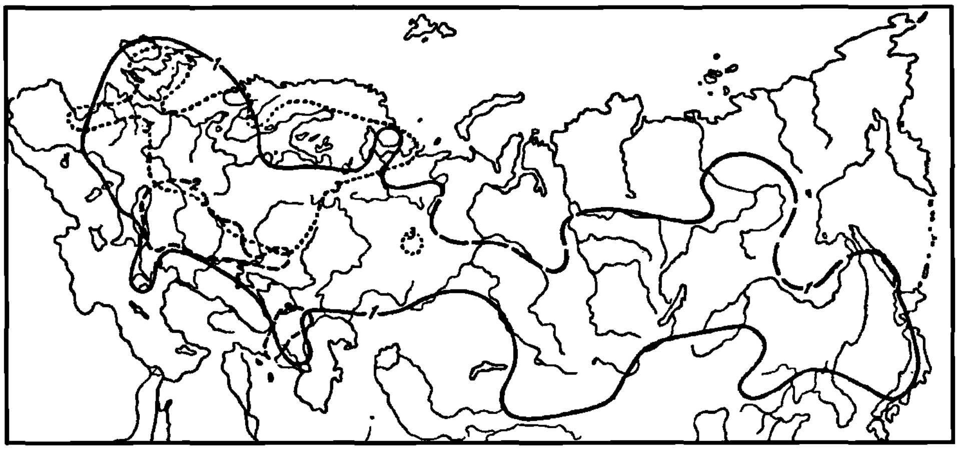

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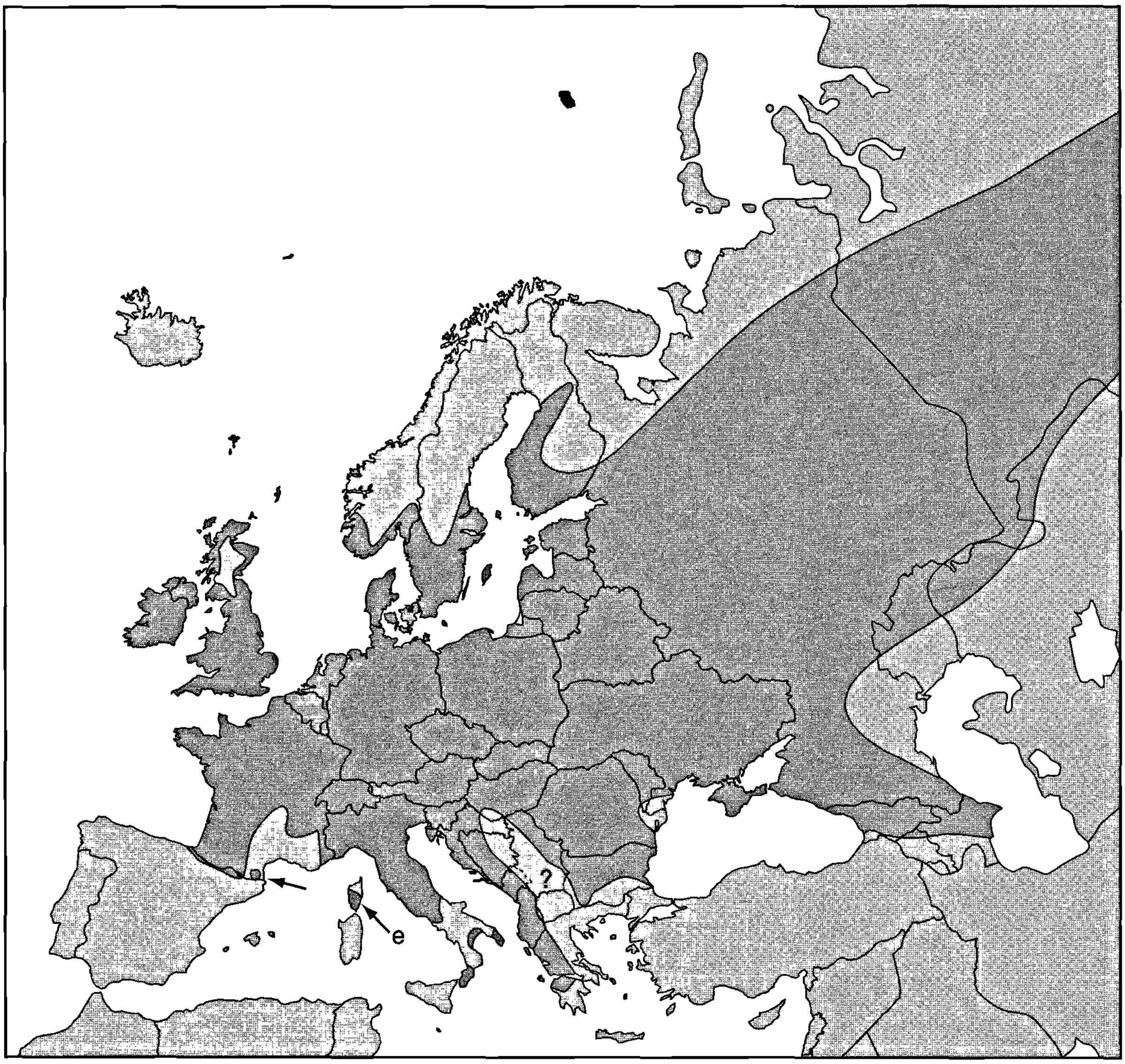

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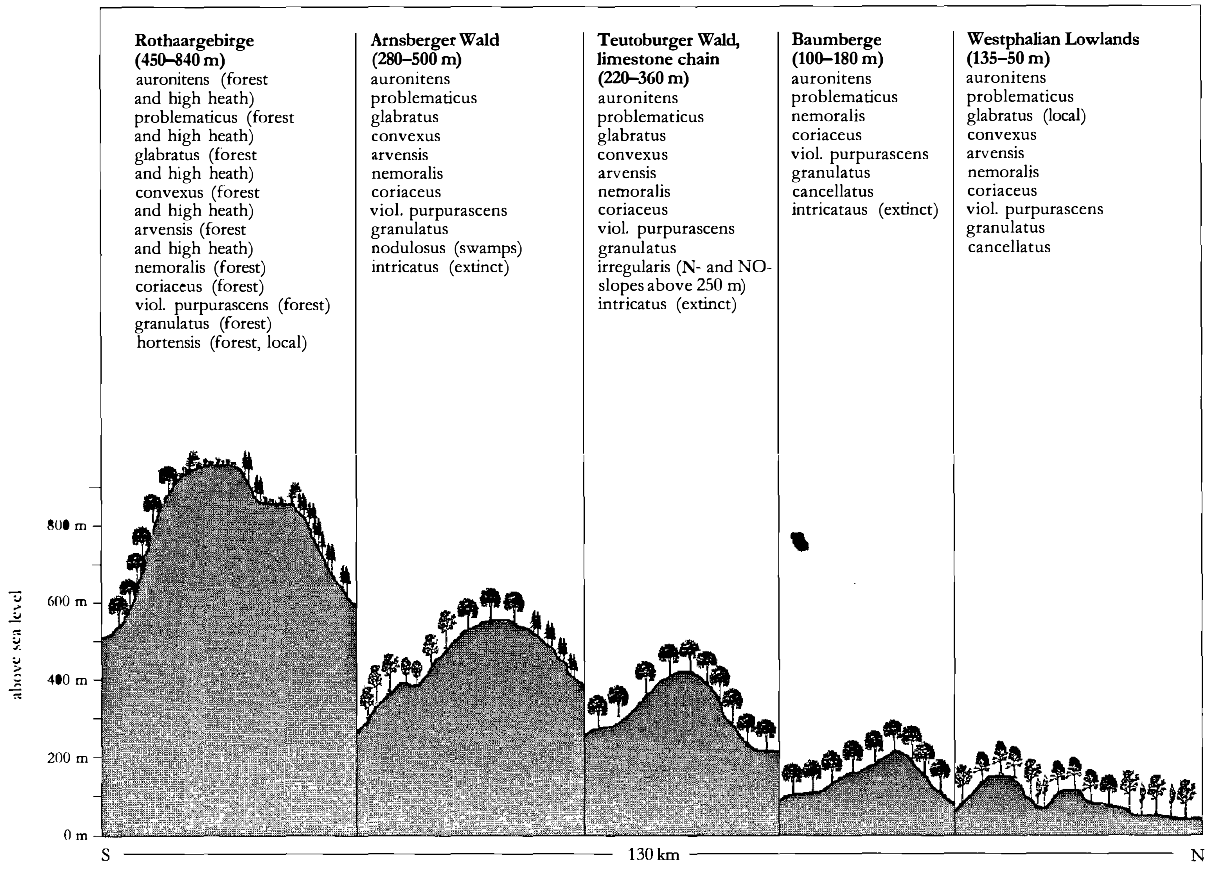


Fig. I-1
Macrotransect of the distribution of Carabus species in Westphalia, Germany (compiled by F. Weber).

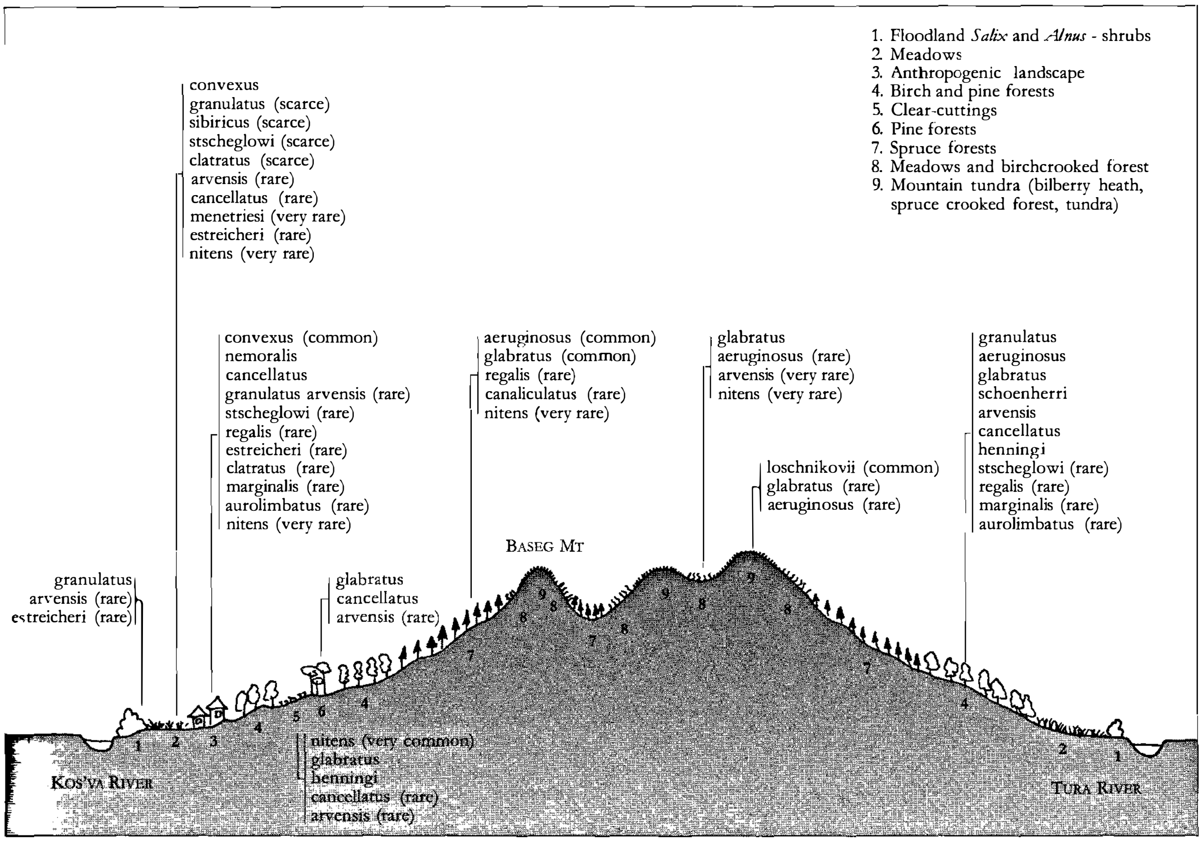


Fig. I-2
Macrotransect of the distribution of Carabus species in the Central Urals, Baseg Mt. (compiled by K. Makarov, after Voronin, 1999).

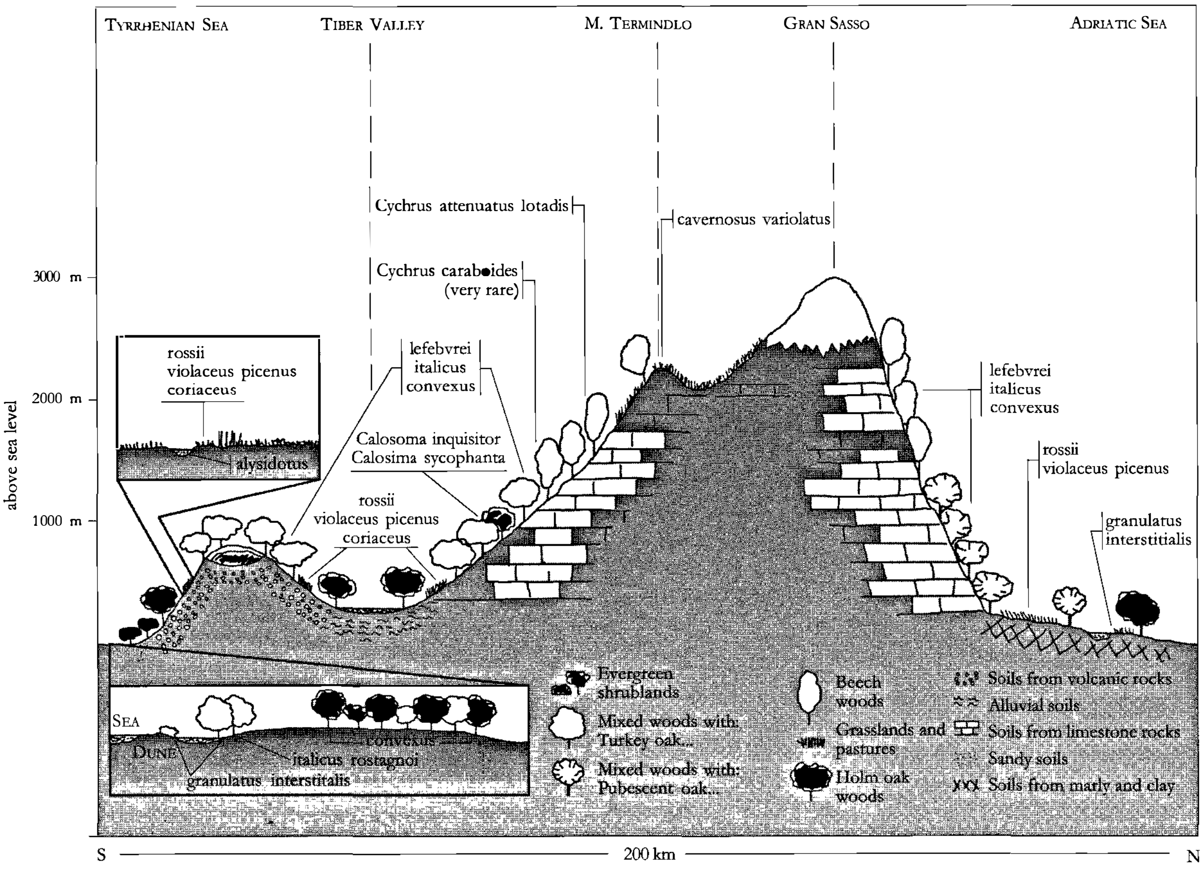
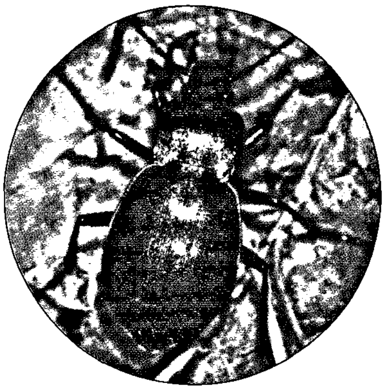


Fig. I-3
Macrotransect of the distribution of Carabus species in Central Italy (compiled by A. Vigna Taglianti and S. De Felici).

Special Part



Chapter 2 **Checklist**

A. Casale & B. Březina

2.1. INTRODUCTION

This checklist is based on the system that was made for the European fauna by A. Casale & O.L. Kryzhanowskij (see checklist in Turin *et al.*, 1993), however, modified according to the most important new developments in phylogeny and classification. It follows, where possible, the authoritative wordlists of Deuve (1991, 1994) and Březina (1999). Because the framework for the present monograph was set by the system used in Turin *et al.* (1993), we decided at an early stage, to maintain the same numbering of the species in order to get a clear infrastructure throughout the chapters of the book. Due to the rapid developments in *Carabus* systematics and in nomenclature, we realise that this clarity could only partly be achieved. On the one hand, some changes make that deviations from Turin *et al.* (1993) are inevitable, while on the other hand, accepting a complete new system like those of Deuve (1994, 1997) or Březina (1999) would be incompatible with the essentials of some chapters and with the insights of the authors. In our opinion, the Chapters 2 (*Checklist*), 3 (*Key to the adults*) and 5 (*Species accounts*) form a basic unity and the numbering and names should be consistent within this unity. The names in other chapters follow this arrangement.

Because this list is an unavoidable compromise between different opinions, especially with respect to significance of subspecies, a solution has been found in 'numbering' all subspecies (indicated: **a-z.** ssp.) recognised in the *Key to the adults* Chapter 3) and in the *Species accounts* (Chapter 5). This includes also the names that belong to the status of synonymy in Březina (1999). Subspecies that have not been mentioned by Březina (1999), and not treated in detail in the present work, but merit further investigation, have been indicated by '(ssp.)'. In this checklist, the numbering of the subspecies follows an order that is not alphabetic, because it follows the order of treatment in the Chapter 3. *Key to the adults* and Chapter 5. *Species accounts*, and as far as applicable, the original order in the worldlist of Březina (1999). For any taxon, only synonyms described from European localities are cited.

LEGEND:

species
  major subspecies (well geographically limited and morphologically defined, italic and bold)
  minor subspecies (in global faunistic view, numerous taxa can be treated as synonyms, italic)
    =*synonym, local form etc.* (in local faunistic view, some taxa can be treated as subspecies)
    ~*permanently invalid name* (mostly junior homonym or unavailable infrasubspecific name)

cos	correct original spelling
fos	fossil form
hyb	hybrid form
inc	taxon incertae sedis
ios	incorrect original spelling
iss	incorrect subsequent spelling
lsu	junior homonym treated as valid name due to long standing use
nud	nomen nudum
spn	suppressed name
(ssp)	questionable subspecies
un	unavailable (mostly infrasubspecific) name
HT	holotype
LNF	type locality not fixed

◀ **C. intricatus × arcadicus.** Greece, Pindus, Katara Pass. Photo by A. Vigna Taglianti.

LT	lectotype
NT	neotype
TNF	type not fixed
underlined	type locality
1m/1f	only 1 male/1 female specimen known

2.2. CHECKLIST

Genus ***CARABUS*** Linnaeus, 1758

01. ***LIMNOCARABUS*** Géhin, 1876; type species *Carabus clatratus* Linnaeus

001 ***clatratus*** Linnaeus, 1761	N,C,S-Europe, Brit.Isles, Balcans, Turkey, Russia, Central Asia, Siberia, Far East, Japan
a. ssp. ***clatratus*** Linnaeus, 1761	N,C-Europe, Russia, Central Asia, Siberia; LNF(?N-Germany)
=*clathratus* Auct.	
=*aeneopunctatus* DeGeer, 1774	
=*longus* Voet, 1778	
=*adspersus* Gmelin, 1788	
~*eversmanni* Motschulsky, 1846, nec Fischer von Waldheim, 1832	"Ichym"
~*detritus* Letzner, 1850; un	"Silesia"
~*cupreus* Schilsky, 1888, nec Linnaeus, 1758	N-Germany:Borkum Island, Warnemünde, Zingst
~*multipunctatus* Kraatz, 1890, nec Linneaus, 1758	"Westpreussen"
~*borealis* Born, 1908, nec Paykull, 1790	
=*foveolatoseriatus* Reitter, 1896	Altays
=*boreus* Csiki, 1927; nom.pro *borealis* Born, 1908	
~*aeratus* Culot, 1986; un	
b. ssp. *jansoni* Kraatz, 1890	Brit. Isles: Scottland
c. ssp. *auraniensis* Müller, 1902	Austria, S-Moravia, Hung., SE-France; Italy(?), Balkans(?"Fiume"=Rijeka); Cauc., Armen., Turkey
=*epirensis* Purkyně, 1928	NW-Greece:Ipeíros:"Janina"(=Ioánnina)
~*laccophilus* Reitter, 1896; un	"Caucasus:Mahmutli"
e. ssp. *arelatensis* Vacher de Lapouge, 1903	S-France:Camargue, Montpellier
d. ssp. *antonellii* Luigioni, 1921	N,C-Italy:Latium:Maccarese, Fiumicino, Roma env.

02[1]. ***MORPHOCARABUS*** Géhin, 1885; type species *Carabus monilis* Fabricius
=*Apostocarabus* Reitter, 1896; type species *Carabus odoratus* Motschulsky
=*Pancarabus* Reitter, 1896; type species *Carabus aeruginosus* Fischer von Waldheim
=*Amorphocarabus* Vacher de Lapouge, 1930; type species *Carabus henningi* Fischer von Waldheim
=*Basilicocarabus* Vacher de Lapouge, 1930; type species *Carabus regalis* Fischer von Waldheim

Note: In agreement with the checklists of Březina (1994, 1999), Kleinfeld & Schütze (1999) and Kryzhanovskij *et al.* (1995), the genus ***Trachycarabus*** Géhin, has been re-accepted as a valid subgenus. In the checklists of Deuve (1991) and Turin *et al.* (1993) all species were placed in ***Morphocarabus*** Géhin.The original numbering of the species according to Turin *et al.* (*l.c.*), however, has been maintained in the present work for reasons of consistency. In this checklist, the species have been splitted accordingly, but in the *Key to the adults* (Chapter 3) they have for practical reasons been treated in one group, together with ***Eucarabus*** Géhin.

001 ***aeruginosus*** Fischer von Waldheim, 1822	E-Eur.Russia, Siberia, Altays, Sayans
a. ssp. ***aeruginosus*** Fischer von Waldheim, 1822	E-Eur.Russia, Siberia, Altays("Ridders"=Leninogorsk; ?by error), Sayans
=*aereus* Dejean, 1826	
=*gmelini* Fischer von Waldheim, 1827	
(ssp.) *hermani* Mannerheim, 1827	Urals(Zlatoust), W-Siberia

(ssp.) *salechardensis* Obydov, 1999	NW-Siberia(Salekhard env.) & NE-Eur.Russia; ?NC-Siberia
(002-003 see 02$^{\text{II}}$ *Trachycarabus*)	
004 *comptus* Dejean, 1831	CW-Romania:Retezat Mts.to Bihor Mts.; "Banat"
~*hopffgarteni* Kraatz, 1880, nec Kraatz, 1878	"S-Hungary"(inexact; ?Godeanu & Tarcu Mts.)
~*merkli* Kraatz, 1880, nec *merklii* Hopffgarten, 1878	
~*merklianus* Géhin, 1885; un; nom.pro *merkli* Kraatz	
=*dieneri* Merkl, 1900	"Szöreny Mts."(=Godeanu/Tarcu Mts.)
=*diffinis* Csiki, 1906	"Komitat Kolosz"(=Cluj)
=*szoerenyensis* Csiki, 1908; nom.pro *hopffgarteni* Kraatz	"S-Hungary"(inexact; ?Godeanu/Tarcu Mts.)
~*ulrichhofmanni* Kleinfeld & Korell, 1986; un	SW-Romania:30km SE of Lugoj:Cavaran
~*cavarani* Lie, 1989; un	SW-Romania:30km SE of Lugoj:betw.Cavaran/Tincova
=*ulrichhoffmanni* Lie, 1989	SW-Romania:ca 20km E of Lugoj:Nadrag env.:Gosta Hut nr.Nadrag
(005-006 see 02$^{\text{II}}$ *Trachycarabus*)	
007 *excellens* Fabricius, 1798	NE-Romania, Moldavia, Ukraine; W-Russia: Kursk env.; Byelorussia
=*goldeggi* Duftschmid, 1812	"Podolia"
=*erythromerus* Dejean, 1826	Moldavia:Bendery
=*erythrocnemus* Fischer von Waldheim, 1827	
=*erythrodes* Fischer von Waldheim, 1827	
~*chrysitis* Letzner, 1850; un	
~*polonicus* Lomnicki, 1886, nec Motschulsky, 1850	"Galicia:Lubaczow"(=SE-Poland:Lubaczow E of Rzeszów)
=*frivaldskyi* Kraatz, 1887	"Galicia"
=*lomnitzkii* Reitter, 1896; nom.pro *polonicus* Lomnicki	"Galicia:Lubaczow"(=SE-Poland:Lubaczow E of Rzeszów)
=*sturmi* Schilsky, 1899	
=*moldaviensis* Born, 1903	S-Moldavia
=*jasilkowskii* Born, 1905	"Moldavia:Bojan"
~*pulchellus* Csiki, 1906, nec Brüggemann, 1873	"Tavarnók"(=SW-Slovakia:Tovarníky; error)
~*indiconotus* Vacher de Lapouge, 1906; un	
~*paradoxus* Vacher de Lapouge, 1906; un	
~*rubicundus* Vacher de Lapouge, 1906; un	
~*pseudomoldaviensis* Hormuzaki, 1907; un	NE-Romania:"Jassy"(=Iaşi)
=*pyretanus* Hormuzaki, 1907	N-Moldavia
=*rareulensis* Born, 1907	NE-Romania:Rarau Mts.(alpine form)
~*paradoxalis* Vacher de Lapouge, 1909; un	
=*feketei* Csiki, 1926; nom.pro *pulchellus* Csiki	"Tavarnók"(=SW-Slovakia:Tovarníky; error)
~*botezati* Marcu, 1934; un	
~*striatulus* Marcu, 1934; un	
(008 see 02$^{\text{II}}$ *Trachycarabus*)	
009 *hampei* Küster, 1846	NW,C,?SW-Romania; NE-Hungary; W-Ukraine
a. ssp. ***hampei*** Küster, 1846	NW,C,?SW-Romania; NE-Hung.:Szabolcz-Szatmár; W-Ukraine:Mukachevo; "Siebenburgen"
~*schaumi* Birthler, 1886, nec Gaubil, 1849	"Serbia"(?inexact)
=*aurosericeus* Kraatz, 1880	"Maros-Vasarhely"(=Tirgu Mures)
=*marusii* Ormay, 1890	"Gyula-Fehervar & Nagy Enyed"(=Alba Iulia & Aiud)
=*ormayi* Reitter, 1896	"Beregszasz"(=Beregovo)
=*liebli* Dietl, 1897	"Komitat Kis-Küküllö"(=Tirnava Mic)
~*marginatus* Kraatz, 1900; un	?"Maros-Vasarhely"(=Tirgu Mures)
=*zoppai* Kraatz, 1900	?"Maros-Vasarhely"(=Tirgu Mures)
=*dacicus* Csiki, 1906	"Szamosujvar & Naszod"(=Gherla & Bistrita Nasaud)
=*eximius* Csiki, 1906	"Nagyvarad"(=Oradea)
=*fraternus* Csiki, 1906	"Maros-Vasarhely"(=Tirgu Mures)
~*mendax* Csiki, 1906, nec Rossi, 1790	"Komitat Marmaros"(=Maramureş)

~*validus* Csiki, 1906, nec Kraatz, 1884	"Komitat Hunyad:Nagayg"(=Hunedoara:ca.40km NE of Deva:Sacarimb)
~*vitiosus* Csiki, 1906; un	
~*zilahiensis* Csiki, 1906; un	"Komitat Szilagy:Zilah"(=Salaj:Zalau)
~*concinnus* Vacher de Lapouge, 1916; un; nom.pro *schaumi* Birthler	"Serbia"(?inexact)
=*hunyadensis* Csiki, 1926; nom.pro *validus* Csiki	"Komitat Hunyad:Nagayg"(=Hunedoara:ca.40km NE of Deva:Sacarimb)
=*bokori* Csiki, 1927; nom.pro *concinnus* Vacher de Lapouge	"Serbia"(?inexact)
=*telekii* Csiki, 1937	?"Banat"(?inexact)
=*gutiiensis* Takács & Lie, 1992	NW-Romania:NE of Baia Mare:Gutii Mts.
=*praedacicus* Takács & Lie, 1992	C-Romania:WNW of Alba Iulia:Zlatna
b. ssp. ***incompsus*** Kraatz, 1880	NC,C-Romania:Rodna Mts.to Harghita Mts.; "S-Hungary:Brasso env."(=Braşov)
~*elegantissimus* Csiki, 1906; un	
=*mehelyanus* Csiki, 1906	"Komitat Csik:Vigyazok-Tarko"(=ca.Harghita Mts.)
=*spectabilis* Csiki, 1906	Rodna Mts.
010 ***henningi*** Fischer von Waldheim, 1817	E-Eur.Russia, Urals; C,W-Siberia, Altays, Sayans; ?N-Mongolia
a. ssp. ***henningi*** Fischer von Waldheim, 1817	E-Eur.Russia, Urals, W-Siberia(Barnaul), Altays, Sayans
=*uralicus* Born, 1922	Urals
b. ssp. ***oviformis*** Beheim & Breuning, 1943	Arctic W. Siberia, Polar Ural, Vorkuta
c. ssp. ***peczoricus*** Obydov, 2000	Rep. Komi, Kosiyu River mouth, Pechora bassin
011 ***hummeli*** Fischer von Waldheim, 1823	Siberia; Altays, Sayans, Mongolia, Far East, Korea, NE-China
(ssp.) *dshvangi* Menshikov & Gorbunov, 1997	Polar Trans Uralia, Yamal Peninsula
ssp. ***hummeli*** Fischer von Waldheim, 1823	C,W,E-Siberia(Nerchinsk); Altays, Sayans, Mongolia
=*burnaschewi* Dejean, 1826	"Siberia"
012 ***karpinskii*** Kryzhanovskij & Matveev, 1993	SW-Siberia:South Urals:Mt.Iremel, Yamantau, Zigalga
013 ***kollari*** Palliardi, 1825	SW-Romania:Banat Mts.; Serbia, Bosnia, W-Croatia
a. ssp. ***kollari*** Palliardi, 1825	SW-Romania:Banat Mts.(Mehadia)
=*magnificus* Kraatz, 1878	
b. ssp. *semetricus* Kraatz, 1878	"Banat"
=*negotinensis* Reitter, 1896	Serbia:Negotin
~*paroecus* Csiki, 1906; un	
~*sejunctus* Csiki, 1906; un	
=*joergeri* Born, 1927	"Walachei"
e. ssp. ***praecellens*** Palliardi, 1825	Serbia:Novi Sad, Fruska Gora Mts.("Futtak"=Futog)
~*kollarioides* Mandl, 1966; un	Serbia:Fruska Gora Mts.
c. ssp. ***illigeri*** Dejean, 1826, nec Panzer, 1806; lsu	Bosnia; W-Croatia:Dinara planina
=*laticollis* Sturm, 1826	
=*stentzi* A.& G.B.Villa, 1833	"Hungary"(?error)
~*parallelus* Kraatz, 1878, nec Faldermann, 1835	Pljesevica Mts.
=*unanensis* Born, 1909	Bosnia:Bihac
d. ssp. *curtulus* Ganglbauer, 1892	Mts.nr.Sarajevo
= *bjelasnicensis* Apfelbeck, 1902	Mts of Bosnia (Bjelasnica) and Serbia (Kopaonik)
=*koschanini* Csiki, 1904	Serbia:Kopaonik Mts.
~*transfugus* Apfelbeck, 1907, nec Semenov, 1898	Sarajevo env.
~*cerensis* (Toševski, 1990); un	NW-Serbia:Cer Planina(=SW of Sabac), Korenita nr.Loznica
~*tarensis* (Toševski, 1990); un	W-Serbia:Tara Mts.:Mitrovac
014 ***monilis*** Fabricius, 1792	France, Belgium, Holland, Switzerland, Germany(Halle), Brit.Isles, Ireland, Italy (W. Alps)

Note: According to Březina (1999), no valid subspecies of *C. monilis* are recognizable morphologically.

a. ssp. ***monilis*** Fabricius, 1792	NC-Europe, British Isles, S to the W-Alps
~*affinis* Panzer, 1798, nec Schrank, 1781	Germany:Würzburg
=*kronii* Hoppe & Hornschuch, 1825	Salzburg(error) & Mühlhausen
=*amoenus* Baudet-Lafarge, 1836	Puy-de-Dome:Mt.Doré
=?*helveticus* Heer, 1837; ?hyb	Switzerland:?"Guttannen, Herzogenbuchsee"; ?hyb *monilis/cancellatus*
=*gracilis* Küster, 1846	"Bayern"
~*regularis* Wissmann, 1848, nec Fischer von Waldheim, 1823	"Thüringen"
=*scolecaster* Gistl, 1857	"Helvetia"
=*veris* Gistl, 1857	"Germany"
=*rufofemoratus* Motschulsky, 1865	"Helvetia"
~*femoralis* Géhin, 1876, nec Motschulsky, 1865	
~*azurescens* Dalla Torre, 1877; un	
~*viridescens* Dalla Torre, 1877; un	
=*anomalus* Géhin, 1880	Switzerland:Mt.Pilatus
=*femoratus* Géhin, 1880	
=*interpositus* Géhin, 1880	"Parigi"
=*rugatinus* Géhin, 1880	
=*bavaricus* Beuthin, 1896	Bayern:Lechfeld
~*interruptus* Beuthin, 1896, nec Fabricius, 1775	
=*moestulus* Beuthin, 1896	
=*sengstacki* Beuthin, 1896	
=?*subschartowi* Vacher de Lapouge, 1898; ?hyb	Haute-Garonne:Luchon; ?hyb *monilis/cancellatus*
=*meridionalis* Born, 1905	S-France
~*anglicus* Vacher de Lapouge, 1906; un	England:?
~*externus* Vacher de Lapouge, 1906; un	
~*gaultieri* Vacher de Lapouge, 1906; un	Loire-Atlantique:Nantes
=*tugenus* Vacher de Lapouge, 1906	"Kanton Appenzell"
=*perreti* Born, 1907	Isère:Notre-Dame-la-Salette(alpine form)
~*arvernus* Barthe, 1908; un	Puy-de-Dome:Mt.Doré
~*insularis* Born, 1908, nec Hope, 1837	England:?
~*bavariensis* Vacher de Lapouge, 1909; iss of *bavaricus* Beuthin	-
=*pustulatus* Vacher de Lapouge, 1909	Puy-de-Dome
=*tigurinus* Vacher de Lapouge, 1909	
~*kellneri* Hubenthal, 1910; un	"Thüringen"
=*nicodii* Pic, 1910	
=*rhodanicus* Vacher de Lapouge, 1916	S-France:?
=*sequanus* Vacher de Lapouge, 1916	Cote-d'Or:Brazay en Morvan
=*succisus* Vacher de Lapouge, 1916	France:St.Gaudens
~*charbonieri* Sirguey, 1931; un	Puy-de-Dome:Mt.Doré
~*cylindricus* Sirguey, 1931, nec Herbst, 1784	Puy-de-Dome
~*cylindricusniger* Sirguey, 1931; un	Puy-de-Dome
~*cylindricusviolaceus* Sirguey, 1931; un	Puy-de-Dome
~*femoratusviolaceus* Sirguey, 1931; un	
=*incostatus* Sirguey, 1931	Puy-de-Dome
~*incostatusfemoralis* Sirguey, 1931; un	Puy-de-Dome
~*incostatusniger* Sirguey, 1931; un	Puy-de-Dome
~*incostatusviolaceus* Sirguey, 1931; un	Puy-de-Dome
~*interposituscyaneus* Sirguey, 1931; un	
~*interpositusniger* Sirguey, 1931; un	
~*interpositusviolaceus* Sirguey, 1931; un	
=*lavagnei* Sirguey, 1931	Puy-de-Dome:Mt.Doré
~*marcoti* Sirguey, 1931; un	

~*pustulatusniger* Sirguey, 1931; un	?Puy-de-Dome
~*pustulatusviolaceus* Sirguey, 1931; un	?Puy-de-Dome
~*rhodanicusviolaceus* Sirguey, 1931; un	
~*sequanusniger* Sirguey, 1931; un	S-France:?
~*sequanusviolaceus* Sirguey, 1931; un	S-France:?
~*theroudi* Sirguey, 1931; un	
=*theryi* Sirguey, 1931	
~*trapeti* Sirguey, 1931, nec Bleuse, 1885	Puy-de-Dome:Mt.Doré
~*trilineatusniger* Sirguey, 1931; un	?"Schweizer Jura"
~*trilineatusviolaceus* Sirguey, 1931; un	?"Schweizer Jura"
=*rosayanus* Dufour, 1978	Cote-d'Or:Rosay
=*fagnensis* Grotz, 1978	
~*nepos* Ivanovs, 1981; un	N-Germany:Niedersachsen:Verden an der Aller(=SE of Bremen)
=*alpigradus* Sermet, 1985	
~*vincentianus* Devecis, 1991; un	Cantal:Col d'Aulac
f. ssp. *schartowi* Heer, 1837	"Jura"
=*sabaudus* Géhin, 1880	"Jura"
~*nigritulus* Kraatz, 1881, nec Kraatz, 1876	"Grande Chartreuse"
~*rubricrus* Géhin, 1885; un; nom.pro *rufofemoratus* Motschulsky	"Helvetia"
~*trilineatus* Haller, 1885, nec Fabricius, 1792	"Schweizer Jura"
~*varicolor* Joerin-Gerber, 1888; un	"Jura"
=*taunicus* Heyden, 1871	W-Germany:"Mt.Taunus & Vogelsberg"(alpine form)
~*meneensis* Grotz & Grotz, 1975; un	Drôme:Col de Menée
e. ssp. *consitus* Panzer, 1809	Bern
d. ssp. *saouensis* Mandl, 1967; un	Drôme:Ft.de Saou, Vercors
=*marsannensis* Machard, 1979	
=*aoustensis* Machard, 1979	
=*proncelensis* Machard, 1979	
c. ssp. *alticola* Bellier, 1880	Alpes-Hte-Provence:Digne env.
=*daniellae* (Bellon & Tarrier, 1972)	?Alpes-Maritimes:Col de Champs
=*ventusicus* (Bellon & Tarrier, 1972)	Mont Ventoux
b. ssp. *subpyrenaeus* Vacher de Lapouge, 1925	Haute-Garonne:St.Gaudens, Col d'Aspin
(ssp.) *norensis* Pham, 1977	Aude:Pic de Nore
(ssp.) *montichares* (Hansen & Gaskowiak, 1973)	Ariège:Pailhéres
=*pailherensis* Machard, 1979	
=*ourthizetensis* Machard, 1979	
=*brunetensis* Machard, 1979	
(ssp.) *dupeuxi* Deuve, 1974	Charente:Forêt de Braconne
=*benoiti* (Devecis, 1975)	Corrèze:Albussac
=*chabroli* Devecis, 2000	
015 ***odoratus*** Motschulsky, 1844; ?non priority	Siberia, Altays, Sayans; ?N-Mongolia
a. ssp. *septentrionalis* Breuning, 1932	NW,NC-Siberia:arctic Urals("Obdorsk"=Salekhard) to Yenisey River
(016 see 02^{II} *Trachycarabus*)	
017 ***regalis*** Fischer von Waldheim, 1822	E-Eur.Russia; C,W-Siberia, Altays, Sayans; N-Mongolia
ssp. ***regalis*** Fischer von Waldheim, 1822	E-Eur.Russia; W-Siberia(Barnaul)
=*cuprinus* Fischer von Waldheim, 1822	
=*cyanicollis* Dejean, 1826	
=*pasianax* Fischer von Waldheim, 1827	
~*viridicinctus* Kraatz, 1882, nec Schaufuss, 1872	
=*viridicollis* Kraatz, 1882	
=*jureceki* Born, 1922	"Mts.nr.Simbirsk"(=Ulyanovsk)
=*volgensis* Csiki, 1927; nom.pro *jureceki* Born	"Mts.nr.Simbirsk"(=Ulyanovsk)

018 ***rothi*** Dejean, 1829	Romania, NE-Hungaria, W-Ukraine
a. ssp. *rothi* Dejean & Boisduval, 1829	C-Romania:Sibiu env.; "Transsylvania"
=*aequistriatus* Kraatz, 1878	
=*latestriatus* Kraatz, 1878	
=*quadricatenatus* Kraatz, 1878; nec ?	
=*varistriatus* Kraatz, 1878	
=*birthleri* Reitter, 1885	
~*rugulosus* Birthler, 1885; un	
~*ignoscus* Csiki, 1906; un; nom.pro *quadricatenatus* Kraatz	
b. ssp. *alutensis* Savulescu, 1972	C-Romania:Olt River:Rimnicu Vilcea env.(Calimaneşti)
(019-020 see 02^{II} *Trachycarabus*)	
021a ***scheidleri*** Panzer, 1799	CE-Europe, W-Carpathians
a. ssp. ***scheidleri*** Panzer, 1799	N,E-Austria(Wien); SE-Germany:Passau, Regensburg; S-Bohemia; S-Moravia; NW-Hungary
~*caeruleus* Panzer, 1812, nec *coeruleus* Steven, 1808	Wien
=*aeneipennis* Sturm, 1815	
=*purpuratus* Sturm, 1815	
~*virens* Sturm, 1815, nec Müller, 1776	
~*niger* Letzner, 1850; un	
~*purpureomarginatus* Letzner, 1850; un	
~*purpureus* Letzner, 1850; un	
~*viridiaeneus* Letzner, 1850; un	
~*viridimarginatus* Letzner, 1850; un	
~*viridis* Letzner, 1850; un	
=*gibbicollis* Motschulsky, 1865	
~*aerescens* Dalla Torre, 1877; un	
~*aeruginescens* Dalla Torre, 1877; un	
~*aurescens* Dalla Torre, 1877; un	
~*coerulescens* Dalla Torre, 1877; un	
~*elegans* Dalla Torre, 1877; un	
~*fuscescens* Dalla Torre, 1877; un	
~*metallescens* Dalla Torre, 1877; un	
~*nigrescens* Dalla Torre, 1877; un	
~*violescens* Dalla Torre, 1877; un	
~*virescens* Dalla Torre, 1877; un	
=*dominus* Reitter, 1885	
=*graciosus* Géhin, 1885; un	
=*jucundus* Csiki, 1906	W of Budapest:Pilis Mts.
~*duchoni* Vacher de Lapouge, 1906; un	"Krain"(error)
~*prolifer* Vacher de Lapouge, 1906; un	"Krain"(?error)
b. ssp. *preysleri* Duftschmid, 1812	Niederösterrieich; Puchberg am Schneeberg(LT)
~*atrocoeruleus* Letzner, 1850; un	
~*aureus* Letzner, 1850; un	
~*cyaneus* Letzner, 1850; un	
~*purpureoaureus* Letzner, 1850; un	
=*ambitiosus* Schaufuss, 1872	
=*improbus* Schaufuss, 1872	
=*principatus* Schaufuss, 1872	
=*superbus* Schaufuss, 1872	
=*viridicinctus* Schaufuss, 1872	
~*cuprescens* Dalla Torre, 1877; un	
=*maderianus* Mandl, 1957	Niederösterrieich:Aspang
~*pseudoscheidleri* Mandl, 1964; un	NE-Austria:Leitha Mts.:Winden env.
~*punctatocostatus* Mandl, 1964; un	Leitha Mts.:Winden env.

(*reductecostatus* Mandl, 1964; un	Leitha Mts.:Winden env.
d. ssp. *styriacus* Kraatz, 1887	"Styria"(=Steiermark), CW-Hungary
=*limbifer* Reitter, 1889	
=*burghauseri* Fleischer, 1899	
=*floriani* Penecke, 1905	Steiermark:Gratwein
=*pannonicus* Csiki, 1906	C-Hungary:Fejér:Székesfehérvár
~*coeruleocinctus* Fleischer, 1925; un	
~*elegans* Fleischer, 1925; un	
=*gebhardti* Bodemeyer, 1927	SW-Hungary:Tolna:Dombovar
~*baderlei* Mandl, 1965; un	NE-Austria:Burgenland:Parndorfer Platte(SE of Wien)
~*praescheidleri* Mandl, 1965; un	SW-Hungary:Baranya:Mescek Mts.
~*pseudojucundus* Retezár, 1974; un	W-Hungary:Komárom:Gerecse Mts.
~*vertesensis* Retezár, 1974; un	W-Hungary:Fejér:Vértes Mts.
c. ssp. *helleri* Ganglbauer, 1892; ?non priority	Slovakia("Kom.Neutra"=Nitra); N,C,E-Moravia; N-Bohemia; ?W-Ukraine; E-Hungary
=*repercussus* Drapiez, 1819; ?priority	"Karpathen"
~*morawitzi* Kraatz, 1887, nec Ganglbauer, 1887	?"Bohemia"
~*distinguendus* Csiki, 1906, nec Duftschmid, 1812	E of Budapest:Rakosfeld
=*kollarisans* Sokolar, 1907	"Moravia"
~*cupripennis* Fleischer, 1925; un	
~*pseudoambitiosus* Fleischer, 1925; un	
~*pseudoexcellens* Fleischer, 1925; un	
~*pseudosuperbus* Fleischer, 1925; un	
~*viridipennis* Fleischer, 1925; un	
~*pseudopreyssleri* Breuning, 1932; un; nom.pro *morawitzi* Kraatz	?"Bohemia"
=*giuseppemuelleri* Hildebrand, 1955	S-Moravia:"Brünn"(=Brno)
~*bieneri* Mandl, 1965; un	C-Slovakia:Kralovany
~*subparvulus* Mandl, 1965; un	NC-Hungary:Börzsöny Mts.:Dios Jenö
~*subtilepunctatus* Mandl, 1965; un	
021b ***versicolor*** E. Frivaldszky, 1835	Bulgaria, NE-Serbia
a. ssp. ***versicolor*** E. Frivaldszky, 1835	Bulgaria:Stara planina Mts.(Sliven)
=*buresi* Hanuš, 1923	Stara planina Mts.
b. ssp. ***simulator*** Kraatz, 1876	NE-Serbia:Majdanpek env.
=*serbicus* Hopffgarten, 1878	?"Serbia"
=*polychloros* Beuthin, 1885	
~*tekijensis* (Toševski, 1990); un	NE-Serbia:Tekija:Djerdapska klisura, 50m(=Dunav right bank opposite to Orşova)
(022 see 02$^{\text{II}}$ *Trachycarabus*)	
023a ***zawadzkii*** Kraatz, 1854	E-Slovakia, NE-Hungary, W-Ukraine, N-Romania
a. ssp. ***zawadzkii*** Kraatz, 1854	E-Slovakia, NE-Hungary, W-Ukraine
=*dissimilis* Csiki, 1906	"Kom.Ung"(=W-Ukraine:Uzhgorod env.)
(ssp.) *seriatissimus* Reitter, 1896	W-Ukraine:Carpathians:Hoverla Massif; ?"Marmaros"
=*beheimi* Niedl, 1957	W-Ukraine:Mukachevo
~*marmaroschensis* Mandl, 1965; un	"Marmaros"
(ssp.) *ronayi* Csiki, 1906	E-Slovakia("Kom.Zemplén & Ung"), NE-Hungary
023b ***zherichini*** Shilenkov, 1990	N-Siberia:Polar Urals toKolyma Riv. (not in key: see p. 178).

02$^{\text{II}}$ *TRACHYCARABUS* Géhin, 1885; type species *Carabus scabriusculus* Olivier
=*Lyperocarabus* Vacher de Lapouge, 1930; type species *Carabus estreicheri* Fischer von Waldheim

(001 see 02$^{\text{I}}$ *Morphocarabus*)	
002 ***besseri*** Fischer von Waldheim, 1822	NE-Romania, Moldavia("Süd-Podolien"), Ukraine
=*dimorphus* Vacher de Lapouge, 1908	
=*pseudobesseri* Vacher de Lapouge, 1908	

003 *bosphoranus* Fischer von Waldheim, 1823	Taman Peninsula, Krym Peninsula, W-foot of Caucasus
~*carbonarius* Motschulsky, 1850, nec Rossi, 1790	S-Russia:?
=*jailensis* Breuning, 1932	Krym Peninsula:Jaila Mts.
(004 see 02^1 *Morphocarabus*)	
005 *errans* Fischer von Waldheim, 1823	Ukraine; SW-Russia:Rostov; "Tauria"
=*krynickii* Fischer von Waldheim, 1827	Ukraine:Odessa
=*cribricollis* Motschulsky, 1846	"Sarepta"(=lower Volga basin; LT)
=*maritimus* Motschulsky, 1850	"Litt.m.Pont.:Odessa"
~*acutangulus* Eichler, 1924, nec Chaudoir, 1879	Rostov env.:Morskaya
~*acutangulatus* Csiki, 1927; un; nom.pro *acutangulus* Eichler	Rostov env.:Morskaya
=*retowskianus* Mandl, 1955	SC-Ukraine:Odessa
006 *estreicheri* Fischer von Waldheim, 1822	Ukraine("Proskurov"=Khmelnitskiy), SW-Russia; W-Siberia:Tyumen, Tobolsk
=*adoxus* Fischer von Waldheim, 1823	"Kaukasus"(error)
~*modestus* Fischer von Waldheim, 1823, nec Fabricius, 1801	"Dauria, Südrussland"
=*jaegeri* Ménétriés, 1827	?Voronezh
=*accuratus* Chaudoir, 1848	"Bessarabia, Cherson"
~*rufofemoratus* Lomnicki, 1892, nec Motschulsky, 1865	
~*erythromerus* Semenov, 1898, nec Dejean; nom.pro *rufofemoratus* Lomn.	
~*rubidofemoratus* Csiki, 1927; un; nom.pro *erythromerus* Semenov	
=*basirufus* Marcu, 1937	
(007 see 02^1 *Morphocarabus*)	
008 *haeres* Fischer von Waldheim, 1823	N-Ukraine; SW-Russia:Voronezh, Tula, Ryazan'
a. ssp. ***haeres*** Fischer von Waldheim, 1823	Ryazan'
b. ssp. *fossulatus* Dejean, 1826, nec Quensel, 1806	W-Kursk prov., N,E-Ukraine
(009-015 see 02^1 *Morphocarabus*)	
016 *perrini* Dejean, 1831	SE-Ukraine, Krym Peninsula, SW-Russia, Georgia
ssp. ***perrini*** Dejean, 1831	Krym Peninsula("Sudrussland, Krym")
=*orbicollis* Motschulsky, 1846	"Russ.mer."(LT)
=*campicola* Reitter, 1896	Krym
(ssp.) *planus* Géhin, 1885, nec Fabricius, 1792; lsu; nom.pro *planatus* Motschulsky	SE-Ukraine, SW-Russia:Rostov, Maykop; Georgia; "S-Russia"
~*campestris* Fischer von Waldheim, 1822, nec Adams, 1817	"Tiflis"(=Tbilisi; ?inexact)
=*transcaucasicus* Csiki, 1927; nom.pro *campestris* Fischer von Waldheim	"Tiflis"(=Tbilisi; ?inexact)
~*parallelus* Fischer von Waldheim, 1844, nec Faldermann, 1835	"S-Russia"
~*planatus* Motschulsky, 1850, nec Chaudoir, 1843; nom.pro *parallelus* Fisch.	"S-Russia"
(017-018 see 02^1 *Morphocarabus*)	
019 *rybinskii* Reitter, 1896	W-Ukraine:Ternopol
020 *scabriusculus* Olivier, 1795	SC-Europe, Carpathians, Balcans, Ukraine, S-Russia, W-Turkey, SE-Europe
a. ssp. ***scabriusculus*** Olivier, 1795	Austria, Moravia, Slovakia, Hungary, W-Romania, Ukraine
=*agrestis* Creutzer, 1799	Moravia
~*erythropus* Fischer von Waldheim, 1822, nec Marsham, 1802	
=*hoffmanni* Motschulsky, 1845	
c. ssp. *lippii* Dejean, 1826	SE-Hungary; Romania, Moldavia

=?*laevior* Krynicki, 1830	"Moldavia, Bessarabia"
=*curvatus* Motschulsky, 1845	"Altays"(error)
~*cruralis* Vacher de Lapouge, 1908; un	
~*costulatus* Petri, 1912, nec Kraatz, 1889	"Transsylvania"
retyezaticus Csiki, 1927; nom.pro *costulatus* Petri	"Transsylvania"
~*macrolippii* Lie, 1996; un	C-Romania:S of Alba-Iulia:Sebeş-Alba env.
b. ssp. *inapertus* Motschulsky, 1850	Ukraine(Kharkov-LT), S-Russia
~*longulus* Vacher de Lapouge, 1908; un	
d. ssp. *bulgarus* Vacher de Lapouge, 1908	SC,SE-Romania, Bulgaria, Serbia, Bosnia, N. Macedonia, Eur.Turkey
~*interruptus* Born, 1902, nec Fabricius, 1775	S-Romania:Vlasca:Comana
=*laceratus* Csiki, 1927; nom.pro *interruptus* Born	S-Romania:Vlasca:Comana
022 *sibiricus* Fischer von Waldheim, 1822	S,C-Siberia; SW-Russia; ?NW-China:Xinjiang
a. ssp. *kareLini* Fischer von Waldheim, 1830	SW-Russia:Saratov, Orenburg, Samara; "Südrussland"
= *kolosovi* Zinovjev, 1997	S.Urals
(023 see 02^1 *Morphocarabus*)	

03. ***CARABUS*** Linnaeus, 1758; type species *Carabus granulatus* Linnaeus
~*Paracarabus* Vacher de Lapouge, 1930, nec Reitter, 1930; type species *Carabus granulatus* Linnaeus
~*Neocarabus* Hatch, 1949, nec Vacher de Lapouge, 1930; type species *Carabus granulatus* Linnaeus

001 *granulatus* Linnaeus, 1758	Europe, Brit.Isles, Balcans, Turkey, Siberia, Far East, Japan; introduced: Canada, USA
a. ssp. ***granulatus*** Linnaeus, 1758	C,W,N-Europe, Brit.Isles, Balcans; S-Russia; introd.: SW-Canada:Brit.Columbia; ?LNF
=*chalybaeus* Voet, 1776	
=*campestris* Adams, 1817	Volga River Bank
=*confluens* Fischer von Waldheim, 1827	Volga River
=*parallelus* Faldermann, 1835	Volga River
~*niger* Letzner, 1850; un	
~*nigrescens* Letzner, 1850; un	
~*rufofemoratus* Letzner, 1850; un	
~*virescens* Letzner, 1850; un	
~*rubripes* Géhin, 1876, nec Duftschmid, 1812	
~*cupreoaeneus* Dalla Torre, 1877; un	
~*nigroaeneus* Dalla Torre, 1877; un	
~*viridiaeneus* Dalla Torre, 1877; un	
=*forticostis* Kraatz, 1878	
=*haematomerus* Kraatz, 1878	
=*parvicollis* Kraatz, 1878	?"Steiermark"
~*fulvipes* Géhin, 1885, nec Fabricius, 1792	
=*wimmeli* Schultz, 1900	Hamburg
~*hudsonicus* Vacher de Lapouge, 1924, nec Motschulsky, 1865	?Hudson Bay
=*granulatulus* Mandl, 1955	
e. ssp. *crimeensis* Breuning, 1933; un	Krym Peninsula:?Jaila Mts.
b. ssp. *hibernicus* Lindroth, 1956	Ireland:Kerry Co.:Killarney; Hebrides; introduced: Quebec, N.Brunswick, N.Scotia
~*atrocyanescens* Lamy, 1973; un	
c. ssp. ***interstitialis*** Duftschmid, 1812	S-Austria(Sudkärnten); N-Italy
=*debilicostis* Kraatz, 1878	?Piemonte
=*palustris* Dejean, 1826	Roma env.
d. ssp. *aetolicus* Schaum, 1857	C-Greece:"Missolunghi"(=Mesolóngi), Corsica, S-Balcans; Turkey:Konya, Denizli, S-Italy (Apulia, Calabria)
=*miridita* Apfelbeck, 1901	N-Albania:"Velipoja nr.Alessio"(=Lezhë)

=*paludicola* Müller, 1903	Herzegovina:Narenta River nr.Metkovich
=*corsicus* Born, 1906	Corsica:Folelli
f. ssp. *parallelus* Faldermann, 1835	Russia: Lower Volga, N-Caucasus
g. ssp. *duarius* Fischer von Waldheim, 1844	E-European Russia, Siberia, Altays, Sayans, Kazakhstan, Kyrgyzstan, N-Mongolia:"Dzhungaria"
h. ssp. *calabricus* Spettoli & Vigna Taglianti, 2001	S-Italy, Serre Calabre: Colle del Monaco
002 ***menetriesi*** Hummel, 1827	EC-Europe, NE-Europe, N-Russia, Finland, Byelorussia, Latvia
a. ssp. ***menetriesi*** Hummel, 1827	N-Europe, Finland, N-Russia(Novgorod env.), Byelorussia, Latvia; N-Slovakia:Oravská Lesná
b. ssp. ***pacholei*** Sokolar, 1911	Austria:Oberöst.(Tanner Moor nr.Königswiesen), Niederöst., Tirol; S,W,N-Bohemia: Šumava Mts. to Ústí n.Lab; NE,SE-Germany: Mecklenburg-Vorpommern, Sachsen, Bayern, ?Bulgaria
~*bohemicus* Tanzer, 1934; un	S-Bohemia:"Mt.Schreiner foot:Schneider- & Oberschlag"(=Mt.Bobík:Krejčovice, Milešice)
(ssp.) *knabli* Mandl, 1951	E-Austria:"Nordtirol:Gem.Breitenwang bei Reutte"(=ca.60km WNW of Innsbruck); 1m
(ssp.) *pseudogranulatus* Nüssler, 1965	Germany:Sachsen:Hermannsdorfer Wiesen

04. ***EUCARABUS*** Géhin, 1885; type species *Carabus ulrichii* Germar
=*Eutelocarabus* Reitter, 1896; type species *Carabus arvensis* Herbst
=*Loxocarabus* Reitter, 1896; type species *Carabus obsoletus* Sturm
=*Xystrocarabus* Reitter, 1896; type species *Carabus catenatus* Panzer = *Carabus catenulatus* Scopoli
=*Tmesicarabus* Reitter, 1896; type species *Carabus cristoforii* Spence
=*Apocarabus* Vacher de Lapouge, 1930; type species *Carabus stscheglowi* Mannerheim

001 ***arvensis*** Herbst, 1784	Europe, Siberia, Far East, Japan
(see note: Chapter 5, p. 182)	
a. ssp. ***arvensis*** Herbst, 1784	N,C-Europe:Slovenia to Scandinavia; W-Eur.Russia; "Pommern"(=NW-Poland)
~*arcensis*: auct.; iss of *arcensis* Herbst	-
=*pomeranus* Gmelin, 1788	"Pommern"(=currently NW-Poland)
~*aereus* Dejean, 1826, nec Dejean, 1826	"Alps of Steiermark"
=*seileri* Heer, 1837	Switzerland:Schaffhausen
~*cupreoaeneus* Letzner, 1850; un	
~*marginatus* Letzner, 1850; un	
~*niger* Letzner, 1850; un	
~*nigrescens* Letzner, 1850; un	
~*purpurescens* Letzner, 1850; un	
~*versicolor* Letzner, 1850; un	
~*viridiaeneus* Letzner, 1850; un	
~*viridis* Letzner, 1850; un	
~*ziegleri* Géhin, 1876, nec Duftschmid, 1812; nom.pro *aereus* Dejean	"Alps of Steiermark"
~*cuprescens* Dalla Torre, 1877; un	
~*fuscescens* Dalla Torre, 1877; un	
~*virescens* Dalla Torre, 1877; un	
~*nigrescens* Westhoff, 1881; un	
~*nigrinus* Westhoff, 1881, nec Motschulsky, 1865	
~*aeratus* Géhin, 1885, nec Quensel, 1806; nom.pro *ziegleri* Géhin	"Alps of Steiermark"
~*ruficrus* Géhin, 1885; un	
~*nigrinopomeranus* Rade, 1895; un	
=*austriae* Sokolar, 1907	?Wienerwald

~*detritus* Vacher de Lapouge, 1908, nec Drapiez, 1821	N-Germany:?
~*simplex* Vacher de Lapouge, 1908; un	"S-Germany & Austria"
b. ssp. *noricus* Sokolar, 1910	Austria:Alps:Wechsel
=*decipiens* Lengerken, 1911	"Bayern"
=*germaniae* Lengerken, 1911	Germany:?
=*borussicus* Csiki, 1927; nom.pro *detritus* Vacher de Lapouge	N-Germany:?
~*baldiai* Mandl, 1963; un	Austria:Vorarlberg:Hochfreschen, 1900m
~*haideri* Mandl, 1963; un	Kärnten:Schleinitz, Lienzer Hütte env.
(ssp.) *baschkiricus* Breuning, 1932	CE-Russia(Kazan'); C-Urals
~*laticollis* Motschulsky, 1850, nec Sturm, 1826	Baschkiria:Mt.Ilmen(=?Ilmen' ca.20km NE of Zlatoust)
e. ssp. ***sylvaticus*** Dejean, 1826	W-Europe:France(Seine-Marne:Ft.d'Eu), W-Switz., Belgium, Holland, W-Germany, Brit.Isles
=*schrickelli* Dejean, 1826	LNF
=*alpicola* Heer, 1837	?Switzerland:Mt.Pilatus
=*anglicus* Motschulsky, 1865	Windsore nr.London
~*irregularis* Beuthin, 1896, nec Fabricius, 1792	Haute-Loire
=*raetzeri* Born, 1898	Switzerland:Neuenburger Jura
=*brugeli* Devecis, 2000	
~*costalis* Vacher de Lapouge, 1908; un	France:Cévennes:Gerbier des Jonc
=*liebmanni* Lengerken, 1911	W-France:Vosges
=*spencei* Lengerken, 1911	"Pyrénées"(error)
=*sugintensis* Brunier, 1922	W-France:Haut-Rhin:Sundgau(=area betw.Basel/ Mulhouse)
=*subsylvaticus* Perraudin, 1965	?"Stoccarda"
=*jarrigei* Colas, 1971	Cote d'Or:Chatillon; TNF
=*thebaudi* Colas, 1971	Corrèze:Les Monédières; TNF
~*bicolor* (Keith, 1989); un	
c. ssp. ***carpathus*** Born, 1902; ?non priority	Carpathians(C-Romania:Bucegi Mt.R., Mt.Negoi); E-Europe, S-Eur.Russia
=?*eremita* Fischer von Waldheim, 1823; ?priority	"Kaukasus"(error)
~*romanus* Marcu, 1937; un	Romania:?
=*csikensis* Csiki, 1942	CE-Romania:Haghimas Mts.nr.Balan
=*pseudonoricus* Kenyery, 1983	Slovenia:"Bachergebirge:N-slope:1km S of Podvelka, 350m"(=ca.betw.Celje/Zagreb)
d. ssp. *venetianus* Bernau, 1914	NE-Italy:Dolomiti, Veneto(Bosco del Cansiglio); Slovenia
002 *catenulatus* Scopoli, 1763	Slovenia, Croatia, Bosnia, NE-Italy
a. ssp. *catenulatus* Scopoli, 1763	Slovenia("Kranj"); Croatia, Bosnia; NE-Italy:Trieste env., SE-Alps; Switzerland:Lugano env.
=*catenatus* Panzer, 1805	"Kranj"
=*herbsti* Dejean, 1826	"Mts.of Croatia"(alpine form)
=*alternatus* Haury, 1855	
=*subvirescens* Motschulsky, 1865	"Idria"
~*atropurpureus* Dalla Torre, 1877; un	
~*atrovirescens* Dalla Torre, 1877; un	
~*purpurescens* Dalla Torre, 1877; un	
~*virescens* Dalla Torre, 1877; un	
=*korlevici* Hoffmann, 1883	Croatia:"Lic plateau"
=*albanensis* Géhin, 1885	
~*subvirens* Haury, 1885; iss of *subvirescens* Motschulsky	
=*troyeri* Born, 1911	Croatia:Gospic
~*aenescens* Depoli, 1929; un	
=*hosti* Depoli, 1929	"Fiume env."(Rijeka)
=*rattii* Mandl, 1966	Mt.Palanzone nr.Lago de Como(=ca.20km NE of Como)
b. ssp. *fontanellae* Reitter, 1896	Croatia:Adriatic Sea coast & islands; "Zara"(=Zadar)

=*dinaricus* Apfelbeck, 1904	Dinara Mts.:Troglav, Kamesnica
=*mosorensis* Müller, 1930	"Mosor"(=nr.Split)
003a. *cristoforii* Spence, 1823	Pyrénées:N-Spain, S-France(Hautes-Pyrénées:Pic du Bréveu), Andorra
=*nicolasi* Reitter, 1888	Pic de Nère
~*obtritus* Vacher de Lapouge, 1898, nec Chaudoir, 1857	
~*rufipes* Nicolas, 1898, nec DeGeer, 1774	Pic de Nère
=*beuthini* Schulz, 1899	
003b. *deyrollei* Gory, 1839	NW-Spain(Galicia:Sierra de Perache); N-Portugal
~*luctuosus* Géhin, 1885, nec Villers, 1789	N-Portugal:Braga
~*chloromorphus* Brañes, 1985; un	
~*cyaneomorphus* Brañes, 1985; un	
~*goryi* Brañes, 1985; un	
~*miniresplendens* Brañes, 1985; un	
~*neotristis* Brañes, 1985; un	
~*pecoudi* Brañes, 1985; un	
~*splendidulus* Brañes, 1985; un	
004 *italicus* Dejean, 1826	N,C-Italy, S-Switzerland
a. ssp. *italicus* Dejean, 1826	N-Italy(Piemonte), S-Switzerland (Tessin)
=*halbherri* Vacher de Lapouge, 1898	
=*ronchettii* Born, 1900	Lombardia:Val Sassina
~*battonianus* Mandl, 1966; un	Liguria:Pra:Mt.Riondo
b. ssp. *rostagnoi* Luigioni, 1904	C,S-Italy(Latium:Maccarese, Cisterno,Campania)
~*rostagnonis* Seidlitz, 1904; iss of *rostagnoi* Luigioni	-
005 *obsoletus* Sturm, 1815, nec Rossi, 1790; lsu	Carpathians
a. ssp. *obsoletus* Sturm, 1815, nec Rossi, 1790; lsu	Carpathians:Mor., Slov., SE-Poland, N-Hungary, E-Ukr., N,C-Rom.; "Österreich"(=?Moravia)
=*aureocupreus* Reitter, 1880	"Trencsen"(=CW-Slovakia:Trenčín)
c. ssp. *prunneri* Mallasz, 1901	"Kom.Bestercze-Naszod"(=NC-Romania:Bistrita-Nasaud) "Kom.Also-Fehér"(=Alba Iulia)
=*csikii* Mallasz, 1901	
~*mallaszi* Vacher de Lapouge, 1908; un	"N-Hungary"(=currently NW-Romania)
~*uhligi* Vacher de Lapouge, 1908; un	
b. ssp. *uhligi* Vacher de Lapouge, 1908	"Ceahlau, Caliman, Rareul, Nagy-Hagymas"(=Rarau, Haşmaşul Mare)
=*dudichi* Csiki, 1927	
~*bicoloratus* Fleischer, 1930; un	
~*mallaszianus* Breuning, 1932; un; nom.pro *uhligi* Holdhaus	
~*tesari* Niedl, 1957; un	M-Ukraine:Mukachevo
e. ssp. *carpathicus* Palliardi, 1825	C,SW-Romania:Fagaraş Mt.R. to Banat; "Transsylvanian Alps"
=*euchromus* Palliardi, 1825	"Banat"
~*sacheri* Thomson, 1875; un	
=*bielzi* Birthler, 1886	C-Romania:"Çibin"(Çindrel Mt.R.)
=*deubelianus* Fleischer, 1911	"Kapellenberg nr.Kronstadt"(=Braşov)
(ssp.) *nagyagensis* Seidlitz, 1888; nom.pro *procerus* Bielz	W-Romania:Bihor Mts.; Cluj; Hunedoara & Alba:("Nagyag, Zalatna"=Sacarimb, Zlatna)
~*carpathicusnagyagensis* Birthler, 1886; un	"Nagyag, Zalatna"(=Sacarimb, Zlatna)
~*procerus* Bielz, 1887, nec Reitt.; nom.pro *carpathicusnagyagensis* Birth.	"Nagyag, Zalatna"(=Sacarimb, Zlatna)
d. ssp. *fossulifer* Fleischer, 1893	"Kom.Bihar:Hadymadfalva"
~*cupreus* Fleischer, 1930; un	
~*viridis* Fleischer, 1930; un	
=*tippmanni* Breuning, 1936	"Zalatna"(=Alba:Zlatna)

~*paranagyagensis* Lie, 1990; un	Arad/Hunedoara:Savirsin, Pojoga
006 *parreyssii* Palliardi, 1825; ?iss of *paraysi* Palliardi	Croatia, Bosnia; Montenegro, Serbia
a. ssp. ***parreyssii*** Palliardi, 1825; ?iss of *paraysi* Palliardi	Croatia, Bosnia; Montenegro:Volujak, Durmitor Massif
~*paraysi* Palliardi, 1825; ?cos of *parreyssi* Palliardi	-
=*pareysi* Auct.	
=*gattereri* Géhin, 1882	"Steiermark"(error)
=*purpurifer* Reitter, 1885	
=*dobiaschi* Beuthin, 1894	"Bosnia"
=*padewiethi* Csiki, 1906	S-Velebit Mts.:Stirovaca
~*ganglbaueri* Apfelbeck, 1890, nec Reitter, 1888	S-Bosnia:?
=*planinaecola* Csiki, 1906; nom.pro *ganglbaueri* Apfelbeck	S-Bosnia:?
=*squamisculptus* Reitter, 1908; nom.pro *ganglbaueri* Apfelbeck	S-Bosnia:?
b. ssp. *plassensis* Born, 1907	Bosnia:Adriatic Sea coast(Plasa);
=*strauchi* Born, 1908	N-Bosnia:Bihac env.
(ssp.) *tippmannianus* Breuning, 1943	E-Serbia:Frushka Gora; E-Serbia:Frushka Gora
007 *stscheglowi* Mannerheim, 1827	E-Ukraine, E-Eur.Russia; C,S-Urals(Zlatoust betw.Ufa/Chelyabinsk)
=*zakharschewskii* Motschulsky, 1845	Ukraine:"Charcov:Tschuguev"(=Kharkov:Chuguevka); "Rus.mer.:Svatova Luchka"(LT)
008 *ulrichii* Germar, 1824	C,E-Europe, Hungary, Ukraine, Romania, Bulgaria, Slovenia, Croatia, Bosnia, Serbia
a. ssp. ***ulrichii*** Germar, 1824	S,C,E-Germany, S-Poland, Bohemia to Slovakia, E-Hung., Moldova, W. Ukraine, N. Croatia, N. Serbia, N,C,E-Romania; "Schlesien", Austria
~*ullrichi* Germar, 1824; ?iss of *ullrichii* Germar	
=*leuckarti* Petri, 1885	"Siebenburgen:Schässburg"(=Sighişoara)
=*podolicus* Semenov, 1898	"Vinnitza"(=W-Ukraine:Vinnitsa)
=*comanensis* Born, 1902	SE-Romania:Dobrogea lowland:Comana, Braila; NE-Bulgaria:Razgrad
=*pavlitscheki* Born, 1907	"Bukowina"
=*tigancanus* Born, 1908	SE-Romania:Dobrogea lowland:"Tiganca"
=*baranyensis* Sokolar, 1908	SC-Hungary:"Kom.Baranya"
=*intercessor* Sokolar, 1912	NC-Hungary:Nógrád:Rétság
~*kardaschi* Fleischer, 1926; un	"Vlarapass"(=Moravia:Vlárský průsmyk)
=*volhynicus* Lutshnik, 1927	"Wolhynia"
=*planitiae* Csiki, 1929	E-Hungary(Alföld region:?Debrecen, ?Gyula)
=*donovalensis* Smetana, 1951	C-Slovakia:Nízké Tatry Mt.R.:Donovaly
~*germanicus* Sokolar, 1908, nec Semenov, 1898	"Germany, Nieder- & Oberösterreich"
=*alamannicus* Csiki, 1927; nom.pro *germanicus* Sokolar	"Germany, Nieder- & Oberösterreich"
~*stegmanni* Mandl, 1969; un	Niederbayern:Straubing
~*cupreoaeneus* Dalla Torre, 1877; un	"Oberösterreich"
~*picipes* Dalla Torre, 1877; un	
~*viridiaeneus* Dalla Torre, 1877; un	
=*viridulus* Kraatz, 1878	
~*parvus* Géhin, 1885; un	"Steiermark"
=*sokolari* Born, 1904	S-Austria:Leitha Mts.
c. ssp. *rhilensis* Kraatz, 1876	S-Hung., CW-Romania; Bulgaria(Rila Mts.), Slovenia, Croatia, Bosnia, S. Serbia
~*stussineri* Géhin, 1885; un	Slovenia:"Krain"
=*jaroslawi* Fleischer, 1898	"Kom.Bihar"
=*werneri* Reitter, 1899	Bosnia:Vradac
=*papukensis* Koca, 1900	Serbia:Slavonia:Papuk Mts.

~*fabrizioi* Battoni & Breuning, 1970; un	E-Serbia:Negotin
~*serbomacedonicus* Kenyery, 1970; un	SE-Serbia(70km S of Nis)
=*pernix* Csiki, 1904	
=*slivensis* Apfelbeck, 1904	CE-Bulgaria:Sliven
b. ssp. ***fastuosus*** Palliardi, 1825	SW-Romania:Banat(Mehadia), E-Serbia
~*cupreonitens* Kraatz, 1878, nec Chevrolat, 1861	
~*parallelus* Kraatz, 1878, nec Faldermann, 1835	"Banat:Nemet Bogsan"(=Bocsa nr.Reşita)
~*robustus* Kraatz, 1878, nec Deyrolle, 1869	"Banat"
~*superbus* Kraatz, 1878, nec Schaufuss, 1872	"Banat:Moldowa"(=Moldova Noua)
~*viridilimbatus* Kraatz, 1878, nec Motschulsky, 1859	"Banat:Nemet Bogsan"(=Bocsa nr.Reşita)
=*glaucus* Haury, 1878	Banat:Bazias
~*cyaneus* Bodemeyer, 1881, nec Fabricius, 1776	Banat:Reşita
~*cuprinus* Vacher de Lapouge, 1902; un	Banat:Bazias
~*kucajensis* Pavićević & Toševski, 1988; un	NE-Serbia:Kučaj Mts.:Babina Glava:above Resavska pečina Cave
~*transdiernae* Pavićević & Toševski, 1988; un	NE-Serbia:Tekija(=Dunav right bank opposite to Orşova)
~*alionidiernae* Lie, 1989; ?nud	Banat:Alion nr.Orşova
~*superboides* Lie, 1989; ?nud	Banat:"sanatoriul Marilla de linga Oravita"(=Oravita env.)
~*alioni* Lie, 1990; un; ?nom.pro *alionidiernae* Lie	Banat:Alion nr.Orşova
~*ciutagrosi* Lie, 1990; un	Banat:dealul Ciuta nr.Groşi(=ca.15km NE of Faget)
~*feregarii* Lie, 1990; un	Banat:Feregari/Domogled valley nr.Baile Herculane
~*subfastuosus* Lie, 1990; un	Banat: betw.Cavaran/Tincova(=ca.30km SE of Lugoj)
~*subsuperbus* Lie, 1990; un; ?nom.pro *superboides* Lie	Banat:"sanatoriul Marilla de linga Oravita"(=Oravita env.)
~*topeniae* Savulescu, 1992; un	Banat:Topenia valley(=NE of Baile Herculane)
=*subfastuosus* Lie, 1996	Banat: betw.Cavaran/Tincova(=ca.30km SE of Lugoj)
~*subsuperbussuperboides* Lie, 1996; un	Banat:"sanatoriul Marilla de linga Oravita"(=Oravita env.)
~*umbrosus* Lie, 1996; un	Banat:Poiana Rusca Mts.:Nadrag & Borlova env.
d. ssp. *arrogans* Schaum, 1858	NE-Serbia:Majdanpek, Donji Milanovac; "Serbia"
~*ceremosnjensis* Pavićević & Toševski, 1988; un	NE-Serbia:Homolje Mts.:Ceremošnja
~*gornjakensis* Pavićević & Toševski, 1988; un	NE-Serbia:Šetonje:Gornjak monastery env.
~*pseudoarrogans* Pavićević & Toševski, 1988; un	NE-Serbia:Donji Milanovac

05. *TACHYPUS* Weber, 1801; type species *Carabus auratus* Linnaeus
=*Autocarabus* Seidlitz, 1887; type species *Carabus auratus* Linnaeus
~*Goniocarabus* Reitter, 1896, nec Géhin, 1885; type species *Carabus cancellatus* Illiger
=*Cancellocarabus* Lutshnik, 1924; nom.pro *Goniocarabus* Reitter

001 ***auratus*** Linnaeus, 1761	W,NC-Europe
a. ssp. ***auratus*** Linnaeus, 1761	W,NC-Europe:NC-Spain:Viella; SC,C,N-France to Bohemia, ?W-Poland; "Sweden"(error)
=*sulcatus* DeGeer, 1774	
~*coeruleomicans* Letzner, 1850; un	
~*contortus* Letzner, 1850; un	
~*picipes* Letzner, 1850; un	
=*laniarius* Gistl, 1857	
~*nigripes* Dalla Torre, 1877; un	
~*opacoviridis* Dalla Torre, 1877; un	
~*viridiauratus* Dalla Torre, 1877; un	
=*brullei* Géhin, 1885	
=*catalaunicus* Géhin, 1885	"Champagne"
=*obscuricornis* Beuthin, 1894	
=*worleei* Beuthin, 1894	"Harz"
~*rotundatus* Born, 1895, nec Paykull, 1798	Col de Balme nr.Chamonix
=*auratoides* Reitter, 1896	"Vogesen"(=Vosges Mts.)

=*perauratus* Reitter, 1896	Austria:Vorarlberg:Dornbirn
=*sulcatissimus* Vacher de Lapouge, 1898	
=*confluentinus* Bockleth, 1904	C-Germany:Rheinland:Koblenz
=*laticollaris* Bockleth, 1904	
=*quadricostatus* Bockleth, 1904	
=*labittei* Clément, 1904	Paris env.
~*perviridis* Born, 1915; un; error for *perauratus* Reitter	-
~*anthracinus* Barthe, 1921; un	"Pyrénées"
=*bettingeri* Barthe, 1921	Savoie:St.Pierre d'Albigny
~*dufouri* Barthe, 1922, nec Dejean, 1829	Auvergne:Clermont-Ferrand
~*barthei* Lebis, 1924; un	
=*dufouranus* Csiki, 1927; nom.pro *dufouri* Barthe	Auvergne:Clermont-Ferrand
=*clementi* Sirguey, 1931	
~*clermonti* Sirguey, 1931; un	
~*meyeri* Sirguey, 1931, nec Born, 1898	
=*rivalieri* Bourgin, 1948	Seine-et-Marne:?
=*concyri* Machard, 1973	
~*plonnieri* Machard, 1973; un	
=*isignyensis* Machard, 1977	
~*margaritae* Hecq, 1996, un	Marne/Meuse:Ft. d'Argonne(Chatrices S of Sainte Menehould)
d. ssp. *honnoratii* Dejean, 1826	SE-France:Alpes-de-Haute-Provence(?"Mts.of Basses Alpes:Banon"), Vaucluse, Var
~*atripes* Géhin, 1885; un	"Basses Alpes"(=Alpes-de-Haute-Provence)
~*nicolasi* Chobaut, 1897, nec Reitter, 1888	Vaucluse:Mt.Ventoux
=*ventouxensis* Nicolas, 1904	Vaucluse:Mt.Ventoux
=*bnicolasi* Chobaut, 1908; ?nom.pro *nicolasi* Chobaut	Vaucluse:Mt.Ventoux
~*baeri* Bleuse, 1914, nec Ménétriés, 1851	"Basses Alpes"(=Alpes-de-Haute-Provence)
=*diversicolor* Bleuse, 1914	"Basses Alpes"(=Alpes-de-Haute-Provence)
~*olivarius* Nicolas, 1919; un	Alpes-de-Haute-Provence:Digne
~*nicolasianus* Csiki, 1927; un; nom.pro *nicolasi* Chobaut	Vaucluse:Mt.Ventoux
=*fabrei* Colas, 1962	Vaucluse:Mt.Ventoux
=*vadoni* Colas, 1962	Var:Rians
=*aufrerei* Colas, 1964	Alpes-de-Haute-Provence:Les Dourbes
~*diensis* Tarrier, 1975; un	Drôme:Forêt de Saou
~*blayeulensis* Machard, 1977; un	Alpes-de-Haute-Provence:Mt.de Blayeul
~*lardierensis* Machard, 1977; un	
~*lurensis* Machard, 1977; un	
~*grimonensis* Machard, 1977; un	
~*malcorensis* Machard, 1977; un	
~*seirinensis* Machard, 1977; un	
~*ignescens* Darnaud, 1980; un	Vaucluse:Mt.Serein
~*astridae* Fiévet, 1991; un	
~*camardi* Darnaud, 1995; un	Vaucluse:Buoux
c. ssp. *lotharingus* Dejean, 1826	SC,SE-France:Gard, Hérault, Aude, Vaucluse, Bouch.du Rh., Ardèche; Moselle:Metz(error)
=*siculus* Ragusa, 1881	"Sicilia"(error)
=*monspessulantus* Vacher de Lapouge, 1898	Gard:Montpellier
=*transiens* Cleu, 1952	
=*incognitus* Bourgin, 1953	Hérault:?
=*puisseguri* Bourgin, 1953	Hérault:Les Thiéres
=*gangensis* Schaefer, 1962	Hérault:Ganges
=*billieriensis* (Schaefer, 1969)	Hérault:Les Billieres
=*carouxensis* (Schaefer, 1969)	Hérault:Mt.Caroux

=*virenquensis* (Schaefer, 1969)	Aveyron:La Virenque
=*avenionensis* (Schaefer, 1973)	Vaucluse:Avignon
=*larzacensis* (Schaefer, 1973)	Hérault:Le Caylar
=*mourguesi* (Schaefer, 1973)	?Hérault:Cros env.:La Virenque
=*sambucensis* (Schaefer, 1973)	Bouches-du-Rhône:Le Sambuc
=*gagates* Forel & Leplat, 1995	Hérault: Brassac
b. ssp. *lasserrei* Doué, 1855	SW,SC-France(Dep.Ardèche)
=*ligericinus* Fairmaire, 1886	Lozère:S-part
=*sudresi* Vacher de Lapouge, 1898	Lozère:Mt.de la Margeride
~*ruthenus* Vacher de Lapouge, 1908; un	
=*magdelainei* Bleuse, 1914	Ardèche
=*ispaniacus* Nicolas, 1919	Lozère:Ispagnac
=*pseudolotharingus* Barthe, 1921	Aude:?
~*taranicus* Cleu, 1952; un	Ardèche
~*ligericinulus* Mandl, 1955; un	
=*millavensis* (Schaefer, 1969)	Aveyron:?
~*mouriesi* (Schaefer, 1969); un	
~*rabili* Raynaud, 1971; un	Tarn:Forêt de Grésigne
=*brunieri* Barthe, 1921	Aude:Salvezines
~*erythropus* Barthe, 1921; un	"C-Pyrénées"
=*hilairei* Gavoy, 1925	Pyrénées:Val d'Aran
~*nigricatus* Csiki, 1927; un; nom.pro *anthracinus* Barthe	"Pyrénées"
~*rutilipes* Csiki, 1927; un; nom.pro *erythropus* Barthe	"C-Pyrénées"
=*mazametensis* Prunier, 1999	Mazamet
(ssp.) *navarricus* Vacher de Lapouge, 1924	?"W-Pyrénées"; ?"Navarra"
002 ***cancellatus*** Illiger, 1798	W,N,C-Europe, Balcans, S-Scandinavia, W-Russia, Siberia
a. ssp. ***cancellatus*** Illiger, 1798	N-Germany, S-Scandinavia, Poland, N-Moravia, Ukraine, W-Russia, Siberia; ?"Ost-Preussen"
=*tuberculatus* Dejean, 1826	"N-Germany"
=*conjunctus* Lomnicki, 1892	
=*sajanensis* Reitter, 1896	"Ostsajan"(=East Sayans)
~*anderseni* Beuthin, 1896; un	
~*bicolor* Beuthin, 1896, nec Walker, 1866	
=*conspersus* Vacher de Lapouge, 1902	?"Russia"; ?Byelorussia:Baranovichi
~*rossicus* Vacher de Lapouge, 1902; un	C-Russia:?
~*adelphus* Kolbe, 1912, nec Rost, 1892	"Mark Brandenburg"
=*amitinus* Kolbe, 1912	
=*avunculus* Kolbe, 1912	"Westpommern:?Negast nr.Stralsund"
~*fallax* Kolbe, 1912, nec Olivier, 1795	CW-Poland:"Krossen"(=Krosno)
=*genuinus* Kolbe 1912	
=*marchicus* Kolbe, 1912	Berlin env.
=*rauterbergi* Kolbe, 1912	Niedersachsen:Hildesheim
=*saxonicus* Kolbe, 1912	"Sachsen:?"
=*kniehopfi* Langenhan, 1913	"Pommern:Stolp"
=*setteli* Langenhan, 1913	?Hannover
=*kuennemanni* Langhenhan, 1913	?Bremen
~*balticus* Bernau, 1915; un	Latvia:"Lennewaden nr.Riga"
~*charcoviensis* Bernau, 1915; un	Ukraine:Kharkov
=*pratensis* Bernau, 1915	"Südrussland"(error)
=*suspicax* Everts, 1915	Holland:?
~*rapax* Kolbe, 1915; un	N-Moravia:Paskov
=*wankae* Sokolar, 1919	"Teschen & Saybusch"
=*munsteri* Born, 1926	SE-Norway:?
=*dolosus* Csiki, 1927; nom.pro *fallax* Kolbe	CW-Poland:"Krossen"(=Krosno)

~*nowotnyi* Eidam, 1930; un	"Emanuelsegen"
~*semnonicus* Csiki, 1927; un; nom.pro *adelphus* Kolbe	"Mark Brandenburg"
=*kuntzeni* Eidam, 1930	Denmark:"Jutland:Sandbl.Leijord, Sandet, Muldjord, Klitplantage, Svingelbjerg"
=*obscuriusculus* Eidam, 1930	"Oberschlesisches Industriegebiet"
=*ingulensis* Eidam, 1941	Ukraine:"Elisabethgrad, Cherson, Charkow"
(ssp.) *scythicus* Schaum, 1857	Romania & W-Ukraine:N,C-Carpathians; ?Carpathians of C-Romania
=*bucsecsianus* Born, 1902	"Gipfelregion des Bucsecs"(=Bucegi Mt.R.; alpine form)
~*pseudoscythicus* Vacher de Lapouge, 1902; un	
~*pseudotuberculatus* Vacher de Lapouge, 1902; un	?Carpathians of NC Romania
~*transsylvanicus* Petri, 1912; un	"Transsylvania:Schulergebirge, Schässburg"(=Sighişoara)
=*assiduus* Kolbe, 1913	Fagaraş Mt.R.:Mt.Negoi
=*bucovinianus* Kolbe, 1913	"Bucowina"(=NE-Romania)
~*gracilis* Kolbe, 1913, nec Küster, 1846	"Galicia:Radymno"
~?*infernalis* Kolbe, 1913; un	"Ungarn"(=?W-Romania)
=*moldavicus* Kolbe, 1913	Bacau
=*oligoscythus* Kolbe, 1913	NE-Romania:"Berlad valley"(=Birlad River)
=*oriundus* Kolbe, 1913	"Czernowitz & Bojan"(=W-Ukraine:Chernovtsy)
=*romaniacus* Kolbe, 1913	"Romania:Parban"
~*dobrudschensis* Bernau, 1913; un	Dobrogea Lowland(?error)
~*subfallax* Bernau, 1913; un	"Bukowina:Bojan"
~*scythicoides* Bernau, 1913; un	"Walachei"
~*vorax* Bernau, 1913; un	"Kronstadt"(=Braşov)
~*subscythicus* Lie, 1996; un	C-Romania:NE of Simeria:Sibot env.
(ssp.) *durus* Reitter, 1896	W-Carpathians:Slovakia("Trencsener Bergen"=Mts.nr. Trenčín), SW-Ukraine, NC-Romania
=*pseudograniger* Reitter, 1896	"Trencsén"(=SW-Slovakia:Trenčín)
=*ungensis* Csiki, 1905	?"Kom.Ung"(=W-Ukraine:Uzhgorod env.)
~*carpathicus* Kolbe, 1913, nec Palliardi, 1825	"Szinever & Nadvorna"(=?Carpathians of W-Ukraine)
=*enitens* Kolbe, 1913	"Galicia"
=*strictus* Kolbe, 1913	"Galicia & Karpathen"
(ssp.) *sulinensis* Born, 1902; ?non priority	NE-Romania("Letea nr.Sulina/Dunarea confluence"), Moldavia, Krym Peninsula
=?*semistriatus* Fischer von Waldheim, 1823; priority	"Caucasus"(error)
=*scabridus* Eidam, 1941	LNF(?Moskva, Ryazan', Kazan')
b. ssp. ***emarginatus*** Duftschmid, 1812, nec Olivier, 1795; lsu	N,NC-Italy, W-Slovenia, SW-Switzerland, SE-Austria, ?"Krain"
~*affinis* Duftschmid, 1812, nec Schrank, 1781	
~*oblongus* Sturm, 1815, nec Fabricius, 1792	LNF(?Italy/Slovenia/Austria borders region)
=*dahli* Heer, 1841	Alpi Orobie:Mt.Generoso
=*duftschmidi* Géhin, 1876; nom.pro *affinis* Duftschmid	
=*trentinus* Kraatz, 1877	"Trient"(=Trento)
=*bohatschi* Reitter, 1881	Lago Maggiore
~*ziegleri* Kraatz, 1883, nec Duftschmid, 1812	?LNF(unlabelled HT); ?"Styria"
~*tridentinus* Bertolini, 1887; ?iss of *trentinus* Kraatz	-
=*penninus* Vacher de Lapouge, 1896	"Monte Rosa"
~*sequensi* Beuthin, 1898; un	CW-Croatia:Gospic
~*generoso* Born, 1900; ?nud	Alpi Orobie:Mt.Generoso(alpine form)
~*collaris* Vacher de Lapouge, 1902; un	"S-Tyrolia:?
=*generosensis* Born, 1906	Alpi Orobie:Mt.Generoso(alpine form)
~*karstianus* Bernau, 1911; un	SW-Slovenia("Heidenschaft"=Ajdovščina)
~*tolminensis* Bernau, 1911; un	Italy/Slovenia:Isonzo valley:Tolmin env.
=*luganensis* Born, 1914	"Ticino:Locarno & Lugano"
=*picciolii* Bernau, 1915	"N-Apennines"

=*ticinus* Born, 1920	"Tessin"
=*poschiavinus* Born, 1922	Lombardia:Bernina Massif:Val Poschiavo
~*pustuliger* Eidam, 1941; un	"Tyrolia:Ampezzo Tal:Schluderbach"
~*obscuripennis* Mandl, 1961; un	"Kärnten:Waidischtal:Hudajama-Graben"
=*neoziegleri* Deuve, 1991; nom.pro *ziegleri* Kraatz	?LNF(unlabelled HT); ?"Styria"
~*planitialis* Ghiretti, 1994; ?un	Lombardia:Mantova
g. ssp. **carinatus** Charpentier, 1825, nec Duftschmid, 1812; lsu	France, NW,NC-Spain, W-Switzerland("Genf"= Genève), W-Germany, Belgium, S-Holland
=*fusus* Palliardi, 1825	Savoie
=*dolens* Kraatz, 1879	"Pyrénées"
=*tarnensis* Géhin, 1885	Tarn
=*aveyronensis* Beuthin, 1895	Aveyron
~*nigrinus* Beuthin, 1896, nec Motschulsky, 1865	
~*pseudocarinatus* Beuthin, 1896; un	"Rheinland"
=*astur* Vacher de Lapouge, 1898	"Asturia"
=*celticus* Vacher de Lapouge, 1898	"Intérieur de France"
=*crassus* Vacher de Lapouge, 1898	"Batz & Le Croisic"
=*misellus* Vacher de Lapouge, 1898	"Margeride Mts."; alpine form
=*pyrenaicus* Vacher de Lapouge, 1898	S-France:?
~*acicularis* Vacher de Lapouge, 1902; un	
~*asidoides* Vacher de Lapouge, 1902; un	"S-France"
~*inornatus* Vacher de Lapouge, 1902; un	
~*confinis* Vacher de Lapouge in Barthe, 1909; un	
=*progressivus* Kolbe, 1912	"Westfalen"
~*subcarinatus* Kolbe, 1912; un	"Rheinprovinz"
=*houlberti* Bleuse, 1913	Ille-et-Vilaine
=*nigellus* Bleuse, 1913	Ille-et-Vilaine
~*ehlersi* Bernau, 1915; un	"N-Spain:Gorbea"
~*pyrenaeus* Bernau, 1915; un; error for *pyrenaicus* Vacher de Lapouge	-
~*simulator* Everts, 1915, nec Kraatz, 1876	
~*viridis* Everts, 1918; un	Holland:?
~*delaunayi* Barthe, 1924; un	Orne:Domfront
=*eques* Vacher de Lapouge, 1925	"Navarra & Dep.Landes"
=*pelissieri* Darnaud, 1978	Bouches-du-Rhone:Arles:moor area
f. ssp. ***graniger*** Palliardi, 1825	SW,C-Romania:Banat(Mehadia), Bihor; CE-Serbia
~*assimilis* Duftschmid, 1812, nec Paykull, 1790	"Banat"
~*moestus* Dejean, 1831, nec Duftschmid, 1812	
=*nicanor* Haury, 1880	
=*muehlfeldi* Géhin, 1885, nec Duftschmid, 1812	?Retezat Mts.
=*szobroniensis* Géhin, 1885	?SE-Romania:Comana
=*basalis* Beuthin, 1896	
=*biharicus* Reitter, 1896	
=*rufoscapus* Beuthin, 1896	
=*subgraniger* Reitter, 1896	"Klausenburg"
~*ater* Fleischer, 1898, nec Villers, 1789	
=*coloripes* Fleischer, 1898	
=*nigripennis* Fleischer, 1898	
=*oxycancellatus* Fleischer, 1898	
=*mazurai* Fleischer, 1910	C-Romania:"Retezat:Kimpuluinyag"(=Cimpu lui Neag W of Petroşani)
=*disseptus* Kolbe, 1913	"Moldova"
~*fraternus* Kolbe, 1913, nec Csiki, 1906	
=*insperatus* Kolbe, 1913	"Serbia"
=*rbanyensis* Bernau, 1913	"Banat:Resitzabanya"(=Reşita)

=*resiczabanyensis* Csiki, 1913; nom.pro *rbanyensis* Bernau	
=*romaniensis* Kolbe, 1913	"Romania"
=*geta* Vacher de Lapouge, 1925; nom.pro *szobroniensis* Géhin	
~*pompilii* Savulescu, 1992; un	Banat:Topenia valley(=ca.24km NE of Baile Herculane)
=*bibanensis* Lie, 1994	Banat:Semenic Mts.:Biban valley(=ca.30km S of Caransebeş)
(ssp.) *excisus* Dejean, 1826	Austria("Wien:Kahlen- & Leopoldsberges"), NE-Switzerland, S-Germany, Bohemia, S-Moravia
=*verrucosus* Heer, 1837	?Switzerland
~*marginatus* Letzner, 1849; un	
~*rufofemoratus* Letzner, 1849; un	
~*viridis* Letzner, 1849; un	
~*affinis* Gistl, 1857, nec Schrank, 1781	München
~*punctulatus* Schaum, 1857, nec Schaller, 1783	
~*cupreoaeneus* Dalla Torre, 1877; un	?"Oberösterreich"
~*rubrofemoratus* Dalla Torre, 1877; un	
~*viridiaeneus* Dalla Torre, 1877; un	
~*haematomerus* Kraatz, 1879, nec Kraatz, 1878	
=*letzneri* Kraatz, 1879	
~*rufipes* Kraatz, 1879, nec DeGeer, 1774	
~*femoralis* Géhin, 1885, nec Motschulsky, 1865	
~*sudeticus* Schulz, 1901; un	
=*superior* Sokolar, 1907	Oberösterreich:Steyr env.
=*brevituberculatus* Roubal, 1909	?"Bohemia"
=*interior* Sokolar, 1910	
~*opolanus* Bernau, 1910; un	C-Bohemia:"Opolan bei Podiebrad"(=Opolany nr.Poděbrady)
=*pseudoemarginatus* Bernau, 1910	
=*thuringianus* Born, 1911	"Thüringen"
=*brdensis* Sokolar, 1911	C-Bohemia:Brdy Mts.
~*bavaricus* Kolbe, 1912, nec Beuthin, 1896	Bayern:?
=*spaneyi* Kolbe, 1912	S-Germany:?
=*transitivus* Kolbe, 1912	"Thüringen"
=*lapougeanus* Langenhan, 1913	"Schweiz"
=*planianensis* Bernau, 1913	"Planian"(=?C-Bohemia:Plaňany W of Kolín)
~*pseudobavaricus* Bernau, 1913; un	Pfarrkirchen
=*danubialis* Bernau, 1915	S-Germany:?
=*maderi* Born, 1915	?Wechsel Mts.
~*tersculptus* Fleischer, 1917; un	"Böhmerwald"(=S-Bohemia:Šumava Mts.)
=*transversus* Eidam, 1941	"Steiermark"
~*baldianus* Mandl, 1955; un	
~*regressivus* Poschinger, 1955; un	
~*gotzi* Mandl, 1964; un	Marchauen nr.Marchegg(=betw.Wien/Bratislava)
~*hanauensis* Niedl, 1964; un	SC-Germany:Hessen:Hanau
~*kubinyii* Mandl, 1964; un	Niederösterreich:Waldviertel:Gross-Pertenschlag, Sölling, Kasterslehen, Purgstall env.
~*wirthumeri* Mandl, 1964; un	Oberösterreich:Steyr:Reichraming & Kleiberggipfel nr.Schön-Klaus,
e. ssp. ***intermedius*** Dejean, 1826	S-Croatia:Dalm., Bosn.-Herz., Slovenia
=*apfelbecki* Born, 1904	Bosnia:?
=*islamitus* Born, 1904	Bosnia:Zepce
=*livnensis* Born, 1906	SW-Bosnia:Livanjsko Polje
=*annisus* Kolbe, 1913	

=*duvnensis* Bernau, 1914	Bosnia:Duvno Polje
(ssp.) *maximus* Haury, 1880	Bosnia, NE-Croatia; ?LNF
~*zoufali* Fleischer, 1922; un	
(ssp.) *aurosplendens* Born, 1910	?SE-Croatia, ?NW-Bosnia, Slovenia
(ssp.) *balcanicus* Born, 1899	E-Serbia; Bulgaria(“Stara Planina nr.Klisura”); ?Eur.Turkey:“Adrianopel”(=Edirne)
=*kocae* Born, 1910	“Serbia:Slavonia:?”
~*drenskyi* Breuning, 1928; un	S-Bulgaria:Rodopes(“Hassa Korja”); alpine form
=*simeoni* Eidam, 1941	
(ssp.) *mimus* Kolbe, 1913	N-Slovenia; SE-Austria, SW-Hungary(“Satoristye”)
~*nigricornis* Dejean, 1826, nec Fabricius, 1787	“S-Styria”
~*pseudocancellatus* Fleischer, 1898; un	“Banat”(error)
=*ambicornis* Sokolar, 1907; nom.pro *nigricornis* Dejean	-
c. ssp. ***corpulentus*** Kraatz, 1880	Croatia, Montenegro:Dalmatian coast; ?LNF
=*atroviridulus* Müller, 1898	“Zara”(=Zadar)
=*novaki* Müller, 1898	“Vrana Lake”(=Vransko Lake)
=*nudilabrus* Müller, 1898	“Zara”(=Zadar)
=*schatzmayri* Born, 1912	“Pago Island”(=Pag)
~*beszedesi* Depoli, 1915; un	“Abbazia”
=*ventricosus* Bernau, 1915	“Budua”
d. ssp. ***alessiensis*** Apfelbeck, 1901	N-Albania(“Velipoja nr.Alessio”)
=*hypsobius* Apfelbeck, 1918	“Nordalbanian Alps:Vunsaj env., karst, 1100-1800m”
h. ssp. ***tibiscinus*** Csiki, 1905	Hungary(?“Tisa Lowland”), NE-Serbia, E-Austria, W,NC-Slovakia, CW-Romania:Timis
~*soproniensis* Dejean, 1826; nud	“Hungary:Oedenburg”(=Sopron)
=*adeptus* Kolbe, 1913	?NW-Hungary
=*electus* Kolbe, 1913	?W-Slovakia
=*inceptus* Kolbe, 1913	?LNF
=*nattereri* Kolbe, 1913	“Temesvár”(=Timişoara)
~*tatricus* Kolbe, 1913, nec Reitter, 1896	NC-Slovakia:Tatry Mts.
=*vogeli* Breuning, 1933	NW-Hungary:Sopron
=*budensis* Csiki, 1946	Budapest env.:?Pilis Massif
=*leithaicus* Mandl, 1955	Burgenland:Leitha Mts.:?
004 ***vagans*** Olivier, 1795	SE-France:Alpes-Maritimes, Var(Frejus); NW-Italy:Liguria
~*liguricus* Vacher de Lapouge, 1898, nec Born, 1898	Var:Collobrières
=*matheyi* Born, 1917	Alpes-Maritimes:Grasse
~*borni* Barthe, 1921; un	
=*ligustinus* Csiki, 1927; nom.pro *liguricus* Vacher de Lapouge	“Dep.Var”
=*triglyphicus* Ochs, 1965	Var:Collobrières

06. ***ARCHICARABUS*** Seidlitz, 1887; type species *Carabus nemoralis* Müller
=*Aptocarabus* Reitter, 1896; type species *Carabus rossii* Dejean
=*Deuterocarabus* Reitter, 1896; type species *Carabus montivagus* Palliardi
=*Rhipocarabus* Reitter, 1896; type species *Carabus alysidotus* Illiger
=*Nemoralus* Schuler, 1976; type species *Carabus nemoralis* Müller

001 ***alysidotus*** Illiger, 1798	NW,CW-Italy; SE-France:Alpes-Maritimes to Hérault; “Italy”
a. ssp. ***alysidotus*** Illiger, 1798	Italy
=*pomptinus* Vacher de Lapouge, 1916	Italy:Maremma
b. ssp. *stagnalisaequalis* Vacher de Lapouge, 1916	Hérault:Lattes nr.Montpellier
=*stagnalis* Breuning, 1932; nom.pro *stagnalisaequalis* Vacher de Lapouge	-
=*bucheti* (Ochs, 1949)	

002 ***monticola*** Dejean, 1826	SE-France & NW-Italy:Alps
a. ssp. ***monticola*** Dejean, 1826	SE-France: Alp.Hte.Prov.("Basses Alpes"), Alp.Marit.; NW-Italy:Liguria
=*asperus* Beuthin, 1892	?"Basses Alpes"(=Alpes-Hte-Provence)
=*jordani* Beuthin, 1892	?"Basses Alpes"(=Alpes-Hte-Provence)
=*maritimensis* Born, 1923	Alpes Maritimes
=*megasomus* (Tarrier, 1972)	Alpes Maritimes:?lower Vésubie valley
~*bleonensis* Raynaud, 1973; un	Alpes-Hte-Provence:Bléone valley:Prads
(ssp.) *liguricus* Born, 1898	NW-Italy:Alpi Liguri(Colle dei Signori)
= *roccae* Born, 1923	NW-Italy:Monte Viso, Albergian, Val di Susa, Col Coupé;
~*sturanii* Mandl, 1966; un	Tessin:Savona env.:Monte San Giorgio; hills betw.Savona/Torino
(ssp.) *fontanae* Born, 1906	Tessin:Monte Generoso
=*biellensis* Born, 1923	Biella env.
003 ***montivagus*** Palliardi, 1825	Balcans, Romania, Hungary, SE-Slovakia, NE-Italy (introduced)
a. ssp. ***montivagus*** Palliardi, 1825	C,W,E-Bulgaria; C,W-Romania("Banat"), E-Serbia, E-Macedonia; NE-Greece, Eur.Turkey
=*kalofirensis* Apfelbeck, 1904	Bulgaria:"Kalofer"(=Kalofer Planina Mts.).
~*ponticus* Apfelbeck, 1904, nec Deyrolle, 1869	E-Bulgaria:Burgas
~*rosalitanus* Apfelbeck, 1904; un	"Balkan Mts.:Rosalita Pass env.(=Stara Planina Mt.R.)
=*bulgaricus* Csiki, 1927; nom.pro *ponticus* Apfelbeck	E-Bulgaria:Burgas
b. ssp. *vellepiticus* Hampe, 1850	Croatia(Velebit Mts.), Bosnia, Montenegro; N-Albania
~*illyricus* Kraatz, 1880, nec Kraatz, 1878	?"Ternowaner Wald"(=Slovenia:Trnovski Gozd)
=*illyriensis* Géhin, 1885; nom.pro *illyricus* Kraatz	?"Ternowaner Wald"(=Slovenia:Trnovski Gozd)
=*sutomorensis* Reitter, 1885	Montenegro:"Sutomore"
=*leonhardi* Born, 1904	?"N-Herzegovina"
=*medius* Vacher de Lapouge, 1908	"Romania, Bulgaria, Serbia, Bosnia & Croatia"
=*goljensis* Born, 1910	W-Bosnia:Golja Planina
(ssp.) *blandus* Frivaldszky, 1865	S-Slovakia, Hungary("Kom.Abauj-Torna & Heves")
004 ***nemoralis*** O.F. Müller, 1764	N,C,S,E-Europe; introduced:N.America, Kazakhstan
a. ssp. ***nemoralis*** O.F. Müller, 1764	Europe:France – Brit.Isles – Scandinavia – Eur.Russia; Germany, N-Italy; introd.:N.America, Kazakhstan
=*foetens* Voet, 1778	
~*nigrescens* Letzner, 1850; un	"Silesia"
~*virescens* Letzner, 1850; un	"Silesia"
~*tristis* Dalla Torre, 1877; un	Oberösterreich
~*krasae* Roubal, 1903; un	SW-Bohemia:"Klattau"(=Klatovy)
~*brunnipes* Vacher de Lapouge, 1908; un	
~*lucidus* Vacher de Lapouge, 1908, nec Duftschmid, 1812	?N,C-France
~*canadensis* Vacher de Lapouge, 1908, nec Melsheimer, 1853	N.Brunswick & Newfoundland(introduced)
~*deletus* Vacher de Lapouge, 1908; un	"Russia & Hungary"
~*auratus* Heuer, 1926, nec Linnaeus, 1758	Frankfurt a.M.
~*lestagei* Basilewsky, 1930; un	
=*nicollei* Bourgin, 1947	Aube:?Ft.du Grand Orient
=*nigrotinctus* Mandl, 1955	
~*pseudomontivagus* Mandl, 1961; un	"Kärnten:Weidisch:Javornik"
=*verdonensis* Puisségur, 1961	Alpes-Hte-Provence/Var:Verdon valley:Les Dourbes
=*colasi* (Bourgin, 1963)	Massif des Maures
=*miolansicus* Tarrier, 1965	Esteron valley
=*cantalicus* Jeanne, 1970	Cantal:Plomb du Cantal, 1850m
~*aubersoni* (Raynaud, 1973); un	Switzerland:Pomy
=*borealensis* (Raynaud, 1973)	England:Oundle, Ashton Wold

~*cantalicus* Machard, 1974, nec Jeanne, 1970	C-France:Cantal:?
=*fayardensis* Machard, 1974	Alpes-Hte-Provence:Lardier
~*freneyi* Tarrier, 1975; un	Maine-et-Loire:Bois du Mouliherne
~*montisdiniensis* Tarrier, 1975; un	Alpes-Hte-Provence:Les Dourbes
=*waltersachi* Mandl, 1984	Austria:Steiermark:Rotemanner Tauern:Strechengraben
b. ssp. ***prasinotinctus*** Heyden, 1880	SW-France, NC-Spain; Lozère & N-Spain
=*contractus* Géhin, 1885	Hautes-Pyrénées
=*kraatzianus* Beuthin, 1889	?“S-France”
=*nisseni* Beuthin, 1889	?“S-France”
~*pulcherrimus* Beuthin, 1889; un	?“S-France”
=*atavus* Vacher de Lapouge, 1908	LNF(unlabelled HT)
~*discolor* Vacher de Lapouge, 1908; un	
~*meridionalis* Vacher de Lapouge, 1908, nec Born, 1905	Ariège
=*pascuorum* Vacher de Lapouge, 1908	S-France:Cévennes; Lozère:St.Germain-de-Calberte(NT)
=*quinqueseriatus* Vacher de Lapouge, 1908	Landes
~*setosus* Vacher de Lapouge, 1910; un	
~*indigotinctus* Codina, 1927; un	N-Spain:Burgos:Pancorbo
~*meridianus* Csiki, 1927, nec Linn., 1767; nom.pro *meridionalis* Vacher de Lapouge	Ariège
~*venustus* (Raynaud, 1973), nec Morawitz, 1862	Lot:Leymes
~*litigiosus* Tarrier, 1975; un	Aude:Ft.de Monthaut nr.Rennes-les-Bains
(ssp.) *lamadridae* Born, 1895	NW-Spain:Lugo, Oviedo, Leon, Coruna; “Asturia:Llanos”
~*layrei* Tarrier, 1975; un	NW-Spain:Lugo:Puertomarin
005 ***pseudomonticola*** Vacher de Lapouge, 1908	S-France:Pyrénées-Orientales(Serralongue; NT); NE-Spain:Gerona, Barcelona
=*sorredensis* Reymond, 1935	Pyrénées-Orientales:Forêt de Sorrède
~*catenus* (Raynaud, 1973); un	“Casteil”
~*lunatus* (Raynaud, 1973); un	“Col des Ares”
~*hispanicus* Tarrier, 1975; un	Barcelona:Montserrat
=*pseudopascuorum* Tarrier, 1975	Barcelona:N.S.de Queralt nr.Berga
006 ***rossii*** Dejean, 1826	Italy:Piemonte to Calabria
=*dragonettii* Rozzi, 1839	Gran Sasso Massif
~*castaneipennis* Costa, 1857, nec Ménétriés, 1832	
~*minor* Pirazzoli, 1871, nec Kraatz, 1860	Abruzzi Mts.
=*pirazzolii* Géhin, 1876; nom.pro *minor* Pirazzoli	Abruzzi Mts.
=*costae* Géhin, 1885; nom.pro *castaneipennis* Costa	
=*stoecklini* Lopez, 1891	Livorno
~*intermedius* Porta, 1923, nec Dejean, 1826	
=*portae* Csiki, 1927; nom.pro *intermedius* Porta	
007 ***steuartii*** Deyrolle, 1852	NW-Spain:Orense, Zamora, Lugo, Léon; N-Portugal:Braga to Guarda(“Oporto env.”=Porto)
=*heydeni* Oliveira, 1876	Portugal:?Serra de Gerez
=*barrosi* Vacher de Lapouge, 1908	
=*fusarius* Vacher de Lapouge, 1908	
=*moreli* Vacher de Lapouge, 1908	Spain
=*nodicornis* Vacher de Lapouge, 1908	
=*fabriciiruspolii* Breuning, 1966	NW-Spain:Léon:Peña Rubia
=*durani* Raynaud, 1974	NW-Spain:Lugo:Samos
=*bastiani* Lassalle, 1982	Portugal:Guarda:Manteigas env.
008 ***wiedemanni*** Ménétriés, 1836	Turkey, SE-Bulgaria
(ssp.) ***wiedemanni*** Ménétriés, 1836	NW-Turkey:Istanbul to Sinop; SE-Bulgaria; NE-Greece:Alexandroupoli; “Turkey”
=*vaitoiani* Strasser, 1900	“Phillipoppel”(=Plovdiv)
=*burgassiensis* Apfelbeck, 1904	SE-Bulgaria:Burgas env.

07. ***HEMICARABUS*** Géhin, 1876; type species *Carabus nitens* Linnaeus

001 ***nitens*** Linnaeus, 1758	N,W,C-Europe:SW-France to Scandinavia; British Isles, Ukraine, W-Siberia
=*aureus* DeGeer, 1774	
~*marginatus* Voet, 1778, nec Linnaeus, 1758	
=*hookeri* Nodier, 1821	Scotland
~*aureomicans* Letzner, 1850; un	
~*virescens* Letzner, 1850; un	
=*pulchellus* Brüggemann, 1873; nom.pro *nitens* Linnaeus	-
~*cupreus* Westhoff, 1881, nec Linnaeus, 1758	
~*interruptus* Westhoff, 1881, nec Fabricius, 1775	
=*fennicus* Géhin, 1885	?Finland
~*niger* Semenov, 1886, nec Linnaeus, 1761	Arkhangelsk
=*subnitens* Reitter, 1896	
~*funebris* Csiki, 1927; un; nom.pro *niger* Semenov	Arkhangelsk
~*willemsi* (Culot, 1986); un	
=*aquitaniensis* Mollard, 1996	Gironde:Bassin d'Arcachon

08. ***DIOCARABUS*** Reitter, 1896; type species *Carabus loschnikovii* Fischer von Waldheim

001 ***loschnikovii*** Fischer von Waldheim, 1823	N-European Russia, Altays(Kolyvan'nr.Zmeinogorsk), Sayans, Baykal Lake, N-Mongolia
002 ***truncaticollis*** Eschscholtz, 1833	Alaska, NW-Canada, N-Siberia, N-Eur.Russia, CE-Siberia, ?N-Mongolia
a. ssp. *truncaticollis* Eschscholtz, 1833	
ssp. ***polaris*** Poppius, 1905; ?non priority	N-Siberia("Obdorsk"=Salekhard nr.Ob' River mouth), arctic Russia
~*tristis* Motschulsky, 1850, nec Schaller, 1783	"Ural.bor."
=*degeneratus* Sahlberg, 1885; ?un; ?priority	
=*sahlbergianus* Géhin, 1885; ?un; ?priority	

09. ***AULONOCARABUS*** Reitter, 1896; type species *Carabus canaliculatus* Adams

001 ***canaliculatus*** Adams, 1812	Ural, C,E-Siberia, Sayans, N-Mongolia, Far East, Shanxi, NE-China, N-Korea; N,C-Sakhalin
ssp. ***canaliculatus*** Adams, 1812	Ural, C,E-Siberia(Lena River), Sayans, N-Mongolia, Far East, Shanxi, NE-China

10. ***MESOCARABUS*** C.G. Thomson, 1875; type species *Carabus catenulatus*: Fabricius, non Scopoli = *Carabus problematicus* Herbst

=*Hadrocarabus* C.G. Thomson, 1875; type species *Carabus latus* Fabricius = *Carabus lusitanicus latus* Fabricius

001 ***dufourii*** Dejean & Boisduval, 1829	S-Spain; "S-Spain & Tanger"(?error)
=*rosalesi* Reiche, 1863	Cordoba
~*papillatus* Vacher de Lapouge, 1902; un	Gibraltar
~*scaber* Vacher de Lapouge, 1902; un	Granada
=*salebrosus* Csiki, 1927; nom.pro *scaber* Vacher de Lapouge	Granada
~*granadensis* Brañes, 1987; un	Granada:Purullena
002 ***lusitanicus*** Fabricius, 1801	Portugal, Spain
a. ssp. ***lusitanicus*** Fabricius, 1801	Portugal; CW-Spain:Salamanca:CW-part
i. ssp. *egesippei* LaFerté Sénectère, 1847	N-Portugal:"Oporto"(=Porto)

=*sabrosensis* Reitter, 1896	N-Portugal:Sabrosa
b. ssp. *schaumi* Gaubil, 1849	"Portugal"
=*hellwigi* Schaum, 1862	
=*descensus* Schaufuss, 1871	
=*vieirae* Oliveira, 1875	CW-Portugal:Leiria
=*mediotuberculatus* Schaufuss, 1882	
=?*vivesi* Jeanne, 1973	
h. ssp. *castilianus* Dejean, 1826	CW-Spain:Salamanca:N-part(Los Santos)
c. ssp. *bolivari* Breuning, 1926	Salamanca:S-part(Bejar); Caceres:N-part; Avila:S-part
=*fuentei* Breuning, 1926	Salamanca:SW-part(Sierra de la Pena de Francia)
d. ssp. ***brevis*** Dejean, 1826, nec Duftschmid, 1812; lsu	C-Spain:Avila, Madrid, Guadalajara, Segovia, Burgos, Soria, Logrono, Cuenca, Teruel
e. ssp. *complanatus* Dejean, 1826, nec Linnaeus, 1767	Castrogeriz nr.Burgos
=*aragonicus* Ganglbauer, 1886	Zaragoza:Sierra de Moncayo:San Martin de Moncayo
=*complantus* Morawitz, 1890	?Avila; ?Burgos:Castrojeriz
~*logronicus* Breuning, 1926; un	Logrono:?
=*sorianus* (Jeanne, 1972)	Soria:Puerto de Oncala. 1450m
g. ssp. *helluo* Dejean, 1826	CE-Spain:Alicante, Valencia, Teruel, Castellon; ?"Spain"; ?"S.de Albarracin"
=*alicantinus* Ganglbauer, 1886	"Alicante"
k. ssp. *albarracinus* Ganglbauer, 1886	Teruel:Sierra de Albarracin
m. ssp. ***baguenai*** Breuning, 1926	SE-Spain:Almeria, Granada, Murcia; ?Almeria:Águilas
~*nevadensis* Brañes, 1989; un	Granada:Guadix
l. ssp. ***latus*** Dejean, 1826, nec Linnaeus, 1758; lsu	SW,SC-Spain(Caceres:Navalmoral de la Mata); CW-Portugal
=*luczotii* Castelnau, 1832	
=*gougeleti* Reiche, 1863	"Malaga & Córdoba"
=*leptopus* Thomson, 1876	
=*alcaracinus* Kraatz, 1886	Albacete:?betw.Alcaraz/Riopar; ?Ciudad Real:Pozuelo de Calatrava
f. ssp. *molossoides* Lassalle, 1984; un	Caceres:NE-part:Piornal
j. ssp. *antiquus* Dejean, 1826	S-Portugal; CW-Spain:Caceres/Badajoz:W-part; "Hispania"
=*mertolaensis* Breuning, 1975	S-Portugal:betw.Beja/Faro:Mertola
=*portalegrensis* Reitter, 1896	CW-Portugal:Portalegre
n. ssp. ***trabuccarius*** Fairmaire, 1857	NE-Spain:Tarragona, Barcelona; Huesca:NE-part; Pyrénées-Or.:Col de Perthus(?error)
=*catalonicus* Ganglbauer, 1886	Barcelona
~*problematicusoides* Tarrier, 1974; un; ?hyb	Barcelona:Collado d'Estenalles; ?hyb *lusitanicus/problematicus*
=*trypalsi* Breuning, 1975	Huesca:Mont Perdu Massif:E-slope:Plan de Trypals, 2000m
~*troncedoensis* Meyer & Mollard, 1990; nud	Huesca:Troncedo N of Barbastro
=*benabarrensis* Meyer & Mollard, 1996	Huesca:Calvera N of Benabarre
=*galardonensis* Meyer & Mollard, 1996	Huesca:Sierra de Galardon:Pto del Sarrablo
003 ***macrocephalus*** Dejean, 1826	N-Spain, SE-France:Pyrénées
a. ssp. ***macrocephalus*** Dejean, 1826	NW-Spain:Oviedo; Leon:N-part; "Asturia"; S of Puerto de Pajares:Busolongo(NT)
=*brabeus* Schaufuss, 1876	?Guipuzcoa:Mt.Aralar
e. ssp. *joaquini* Breuning & Toulgoet, 1974	Leon:N-part:Torrebarrio env.
=*guardoensis* Meyer & Mollard, 1996	Palencia:W of Guardo:Prado de Guzpena
=*rodriguezi* Meyer & Mollard, 1998, nec Breuning & Ruspoli, 1977	Burgos:10km W of Poza de la Sal

c. ssp. *cantabricus* Chevrolat, 1840	NW-Spain:Pontevedra(Sierra de Caniza), La Coruna, Lugo; Orense, Oviedo & Leon:W-part
=*liebei* Eidam, 1925	La Coruna
d. ssp. *asturicus* Born, 1925	Oviedo:W-part:Los Cabos nr.Pravia
h. ssp. *barcelecoanus* Vacher de Lapouge, 1924	NC-Spain:Santander to Pamplona; Pyr.-Atl.("Col Barceleco sur la Rhune"=Col des 3 Fontaines)
=*ahascoanus* Vacher de Lapouge, 1924	Navarra:Mt.Ahascoa
b. ssp. *macrocephaloides* (Jeanne, 1972)	Navarra(Sierra de Andia:Venta de Zumbelz, 1000m)
~*amayensis* Lassalle, 1984; un	Palencia/Burgos:Puerta de Amaya
f. ssp. *moroderi* Breuning, 1926	Mts.of Leon Province"
=*magdalenai* Meyer & Mollard, 1996	León:Pto.de la Magdalena
g. ssp. *breuningi* Csiki, 1927; nom.pro *kricheldorffi* Breuning	NW-Spain:Orense(Sierra de Queija), Zamora
~*kricheldorffi* Breuning, 1926, nec Le Moult, 1913	Orense:Sierra de Queija
004 ***problematicus*** **Herbst, 1786**	C,W,N-Europe, Scandinavia, Iceland, Kola Peninsula
a. ssp. ***problematicus*** Herbst, 1786	Austria, N-Italy, Alps; Moravia, Slovakia; "Österreich"
~*catenulatus* Fabricius, 1792, nec Scopoli, 1763	-
~*austriacus* Sturm, 1815, nec Fabricius, 1801	"Österreich"(inexact; ?Moravia)
=*cyanescens* Sturm, 1815	?"Mts.of Austria"
~*azurescens* Dalla Torre, 1877; un	"Oberösterreich"
~*marginatus* Dalla Torre, 1877; un	"Oberösterreich"
~*nigrescens* Dalla Torre, 1877; un	"Oberösterreich"
=*angustior* Born, 1885	Lugano env.(Mt.Generoso); SC-Switzerland:Ticino
=*clairvillei* Vacher de Lapouge, 1916	Savoie:Col du Petit St.Bernard
~*iserensis* Breuning, 1933; un	Isère:Villars de Lans
d. ssp. *harcyniae* Sturm, 1815	C,N-Germ.(Harz); N,C-France, Belg., Holl., Denm., Br.Isles; Bohemia, N-Poland, S-Scandin.
=?*dissitus* Fischer von Waldheim, 1826	"Bessarabia"(error)
=?*beauvoisi* Dejean, 1826	"North America"(error)
=?*californicus* Motschulsky, 1865	"California"(error)
=*solutus* Oberthür, 1884	N-France:Ft.Lorges
=*gallicus* Géhin, 1885	"Vogesen"
~*tibialis* Bleuse, 1896, nec Paykull, 1790	N-France:?
=*muelverstedti* Reitter, 1896	N-Poland:"W.Preussen:Rosenberg"=?Susz)
=*wockei* Born, 1898	C-Norway:"Dovrefield"
~*arvernus* Vacher de Lapouge, 1902; un	Auvergne
=*bayeri* Vacher de Lapouge, 1910	Switzerland/Germany:Bodensee
=*belgicus* Vacher de Lapouge, 1913	Belgium:"Liège, Luxemburg"
=*cychriformis* Bleuse, 1913	N-France:?
~*veneti* Auzat, 1915; un	Clermont-Ferrand
~*anthracinus* Everts, 1918, nec Illiger, 1798	Holland:?
~*progressus* Vacher de Lapouge, 1924, nec Semenov, 1888	British Isles:?
=*scandinavicus* Born, 1926	S-Norway & S-Sweden
=*cruris* Csiki, 1927; nom.pro *tibialis* Bleuse	N-France:?
=*procedens* Csiki, 1927; nom.pro *progressus* Vacher de Lapouge	British Isles:?
=*obenbergerianus* Breuning, 1927	W,S-Bohemia("Preitenstein, Scheiben, Rakovitz"=Nečtiny, Šejby nr.Nové Hrady, ?Rakovice)
~*lhommei* Hoffmann, 1928; un	N-France:?
=*alluaudi* Colas, 1936	
~*diluvialis* Blumenthal & Nüssler, 1967; un	Niedersachsen:Lüneburger Heide
=*oceanicus* (Jeanne, 1971)	Gironde:Le Porge-Océan
~*campinus* Delacre, 1975; un	Belgium:Anvers:Zoersel
~*pseudogallicus* Delacre, 1975; un	Belgium:Brabant:Forêt de Soignes

~*lovervalensis* (Mal, 1981); un	Belgium:Hainaut:Bois de Loverval S of Charleroi
~*montanus* Venet, 1930; un	Auvergne
c. ssp. *inflatus* Kraatz, 1878	SE,SC-France:Alpes-Marit.; NW-Italy:Liguria;"Marseille, Basses-Alp.& Pyr.-Or."; N-Apennines
~*quadraticollis* Vacher de Lapouge, 1899; un	"Basses-Alpes:Riez"(=Alpes-Hte-Provence)
~*dellabeffae* Breuning, 1933; un	Alpes-Maritimes:Mt.Mounier
~*battonii* Mandl, 1966; un	Liguria:Savona:Osiglia
=*falsinflatus* Ochs, 1967	
~*moderatus* (Raynaud, 1971); un	Alpes-de-Hte-Provence:Vallée de la Gordolasque:St-Grat
b. ssp. *planiusculus* Haury in Géhin, 1885	E,C,W-Pyrénées(Hautes-Pyrénées:Gavarnie); SC-France: Tarn; SE-Spain:Barcelona, Gerona
~*brisouti* Fauvel, 1863; un	Pyrénées-Orientales:Vallée d'Eyne
=*solidus* Vacher de Lapouge, 1902	Pyrénées-Orientales:Vernet-les-Bains
=*prunieri* Pham, 1978	Pyrénées-Orientales:Puigmal Massif
=*mayeti* Géhin, 1885	"Alpes et Pyrénées"
=*mulsanti* Géhin, 1885	?Hautes-Pyrénées
=*trapeti* Bleuse, 1885	Hautes-Pyrénées:Baréges env.:Montferrat Glacier Vignemale Massif
~*niger* Nicolas, 1898, nec Linnaeus, 1761	Hautes-Pyrénées:Pic de Nère
=*andorranus* Vacher de Lapouge, 1902	Andorra
=*cunii* Vacher de Lapouge, 1903	?Gerona:Rosas
=*bepmalei* Vacher de Lapouge, 1904	"Aragonia:Huesca:Col de Basibé"
=*jugicola* Vacher de Lapouge, 1908	Haute-Garonne:Luchon env.
=*occitanus* Vacher de Lapouge, 1910	Tarn(Montagnes-Noires) to C-Pyrénées
~*impar* Vacher de Lapouge, 1910; un	Tarn:Montagnes-Noires
~*amplicollis* Bleuse, 1913, nec A.& J.B.Villa, 1844	
~*gracilis* Bleuse, 1913, nec Küster, 1846	
=*xaxarsi* Born, 1917	Barcelona:Centellas(LT)
~*secundariofilicatus* Codina, 1921; un	Gerona:Setcasas
=*oberthueri* Venet, 1930	?Andorra
~*nicolasi* Venet, 1932, nec Reitter, 1888	Ariège:Fôret de Bosc
~*navarrensis* Breuning, 1933; un	Navarra:Mt.Urculo
=*nicolasiellus* Breuning, 1934; nom.pro *nicolasi* Venet	Ariège:Fôret de Bosc
=*laurentianus* Forel & Laplat, 1995	Pyrénées, lac de Laurenti
f. ssp. *feroensis* Vacher de Lapouge, 1910	Faer Islands, Hebrides, Shetland & Orkney Isles
~*fairensis* Breuning, 1966; un	Fair Isle(=betw.Shetland/Orkney Isles)
(ssp.) *holdhausi* Born, 1911	C-Romania:Carpathians; ?"Siebenburgen:Ceahlau"
e. ssp. *strandi* Born, 1926	N-Scandinavia(N-Norway:Lappland:Faestnigstuen); Kola Peninsula
g. ssp. *islandicus* Lindroth, 1968	SE-Iceland:Höfn env.:Hornafjördur
h. ssp. *relictus* Hellén, 1934, nec Semenov, 1898	Russia:Hogland Island(=btw.Helsinki/St.Petersburg)

11. ***ORINOCARABUS*** Kraatz, 1878; type species *Carabus sylvestris* Panzer
=*Carpathophilus* Reitter, 1896; type species *Carabus linnei* Panzer
=*Cavazzutiocarabus* Imura, 1998; type species *Carabus latreilleanus* Csiki

Note: During the preparation of this book for printing, some important nomenclatorial changes in the subgenus *Orinocarabus* have been established by Deuve (2002) (see Addendum).

001 ***adamellicola*** Ganglbauer, 1904	NE-Italy:Adamello Massif(Mt.Frerone & Val di Leno), Brenta Massif
002 ***alpestris*** Sturm, 1815	E-Alps:NE-Italy:Alpi Carniche, Dolomiti; Slovenia; S-Austria

a. ssp. ***alpestris*** Sturm, 1815	SC,C-Austria(Schneeberg)
=*olivaceus* Géhin, 1876	
=*illyricus* Kraatz, 1878	?"Illyria"
~*hickeri* Breuning, 1927; un	"Böses Weibele"(=Lienz)
c. ssp. *hoppei* Germar, 1824; ?iss of *hoppii* Germar	E-Alps:NE-Italy:Alto Adige; S-Austria:Tirol, Salzburg, Kärnten; "Austria"
~*hoppii* Germar, 1824; ?cos of *hoppei* Germar	-
=*tyrolensis* Kraatz, 1876	Tirol:Zillertaller Alpen:Hocheder
=*brevicornis* Kraatz, 1878	
~*puncticollis* Kraatz, 1878, nec Paykull, 1798	
~*niger* Schilsky, 1888, nec Linnaeus, 1761	Zirbitzkogel
~*viridis* Schilsky, 1888, nec Dejean, 1826	Zirbitzkogel
=*rottenmannicus* Sokolar, 1907	Rottenmanner Tauern:Steinamandl
~*confluens* Born, 1913, nec Fischer von Waldheim, 1827	Rottenmanner Tauern:Hochschwung
~*tauernicus* Csiki, 1927; un; nom.pro *confluens* Born	Rottenmanner Tauern:Hochschwung
=*latschuranus* Born, 1921	Kalkalpen:Latschur
b. ssp. *dolomitanus* Mandl, 1956	NE-Italy:Dolomiti:Mt.Plose; N-Slovenia
003 *bertolinii* Kraatz, 1878	NE-Italy:Dolomiti("Malga Fornasa"=?Colle di Fornace); Belluno env.
(ssp.) *cavallensis* Bernau, 1914	Belluno env.:Mt.Cavallo
004 *carinthiacus* Sturm, 1815	E-Alps:NE-Italy; S-Austria; C-Austria:Rottm.Tauern; Slovenia(Karavanke:Zelenica), Bosnia
=*mollii* Dejean, 1826	
~*borni* Csiki, 1905, nec Meyer-Darcis, 1902	Bosnia:?
=*moosbruggeri* Born, 1913	Rottenmanner Tauern:?
=*friaulicus* Born, 1914	Mt.Cavallo & Musič nr.Bergogna
=*kendii* Csiki, 1926; nom.pro *borni* Csiki	Bosnia:?
005 *castanopterus* A.& G.B.Villa, 1833	NC-Italy/S-Switzerland:Alpi Orobie; Bernina Massif; "Alps of Lombardia"
=*lombardus* Kraatz, 1878	Lombardia:?
=*danieli* Reitter, 1896	Alpi Orobie:Val Arigna
=*mesolcinus* Born, 1906	Switzerland:passo della Forcola
=*montarerae* Bernau, 1914	Alpi Orobie:Mt.Arera
006 *cenisius* Kraatz, 1878	NW-Italy:Alpi Graie, Alpi Cozie
a. ssp. ***cenisius*** Kraatz, 1878	NW-Italy:Alpi Graie:Val Orco-Val Stura-Dora Riparia; Mt.Cenis Massif
=*sellae* Kraatz, 1878	LNF
=*sturensis* Born, 1899	Alpi Graie:Colle della Pietra Scritta
~*mauriennensis* Carret, 1904; un	
=*nigrocyanescens* Carret, 1904	
(ssp.) *iseranicus* Deuve & Simard, 1977	SE-France:Savoie:Iseran Massif (Col de l'Iseran,2500m)
c. ssp. *ceresiacus* Born, 1896	NW-Italy:Alpi Graie:Alpe Pian della Moglie:Ceres env.
b. ssp. ***fenestrellanus*** Beuthin, 1899	NE-Italy:Alpi Cozie:Col delle Finestre, Albergian, Sestriere
007a *concolor* Fabricius, 1792	Italy/Switzerland:Trentino; Alpi Pennine, Berner Alpen
~*alpinus* Dejean, 1826, nec Paykull, 1790	"Alps of Italy & Switzerland"(=Alpi Pennine)
=*amplicollis* A.& G.B.Villa, 1844	"Lombardische Alpen"
=*bernhardinus* Kraatz, 1878	Italy/Switzerland:Gr.St.Bernhard Pass
=*mimethes* Kraatz, 1878	Mte.Rosa
~?*minor* Kraatz, 1878, nec Kraatz, 1860	
=*bernensis* Born, 1895	Switzerland:?"Berge links des Haslitales von der Grimsel bis zum Urbachtal"
007b *lepontinus* Born, 1908	NW-Italy:Alpi Lepontine

008 ***fairmairei*** Thomson, 1875	W-Italy:Alpi Cozie; SE-France:Savoie
a. ssp. *fairmairei* Thomson, 1875	W-Italy:Alpi Cozie:upper Pellice & Po valley; "Pyrénées"(error)
=*baudii* Kraatz, 1878	Mte.Viso
~*cavazzutii* Raynaud, 1971; un	Val Chisone: S-W Fenestrelle (error)
c. ssp. *stecki* Born, 1902	SE-France, NW-Italy:Alpi Cozie:Col Longet, Col de Mary
b. ssp. *pelvicus* Cavazzuti, 1973	NW-Italy:Val Varaita(Mt.Pelvo d'Elva)
009 ***heteromorphus*** K. Daniel, 1896	NW-Italy:Alpi Graie:Col Nuovo
010 ***latreilleanus*** Csiki, 1927; nom.pro *latreillei* Dejean; ?non priority	W-Alps:NW-Italy, S-Switzerland:Alpi Pennine; "Alps of Piemonte"
~*latreillei* Dejean, 1826, nec Fischer von Waldheim, 1822	"Alps of Piemonte"
=*bremii* Stierlin, 1881; ?un; ?priority	
=*neglectus* Kraatz, 1887	
=*schilskyi* Kraatz, 1887	
011 ***linnaei*** Duftschmid, 1812	C-Europe(Germany:Harz Mts.), NE-Italy, Carpathians
~*linnei* Panzer, 1812; ?cos of *linnaei* Panzer	"Austria"
~*angustatus* Panzer, 1812, nec Fabricius, 1787	"Austria"
=*scopolii* Dejean, 1826	"Wolhynien"
~*brunneofemoratus* Letzner, 1850; un	
~*cupreoaureus* Letzner, 1850; un	
~*cupreus* Letzner, 1850; un	
~*nigricornis* Letzner, 1850; un	
~*obscurus* Letzner, 1850; un	
~*versicolor* Letzner, 1850; un	
(ssp.) *macaierei* Dejean, 1826	S-Carpathians:SW-Romania("Mts.of Banat")
= *macairei* Breuning, 1933	
=*hopffgartenianus* Beuthin, 1885	"Transsylvania:Kerzeschora"
=*bescidensis* Reitter, 1896	"Beskiden"(=N-Moravia:Moravskoslezské Beskydy Mts.)
=*ludovicus* Dietl, 1896	"Rotenturmpass"(=C-Romania:Turnu Rosu Pass)
=*quadraticollis* Petri, 1912	Romania:"Schässburg"(=Sighişoara)
=*quinquecostatus* Petri, 1912	"Schässburg & Kronsdtadt"(=Romania:Sighişoara & Braşov)
(ssp.) *folgariacus* Born, 1913	E-Alps:NE-Italy, Austria(?"Südtirol"); SE-Austria: Burgenland
=*transdanubialis* Kenyery, 1983	Burgenland:Mt.Geschriebenstein
=*tauernensis* Mandl, 1985	?Rottenmanner Tauern
012 ***putzeysianus*** Géhin, 1876; nom.pro *putzeysi* Thomson	SE-France & NW-Italy:Alpes-Maritimes, Alpi Liguri, Alpi Cozie
a. ssp. ***putzeysianus*** Géhin, 1876; nom.pro *putzeysi* Thomson	SE-France & NW-Italy:Alpes-Maritimes:Val Stura-Col de Tenda; "Switzerland"(error)
~*maritimus* Schaum, 1856, nec Motschulsky, 1850	"Seealpe"(=Alpes Maritimes)
~*putzeysi* Thomson, 1875, nec Mors, 1863	"Switzerland"(error)
e. ssp. ***pedemontanus*** Ganglbauer, 1892	NW-Italy:Alpi Liguri(Mt.Jurin); Alpi Marittime:Col di Tenda env.
=*tendanus* Born, 1898	Alpi Marittime:Col di Tenda env.
d. ssp. ***omensis*** Born, 1901	NW-Italy:Alpi Marittime:Val Maira-Val Stura; Mt.Omo & Mt.Baudia
c. ssp. ***germanae*** Casale & Cavazzuti, 1977	NW-Italy:Alpi Marittime:Cuneo:Mt.Saccarello & Mt.Fronte
b. ssp. ***raynaudianus*** Deuve & Simard, 1977	SE-France:Alpes-Maritimes:Colla Lunga
f. ssp. ***bisioi*** Cavazzuti & Meli, 1999	NW-Italy:Alpi Cozie:betw. Maira/Varaita valley(Colle di Bellino)
013 ***sylvestris*** Panzer, 1796	C-Europe:Alps; Slovenia, Carpathians
a. ssp. ***sylvestris*** Panzer, 1796	C-Europe:C,W-Alps:France, Switzerland; C-Germany (Harz Mts.), Bohemia, Moravia
~*concolor*. Panzer, 1809, non Fabricius, 1792	?"Harz"
=*nivosus* Heer, 1837	"High Alps of Switzerland"

~*nivalis* Heer, 1841; un; error for *nivosus* Heer	
~*aeneus* Letzner, 1850; un	
~*aeruginosus* Letzner, 1850; un	
~*brunneus* Letzner, 1850; un	
~*detritus* Letzner, 1850; un	
~*purpurascens* Letzner, 1850; un	
~*virescens* Letzner, 1850; un	
=*sylvinus* Gistl, 1857	Tirol
=*thueringianus* Schilsky, 1880	"Thüringen"
=*raxicola* Reitter, 1896	Raxalpe
=*silesiacus* Reitter, 1896	"Oberschlesien"
~*extroversus* Vacher de Lapouge, 1903; un	
=*hortensoides* Sokolar, 1910	Stilfserjoch
=*micklitzi* Sokolar, 1910	"Alps of Nieder- & Oberösterreich"
~*blumenthalianus* Mandl, 1963; un	Harz:Bruchberg-Hochmoor
=*slabai* Niedl, 1968	S-Bohemia:Babylon nr.Domažlice
=*guyicolasi* Deuve & Simard, 1976	CW-Switzerland:Jura:Colle d'Aiguillon
d. ssp. ***transylvanicus*** Dejean, 1826	Carpathians; "Transsylvanian Alps"
=*polonicus* Motschulsky, 1850	"Polonia"
~*glacialis* Miller, 1859, nec Gautier des Cottes, 1859	Tatra Mts.(=Slovakia:Tatry Mts.)
=*milleri* Thomson, 1875; nom.pro *glacialis* Miller	Tatra Mts. (=Slovakia:Tatry Mts.)
=*tatricus* Reitter, 1896	?"Hohe Tatra"(=Slovakia:Vysoké Tatry Mts.)
~*ligneus* Vacher de Lapouge, 1903; un	
=*caraimanicus* Marcu, 1934	Romania:?Caraiman Mts.
~*giumaleuensis* Marcu, 1934; un	Romania:?Giumalau Mt.R.
c. ssp. ***redtenbacheri*** Géhin, 1876; nom.pro *angustatus* Redtenbacher	E-Alps:SE-Austria(Schneeberg)
~*angustatus* Redtenbacher, 1849, nec Fabricius, 1787	SE-Austria:Schneeberg
b. ssp. *kolbi* Breuning, 1927	Slovenia:"Triglav Massif & Steiner Alpen"(=Kamniške Alpe)
e. ssp. ***haberfelneri*** Ganglbauer, 1892	E-Alps:SE-Germany, NC-Austria(Niederösterreich: Ötscher Dürrenstein)
~*cupreoaeneus* Dalla Torre, 1877; un	
~*nigroaeneus* Dalla Torre, 1877; un	
~*viridiaeneus* Dalla Torre, 1877; un	
~*fallax* Sokolar, 1910, nec Olivier, 1795	"E-Central Alps"
=*petzianus* Born, 1911	Dachstein
~*vafer* Csiki, 1927, nec Duftschmid, 1812; nom.pro *fallax* Sokolar	"E-Central Alps"

12. *OREOCARABUS* Géhin, 1876; type species *Carabus errans* Gory = *Carabus amplipennis* Vacher de Lapouge

=*Euporocarabus* Reitter, 1896; type species *Carabus hortensis* Linnaeus
=*Phricocarabus* Reitter, 1896; type species *Carabus glabratus* Paykull

001(+007) ***amplipennis*** Vacher de Lapouge, 1924; ?non priority	NW-Spain; N-Portugal
a. ssp. ***amplipennis*** Vacher de Lapouge, 1924; ?non priority	NW-Spain; ?"N-Spain"
~*errans* Gory, 1839, nec Fischer von Waldheim; 1823	Sierra de Caniza
~*femoralis* Beuthin, 1885, nec Motschulsky, 1865	
=*luetgensi* Beuthin, 1886; nom.pro *femoralis* Beuthin; ?un; ?priority	
=*pedator* Reitter, 1887	
=*oliveirae* Csiki, 1927; nom.pro *errans* Gory	Sierra de Caniza

b. ssp. *getschmanni* Vacher de Lapouge, 1924	NW-Spain:Leon, Cantabrian Mts.
c. ssp. ***pseudosteuarti*** Vacher de Lapouge, 1924	N-Portugal
~*steuarti*: Heyden, 1880, non Deyrolle, 1852	-
002 *ghilianii* LaFerté Sénectère, 1847	C-Spain
a. ssp. *ghilianii* LaFerté Sénectère, 1847	C-Spain:Madrid, Segovia:Sra.Guadarrama & Sra.Gredos; Spain
b. ssp. *negrei* Breuning, 1966	C-Spain:Salamanca:Sierra de Bejar
003 *glabratus* Paykull, 1790	NW,C,E-Europe; Scandinavia, Kola Peninsula; N-Italy, Romania, Carpathians; ?NW-Siberia
a. ssp. ***glabratus*** Paykull, 1790	NW,C,E-Europe, Scandinavia, Kola Penins.; W-Romania; ?NW-Siberia; "Finland & Dalmatia"
=*laevigatus* Scriba, 1790; spn	
~*ater* Letzner, 1850; un	
~*coerulescens* Letzner, 1850; un	
~*virescens* Letzner, 1850; un	
b. ssp. *extensus* Kraatz, 1885	SW-Romania:Orsova
=*punctatocostatus* Haury, 1885	"Galicia"
c. ssp. *lapponicus* Born, 1909	NW-Eur.Russia:"Lapland"
~*angustatus* Petri, 1912, nec Fabricius, 1787	"Siebenburgen"
=*liebleri* Bierig, 1918	Ukraine:"Galicia:Brody"
~*sericeus* Csiki, 1945, nec Forster, 1771	
d. ssp. *gibbosus* Heyden, 1866	C,SE-Romania("Banat"); Serbia, ?Bosnia, Croatia, Slovenia; SE,SC-Austria
~*breviusculus* Kraatz, 1885, nec Kraatz, 1876	"Siebenburgen:Kapellenberge"
=*carinthianus* Born, 1915	"Alpen von Kärnten"
=*ottofischeri* Bodemeyer, 1928	Kärnten:Koralpe
e. ssp. *latior* Born, 1895	N,C-Italy ("Piemonte")
=*subglabratus* Reitter, 1896	"Bozen"(=Bolzano)
004 *guadarramus* LaFerté Sénectère, 1847	C,NC,E-Spain(Sierra Guadarrama)
=*duerensis* Raynaud, 1974	Soria:Molinos de Duero
~*sagranus* Brañes, 1985; un	SE-Spain:Granada:Sierra de Sagra, Sierra de Segura
~*hirschfelderi* Brañes, 1987; un	CW-Spain:Salamanca:Navasfrias, Pto de Perales, S.Martin de Trevejo
=*andiaensis* Forel & Leplat, 1998	NE-Spain:Navarra:Sierra de Andia
005 *hortensis* Linnaeus, 1758	C,N,E-Europe; Scandinavia; Eur.Russia; Bulgaria
=*striatus* DeGeer, 1781	
=*gemmatus* Paykull, 1790	
~*cupreoaureus* Dalla Torre, 1877; un	
~*viridiaureus* Dalla Torre, 1877; un	
~*alternans* Kraatz, 1878, nec Fabricius, 1792	
=*duerckianus* Ganglbauer, 1890	München
~*kelecsenyi* Vacher de Lapouge, 1903; un	
=*rhodopensis* Apfelbeck, 1904	
~*sobotkaensis* Šulc, 1907; un	E-Bohemia:Sobotka
=*pillichi* Bernau, 1914	Hungary:Komitat Tolna
006 *preslii* Dejean & Boisduval, 1830	Adriatic Sea Coast; Albania; Greece; S-Italy:Calabria
a. ssp. *preslii* Dejean & Boisduval, 1830	S-Greece:Peloponnesos("Morea"); Greek Islands: Kefallinia, Zakynthos
(ssp.) *pecoudellus* Deuve, 1998	"Peloponnesos:Panankaikon"(=?Panachaikon Massif SW of Patra)
b. ssp. *neumeyeri* Schaum, 1856	Adriatic Sea Coast; NW-Albania; S-Italy:Calabria; "Dalmatia & Montenegro"
=*walteri* Reitter, 1896	Croatia:"Sutomore"
=*huemmleri* Beuthin, 1899	
=*calabrus* Fiori, 1903	S-Italy:Calabria

(ssp.) *jonicus* Apfelbeck, 1904	"Korfu"(=Kerkyra)
~*pindicus* Apfelbeck, 1904; un	C-Greece(?Pindos Mts.); Albania
~*albanicola* Breuning, 1964; un	"Albania:Llogora"
~*hilleri* Mandl, 1964; un	S-Albania:Reza Kanalit:Logara
(ssp.) *herzegowinensis* Apfelbeck, 1904; un	"Herzegovina & Montenegro"
=*ostariensis* Born, 1912	Croatia:Ostaria
=*starygradensis* Born, 1912	Bosnia:Starygrad
~*magdeleinei* Vacher de Lapouge, 1922, nec *magdelainei* Bleuse, 1914	"Macedonia:Florina"(=N-Greece:Makedonía:Florina)
=*dofleini* Csiki, 1927; nom.pro *magdeleinei* Vacher de Lapouge	"Macedonia:Florina"(=N-Greece:Makedonía:Florina)

13. *TOMOCARABUS* Reitter, 1896; type species *Carabus convexus* Fabricius

=*Callistocarabus* Reitter, 1896; type species *Carabus marginalis* Fabricius
=*Procrustides* Semenov, 1905; type species *Carabus bessarabicus* Fischer von Waldheim

(001 *antipai* Panin, 1942)	NE-Romania:Piatra Neamt:Varatec (an aberrant specimen of *C.convexus F.*)
002 *bessarabicus* Fischer von Waldheim, 1823	S-Ukraine, Krym Peninsula; ?Moldavia; SW-Russia; SW,SC-Siberia
a. ssp. ***bessarabicus*** Fischer von Waldheim, 1823	?Moldavia("Bessarabia:Bender"); S-Ukraine; Krym Peninsula
~*tauricus* Roeschke, 1897, nec Bonelli, 1811	Krym Peninsula
b. ssp. ***concretus*** Fischer von Waldheim, 1823	SW-Russia("Sarepta"=lower Volga basin); Caucasus; SW,SC-Siberia
=*platyscelis* Fischer von Waldheim, 1827	"Siberia"
=*melambaphus* Fischer von Waldheim, 1832	"Kirgizsteppe"
=*steppensis* Motschulsky, 1846	"Step.Kirgis., fl.Ischim"(LT)
003 *convexus* Fabricius, 1775	Europe, British Isles, Balcans, Turkey, Russia, Caucasus, Kazakhstan, SC-Siberia
a. ssp. ***convexus*** Fabricius, 1775	C,W,N-Europe(?Germany), British Isles, Russia, Caucasus, Kazakhstan; SC-Siberia:Barnaul
=*aemulus* Fischer von Waldheim, 1823	Siberia:?Tobolsk, ?Barnaul
~*striolatus* Fischer von Waldheim, 1823, nec Fabricius, 1801	"Caucasus:N-slope"
=*simplicipennis* Dejean, 1826	"Silesia"
~*gibbus* Brullé, 1835, nec Fabricius, 1794	
=*turcomannicus* Motschulsky, 1850	"Turkmenia, Samarkand"(error)
~*niger* Letzner, 1850; un	
~*violaceomarginatus* Letzner, 1850; un	
~*viridimarginatus* Letzner, 1850; un	
=*oblongulus* Motschulsky, 1865	"Alp.Cauc."(LT)
~*coeruleomarginatus* Dalla Torre, 1877; un	
~*viridimarginatus* Dalla Torre, 1877; un	
=*merklii* Hopffgarten, 1878	"Siebenburgen"
~*borealis* Géhin, 1885, nec Paykull, 1790	"Sibérie"
=*kiskunensis* Adam & Merkl, 1986	?SC-Hungary
=*barnaulensis* Born, 1922	Siberia:Barnaul
=*henseleri* Bodemeyer, 1922	Frankfurt a.M.
=*longobardus* Depoli, 1927	"Lombardia"
(ssp.) *paganettii* Born, 1905	S-Italy:Calabria:Sta.Eufemia d'Aspromonte
=*appenninus* Depoli, 1927	?"Apennines:Mt.Tresca"
=*bucciarellii* Mandl, 1966	Liguria:N of Savona:Mte.San Giorgio
b. ssp. *pyrenaeicola* Csiki, 1927; nom.pro *pyrenaicus* Born	Pyrénées-Atlantiques:Vallée d'Aspes
~*pyrenaicus* Born, 1907, nec Vacher de Lapouge, 1898	Pyrénées-Atlantiques:Vallée d'Aspes

~*confusus* Tarrier, 1975; un	Aude:Le Linas
c. ssp. *dilatatus* Dejean, 1826	S-Europe, Balcans Peninsula, C-Europe:S-Austria; NE-Italy:Trieste env.; ?Carniolia
=*hornschuchi* Hoppe & Hornschuch, 1825; spn	Hohe Tauern:Heiligenblut
=*perplexus* Schaum, 1857	CE-Greece:"Attika & Parnass"(=Attike & Parnassos Massif)
=*weisei* Reitter, 1883	Adriatic Sea coast:Croatia, Bosnia; ?LNF
=*rufulus* Géhin, 1885	"High Balkan Mts."(=Stara Planina Mt.R.:C-part)
~*proximatus* Reitter, 1896; un	"Südbosnien"
=*cernagorensis* Apfelbeck, 1904	Bosnia:Volujak
=*chionophilus* Apfelbeck, 1904	Bosnia:?
~*latus* Depoli, 1925, nec Linnaeus, 1758	NW-Italy; Croatia: Abbazia, E.Adriatic coast
~*proximatoides* Depoli, 1925; un	NW-Italy; Croatia: Abbazia
=*miliusi* Breuning, 1927	Adriatic Sea coast(numerous localities):S-Dalmatia, Montenegro, N-Albania
=*athesinus* Depoli, 1927	NE-Italy:Trentino:?
~*reductus* Müller, 1930, nec Roeschke, 1896	?"Dalmatia"
(ssp.) *gracilior* Géhin, 1885	SE-Bulgaria, Romania, NE-Greece, Eur.Turkey; "Transsylvania"
~*pygmaeus* Géhin, 1885, nec Fabricius, 1792	
=*pseudogracilior* Panin, 1942	S-Romania:?
d. ssp. *moreanus* Reitter, 1896	Peloponnesos(Taygetos Mts.); ?Euboea Island
004 *marginalis* Fabricius, 1794	NE,?C-Romania; Mold., Ukr.; SW-Hung.:Nagybajom; NE-Poland("Prussia"); C-Siberia:Barnaul
=*chrysochlorus* Fischer von Waldheim, 1812	"S-Russia & Siberia"
~*decorus* Seidlitz, 1891, nec Panzer, 1800	"Siebenburgen:Ratosnya"

14. ***EURYCARABUS*** Géhin, 1885; type species *Carabus numidus* Castelnau = *Carabus famini numidus* Castelnau
=*Apatocarabus* Semenov, 1898; type species *Carabus favieri* Fairmaire = *Carabus famini favieri* Fairmaire

001 *faminii* Dejean, 1826	Sicily, N-Algeria, Tunisia; N,C-Morocco
ssp. ***faminii*** Dejean, 1826	Sicily
002 *genei* Gené, 1839	Corsica, Sardinia(Limbara Mt.)
=*lacrymosus* Vacher de Lapouge, 1899	Corsica:Bastia
=*kraussei* Born, 1908	Sardinia:Oristano

15. ***PACHYSTUS*** Motschulsky, 1865; type species *Carabus hungaricus* Fabricius
=*Melancarabus* Thomson, 1875; type species *Carabus hungaricus* Fabricius

001 *cavernosus* E. Frivaldszky, 1837	S-Balcans, C-Italy
a. ssp. ***cavernosus*** E. Frivaldszky, 1837	Serbia, Bosnia, Macedonia, Albania, Bulgaria; "Rumelia"
=*sterbai* Breuning, 1936	
~*cavernosulus* Mandl, 1961; un	Bulgaria:Stara Planina Mt.R.:Mt.Botev, 2370m
b. ssp. ***variolatus*** O. G. Costa, 1839	C-Italy:Abruzzi Mts.(Gran Sasso Massif)
=*rosti* Beuthin, 1885	
=*seriatofoveatus* Reitter, 1896	
002 *cribellatus* Adams, 1812	Siberia:Ural-Yakutsk; Altays, Sayans; "Ostsiberien"
=*perforatus* Fischer von Waldheim, 1822	"Ural"
~*thoracicus* Germar, 1824, nec Thunberg, 1784	
=*variolaris* Ménétriés, 1849	"Kisilkum"(=Kyzyl-kum desert)
003 *graecus* Dejean, 1826	Greece, Bulgaria, Albania, Macedonia, S-Romania, Turkey
a. ssp. ***graecus*** Dejean, 1826	S,C-Greece; "Greek Islands"
=*thessalonicensis* Apfelbeck, 1904	NE-Greece:Thessalonike
~*winkleri* Breuning, 1933, nec Weyenberg, 1869	S-Albania:"Maj'e Tartarit"
=*neowinkleri* Deuve, 1991; nom.pro *winkleri* Breuning	S-Albania:"Maj'e Tartarit"

b. ssp. ***morio*** Mannerheim, 1830, nec Duftschmid, 1812; lsu	Turkey(Kop Dag nr.Bayburt);
=*cavernicola* Kraatz, 1880	"Dobrudzha"
004 ***hungaricus*** Fabricius, 1792	SE-Europe, Ukraine, S-Russia, E-Caucasus
a. ssp. ***hungaricus*** Fabricius, 1792	Hungary, SW-Slovakia, E-Austria, SE-Moravia, SW-Romania; ?"Hungary"
=*viennensis* Kraatz, 1877	NE-Austria:Wien
~*frivaldskyanus* Breuning, 1933; un	SW-Romania:"Temesvar"(=Timisoara)
b. ssp. ***mingens*** Quensel, 1806	SW-Russia:Stavropol; E-Caucasus, Dagestan(Kisljar)
=*vomax* Dejean, 1826	
(ssp.) *gastridulus* Fischer von Waldheim, 1823	Krym Peninsula, S-Ukraine; "Gouv.Taurien"(=Krym)
=*maeotis* Fischer von Waldheim, 1823	"Asov Sea coast"
c. ssp. *scythus* Motschulsky, 1847	Ukraine:Odessa,"Ekaterinoslav"(=Dnepropetrovsk; LT); W-Russia:Voronezh, Saratov
005 ***trojanus*** Dejean, 1826	Andros, Tinos, ?Crete; "Mytilene"(=Lesvos; ?error)
=*hormuzakii* Born, 1907	"Bukowina"(error)
(ssp.) *kykladensis* Breuning, 1961	Kyklades:Naxos, Syra, Milos
(ssp.) *oertzeni* Ganglbauer, 1888	Karpathos Island

16. *CTENOCARABUS* C.G. Thomson, 1875; type species *Carabus galicianus* Gory

001 ***galicianus*** Gory, 1839	NW-Spain:Asturia, León, Galicia(Val Pemache); N-Portugal
=*beirensis* Born, 1924	CW-Portugal:Coimbra

17. *RHABDOTOCARABUS* Seidlitz, 1887; type species *Carabus melancholicus* Fabricius

001 ***melancholicus*** Fabricius, 1798	N-Morocco, Spain, SW-France
(ssp. ***melancholicus*** Fabricius, 1798	N-Morocco: Non European!)
b. ssp. ***costatus*** Germar, 1824	N,C-Spain; N-Portugal; SW-France; "Mts.of Spain"
=*pyrenaeensis* Géhin, 1885	
=*castiliensis* Born, 1924	C-Spain:Madrid:Sierra Guadarrama:Cercedilla
~*leonensis* Breuning, 1964; un	NW-Spain:Leon:Busdongo
~*cuencaensis* Raynaud, 1972; un	CE-Spain:Cuenca:Olivarés
~*exilis* Raynaud, 1972; un	C-Spain:Guadalajara:Villanueva de Alcojon
a. ssp. ***submeridionalis*** Breuning, 1975	SW,SC-Spain(Malaga:Estepona); S-Portugal
~*tietarensis* Brañes, 1987; un	C-Spain:?Tietar River
(ssp.) *dehesicola* Garcia-Paris & Paris, 1996	Cáceres:Torrejón El Rubio

18. *HYGROCARABUS* C.G. Thomson, 1875; type species *Carabus nodulosus* Creutzer = *Carabus variolosus nodulosus* Creutzer

001 ***nodulosus*** Creutzer, 1799	C,E-France, Germany, Switzerland, Austria(Linz env.), CW-Hungary, Slovenia, E-Italy (Trieste)
=*hydrophilus* Reitter, 1896	
=*goricianus* Born, 1911	
002 ***variolosus*** Fabricius, 1787	Carpathians; ?Bohemia; "Transsylvania"
=*weigeli* Panzer, 1801	
=*costulifer* Fleischer, 1898	

19. *CHAETOCARABUS* C.G. Thomson, 1875; type species *Carabus intricatus* Linnaeus

001 ***arcadicus*** Gistel, 1850	C,N-Greece:Olympos Massif, Pindos Mt.R.; ?LNF
=*adonis* Hampe, 1853	?"Greece"
~*parnassicus* Mandl, 1955; un	Parnassós Massif:?

002 ***intricatus*** Linnaeus, 1761	C-Europe(Germany & ?Sweden), France, Holl., N-Italy, Carpath.; Yug, N-Greece, Eur.Turkey
=*cyaneus* Fabricius, 1776	
=*giganteus* Heer, 1837; ?*in litt.*	?Lugano
~*gigas* Heer, 1841, nec Creutzer, 1799	?Lugano
~*bicolor* Letzner, 1850; un	
~*cyanescens* Letzner, 1850; un	
~*tricolor* Letzner, 1850; un	
~*versicolor* Letzner, 1850; un	
~*violaceus* Letzner, 1850; un	
~*virescens* Letzner, 1850; un	
=*angustulus* Haury, 1876	Banat:Bazias
~*obscurus* Dalla Torre, 1877; un	
=*montenegrinus* Kraatz, 1878	Montenegro
~*chlorizans* Dalla Torre, 1879; un	
=*kaadeni* Schaufuss, 1880	
=*bohemicus* Haury, 1881	Bohemia
=*liburnicus* Haury, 1881	Croatia:?
~*minor* Haury, 1881, nec Kraatz, 1860	
~*laticollis* Roeschke, 1896, nec Sturm, 1826	"Mark Brandenburg"
=*germanicus* Semenov, 1898; nec ?; nom.pro *laticollis* Roeschke	"Mark Brandenburg"
=*neustrius* Vacher de Lapouge, 1900	Bretagne
~*aurulentus* Vacher de Lapouge, 1902; un	Bretagne
=*ulcerosus* Vacher de Lapouge, 1902	Banat
=*roeschkeanus* Semenov, 1906; nom.pro *germanicus* Semenov	"Mark Brandenburg"
=*eurynotus* Vacher de Lapouge, 1913	S-Romania:Comana
=*siegwarti* Born, 1914	Locarno
=*exemtus* Kolbe, 1917	"Agram"
=*paniscus* Kolbe, 1917	Wienerwald
=*petax* Kolbe, 1917	"Südtirol:Bozen, Klausen, Gardasee"
=*bosniensis* Born, 1918	Bosnia, Herzegovina & S-Montenegro
=*chionobatus* Born, 1918	Makedonia/Kosovo:Shar Dag
=*starensis* Born, 1918	Bulgaria:"Stara Planina, Sofia env., Vitosha, Klissura, Rila Mts."
=*carnicus* Depoli, 1926	"Alpi Carniche:Mt.Talm"
~*bucovinensis* Marcu, 1934; un	N-Romania:?
=*marchali* Raynaud, 1971	
(ssp.) *macedonicus* Jureček, 1928	S-Macedonia:Pelister Mts.:"Peristeri nr.Monastir"
~*weiratheri* Breuning, 1934; un	NW-Greece:Kerkyra Island; SW-Albania; "Korfu"(=Kerkyra)
(ssp.) *subrhodopensis* Blumenthal, 1976	NE-Greece:Thraki:Silo Massif nr.Essimi
003 ***krueperi*** Reitter, 1896	E-Greece:Thessalia:Magnesia:"Volo"(=Vólos), Larisa: Ossa Massif, Pelio Massif
004 ***lefebvrei*** Dejean, 1826	Sicily; S,C-Italy
a. ssp. ***lefebvrei*** Dejean, 1826	Sicily; S-Italy:Calabria:Aspromonte Massif
=*aspromontanus* Born, 1918	Aspromonte Massif
b. ssp. *bayardi* Solier, 1835	S,C-Italy:Roma env.to Calabria(Napoli)
=*silaensis* Haury, 1881	La Sila Massif
=*leonii* Born, 1902	"Basilicata"
=*molisensis* Born, 1918	Latium:Pagano:nr.Castel di Sangro
=*lombardii* Luigioni, 1927	Firenze(introduced)
005 ***merlini*** Schaum, 1861	S-Greece:Peloponnesos:Taygetos Mt.R.
~*borni* Kolbe, 1917, nec Meyer-Darcis, 1902	Taygetos
=*borniellus* Csiki, 1927; nom.pro *borni* Kolbe	Taygetos

20. ***PLATYCARABUS*** Morawitz, 1886; type species *Carabus depressus* Bonelli
=*Pseudocechenus* Morawitz, 1886; type species *Carabus irregularis* Fabricius
=*Baudiicarabus* Ganglbauer, 1909; type species *Carabus cychroides* Baudi di Selve

001 ***depressus*** Bonelli, 1811, nec Paykull, 1790; lsu	N-Italy, S,C-Switzerland, S-Austria & SE-France:Alps

Note: The name *depressus* Bonelli, 1811, substituted by *bonellii* Dejean, 1826, for reasons of homonymy (Casale *et al.* 1982; Turin *et al.*, 1993), has to be maintained in the opinion of Deuve (1991, 1994), Březina (1999) and by us as "nomen conservandum".

a. ssp. ***depressus*** Bonelli, 1811, nec Paykull, 1790; lsu	N-Italy, S,C-Switzerland, S-Austria & SE-France(Alpi Graie:Val di Lanzo:Usseglio)
~*bonellii* Dejean, 1826, nec Adams, 1817	"Alps of Kärnten"
=*peirolerii* A.& J.B.Villa, 1832	
~*intermedius* Heer, 1837, nec Dejean, 1826	"Graubünden & Wallis"
=*glacialis* Gautier des Cottes, 1859	"Wallis"
=*heerianus* Géhin, 1876; nom.pro *intermedius* Heer	"Graubünden & Wallis"
=*grajus* Reitter, 1896	Alpi Graie:?
=*jurinei* Born, 1901	Mt.Blanc, Col Ferret, Gr.St.Bernhard
=*pseudobonellii* Vacher de Lapouge, 1903	
~*subparallelus* Carret, 1905; un	Val Sessera
~*transversicollis* Carret, 1905; un	
=*velleri* Marceron, 1937	
b. ssp. ***lucens*** Schaum, 1857	NW-Italy & SE-France:Alpi Liguri and Alpi Marittime to Alpi Cozie(Mt.Viso:S-slope)
002 ***creutzeri*** Fabricius, 1801	Slovenia, Croatia; NE-Italy & SC-Austria:Alps
a. ssp. ***creutzeri*** Fabricius, 1801	Slovenia; NE-Italy; SE-Austria; "Carniolia"
~*cupreoaeneus* Dalla Torre, 1877; un	
~*nigroaeneus* Dalla Torre, 1877; un	
~*obscurus* Dalla Torre, 1877; un	
~*viridiaeneus* Dalla Torre, 1877; un	
=*viridimicans* Kraatz, 1878	W-Slovenia("Illyria:Kneza, Krn"); E-Italy:Julijske Alpe; SE-Austria:Karavanke:W-part
=*schencki* Géhin, 1885	
=*tschapecki* Géhin, 1885	
=*araneipes* Vacher de Lapouge, 1903	Slovenia:"Oberkrain:Stein"(=Kranj env.:?)
=*krnensis* Bernau, 1911	W-Slovenia:Krn
=*cohumilis* Bernau, 1913	Slovenia:"Krain"(=Kranj env.)
=*depolianus* Bernau, 1913	Croatia:Risnjak
=*subalpinus* Bernau, 1913	W-Slovenia("Illyria:Tolmin, Julijske Alpe etc.")
=*parumilis* Bernau, 1914	Slovenia:"Krain"(=Kranj env.)
=*sonticus* Bernau, 1914; nom.pro *subalpinus* Bernau	-
=*stolzi* Bernau, 1914	"Steiner Alpen:Grintouc & Karawanken: Bodental" (=Kamnishke Alpe & Karavanke)
=*trnovensis* Bernau, 1914	W-Slovenia:"Ternowaner Wald"(=Trnovski Gozd)
=*posarinii* Rapuzzi, 1999	Slovenia:Koper:Kras Mt.R.:Brkini Mts.:Suhorije env.
c. ssp. *humilis* Bernau, 1911	W-Croatia:"Fuzine env.", Velebit, Kapela Mts.
=*longellipticus* Bernau, 1913	Velebit Mts.
b. ssp. *heros* Vacher de Lapouge, 1924, nec Fabricius, 1801	"Croatia" (error; ?Villach env.)
=*carantanus* Depoli, 1925	Villach
=*pseudoheros* Kenyery, 1983	Slovenia:"Bachergebirge:N-slope:1km S of Podvelka, 350m"(=ca.betw.Celje/Zagreb)
d. ssp. ***kircheri*** Germar, 1824	N-Italy:Alpi Orobie-A.Carniche; Dolomiti; SC-Austria: Gailtaler Alpen; ?LNF

~*fossiger* Kraatz, 1896, nec Chaudoir, 1877	LNF
=*stellifer* Semenov, 1898; nom.pro *fossiger* Kraatz	LNF
=*grignensis* Born, 1902	Bergamasker Alpen:Mt.Grigna
=*latschurensis* Born, 1912	Latschur
=*tesinensis* Bernau, 1913	Pieve di Tesino
=*hamilcaris* Bernau, 1914	Veneto:Belluno env.- Monti Lessini(Mt.Cavallo, Bosco del Cansiglio)
~*fruhstorferi* Born, 1920, nec Roeschke, 1900	Mt.Generoso
=*fruhstorferianus* Csiki, 1927; nom.pro *fruhstorferi* Born	Mt.Generoso
~*fuliginosus* Hölzel, 1950, nec Panzer, 1809	"S of Drau River:Lienzer Dolomiten; N of Drau River:S of Kals:W slopes of Schober Massif"
=*rinaldoi* Meggiolaro, 1958	Veneto:Conegliano env.
e. ssp. ***baldensis*** Schaum, 1857	NC-Italy:Monte Baldo Massif(C.Telegrafo); betw. Trento/Lago di Garda
~*bondonensis* Mandl, 1967; un	Cornetto Massif SW of Trento:(Mt.Cima Verde)
003 *cychroides* Baudi di Selve, 1860	N-Italy:W-Alps: Val Chisone:Mt.Albergian, Colle delle Finestre
=*federicii* Born, 1909	Col di Finestra (= Colle delle Finestre)
004 *fabricii* Duftschmid, 1812	C,SE-Austria, Switzerland & NE-Italy:Alps; Carpathians
a. ssp. *fabricii* Duftschmid, 1812	C,SE-Austria(Niederöst.:Schneeberg); C,W-Switz.; NE-Italy:Alto Adige; W-Carpath.:Slovakia
=*heeri* Germar, 1824	"Glarner Alpen"
=*bugnionii* Chaudoir, 1837	Bern:Faulhorn
=*linderi* Tournier, 1860	
~*nigrinus* Schilsky, 1888, nec Motschulsky, 1865	Niederösterreich:Schneeberg
~*virens* Schilsky, 1888, nec Müller, 1776	Niederösterreich:Schneeberg
=*meschniggi* Born, 1920; ?hyb	"Ostalpen:Ankogel"; ?hyb *fabricii*/*depressus*
=*praeglacialis* Mandl, 1981	C-Austria:Steiermark:N of Liezen:Mt.Hochmolbing
=*feichtauensis* Müller & Sach, 1999	NC-Austria:Oberöst.:Molln:Sengsen Mts.:Feichtaualm: betw.Schöneck/Rotgsol, 1400m
c. ssp. ***malachiticus*** C. G. Thomson, 1875	Carpathians:N-Romania:Rodna, Caliman Mts.
~*fassatii* Smetana, 1955; un	C-Slovakia:Nízke Tatry Mts., 1750m
=*poloniensis* Géhin, 1876; nom.pro *polonicus* Schaum	Carpathians:?
~*polonicus* Schaum, 1856, nec Motschulsky, 1865	Carpathians:?
(ssp.) *ucrainicus* Lazorko, 1951	Carpathians:W-Ukraine:Gorgany Mts., Hoverla, Chorna Gora Massif; LNF
b. ssp. *koralpicus* Sokolar, 1910	E-Karnten:Koralpe
=*pehri* Vacher de Lapouge, 1913	Koralpe
005 *irregularis* Fabricius, 1792	C-Europe, Croatia, Bosnia, Carpathians
a. ssp. *irregularis* Fabricius, 1792	C-Europe:E-France, Switzerland, Belgium, Germany, Austria, Bohemia; LNF(?Germany)
=*regularis* Fischer von Waldheim, 1823	"Iberia"(error)
=*sculptilis* Heer, 1837	France:"Niesen & Saléve"
~*nigrescens* Letzner, 1850; un	
~*versicolor* Letzner, 1850; un	
~*virescens* Letzner, 1850; un	
~*cephalotes* Sokolar, 1909, nec Linnaeus, 1758	?"NE-Alps"
=*jurassicus* Born, 1911	?"C-Jura Mt.R."
=*scheffeli* Born, 1911	Schwäbischen Alb
~*reitteri* Appel, 1916, nec Retowski, 1885	Niederösterreich:Lunz
=*bitschnaui* Born, 1926	Vorarlberg:Freschen
~*denesi* Niedl, 1973; un	S-Bohemia:Hluboká nad Vltavou
c. ssp. *montandoni* Buysson, 1882	Carpathians:Slovakia, SE-Poland, Ukraine, Romania (Rarau Mts.:Cruce)

=*peronae* Hopffgarten, 1885	Romania:"Walachei:Mt.Negoi"
=*brunnipes* Beuthin, 1885	Romania:"Walachei:Mt.Negoi"
=*brostenensis* Jacquet, 1886	NE-Romania:Suceava:Broşteni
=*narosnyi* Csiki, 1946	"Kom.Ung. Poljana"
~*minutulus* Mandl, 1955; un	"Transsylv.Alps:?"
b. ssp. *bucephalus* Kraatz, 1879; un	Slovenia("Kranj")
=*hayeki* Kobmann, 1925	?"S-Steiermark:Possruck"
=*ramanus* Sokolar, 1909	Slovenia, Croatia, Bosnia("Ivan-Sattel"); E-Montenegro: Bjelasica Mts.; SE-Austria:Koralpe

21. *HETEROCARABUS* Morawitz, 1886; type species *Carabus marietti* De Cristoforis & Jan

001 ***marietti*** De Cristoforis & Jan, 1837	N-Turkey, SE-Bulgaria
ssp. ***marietti*** De Cristoforis & Jan, 1837	NW-Turkey:Istanbul("Bospor, Alem Dag"- NT), Kirklareli, Bolu; SE-Bulgaria:Akhtopol env.
=*charetianus* Auvray, 1992	European Turkey:Kirklareli:Yildiz daglari S of Demirkoy

22. *SPHODRISTOCARABUS* Géhin, 1885; type species *Carabus adamsi* Adams

~*Sphodristus* Thomson, 1875, nec Motschulsky, 1865; type species *Carabus varians* Fischer von Waldheim

001 ***varians*** Fischer von Waldheim, 1823	Armenia, Georgia, SW, SC-Caucasus; NE-Turkey
a. ssp. ***janthinus*** Ganglbauer, 1887, nec Duftschmid, 1812; lsu	W-Caucasus; S-Urals:Ilmen' Reserve (introduced)
~*ciscaucasicus* Mandl, 1975; un	Dagomys
~*dvorshaki* Mandl, 1975; un	SW-Caucasus:Pitsunda env., Adler; Bzybsky Mt.R.
~*manfredschmidi* Mandl, 1975; un	Maykop env:Suntuk

23. *MEGODONTUS* Solier, 1848; type species *Carabus caelatus* Fabricius

=*Aulacocarabus* Géhin, 1876; type species *Carabus septemcarinatus* Motschulsky

=*Proteocarabus* Géhin, 1876; type species *Carabus violaceus* Linnaeus

001 ***aurolimbatus*** Dejean & Boisduval, 1829	C,E-Eur.Russia("Ural"); SW,SC-Siberia; Caucasus, Kazakhstan, ?Kyrgyzstan
=*castaneipennis* Ménétriés, 1832	"Kaukasus"
002 ***caelatus*** Fabricius, 1801	Slovenia, Bosnia, Croatia; N,C-Albania; NE-Italy
a. ssp. ***caelatus*** Fabricius, 1801	C,E-Slovenia; ?E-Austria:Karawanken; NE-Italy:Friuli; NW-Croatia; "Krain"
=*carniolicus* Crotch, 1871	
d. ssp. *sarajevoensis* Apfelbeck, 1890	Bosnia:Sarajevo env.
=*volujakianus* Apfelbeck, 1894	Bosnia:Volujak Massif; alpine form
=*hilfi* Born, 1907	Bosnia:Vran Planina & Cvrsnica Planina; alpine form
=*malissorum* Apfelbeck, 1919	?Montenegro:Durmitor; alpine form
=*metalkanus* Apfelbeck, 1919	SE-Bosnia:"Metalka Pass"(=SE of Gorazde)
=*grmecensis* Born, 1910	Bosnia:Grmec Planina
b. ssp. *schreiberi* Kraatz, 1877	NE-Italy:Trieste; SW-Slovenia("St.Canziano, Schneeberg" =?Sneznik), W-Croatia; NW-Bosnia
c. ssp. ***dalmatinus*** Duftschmid, 1812	Adriatic Sea Coast:Rijeka to N-Albania; ?LNF
=*macretus* Kraatz, 1877	Dinara Planina; alpine form
~*ljubinjensis* Haury, 1885; un	Bosnia:Ljubinje
=*procerus* Reitter, 1885	"W-Montenegro"
=*cabuljensis* Apfelbeck, 1919	Bosnia:Mostar env.:Cabulja Planina; alpine form
=*dinaricola* Müller, 1930	?"Dinarische Alpen"(=Dinara Planina)
003 ***croaticus*** Dejean, 1826	Slovenia, Croatia, Bosnia, Montenegro, N-Macedonia, N-Albania

a. ssp. ***croaticus*** Dejean, 1826	S-Slovenia, W-Croatia & W-Bosnia:Adriatic coast mts.; Croatia:"Ostaria btw.Gospic/Carlopago"
~*carniolicus* Géhin, 1885; un	?"Krain:Mt.Nevoso"
=*schmidti* Apfelbeck, 1890	Bosnia:"Vucja Luka nr.Sarajevo"
=*primarius* Vacher de Lapouge, 1902	Croatia:Velebit Mts.
=*frankenbergeri* Obenberger, 1914	NW-Croatia:"Gr.Capella"(=Velika Kapela Mts.)
~*mediterraneus* Apfelbeck, 1919, nec Born, 1906	Bosnia:Cabulja Planina nr.Mostar
~*carnicus* Csiki, 1927, nec Depoli, 1925; nom.pro *carniolicus* Géhin	?"Krain:Mt.Nevoso"
=*fodori* Csiki, 1927; nom.pro *mediterraneus* Apfelbeck	Bosnia:Cabulja Planina nr.Mostar
=*albiensis* Depoli, 1938; ?nom.pro *carnicus* Csiki	?"Krain:Mt.Nevoso"
b. ssp. ***bosnicus*** Apfelbeck, 1890	C,N-Bosnia(Treskavica Mts.)
=*kobingeri* Apfelbeck, 1904	C-Bosnia:"Mts.near Foinica & Travnik"
~*travnikanus* Apfelbeck, 1904; un	C-Bosnia:?Travnik
~*leonhardianus* Breuning, 1932; un	C-Bosnia:Cvrstnica Planina
=*pretneri* Krätschmer & Drovenik, 1977	N-Bosnia:Ostrelj env.(Ostrelj, 1000m), Srnetica Mts.
c. ssp. *zepcensis* Reitter, 1902	E-Bosnia:Zepce env.; Ravan, Zvijezda, Javor, Ozren Mts.; CW-Serbia:Murtenica planina
=*bosiljevici* Drovenik & Pavićević, 1985	CW-Serbia:50km S of Titovo Uzice:Murtenica planina: Brijac
d. ssp. *durmitorensis* Apfelbeck, 1904	Montenegro(Durmitor Massif) & NE-Albania:Prokletije Mts.; Kosovo; N-Albania, W-Maced.
f. ssp. *babinjensis* Apfelbeck, 1919	Montenegro & NE-Albania:Prokletije Mts.:"Babinje Planina"
e. ssp. *ljubetensis* Apfelbeck, 1918	Serbia/Macedonia/Albania borders region:Sar planina Mts.:Ljubeten
=*droveniki* Krätschmer, 1984	SW-Macedonia:Galicica Mts., Baba Mts., Pelister
=*kraetschmeri* Drovenik, 1978	SE-Montenegro:betw.Ivangrad/Rozaj:Turjak
004 *exaratus* Quensel, 1806	N-Caucasus:Anapa to Mt.Kazbek; Krasnodar:Taman Pen.to Manych R..; "Kislar"(=?Kizlyar)
~?*seriatus* Motschulsky, 1850, nec Wiedemann, 1821; ?hyb	?Balkaria; ?hyb *exaratus/ aurolimbatus*
005 *germarii* Sturm, 1815 (*exasperatus* Auct.); lsu	Austria, Switzerland, N-Italy, Slovenia, S-Moravia, Hungary, Croatia, Bosnia

Note: By several authors regarded as a subspecies of *C. violaceus* L. (e.g.: Březina, 1994; 1999). To our knowledge, no hybrid zones exist between *C. germarii* and *C. violaceus*. Furthermore, in N.W. Italy the two species are parapatric, without introgressive forms. According to Lorenz (1998a), a neotype selection is needed for stabilization of the nomenclature in this case.

d. ssp. ***exasperatus*** Duftschmid, 1812	NE,CE-Austria:Graz, Wien env.; S-Moravia; NW,NC-Hungary:Gyor, Budapest env.
=*glabrellus* Dejean, 1826	"Austria"
=*pseudoviolaceus* Kraatz, 1886	S-Moravia:"Brünn"(=Brno)
=*rakosiensis* Csiki, 1905	NC-Hungary:"Rakosfeld"(=Pest:E of Budapest)
c. ssp. ***germarii*** Sturm, 1815; lsu	Alps:SC-Switz, N-Italy, SC,SE-Austria; Slovenia, E-Croatia, Slavonia, S-Hungary; "Krain"
=*detritus* Drapiez, 1821	
=*obliquus* Thomson, 1875	?Slavonia:Frushka Gora
b. ssp. *savinicus* Hammer, 1906	S-Austria:Villach env.:"Ober-Seeland"
=*rombonensis* Bernau, 1911	NW-Slovenia:"Mt.Rombon bei Flitsch"(=Julijske Alpe:Bovec)
~*jureceki* Sokolar, 1913; un	Trentino:Folgaria(=S of Trento)
=*ticinensis* Born, 1920	"Tessin"(=SC-Switzerland)
=*poussielguei* Nicolas, 1924	Monti Lessini:Sette Communi(=N of Verona)

f. ssp. *neesi* Hoppe & Hornschuch, 1825	SC,E-Austria(Kärnten:Heligenblut) to SW-Switzerland; NE-Italy:Alto Adige:Alpi Atesine
~*laevigatus* Dejean, 1826, nec Scriba, 1790	Steiermark:Rottenmanner Tauern:alpine zone
=*kunzei* Heer, 1837	
~*buendneri* Breuning, 1934; un	CE-Switzerland:"Graubünden, Bonaduzer Alpen" (=W of Davos:Bonaduz env.)
e. ssp. *styriensis* Breuning, 1932; un; nom.pro *laevigatus* Dejean	C-Austria:Steiermark(Rottenmanner Tauern:alpine zone), NE-Kärnten
=*pseudoneesi* Mandl, 1984	C-Austria:Salzburg:E-part; Steiermark:NW-part (Ramsau, 1300m); alpine form
h. ssp. ***vlasuljensis*** Apfelbeck, 1894	Bosnia/Montenegro:Volujak Mts., Vlasulje; alpine form
g. ssp. *scordiscus* Vacher de Lapouge, 1901	Bosnia
=*igmanensis* Eidam, 1927	Bosnia:Igman planina
=*narentinus* Eidam, 1927	Bosnia:E of Narenta:Prenj planina:low altitude
i. ssp. *prenjus* Eidam, 1927	Bosnia:Prenj planina:high altitude
a. ssp. ***fiorii*** Born, 1901	NC, NW-Italy(Emilia:Casinalbo) to Alpi Liguri; SW-Switz.; E-France:Savoie, Alp.Hte.Prov.
~*pedemontanensis* Breuning, 1935; un	Alpi Liguri:"Viozene"
=*dechambrei* (Colas, 1952)	Alpes-Hte-Provence:Vallée de l'Ubaye:Col de Larche
~*adelus* Tarrier, 1974; un	NW-Italy:Liguria:Imperia:Nava, 800m
006 ***gyllenhali*** Fischer von Waldheim, 1827, nec Paykull, 1790; lsu; nom.pro *dejeani* Fischer von Waldheim	Krym Peninsula
~*dejeani* Fischer von Waldheim, 1823, nec Fischer von Waldheim, 1822	Krym Peninsula
=*blakistoni* Newman, 1857; ?priority	
007 ***planicollis*** Küster, 1846	C-Romania:Carpathians
a. ssp. ***planicollis*** Küster, 1846	C-Romania:Carpathians W of Olt River:Cindrel – Retezat – Godeanu Mts.; ?"Siebenburgen"
(ssp.) *verae* Csiki, 1905	C-Romania:Carpathians E of Olt River:Fagaraş to Bucegi Mts.; "Bucsecs"(=Bucegi Mts.)
008 (previously: *C. purpurascens* F. see **010** *C. violaceus* L.)	
009 ***septemcarinatus*** Motschulsky, 1840; nom.pro *carinatus* Motschulsky	S-Caucasus:Mt.Fisht to Lagodekhi; "Kachetia"; Tbatani (LT); imported and established in Crimea; Georgia; W-Armenia; NE-Turkey
~*carinatus* Motschulsky, 1839, nec Duftschmid, 1812	"Kachetia"; Tbatani(LT)
010 ***violaceus*** Linnaeus, 1758	Europe:Pyrénées to Scandinavia, Balcans
e. ssp. ***violaceus*** Linnaeus, 1758	E,S,N-Germany, Scandinavia, Kola Penins., Bohemia, Moravia, W-Slovakia; Brit.Isles; ?LNF
=*sublaevis* Drapiez, 1820	"Russia"(?error)
~*bicolor* Letzner, 1850; un	
~*coerulescens* Letzner, 1850; un	
~*cyanescens* Letzner, 1850; un	
~*marginatus* Letzner, 1850; un	
~*blumenthali* Blumenthal, 1961; un	NC-Germany:Lüneburg:Lüneburger Heide: Königsmoor nr.Tostedt
~*intermarinus* Blumenthal & Staven, 1985; un	NC-Germany:Schleswig-Holstein:Osterwohld W of Albersdorf
f. ssp. *candisatus* Duftschmid, 1812	"Österreich & Böhmen"(=Austria & Bohemia)
~*nivalis* Letzner, 1850; un	NE-Bohemia:"Riesengebirge"(=Krkonoše Mts.)
~*purpureomarginatus* Letzner, 1850; un	
~*violaceomicans* Letzner, 1850; un	
~*virescens* Letzner, 1850; un	
~*viridicoeruleus* Letzner, 1850; un	
=*psilopterus* Kraatz, 1879	"Thüringen & Böhmen"
=?*albinae* Haury in Géhin, 1885	

=*niveus* Géhin, 1885; nom.pro *nivalis* Letzner	NE-Bohemia:"Riesengebirge"(=Krkonoše Mts.)
~*duftschmidi* Vacher de Lapouge, 1922, nec Géhin, 1876	Austria:Linz env.
~*pseudocandistatus* Eidam, 1927; un	
~*pseudolaevigatus* Breuning, 1934; un	Moravia:"Prossnitz"(=Prosečnice)
=*subpurpurascens* Eidam, 1941; nom.pro *duftschmidi* Vacher de Lapouge	Austria:Linz env.
~*subcarbonatus* Niedl, 1975; un	S-Bohemia:Mt.Klee nr.Český Krumlov
h. ssp. *sollicitans* Hartert, 1907	?England
=*britannicus* Born, 1908	British Isles:?
(ssp.) *browni* Deuve, 1999	NW-Scotland:Raasay Island
i. ssp. ***ottonis*** Csiki, 1909	S-Norway:Trondheim
=*lindbergi* Burkard, 1921	Finland:Helsingfors(=Helsinki)
=*carelicus* Hellén, 1934	Karelia:?Kivenkappa(currently:NW-Russia:W of Ladozhskoe Lake)
j. ssp. *lindrothi* Silfverberg, 1977; nom.pro *arcticus* Sparre-Schneider	C-Sweden:(Jämtland:Areskutan); Kola Peninsula
~*arcticus* Sparre-Schneider, 1888, nec Olivier, 1795	C-Sweden:Jämtland:Areskutan
~*pseudarcticus* Mandl, 1962; un	LNF(?N-Finland, Sweden & Norway)
~*pseudolindbergi* Mandl, 1962; un	LNF(?Sweden:Uppland)
~*pseudottonis* Mandl, 1962; un	LNF(?S-Sweden)
o. ssp. ***andrzejuscii*** Fischer von Waldheim, 1823	C,E-Poland("Wolhynien"), NE-Slovakia, CW-Russia, Ukr., Latv., Lith., Est.; NE-Rom., ?Mold.
=*carbonatus* Schaufuss, 1882	"Podolien"
=*subpolitus* Eidam, 1924	"Podolien"(=W-Ukraine)
=*alterviolaceus* Kolbe, 1925	"?Norddeutschland:E of Oder"
k. ssp. ***volffii*** Dejean, 1826	NW,C,SW-Romania(Banat); E-Hungary; ?SE-Slovakia
=*wolffi* (Auct.)	
=*mehelyi* Ganglbauer, 1896	NC-Romania:Rodna Mts.
=*dacoromanus* Hormuzaki, 1903	SW-Romania:Mehedinti
=*vlascanus* Born, 1909	Walachei(=S-Romania)
~*macilentus* Petri, 1912, nec Olivier, 1795	"Schässburg, Bistra"(=Sighişoara, Bistra)
~*pygmaeus* Petri, 1912; un	Romania:?; alpine form
~*lucidulus* Breuning, 1934; un; nom.pro *macilentus* Petri	"Schässburg, Bistra"(=Sighişoara, Bistra)
=*betuliae* Csiki, 1940	NE-Hungary:Szabolcs-Szatmár:Nyírség lowland
~*balanensis* Csiki, 1942; un	CE-Romania:Mts.nr.Balan:Mt.Nagy-Hagymás (=Haghimas Mts. nr.Balan)
~*ormayanus* Csiki, 1944; un	C-Romania:from Cibin Mts.to Szöreny Mts.(=Godeanu, Tarcu)
~*porolissensis* Csiki, 1944; un	NW-Romania:from left Someş bank S of Rodna Mts.to W-slope of Bihor Mts.
~*serrorum* Csiki, 1944; un	C-Romania:Bucegi to Fagaraş Mts.
g. ssp. ***salisburgensis*** Kraatz, 1879	Austria:Salzburg, Oberöst., Vorarlberg; S-Germany; N,C-Switzerland; CE-France:Doubs, Jura
=*meyeri* Born, 1898	Switzerland:Jura:Creux du Vau
~*hermanni* Born, 1901, nec *hermani* Mannerheim, 1827	Switzerland:Emmental
=*muellerianus* Born, 1902	Vorarlberg:Hochfreschen
=*pauli* Kolbe, 1923	?Simmentaler Alpen
=*sachianus* Mandl, 1981	C-Austria:E of Salzburg:Sensengebirge:Feichtau-Alm, 1400m
u. ssp. ***purpurascens*** Fabricius, 1787	C,N-France, Belgium, Holland; Switzerland; NW,C,S-Germany; ?LNF
=*coeruleus* Voet, 1778; spn	
=?*curtatus* Villers, 1789	?N-France
=*crenatus* Sturm, 1815	"Österreich"

=*asperulus* Kraatz, 1878	
=*palliardii* Gradl, 1881	
=*suffriani* Westhoff, 1881	“Westphalen”
=*scaber* Schaufuss, 1882	“Hessen”
~*subcrenatus* Géhin, 1885; un	?Jura
=*asperipennis* Vacher de Lapouge, 1921	
~*laevicostatus* Vacher de Lapouge, 1921, nec Schulz, 1900	?Belgium:Ft.de Soignes
=*crenatocostatus* Vacher de Lapouge, 1922	N-France:?Bas-Rhin
=*osismius* Vacher de Lapouge, 1922	CW-France:Cotes-du-Nord
~*chatenayi* Sirguey, 1931; un	
~*dayremi* Sirguey, 1931; un	
~*pseudopurpurascens* Breuning, 1934; un; nom.pro *laevicostatus* Lap.	?Belgium:Ft.de Soignes
~*uriensis* Breuning, 1934; un	C-Switzerland:Uri:Reuss valley nr.Erstfeld
~*cyaneocinctus* Cleu, 1937; un	Allier:?
~*perraudini* Mandl, 1962; un	SW-Germany:Baden:Schwarzwald:Nimburg
~*jurassicus* (David & Marchal, 1968), nec Born, 1911	
=*perturbatocostatus* (Grotz & Grotz, 1980)	Belgium:Liège:Rocherath
~*culotianus* (Le Mao, 1986); un	
~*monnayensis* (Branger, 1986); un	
~*enigmaticus* (Devecis, 1988); un	
t. ssp. *fulgens* Charpentier, 1825	Pyrénées;
~*nigrinus* Nicolas, 1898; un	Hautes-Pyrénées:Pic de Nère nr.Baréges
=*subfulgens* Jeanne, 1969	Pyrénées-Atlantiques:Pic d’Orhy, 2000m
r. ssp. *muelleri* Haury, 1878, nec Herbst, 1784	Barcelona env.
=*gerundensis* Born, 1916	NE-Spain:Gerona:Setcasas; SC-France:Pyrénées-Orientales
=*pseudomuelleri* Codina, 1921	Barcelona, Lerida; alpine form; ?Lerida
=*ligneus* Sirguey, 1931	?Lerida
~*parallelus* Sirguey, 1931; un	
s. ssp. *pseudofulgens* Born, 1905	NC-Spain:?Zaragoza; ?“S of Pyrénnées:Logrono, Calahorra”
~*ibericus* (Jeanne, 1976), nec Fischer von Waldheim, 1823	Sierra de la Demanda, Moncayo
p. ssp. *aurichalceus* Kraatz, 1879	N-Spain:Santander & Vizcaya(Reinosa & Portugalete nr.Bilbao), Pic.de Europa, Oviedo
~*europae* Breuning, 1934; un	Picos de Europa:summit area(alpine form)
=*marinae* Maux, 1995	“N-part of Palencia Province”
~*alainsis* Meyer, 1996; un	Palencia:W of Cervera
=*bersoni* Maux, 1998	
q. ssp. *asturiensis* Born, 1925	Oviedo:Los Cabos
=*lugensis* Breuning, 1972	NW-Spain:Lugo:Samos
(ssp.) *baeterrensis* Vacher de Lapouge, 1901	S-France:Aveyron, Tarn, Aude, Hérault(Bessan), Alp. Marit., Gard, Vaucluse, Isère, Ardèche, Drôme, Massif Central
=*provincialis* Born, 1903	Alpes-de-Haute-Provence:Digne
~*gauthieri* Cleu, 1968; un	Drôme:Forêt de Saou(W-part); TNF
~*rectigranosus* Cleu, 1968; un	
=*bicinctus* Born, 1905	Aude:Ft.de Monthaut, Rennes-les-Bains, Ft.de la Loubatière
=*viridilucens* Barthe, 1909	Tarn:Montagnes Noires
=*centralis* Forel & Leplat, 1995	Massif Central
=*cotenayensis* Forel & Leplat, 1995	N-Jura
=*saouensis* David & Marchal, 1968, nec Mandl, 1967	Drôme:Ft. de Saou
~*sicardi* Sirguey, 1931; un	
=*thorencicus* (Ochs, 1967)	Alpes-Maritimes:Logis du Pin

l. ssp. ***azurescens*** Dejean, 1826	Croatia(Velebit Mts.:betw.Gospic/Karlobag); Serbia, Bosnia, Montenegro
=*krajnensis* Born, 1904	CE-Serbia:Krajina, Majdanpek, Negotin
=*hercegovinus* Born, 1913	Bosnia:Vran Planina, Cvrsnica Planina(=SE of Duvno)
=*zabljakensis* Eidam, 1927	Montenegro:Durmitor Massif:Zabljak env., Prokletje Mts.
=*durmitorus* Mandl, 1985	Montenegro:Durmitor Massif; alpine form)
=*shljebensis* Mandl, 1985	Montenegro/Albania:Prokletje Mts.:Zljeb env.; Mokra gora Mts.
d. ssp. *rilvensis* Kolbe, 1887	"Rumelia"; ?SW-Bulgaria, ?Macedonia:?Rila Mts., ?Kozuf Planina(=W of Gevgejija)
~*balcanicus* Vacher de Lapouge, 1901, nec Born, 1899	?W-Balcans
n. ssp. *skombrosensis* Eidam, 1927	CW,C-Bulgaria:Rila Mts., Vitosha Massif; C,W-Stara planina Mt.R.
=*sofianus* Eidam, 1927	CW-Bulgaria:Sofia env.
a. ssp. ***picenus*** A.& G.B.Villa, 1838	C,S-Italy(Ancona env.)
=*romanus* Born, 1905	CW-Italy:Lazio:Roma env.(Castelromano)
=*authionensis* Ochs, 1953	?Alpes-Maritimes:Authion Massif
=*bruschii* Tarrier, 1974	C-Italy:Abruzzi:Campo Imperatore, 1800m
=*liguriensis* Breuning, 1934; ?un	NW-Italia:Liguria:Alpi Liguri, Apennine Ligure(Val Bisagno nr.Genova)
=*hypochora* Tarrier, 1971	Alpes-Maritimes:middle Vésubie valley:Roquebilliere env.
m. ssp. ***dryas*** Gistel, 1857	NE-Greece("Saloniki"=Thesaloniki), SW-Bulgaria, Macedonia, NC-Albania
=*merditanus* Apfelbeck, 1918	NC-Albania:"Mirdite Mts.:Mt.Maj'e Zebes"(=Mirdite Mts.SW of Bicaj); Gjalica Lumes Mts.
=*shardaghensis* Apfelbeck, 1918	Macedonia/Kosovo:?Shar Dagh:Golesnica(=Shar Planina)
~*skripetarum* Breuning, *in litt.*	-
~*korabensis* Csiki, 1944; un	Macedonia/Serbia/Albania borders:Korab Mts.
~*peristericus* Mandl, 1961; un	Macedonia:"Peristeri"(=Pelister Mts.SW of Bitola)
=*letellieri* Blumenthal, 1976	NE-Greece:Pangaion Massif
b. ssp. *bartoni* Mařan, 1930	SW-Bulgaria:"Alibotush"(=Mt.Orvelos)
~*purkynei* Štěrba, 1945; un	SW-Bulgaria:Belasica Mts.(=nr.Petrich)
=*pirinensis* Mandl, 1985	SW-Bulgaria:"Pirin:Sandanski-Popinalka"(=Pirin Mts.: S-part:Popina Lyaka:Sandanski Hut)
c. ssp. *marani* Štěrba, 1945; un	Macedonia:Jablanica Mts.(=W of Ohrid); Peristeri (=Pelister Mts.SW of Bitola)
v. ssp. ***mixtus*** Géhin, 1876, nec Herbst, 1784; lsu	CE-France:Isère(Grande Chartreuse); Savoie; Drôme: N-part
=*cyaneolimbatus* Kraatz, 1879	Isère:Grenoble; "Gallia mer. mont. Costa"(LT)
=*saouensis* David & Marchal, 1968	Drôme:Ft.de Saou
=*neomixtus* Tarrier, 1975; nom.pro *saouensis* David & Marchal	Drôme:Ft.de Saou(=E,C-part)
=*vocontianus* Keith, 1995	Drôme:ca.40km E of Valence:Ft.de Lente

24. ***PACHYCRANION*** Solier, 1848; type species *Carabus schoenherri* Fischer von Waldheim
~*Pachycranius* Solier, 1848; iss of *Pachycranion* Solier
=*Carabulus* Lutshnik, 1924; type species *Carabus ermaki* Lutshnik

001 ***ermaki*** Lutshnik, 1924; nom.pro *amoenus* Chaudoir;	arctic Eur.Russia; N-Siberia; Altays, Sayans ?non priority
~*amoenus* Chaudoir, 1852, nec Baudet-Lafarge, 1836	Altays
=*kantaikensis* Géhin, 1885; ?un; ?priority	?"Kantaika"(=arctic W-Siberia:SW of Noril'sk)
(ssp.) *laetensis* Obydov, 2000	Republic Komi, Usa, Lek-Rogovaia
002 ***schoenherri*** Fischer von Waldheim, 1822	CE-European Russia, C-Siberia, Altays, Sayans
ssp. ***schoenherri*** Fischer von Waldheim, 1822	CE-European Russia; SC-Siberia(Barnaul); Altays, Sayans
=*melanchlorus* Fischer von Waldheim, 1827	

~*gouberti* Géhin, 1885; un	
=*sangilenus* Obydov, 1997	SE-Tuva:Sangilen Mts.:Balyktyk-Khem River valley:50:17N/96:39E, 2100m

25. *INIOPACHYS* Solier, 1848; type species *Carabus pyrenaeus* Audinet-Serville

001 ***auriculatus*** Putzeys, 1872	NW-Spain:Cantabrian Mts.
a. ssp. ***auriculatus*** Putzeys, 1872	NW-Spain:Cantabrian Mts.:Picos de Europa Massif
=*impensus* Reitter, 1896	Picos de Europa Massif
~*emmanueli* Prunier, 1993; un	
b. ssp. *ubinensis* (Puisségur, 1955)	NW-Spain:Cantabrian Mts.:Pena Ubina Massif
~*mestrei* (Puisségur, 1955); un	
(ssp.) *ornizensis* Meyer, 1998	Cantabrian Mts.:Pena de Orniz
002 ***pyrenaeus*** Audinet-Serville, 1821	N-Spain & S-France:Pyrénées
a. ssp. ***pyrenaeus*** Audinet-Serville, 1821	W-Pyrénées:Pic d'Orhy to Pic de Vignemale Massif; Hautes Pyrénées
~*punctatus* Géhin, 1885, nec Castelnau, 1835	
=*ignitus* Reitter, 1896	Hautes Pyrénées
~*cephalotes* Nicolas, 1919, nec Linnaeus, 1758	Pyrénées-Atlantiques:Sède-de-Pan
=*cephalicus* Csiki, 1927; nom.pro *cephalotes* Nicolas	Pyrénées-Atlantiques:Sède-de-Pan
~*punctatulus* Csiki, 1927; un; nom.pro *punctatus* Géhin	
~*punctatulus* (Jeannel, 1941), nec Fabricius, 1792	
~*occidentalis* Jeanne, 1969, nec Born, 1907	Pyrénées-Atlantiques:Pic d'Orhy, 2000m
(ssp.) *cerdanus* Vacher de Lapouge, 1924	Andorra:Mt.Casamanya to Pyr.-Or.:Puigmal Massif; N-Spain:Maladetta nr.Olot:Col d'Envalira
~*laurentii* Rouselle, 1976; un	
(ssp.) *vallierensis* Colas, 1965	C-Pyrénées:Ariège, Val d'Aran, Mt.Vallier:Port d'Aula
c. ssp. *jeanneli* Deuve, 1994	C-Pyrénées:Pic de Vignemale Massif to Viella env.; Huesca:Pt.de Venasque
~*immetallicus* Nicolas, 1898; un	
~*gavarniensis* Pater, 1938; un	
~*viridissimus* Pater, 1938; un	
b. ssp. ***costulus*** Géhin, 1885; nom.pro *costatus* Kraatz	Pyrénées-Orientales:Mt.Canigou Massif; "E-Pyrénées"
~*costatus* Kraatz, 1878, nec Germar, 1824	E-Pyrénées
=*madresensis* Mollard, 1996 un	Aude:Pic du Madres

26.+27. *CHRYSOCARABUS* C. G. Thomson, 1875; type species *Carabus auronitens* Fabricius

=*Sellaecarabus* Sturani, 1947; type species *Carabus olympiae* Sella
=*Dysmictocarabus* Puisségur, 1964; type species *Carabus solieri* Dejean
=*Chrysotribax* Reitter, 1896; type species *Carabus hispanus* Fabricius

Note: *Chrysotribax* Reitter has often been considered to be a separate subgenus (e.g. Březina, 1999; Turin *et al.*, 1993), however, taking into account the latest information (Prüser, 1996), this cannot be maintained, and is has to be regarded synonymous to *Chrysocarabus* Thomson, which is in agreement with Deuve (1994). See also the note in chapter 5 (p. 265). The species of the former *Chrysotribax*, have been re-numbered.

001 ***auronitens*** Fabricius, 1792	C,W-Europe:Pyrénées to Bohemia; Alps, Carpathians
a. ssp. ***auronitens*** Fabricius, 1792	N,C,E-France, Germany, Holl., Belg., Switz., N-Austria, Bohemia, W-Poland; "Sweden"(error)
~*auratonitens* Illiger, 1798; un; error for *auronitens* Fabricius	-
=*zwickii* Heer, 1837	Switzerland:Schaffhausen
~*atratus* Heer, 1841, nec Duftschmid, 1812	
~*coerulescens* Letzner, 1850; un	
~*picipes* Letzner, 1850; un	

~*versicolor* Letzner, 1850; un	
~*viridis* Letzner, 1850; un	
=*putzeysi* Mors, 1863 (*putseysii*)	Belgium
~*nigripes* Heyden, 1875; un	"Domodossola"
~*azureoauratus* Dalla Torre, 1877; un	
~*picipes* Dalla Torre, 1877; un	
~*viridiauratus* Dalla Torre, 1877; un	
=*subcatenulatus* Westhoff, 1881	
=*ignifer* Haury, 1889	"Mühlhausen env."(=Mulhouse)
=*joerini* Stierlin, 1890	Zürich env.
=*perviridis* Reitter, 1896	
=*auropurpureus* Vacher de Lapouge, 1898	Belgium:?
=*cluniensis* Born, 1903	Vorarlberg:Hochfreschen
=*petzi* Sokolar, 1907	S-Austria:?
=*brevipennis* Vacher de Lapouge, 1913	?"Nordsteiermark"
~*gervaisi* Le Moult, 1913; un	Eure:Forêt de Lyons
=*allevardensis* Nicolas, 1919	Isère:Allevard
~*letacqui* Antoine, 1919; un	N-France:?
~*borni* Vacher de Lapouge, 1924, nec Meyer-Darcis, 1902	Switzerland:Emmenthal
~*charlottei* Venet, 1926; un	
=*foveipennis* Lebis, 1926	E-France:?
~*pauli* Csiki, 1927, nec Kolbe, 1923; nom.pro *borni* Vacher de Lapouge	Switzerland:Emmenthal
=*foveatipennis* Csiki, 1927; nom.pro *foveipennis* Lebis	E-France:?
~*oberthueri* Lebis, 1928; un	?N-France
~*aureus* Sirguey, 1931, nec DeGeer, 1774	"Normandia"
~*coeruleomicans* Sirguey, 1931; un	"Normandia"
=*guedeli* Sirguey, 1931	
~*marginatus* Sirguey, 1931; un	"Ft.d'Ecouve & Ft.de Perseigne"
=*normannensis* Sirguey, 1931	"Normandia"
=*normanneus* Sirguey, 1931	"Normandia"
~*purpuratus* Sirguey, 1931, nec Sturm, 1815	"Normandia"
~*sculptipennis* Sirguey, 1931, nec Chaudoir, 1877	"Normandia"
~*viridicollis* Sirguey, 1931, nec Kraatz, 1882	"Normandia"
~*helvetiae* Breuning, 1932; un; nom.pro *pauli* Csiki, 1927	Switzerland:Emmenthal
=*armoricanus* Oberthür, 1935	
=*melanipes* Lienhart, 1936	
~*fuliginosus* Frennet, 1937, nec Panzer, 1809	
=*garactensis* Alluaud, 1937	
~*mormalensis* Leleup, 1938; un	
~*bourgini* Balazuc, 1946; un	
=*duponti* Lebis, 1949	
=*beskydicus* Smetana, 1949	N-Moravia:Moravskoslezské Beskydy Mts. (Lysá hora Mt.)
=*lueneburgensis* Blumenthal, 1949	N-Germany:Niedersachsen:Lüneburger Heide
=*pseudoviridipennis* Lebis, 1949	
~*fritzschei* Korell, 1950; un	
~*edmundi* (Lebis, 1955); un	
~*vulcani* (Lebis, 1955); un	
=*syrmiensis* Mandl, 1955	Serbia:Frushka Gora Massif(?error)
~*christyae* Dorsselaer, 1957; un	
~*schwarzwaldensis* Mandl, 1962; un	Schwarzwald:Goldersbach, 1000m
~*subignifer* Mandl, 1967; un	SC-Germany:Baden:Holzenschallbach nr.Lörrach

~*pumicatoides* Mandl, 1968; un	
~*pseudoceroglossoides* Tarrier, 1975; nud	
~*martinae* (Culot, 1978); un	
~*hennuyi* (Grafteaux, 1980); un	
~*chlorochromus* (Culot, 1981); un	
~*chrysocyaneus* (Culot, 1981); un	
~*deledecquei* (Culot, 1981); un	
=*forsteri* Mandl, 1981	Austria: Niederösterreich: St.Aegyd: Mt.Göller (=betw. Sankt Aegid/Mariazell)
~*grafteauxi* (Hennuy, 1981); un	
~*auverloti* (Thibaudeau, 1983); un	
~*thumseri* (Thibaudeau, 1983); un	
~*inopinatus* (Dachy, 1986); un	
~*rubicundosus* (Branger, 1986); un	
~*noviprati* Maquet, 1991; un	
~*atronitens* Henderickx, 1998; un	?Liège env.
~*bampsi* Henderickx, 1998; un	?Liège env.
~*spinolatus* Maquet, 1999; un	Belgium:Liège env.
~*cauvini* Sirguey, 1931; un	Calvados:Ft.d'Ecouves
~*tourteani* Sirguey, 1931; un	Calvados:Ft.d'Ecouves
(ssp.) *cupreonitens* Chevrolat, 1861	NW-France:Calvados:Ft.de Cerisy
~*fastuosus* Le Moult, 1912; un	?Ft.de Cerisy
~*pseudomelas* Le Moult, 1912; un	?Ft.de Cerisy
~*pseudopurpureus* Le Moult, 1912; un	?Ft.de Cerisy
~*roeschkei* Le Moult, 1912; un	?Ft.de Cerisy
~*rossii* Le Moult, 1912; un	?Ft.de Cerisy
~*pseudonigripes* Machard, 1982; un	
~*nigronitens* (Lacroix, 1986); un	
b. ssp. *costellatus* Géhin, 1882; ?non priority	C,W-France:Lot – Lozère – Cantal – Allier – Finistère – Cotes-du-Nord; "Auvergne"
=*minor* Kraatz, 1860; ?un; ?priority	
=*bleusei* Oberthür, 1884	"Bretagne:Forêt de Lorges"
~*melas* Oberthür, 1884, nec Creutzer, 1799	"Bretagne:Forêt de Lorges"
~*purpureus* Oberthür, 1884, nec Kraatz, 1876	"Bretagne:Forêt de Lorges"
=*subfestivus* Oberthür, 1884	Finistère:Forêt de Lorges
~*viridipennis* Bleuse, 1896, nec Lewis, 1880	
=*semicupreonitens* Schulz, 1900	
=*laevicostatus* Schulz, 1900	
~*guerryi* Born, 1907, nec Born, 1903	"Auvergne:Pic de Sancy"
=*quittardi* Vacher de Lapouge, 1908	?Dep.Cantal
=*bonneti* Le Moult, 1912	Puy-de-Dome:Mt.Doré
~*clermonti* Le Moult, 1912; un	
~*cupreicollis* Le Moult, 1912; un	
~*logreensis* Le Moult, 1912; un	
~*mesmini* Le Moult, 1912; un	
~*nigriformis* Le Moult, 1912; un	Puy-de-Dome:Mt.Doré
~*coeruleus* Barthe, 1924; un	Rennes env.
=*buyssoni* Barthe, 1929	Allier:Moulins env.
~*cupreus* Obenberger, 1935, nec Linnaeus, 1758	
~*leleupi* Hansen, 1968; un	
~*donnoti* (Coupat, 1971); un	
~*lequeti* (Darnaud, 1978); un	
~*artusi* (Le Mao, 1984); un	
~*jacquesi* (Lacroix, 1984); un	
~*quinti* (Lacroix, 1984); un	

~*coatlochensis* (Branger, 1986); un	
~*igneus* (Branger, 1986); un	
~*nigrescens* (Branger, 1986); un	
~*damieni* (Lacroix, 1986); un	
~*delphinae* (Lacroix, 1986); un	
~*nigrinofemoratus* (Lacroix, 1986); un	
~*nigronissimus* (Lacroix, 1986); un	
=*lamberti* Machard, 1995	Correze:Vézere
c. ssp. *kraussi* Vacher de Lapouge, 1898; ?non priority	NE-Italy; N,S,E-Austria; W-Hungary:Vas:Köszeg; ?LNF
=*intercostatus* Gredler, 1854; ?un; ?priority	"Passeiertal"(=NE-Italy)
=*vindobonensis* Kubik, 1901	NE-Austria:Wienerwald Mts.; ?Wien
e. ssp. ***escheri*** Palliardi, 1825	E-Europe:Carpathians:NW-Slovakia to Banat; "Banat"
=*opacus* Haury, 1878	"Transsylvania"
=*rugosipennis* Géhin, 1882	"Transsylvania"
=*fussi* Birthler, 1886	
~*laevipennis* Seidlitz, 1891; un	
=*istratii* Hormuzaki, 1901	"Bukowina"
~*laetus* Vacher de Lapouge, 1902; un	"Serbia"(error)
~*funestus* Csiki, 1905; un	"Transsylvania"
=*decebali* Mallasz, 1929	"Siebenburgen"
~*interruptecostatus* Marcu, 1934; un	
~*palustris* Niedl, 1946; un	?N-Slovakia:Vysoké Tatry Mts.:Tatranská dolina valley
~*cyaneipennis* Breuning, 1947; un	"Russ.subc.:Vihorlat"(=E-Slovakia:Vihorlat Mts.)
~*pseudoputzeysi* Breuning, 1947; un	"Rumänien:Szamosujvar"
~*carpaticus* Niedl, 1948; un	W-Ukraine:Uzhgorod
~*contortus* Niedl, 1948; un	
~*diffisus* Niedl, 1948; un	W-Ukraine:?Uzhgorod
~*havelkai* Niedl, 1948; un	
~*kulti* Niedl, 1948; un	W-Ukraine:Uzhgorod
~*latissimus* Niedl, 1948; un	W-Ukraine:Jasina
~*napravniki* Niedl, 1948; un	W-Ukraine:?Mukachevo
~*punctatus* Niedl, 1948; un	W-Ukraine:?Uzhgorod
~*mandli* Niedl, 1960; un; nom.pro *carpaticus* Niedl, 1948	W-Ukraine:Uzhgorod
~*nitidis* Vicol, 1987; un	
~*takacsi* Vicol, 1987; un	
~*viridis* Vicol, 1987; un	
d. ssp. ***festivus*** Dejean, 1826, nec Panzer, 1796; lsu	SE-France:Aude:N-part; Tarn:S-part(Soréze)
~*holochrysus* Barthe, 1908; un	
~*nigrofemoratus* Barthe, 1908; un	
~*purpureorutilans* Barthe, 1908; un	
~*violaceopurpureus* Barthe, 1908; un	
~*castaneipes* Vacher de Lapouge, 1910; un	
~*crassepunctus* Vacher de Lapouge, 1910; un	
~*holochrysum* Vacher de Lapouge, 1910; un	
~*pumicatus* Vacher de Lapouge, 1910; un	
~*nigricollis* Le Moult, 1912; un	
~*dauphini* Auzat, 1915; un	"Forêt de la Pauze"
~*ceroglossoides* Barthe, 1924; un	
~*auratopumicatus* Sirguey, 1924; un	
=*charpentieri* Sirguey, 1931	
=*gauberti* Sirguey, 1931	
=*lebisi* Sirguey, 1931	
~*claripes* (Alabergere, 1968); un	
~*mirilius* (Alabergere, 1968); un	

~*aveyronnensis* (Raynaud, 1970); un	Aveyron:?
~*jeanimarcianus* (Culot, 1981); un	
~*benedictae* (Lacroix, 1986); un	
~*nigrocyanescens* (Devecis, 1988); un	
~*cyaneonigrescens* (Devecis, 1991); un	
f. ssp. ***punctatoauratus*** Germar, 1824	SC-France:Pyrénées-Orientales(“Mts.E of Mont Louis”-NT); Ariège; “Pyrénées”
=*canigouensis* Schaefer, 1966	Pyrénées-Orientales:Canigou Massif:Pla Guilhem
=*romani* (Raynaud, 1968)	
=*roussellei* (Colas, 1969)	
=*errensis* (Rousselle, 1974)	Pyrénées-Orientales:Vallée d’Err:NW-slopes betw. Puigmale/Pic du Pas dels Lladres
~*holoviridis* (Devecis, 1988; un)	
~*guerroumii* Leplat, 1989; un	Ft.de Nohédes(?Pyrénées-Orientales)
(ssp.) *farinesi* Dejean, 1826	SW-France:Pyrénées-Orientales, Aude, Ariège
=*carlittensis* Barthe, 1910	?Pyrénées-Orientales
=*pseudofestivus* Vacher de Lapouge, 1910	Ariège:Ft.de Bosc
=*barthei* Vacher de Lapouge, 1912	Aude & Ariège:N-part:Belcaire env.& Ft.de Belesta
=*boscensis* Nicolas, 1923	Ariège:Ft.de Bosc
=*bouisseti* Barthe, 1936	
=*aubryi* (Colas, 1969)	Ariège:Cirque d’Anglade nr.Salau
~*ninini* (Colas, 1969); un	Ft.de Gravas
=*raynaudi* (Colas, 1969)	?Pyrénées-Orientales:Ft.de Boucheville
=*angladensis* (Jeanne, 1969)	Ariège:Salau:cirque d’Anglade, 1400m
~*vallierensis* (Jeanne, 1969), nec Colas, 1964	Ariège:Mt.Vallier Massif:Couflens:Arreou lake, 1800m
~*simardi* (Raynaud, 1970); un	
=*pailherensis* (Jeanne, 1972)	Ariège:Port de Pailhéres, 2000m
=*pseudobarthei* (Schaefer, 1973)	Aude:Massif S of Fajolle
~*ayensis* (Darnaud, 1980); un	Ariège:Ayens
~*caroli* (Darnaud, 1980); un	Ariège:Col des Croisets
~*costessequi* (Darnaud, 1980); un	Ariège:Ft.du Castera
~*philippi* (Darnaud, 1980); un	Ariège:Port de Pailhéres
~*tarasconensis* (Mercier, 1988); un	
~*sylvius* (Delhaye, 1988); un	
=*vicdessoensis* Meyer, 1991	Ft. de Fontanal
=*couseransensis* Meyer, 1991	Couseran
=*mercieri* Remond, 1983	
=*dufisi* Shaefer, 1961	
=*beillensis* Forel & Leplat, 1995	Plateau de Beille
=*pseudoboscensis* Forel & Leplat, 1995	Ft. de Goulier
=*cupreipes* Forel & Leplat, 1995	
=*obscuripes* Forel & Leplat, 1995	
(ssp.) *montanus* Géhin, 1882; ?non priority	Hautes-Pyrénées(Gavarnie); Haute Garronne; Pyrén. Atl.: E-part; NE-Spain:Lerida:C-Pyrénées
=*flavolimbatus* Géhin, 1876; ?un; ?priority	
~*lugubris* Géhin, 1881, nec Duftschmid, 1812	Hautes-Pyrénées:Pic de Nère
=*pandellei* Géhin, 1882	Haute-Garonne:Bagnères de Luchon
~*rubripes* Nicolas, 1898, nec Duftschmid, 1812	Hautes-Pyrénées:Pic de Nère
=*aurocostatus* Vacher de Lapouge, 1902	?Hte-Garonne:Bagnères de Luchon(?inexact: ?in fact: NE-Spain:C-Pyrénées:Val d’Aran env.)
=*bigerrio* Vacher de Lapouge, 1924	Hautes-Pyrénées:Barèges env.
~*illixioni* (Darnaud, 1981); un	Haute-Garonne:“Haute montagne de Luchon”
002 *lineatus* Dejean, 1826	N-Spain, N-Portugal, W-Pyrénées
a. ssp. ***lineatus*** Dejean, 1826	N-Spain:Oviedo:E-part to Navarra:Pamplona; Logrono; C-Spain:Avila; “Asturia”

=*basilicus* Chevrolat, 1837	"Porto Rico"(error)
=*whitei* Deyrolle, 1852	LNF(unlabelled HT)
~*debilicostis* Kraatz, 1896, nec Kraatz, 1878	"Asturia"
~*forticostis* Kraatz, 1896, nec Kraatz, 1878	"Asturia"
~*obscurus* Le Moult, 1913; un	Asturia:Puerto Pajares
~*rufipes* Vacher de Lapouge, 1931; un	
~*fuliginosus* (Puisségur, 1962), nec Panzer, 1809	?Sierra de Andia
~*avilensis* Breuning, 1966; un	Picos de Europa Massif:Aliva refuge(=Avila error)
~*holoidus* (Raynaud, 1969); un	Sierra de Andia
=*numancianus* (Raynaud, 1969)	Soria:Duero River source area
~*poussini* Brañes, 1988; un	Palencia:Revila env.(Cervera de Pisuerga)
b. ssp. *troberti* Kraatz, 1860	NC-Spain:Guipuzcoa; Navarra:NW-part; SW-France:Pyrénées-Atlantiques
=*ursuius* Vacher de Lapouge, 1911	SW-France:Pyrénées-Atlantiques:Mt.Ursuia
=*beharrius* Nicolas, 1916	Pyr.Atlantiques:Mt.Beharria S of St.Jean Pied de Port
=*hochstetteri* Born, 1919	Pyr.Atlantiques:Val d'Urepel
~*incostatus* Nicolas, 1919; un	
c. ssp. ***lateralis*** Chevrolat, 1840, nec Fabricius, 1792; lsu	N-Portugal; NW-Spain:La Coruna, Orense, Pontevedra, Lugo, Leon, Oviedo; "Sra.de Tranquera"
=*miniatulus* Venet, 1930	Pyr.Atlantiques:Val d'Urepel
~*bilineatus* Géhin, 1885; un	"Portugal"
=*strasseri* Lauffer, 1905	Leon:Laceana
=*martinezi* Bolivar, 1922	Leon:Foncebados
~*littoralis* Brañes, 1988; un	Pontevedra
d. ssp. *leonensis* Born, 1918	Leon:Ponferrada
~*subholoviolaceus* (Puisségur, 1962); un	Galicia:Sierra de Arbolente
~*glaucus* (Raynaud, 1969); un	LNF
~*holochlorus* (Raynaud, 1969); un	LNF
~*quasilineatus* Tarrier, 1975; un	Oviedo:Alto del Connio
~*annikae* (Darnaud, 1979); un	Leon:Ponferrada
~*boulbenei* (Darnaud, 1979); un	Leon:Ponferrada
~*bourdeaui* (Darnaud, 1979); un	Leon:Ponferrada
~*caubeti* (Darnaud, 1979); un	Leon:Ponferrada
~*daniellenae* (Darnaud, 1979); un	Leon:Ponferrada
~*rothei* Brañes, 1985; un	
~*sanabriensis* Brañes, 1985; un	Zamora:Sanabria Lake
e. ssp. *salmantinus* Bolivar, 1922	CW-Spain:Salamanca/Caceres:Sierra de Gata; Salamanca: Sequeros
~*subsalmantinus* Brañes, 1985; un	Caceres:St.Martin de Trevejo
=*sainvali* Brañes, 1987	Caceres:Hervas
003 ***olympiae*** Sella, 1855	N-Italy:Piemonte:Biella env.:Sessera valley
~*sellae* Stierlin, 1881, nec Kraatz, 1878	
=*stierlini* Heyden, 1881; nom.pro *sellae* Stierlin	
~*fucatus* Vacher de Lapouge, 1902; un	
004 ***solieri*** Dejean, 1826	Alps of SE-France & NW-Italy
a. ssp. ***solieri*** Dejean, 1826	SE-France:Alpes-de-Haute-Provence(?"Basses-Alpes: Les Dourbes"), Alpes-Maritimes
~*furcillatus* Bleuse, 1913; un	"Basses-Alpes"(=Alpes-de-Haute-Provence)
~*louveti* Clermont, 1922; un	Alpes-Maritimes:St.Martin de Vesubie
=*fuscoaeneus* Clermont, 1925	
=*vesubiensis* (Poncetton & Reymond, 1935)	Alpes-Maritimes:St.Martin de Vesubie
~*fagniezi* Colas, 1959; un	Alpes-Maritimes:St.Martin de Vesubie
=*cavalieri* (Colas, 1965)	Alpes-Maritimes:Col de Braus(=nr.Sospel)
=*altamontanus* (Ochs, 1965)	Alpes-de-Haute-Provence/Alpes-Maritimes:Col de la Cayolle

=*chalcostola* (Ochs, 1965)	Alpes-Maritimes:Collongues
=*tarrieri* (Ochs, 1965)	Alpes-Maritimes:Lantosque
~*ater* (Raynaud, 1970); un	
~*gordolasquensis* (Raynaud, 1970); un	Alpes-de-Haute-Provence:Gordolasque valley
~*smaragdinus* (Raynaud, 1970); un	Alpes-Maritimes:St.Martin de Vesubie
~*viridicupreus* (Raynaud, 1970); un	
~*florettae* Raffaldi, 1971; un	Alpes-de-Haute-Provence:Annot env.
~*hyperchlorus* Tarrier & Bellon, 1972; un	Alpes-Maritimes:St.Martin de Vesubie
~*piezus* Bellon & Tarrier, 1972; un	Alpes-de-Haute-Provence/Alpes-Maritimes:Col des Champs
~*monicae* Tarrier, 1973; un	Alpes-Maritimes:Lantosque
~*carreti* Tarrier, 1975; un	Alpes-Maritimes:St.Etienne-de-Tinée
~*desmon* Bellon & Tarrier, 1975; un	Alpes-Maritimes:Belvédere
~*dujardini* Bellon & Tarrier, 1972; un	Alpes-Maritimes:Sospel
~*rouyricus* Tarrier, 1975; un	Alpes-de-Haute-Provence:Mt.Vial
c. ssp. *clairi* Géhin, 1885	NW-Italy & SE-France:Alpes-Maritimes(?"Mercantour"; ?Col de Tende; ?error)
=*cyaneoviridis* Carret, 1897	
~*azurescens* (Raynaud, 1970); un	
~*viridiater* (Raynaud, 1970); un	
~*axiomorphus* Tarrier, 1971; un	Alpes-Maritimes:La Muselle
~*devillei* Tarrier, 1972; un	
~*strobinoi* Tarrier, 1975; un	Alpes-Maritimes:"Bas vallon de Molliéres:Pierre Blanche"
b. ssp. *liguranus* Breuning, 1932	NW-Italy:Alpi Liguri, Appennino Ligure, Langhe & SE-France:Alpes-Maritimes:Tende env.
~*sturanii* (Raynaud, 1970); un	LNF (type: Liguria, M. San Giorgio)
d. ssp. ***bonnetianus*** Colas, 1937; nom.pro *bonneti* Colas, 1936	SE-France:Var:E-part(St.Cassien des Bois); Tanneron Massif, Esterel
~*bonneti* Colas, 1936, nec Le Moult, 1912	Var:St.Cassien des Bois
e. ssp. *bonadonai* Colas, 1948	Alpes-Maritimes:Séranon
=*canjuersicus* (Ochs, 1965)	Var:NC-part:Ft.Grand Margés:Aiguines
=*curtii* (Ochs, 1965)	Alpes-Maritimes:Vescou
=*belloni* (Tarrier, 1966)	Alpes-Maritimes:Roquestéron
=*caussolsicus* (Bellon, 1971)	Alpes-Maritimes:Caussols env.
~*teillonensis* Tarrier, 1975; un	Alpes-de-Haute-Provence:Mt.de Teillon
005 *splendens* Olivier, 1790	S-France:Aveyron-Pyr.Atl.-Landes; NE-Spain:Lerida, Huesca, Navarra, Alava; Jamaika(error)
=*carolinus* Fabricius, 1792	Carolina(error)
=*viridis* Dejean, 1826	
=*cychricollis* Vacher de Lapouge, 1898	Haute-Garonne:Luchon
~*lineatopunctatus* Vacher de Lapouge, 1898, nec Dejean, 1826	
~*ovipennis* Vacher de Lapouge, 1902; un	
~*seriepunctatus* Vacher de Lapouge, 1902; un	
=*nereensis* Nicolas, 1902	Hautes-Pyrénées:Pic de Néré
~*vittatus* Vacher de Lapouge, 1902; un	Aude:Ft.de Fanye
~*mordoratus* Nicolas, 1908; un	Hautes-Pyrénées & Haute-Garonne:Lourdes & Luchon
~*jeani* Clermont, 1909; un	Ft.de Lestelas
=*ammonius* Vacher de Lapouge, 1909	Tarn:Montagnes Noires
=*pinetorum* Vacher de Lapouge, 1910	"Dep.Landes"
=*pseudotroberti* Vacher de Lapouge, 1910	
~*babaulti* Le Moult, 1912; un	Tarn:Montagnes Noires
~*goliath* Le Moult, 1912, nec Morawitz, 1886	Aude:Ft.des Fanges
~*granulipennis* Le Moult, 1912; un	Tarn:Montagnes Noires
=*pseudocychricollis* Le Moult, 1912	Tarn:Montagnes Noires

=*pseudoovipennis* Le Moult, 1912	Tarn:Montagnes Noires
=*pseudoviridicollis* Le Moult, 1912	Aude:Ft.des Fanges
=*pseudovittatus* Le Moult, 1912	Aude:Ft.des Fanges
=*subcychricollis* Le Moult, 1912	Aude:Ft.des Fanges
=*subovipennis* Le Moult, 1912	Aude:Ft.des Fanges
~*vinosus* Le Moult, 1912; un	Tarn:Montagnes Noires
~*viridicollis* Le Moult, 1912, nec Kraatz, 1882	
~*dombrowskii* Le Moult, 1913; un	Haute-Garonne:Luchon
~*laticollis* Le Moult, 1913; un	Pyrénées:Lerida:Val d'Aran
=*piesbergeni* Le Moult, 1913	
=*lapurdanus* Vacher de Lapouge, 1913	?"Basses Pyrénées:S-part of Bayonne district"(=Pyr.-Atlantiques); ?Pyr.-Atl.:Cambo
=*mascarauxi* Vacher de Lapouge, 1916	"Basses Pyrénées:Vallée de la Bidassoa & Vallée se la Nivelle"(=Pyr.-Atlantiques)
~*cervicis* Csiki, 1917; un; nom.pro *laticollis* Le Moult	Pyrénées:Lerida:Val d'Aran
~*viridicervix* Csiki, 1917; un; nom.pro *viridicollis* Le Moult	
~*pallens* Vacher de Lapouge, 1924, nec Fabricius, 1775	"Basses Pyrénées"(=Pyr.-Atlantiques; alpine form)
=*hemipterus* Sirguey, 1931	
=*palesius* Sirguey, 1931	"Pic Burat"
~*cardinalis* (Raynaud, 1968); un	
~*najacensis* (Raynaud, 1968); un	Aveyron:Ravin de Najac
~*temnoglypha* (Raynaud, 1969); un	
~*ursuiensis* (Raynaud, 1969); un	?Pyrénées-Atlantiques:Mt.Ursuia
~*violaceocyaneus* (Jeanne, 1972); un	Aude:Ft.d'Arques
~*arradoyensis* (Lequet, 1975); un	Pyr.-Atlantiques:Pic d'Arradoy, 600m
~*violaceoviridis* (Rouselle, 1978); un	
~*alberginius* (Remond, 1986); un	
~*michaellae* (Remond, 1986); un	
~*incertus* (Devecis, 1988); un	
~*taffini* (Delaporte, 1988); un	
006 *hispanus* Fabricius, 1787	C,CW,CE,SC-France; "Spain"(error; Lozère: Ispaniac)
=*boudeti* Beuthin, 1892	Gard
~*hispanicus* Thomson, 1875; un; error for *hispanus* Fabricius	-
~*gabalicus* Géhin, 1885; un	Lozère
=*cevennicus* Jacquet, 1886	
=*languedocianus* Vuillefroy, 1892	
~*castaneus* Vacher de Lapouge, 1902; un	Lozère
=*auzati* Le Moult, 1912	Dufourt
=*infernalis* (Lebis, 1958)	Tarn:Forêt de la Grésigne
~*mourguesi* (Puisségur, 1962); un	?LNF
=*berardi* (Raynaud, 1967)	Loire:Saint-Victor-sur-Loire
~*infuscatus* (Raynaud, 1967); un	Tarn:Forêt de la Grésigne
~*semivirescens* (Raynaud, 1967); un	Aveyron:Villecomptal
~*canui* (Darnaud, 1983); un	Corréze:Tulle, Argentat, Beynat
~*ignivorax* (Darnaud, 1983); un	Lozère:St.Germain de Calberte
~*retaudis* (Gorrin, 1991); un	
(ssp.) *latissimus* Vacher de Lapouge, 1910	Aude:Rennes les Bains
~*alarici* (Darnaud, 1983); un	Aude:Rennes les Bains
(ssp.) *dromensis* Forel & Leplat, 1995	Drôme:Forêt de Saou
007 *rutilans* Dejean, 1826	E-Pyrénées; NE-Spain:Barcelona, Lerida
a. ssp. ***rutilans*** Dejean, 1826	E-Pyrénées:Ariège to Pyr.Or.(Prats de Molo); Gerona to Lerida; Barcelona; Tarragona
~*aequatus* Vacher de Lapouge, 1902, nec Motschulsky, 1845	Barcelona:Montserrat

~*rusticus* Vacher de Lapouge, 1902; un	
~*brevicollis* Vacher de Lapouge, 1910, nec Fabricius, 1792	Aude:Ft.de Monthaut nr.Rennes-les-Bains
~*viridis* Ferrer y Vert, 1910; un	Barcelona:Montserrat
~*affictus* Codina, 1913; un	Setcasas
=*aragonensis* Vacher de Lapouge, 1913	Barcelona:Sierra de Montseny
=*codinae* Vacher de Lapouge, 1913	Setcasas
~*montserraticus* Csiki, 1917; un; nom.pro *aequatus* Vacher de Lapouge	Barcelona:Montserrat
~*viridicolor* Csiki, 1927; un; nom.pro *viridis* Ferrer y Vert	Barcelona:Montserrat
~*interseriatus* L'Hoste & Meyer, 1973; un	
~*delacrei* Tarrier, 1975; un	Barcelona:Berga:Nostra Signora de Queralt
~*alberensis* (Darnaud, 1978); un	
~*blanci* (Darnaud, 1978); un	
~*lecumberryi* (Darnaud, 1978); un	
~*pseudoopulentus* (Darnaud, 1978); un	
~*boulbeni* (Blanc, 1980); un	Gerona:Camprodon
~*darnaudi* (Blanc, 1980); un	Barcelona:Sierra de Montseny
~*claveriei* Lassalle & Pham, 1981; un	Barcelona:Sierra de Montseny
~*goalesae* (Cottour, 1984); un	
~*lassallei* Brañes, 1985; un	
(ssp.) *jeannei* Lassalle & Pham, 1981	Tarragona:Sierra de la Mussara
b. ssp. ***perignitus*** Reitter, 1896	Andorra, N-Spain:Lerida; ?"Pyrénées of Spain"
~*foveipennis* Vacher de Lapouge, 1902; un	?Andorra
~*fontyi* (Darnaud, 1980); un	
c. ssp. *opulentus* Oberthür, 1898	NE-Spain:C-Pyrénées:Lerida, Huesca(Col de la Muria)

28. ***MACROTHORAX*** Desmarest, 1850; type species *Carabus aumonti* Lucas = *Carabus morbillosus aumonti* Lucas
=*Dichocarabus* Reitter, 1896; type species *Carabus rugosus* Fabricius
=*Dorcarabus* Reitter, 1896; cos; type species *Carabus morbillosus* Fabricius
~*Dorcocarabus* Reitter, 1896; iss of *Dorcarabus* Reitter
=*Paracarabus* Reitter, 1896; type species *Carabus planatus* Chaudoir

001 ***morbillosus*** Fabricius, 1792	NW-Africa, S-Spain, Baleares, Sicily, Sardinia, Corsica, S-Italy:Calabria, SE-France
a. ssp. ***morbillosus*** Fabricius, 1792	NC,NE-Algeria:Alger env.:Medea, Blida, Tizi Ouzou, Djurdjura Massif; Bejaia; "Barbaria"
(ssp.) *cheminorum* Deuve, 1988	S-France:Var:Frejus; introduced
b. ssp. *constantinus* Vacher de Lapouge, 1899	NE-Algeria:Constantine, Setif; N,CE-Tunisia; NW-Libya:Yafran; Sardinia, Corsica, Lampedusa
=*arborensis* Krausse, 1908	Sardinia:Asuni
=*galloprovincialis* Vacher de Lapouge, 1910	S-France:Var:Muy; introduced
~*relictus* Krausse, 1910, nec Semenov, 1888	S-France:Les Maures; introduced
=*corsicanus* Vacher de Lapouge, 1913	Corsica
=*lampedusae* Born, 1925	Lampedusa Island
c. ssp. ***alternans*** Palliardi, 1825, nec Fabricius, 1792; lsu	Sicily; S-Italy:Calabria
=*servillei* Solier, 1835	
~*viridulus* Ragusa, 1905, nec Kraatz, 1878	
=*bruttianus* Born, 1906	Calabria:?
~*borni* Krausse, 1908, nec Meyer-Darcis, 1902	
=*sicanus* Csiki, 1927; nom.pro *borni* Krausse	
d. ssp. *macilentus* Vacher de Lapouge, 1899, nec Olivier, 1795; lsu	S-Spain:Alicante, Murcia; Baleares
=*ferrugatus* Vacher de Lapouge, 1899	Baleares

=*balearicus* Vacher de Lapouge, 1913	Baleares
002 ***planatus*** Chaudoir, 1843	N-Sicily; LNF(unlabelled NT)
=*thomsoni* Fairmaire, 1857	
003 ***rugosus*** Fabricius, 1775	N,C-Morocco, Spain, Portugal; introduced:SC-France
a. ssp. ***rugosus*** Fabricius, 1775	
b. ssp. ***celtibericus*** Germar, 1824	Portugal; W-Spain:Galicia – Caceres – Huelva; Portugal
=*brannani* Schaufuss, 1871	S-Portugal:?Portalegre; ?Sierra de Estrella
~*semicyanescens* Brañes, 1985; un	
=*condadoensis* Brañes, 1992;	SW-Spain:Huelva:La Palma del Condado
(ssp.) *laufferi* Breuning, 1927	C-Spain:Avila env.
c. ssp. ***boeticus*** Deyrolle, 1852	S-Spain:Sevilla – Granada – Almeria; "Cordillères Bétiques"
~*andalusiacus* Géhin, 1885; un	Andalusia
=*seguranus* Lauffer, 1905	Jaen/Granada:Sierra de Segura Mts.(alpine form)
=*breuili* Alluaud, 1930	Andalusia:Laguna de Janda
~*pseudobaeticus* Brañes, 1985; un	Granada:?
=*pseudoboeticus* Lassalle, 1986	
nom.pro *pseudobaeticus* Brañes, 1985	
(ssp.) *levantinus* Lauffer, 1905	E-Spain(Murcia & Valencia); SC-France:Pyrénées-Orientales(?introduced)
=*barnolai* Xaxars, 1921	Barcelona:St.Boy de Llobregat
=*vermiculosus* Fons, Leplat & Ferrero, 1993	S-France:Pyrénées-Orientales:Albères Massif:E-slope; ?introduced

29. *LAMPROSTUS* Motschulsky, 1865; type species *Carabus spinolae* Cristoforis & Jan = *Carabus torosus spinolae* Cristoforis & Jan

001 ***torosus*** Frivaldszky, 1835	E-Bulgaria; NW,C,NE-Turkey; ?SE-Romania
ssp. ***torosus*** Frivaldszky, 1835	E-Bulgaria; ?SE-Romania; "E-Balcans:Black Sea coast"

30. *PROCRUSTES* Bonelli, 1809; type species *Carabus coriaceus* Linnaeus

001 ***banoni*** Dejean & Boisduval, 1829	Crete Island; Dia Island; Gaudos Island
=*taborskyi* (Mařan, 1948)	
002 ***coriaceus*** Linnaeus, 1758	Europe:France to European Russia; Balcans, Carpathians, Turkey, NW-Syria
a. ssp. ***coriaceus*** Linnaeus, 1758	C,W,NE-Europe:France to European Russia; ?"Germany"
=*punctulatus* Voet, 1778; spn	
=*spretus* Dejean, 1826	NW-Croatia, NW-Bosnia; NE-Italy:Trieste env.; "Fiume"(=Rijeka)
~*angusticollis* Motschulsky, 1859, nec Fabricius, 1801	"Carniolia"
=*cordicollis* Motschulsky, 1865	"Carniolia"(LT)
=*imminutus* Kraatz, 1879	Croatia:Pljesevica Mts.
~*sublineatus* Géhin, 1885; un	"Südrussland"(error)
~*tauricus* Ganglbauer, 1888, nec Bonelli, 1811	"Krym"(error)
=*basilicatus* Born, 1902	C,N-Italy(Basilicata:Val Rondina)
=*pseudorugifer* Sokolar, 1906	"Strassnitz"(=SE-Moravia:Strážnice)
=*occidentalis* Born, 1907	CW-France:Vienne:Poitiers
=*ruscinoensis* Mosconi, 1994	SW-France(Pyrénées Orientales)
~*pueli* Vacher de Lapouge, 1909; un	Bouches-du-Rhône:Ile de la Camargue
~*sabinus* Vacher de Lapouge, 1909; un	C-Italy:?
=*cansiglianus* Bernau, 1914	NE-Italy:Veneto:Bosco del Cansiglio
~*italicus* Vacher de Lapouge, 1924, nec Dejean, 1826	"Basses Alpes:Riez"(=Alpes-Hte-Provence)
=*altercoriaceus* Kolbe, 1925	"Neumark"(=Gorzów env.)

=*italianus* Csiki, 1927; nom.pro *italicus* Vacher de Lapouge	"Basses Alpes:Riez"(=Alpes-Hte-Provence)
=*capellae* Depoli, 1929	"Capella"(=Croatia:Kapela Massif)
~*gracilis* Depoli, 1929, nec Küster, 1846	"Mte.Milonia & Timavo valley"(=?Rijeka env.)
~*holoradiatus* Raynaud, 1966; un	
~*alaricus* (Meyer, 1990); un	
(ssp.) *banaticus* Redtenbacher, 1849	S-Hungary; CW,SW-Romania; Serbia; ?"Austria:Leitha Mts."(error); ?Banat
=*subrugosus* Kraatz, 1877	Banat:Bazias
=*praeillyricus* Szél, 1993	SW-Hungary:Baranya:Villányi Mts.:Szársomlyó
d. ssp. ***mediterraneus*** Born, 1906	S-Italy:Calabria(Cimina, Antonimina), Crotone
(ssp.) *florinensis* Vacher de Lapouge, 1922	S-Macedonia; N,C-Greece:Makedonía ("Florina:Camp. Grosetti"=Florina env.), Pindos Mt.R.
~*pindicola* (MaYan, 1952); un	N-Pindos Mts.:Malakassion(alpine form)
(ssp.) *joniensis* Breuning, 1937; un; nom.pro *graecus* Dejean	S-Albania; NW-Greece:Ioannina env; Kerkyra Island; Ionian Isles
~*graecus* Dejean, 1829, nec Dejean, 1826	"Ionian Isles"
~*nitens* Gautier des Cottes, 1866, nec Linnaeus, 1758	"Ionian Isles"
=*albanicus* Breuning, 1943	"S-Albania:Maj Tartarit"
~*hickerianus* Mandl, 1964; un	"Zante Island:Limne Makry"(=Zakynthos)
=*zanteanus* Breuning, 1964	"Zante Island"(=Zakynthos)
c. ssp. ***excavatus*** Charpentier, 1825, nec Paykull, 1790; lsu	Croatia & ?N-Albania:Adriatic Sea coast; "Pyrénées"(error)
~*rugosus* Dejean, 1826, nec Fabricius, 1775	Dalmatia:Vergorac
=*abchasicus* Motschulsky, 1850	"Abkhasia"(error)
=*nitidior* Reitter, 1881	Dalmatia:"Zara, Lesina"(=Zadar, Hvar Island)
=*dalmaticus* Géhin, 1885	"Dalmatia"
=*proximus* Reitter, 1885	Bosnia & Herzegovina:?
=*monastiriensis* Vacher de Lapouge, 1922	Macedonia:Monastir
~*weiratherianus* Breuning, 1936; un	Montenegro:Lebrsnik
f. ssp. ***cerisyi*** Dejean, 1826	CW,SW-Turkey:Izmir, Manisa, Antalya, Konya; S-Aegean Isles(Mytilene=Lesvos)
=?*vicinus* Waltl, 1838	"Balkan, Constantinopel"(=Istanbul; ?inexact)
~*punctulatus* Reiche & Saulcy, 1855, nec Schaller, 1783	Syra(=Syros Island)
=*impudicus* Gautier des Cottes, 1866	Rhodos
~*minor* Gautier des Cottes, 1866, nec Kraatz, 1860	"Melos Island"(=Milos)
~*sphodrinus* Gautier des Cottes, 1866, nec Fischer von Waldheim, 1844	Rhodos
~*icaricus* Ganglbauer, 1888; un	Samos & Ikaria Island
~*kykladicus* Breuning, 1936; un; nom.pro *punctulatus* Reiche & Saulcy	Syra(=Syros Island)
(ssp.) *foudrasi* Dejean, 1829	S-Greece:Peloponnesos; Kythera Isl.; Morea(=Peloponnesos)
=*obtritus* Chaudoir, 1857	"Graecia"
~*deplanatus* Motschulsky, 1859, nec Fischer von Waldheim, 1823	"Graecia"
~*coraxensis* Beheim & Breuning, 1943; un	S-Greece:"Korax Mts."
(ssp.) *hopffgarteni* Kraatz, 1878	E-Greece, SW,C-Bulgaria, SE-Serbia(Mt.Komska), E-Macedonia
~*semipunctatus* Géhin, 1885, nec Donovan, 1806	Rila Mt.R.
=*emgei* Ganglbauer, 1888	NE-Greece:Thessaloniki, Olympos & Ossa Massif, Parnassos Mt.R.; Euvoia Island
~*oetensis* (Mařan, 1952); un	CE-Greece:Oeta(=?Oite Massif NW of Parnassos)
~*olympicola* (Mařan, 1952); un	NE-Greece:Olympos Massif, 2600m(alpine form)
~*storkani* (Mařan, 1952); un	NE-Greece:Alexandroupoli
~*xanthiensis* (Mařan, 1952); un	NE-Greece:Xanthi(=Xanthé)

~*borchmanni* Mandl, 1959; un	"Stehni-Euböa"(=Euvoia Island)
=*deorum* (Jeanne, 1970)	NE-Greece:Olympos Massif:W-slope:Mt.Agios-Antonios. 2000m
=*roeri* Blumenthal, 1976	NE-Greece:Chalkidiki:Vaydos
e. ssp. ***kindermanni*** Waltl, 1838	SE-Bulgaria:Burgas, Sliven env.; NW-Turkey; ?SE-Romania; "Konstantinopel"(=Istanbul)
=*caraboides* Waltl, 1838	"Balkan"
=*dobrudjensis* Born, 1902	SE-Romania:Mangalia
~*pseudofurax* (Mařan, 1952); un	"Kalofer Balkan"(=Stara Planina Mt.R.nr.Kalofer)
b. ssp. ***rugifer*** (Kraatz, 1877)	Carpathians(?C-Romania:Sinaia)
~*rugulosus* Ganglbauer, 1888; un	C-Romania:Azuga
~*testis* Vacher de Lapouge, 1909; un	C-Romania:Sinaia
(ssp.) *furax* Csiki, 1927; nom.pro *montandoni* Born	SC-Romania(Vlasca:Comana)
~*montandoni* Born, 1902, nec Buysson, 1882	Vlasca:Comana

31. ***PROCERUS*** Dejean, 1821; type species *Carabus scabrosus*: Fabricius, non Olivier = *Carabus gigas* Creutzer

001 ***duponchelii*** (Dejean, 1831)	S-Greece:Peloponnes Peninsula
=*kusdasi* Mandl, 1966	Peloponnes:Chelmos(alpine form)
002 ***gigas*** Creutzer, 1799	Former Yugoslavia, Greece, S-Romania, SW,C,NE-Bulgaria, SE-Austria, NE-Italy
a. ssp. *gigas* Creutzer, 1799	NE-Italy; SE-Austria, former Yugoslavia("Idria, Carniolia"), S-Romania; SW,C,NE-Bulgaria
~*scabrosus*: Fabricius, 1801, non Olivier, 1795	-
~*limbatus* Géhin, 1885; un	
~*olympicus* Vacher de Lapouge, 1902, nec Géhin, 1885	?Olympos Massif
~*limbiger* Csiki, 1927; un; nom.pro *limbatus* Géhin	
(ssp.) *parnassicus* Kraatz, 1884	N, C-Greece, Macedonia, S-Albania
003 ***scabrosus*** Olivier, 1795	SE-Bulgaria; NW,NC-Turkey; Krym Peninsula
a. ssp. ***scabrosus*** Olivier, 1795	SE-Bulgaria, Eur.Turkey("Konstantinopel"=Istanbul)
=*olivieri* Dejean, 1826	?"Konstantinopel"
=?*aegyptiacus* Motschulsky, 1844	"Egypt"(error)
~*cribratus* Motschulsky, 1850, nec Quensel, 1806	"Constantinople"(=Istanbul; LT)
~*angusticollis* Haller, 1885, nec Fabricius, 1801	
~*dejeani* Géhin, 1885; un	
b. ssp. ***tauricus*** Bonelli, 1810	Ukraine:Krym Peninsula; "Crimea meridionale"
=*aeneus* Motschulsky, 1850	"Tauria"(LT)
=*nigritulus* Kraatz, 1876	
=*purpureus* Kraatz, 1876	
=*viridissimus* Kraatz, 1876	
004 ***sommeri*** Mannerheim, 1844	SC-Bulgaria, Turkey
a. ssp. ***bureschianus*** Breuning, 1928	SC-Bulgaria:Rhodopes Mt.R.(Backovo), NE-Greece

HYBRIDS*

MORPHOCARABUS/TACHYPUS
Vacher de Lapouge (1898): hyb *Morphocarabus monilis* × *Tachypus cancellatus*

CARABUS/TACHYPUS
Mandl (1955): hyb *Carabus granulatus* × *Tachypus cancellatus*

EUCARABUS/TACHYPUS
Mandl (1955): hyb *Eucarabus ulrichii* × *Tachypus cancellatus*
Lamy (1908) in Deuve (1994): hyb *Tachypus cancellatus* × *auratus*

EUCARABUS/OREOCARABUS
Roubal (1925): hyb *Eucarabus obsoletus* × *Oreocarabus glabratus*
Mandl (1955): hyb *Eucarabus obsoletus* × *Oreocarabus glabratus*

EUCARABUS/PROCRUSTES
Mandl (1955): hyb *Eucarabus obsoletus* × *Procrustes coriaceus*

EUCARABUS/ARCHICARABUS
Mandl (1955): hyb *Eucarabus parreyssii* × *Archicarabus montivagus*

MESOCARABUS
urculoensis Nicolas, 1919; hyb *Mesocarabus problematicus* × *lusitanicus*
probletanicus Meyer, 1992; hyb *Mesocarabus problematicus* × *lusitanicus*
Lassalle & Delaporte (1989): *Mesocarabus problematicus* × *macrocephalus*

MESOCARABUS/TOMOCARABUS
Mandl (1955): hyb *Mesocarabus problematicus* × *Tomocarabus convexus*

ORINOCARABUS
Born (1897): hyb *Orinocarabus latreilleanus* × *heteromorphus*
Born (1897): hyb *Orinocarabus latreilleanus* × *concolor*
Mandl (1955): hyb *Orinocarabus sylvestris* × *linnaei*

OREOCARABUS
Staven (1990) in Deuve (1991, 1994), Assmann (this book): hyb *Oreocarabus hortensis* × *glabratus*

OREOCARABUS/MEGODONTUS
Mandl (1955): hyb *Oreocarabus glabratus* × *Megodontus violaceus*

PLATYCARABUS
gspani Kobmann, 1925; hyb *Platycarabus creutzeri* × *irregularis*
konscheggi Born, 1912; hyb *Platycarabus creutzeri* × *irregularis*
pseudonothus Kraatz, 1878; hyb *Platycarabus creutzeri* × *irregularis*
?*meschniggi* Born, 1920; ?hyb *fabricii* × *depressus*
sustenensis Born, 1920; hyb *Platycarabus fabricii* × *depressus*
Mandl (1955) in Deuve (1994): hyb *Platycarabus fabricii* × *creutzeri*
Mandl (1955) in Deuve (1994): hyb *Platycarabus fabricii* × *irregularis*
Sturani (1962): hyb *Platycarabus cychroides* × *depressus*

CHAETOCARABUS
Tassi (1968) in Deuve (1994): hyb *Chaetocarabus intricatus* × *arcadicus*

INIOPACHYS/CHRYSOCARABUS
bigorrensis (Camard, 1995); hyb *Iniopachys pyrenaeus* × *Chrysocarabus auronitens*
Deuve (1998): hyb *Iniopachys pyrenaeus* × *Chrysocarabus punctatoauratus*

CHRYSOCARABUS
andronnensis Nicolas, 1923; hyb *Chrysocarabus splendens* × *auronitens*
barthei Le Moult, 1912; hyb *Chrysocarabus splendens* × *auronitens*
boreli Le Moult, 1912; hyb *Chrysocarabus splendens* × *auronitens*
breiti Barthe, 1913; nom.pro *barthei* Le Moult; hyb *Chrysocarabus splendens* × *auronitens*
bugareti Jeannel, 1941; hyb *Chrysocarabus auronitens* × *hispanus*
clarofemoratus Nicolas, 1924; hyb *Chrysocarabus splendens* × *auronitens*
esquieryensis Nicolas, 1923; hyb *Chrysocarabus splendens* × *auronitens*

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* Mostly after Deuve (1994), who cites also several hybrids obtained in laboratory from allopatric species (i.e. *Macrothorax* spp. × *Chrysocarabus* spp., etc.).

eugenieae Raynaud, 1936; hyb *Chrysocarabus splendens* × *auronitens*
faustulus Vacher de Lapouge, 1910; hyb *Chrysocarabus splendens* × *auronitens*
helenae Mollard, 1992; ?emend.pro *helenais* Mollard; hyb *Chrysocarabus auronitens* × *rutilans*
~*helenais* Mollard, 1992; ios; hyb *Chrysocarabus auronitens* × *rutilans*
ignipennis Le Moult, 1912; hyb *Chrysocarabus splendens* × *auronitens*
kricheldorffi Le Moult, 1913; hyb *Chrysocarabus splendens* × *auronitens*
lanieli Le Moult, 1912; hyb *Chrysocarabus splendens* × *auronitens*
lemoulti Vacher de Lapouge, 1910; hyb *Chrysocarabus splendens* × *auronitens*
lucaniusae Fradois, 1940; hyb *Chrysocarabus splendens* × *auronitens*
nigricornis Lebis, 1926; hyb *Chrysocarabus splendens* × *auronitens*
olieri Raynaud, 1943; hyb *Chrysocarabus splendens* × *hispanus*
~*croesus* Oberthür, 1883, nec Fabricius, 1801; hyb *Chrysocarabus rutilans* × *hispanus*
pseudofaustulus Le Moult, 1912; hyb *Chrysocarabus splendens* × *auronitens*
pseudoholochrysus Le Moult, 1912; hyb *Chrysocarabus splendens* × *auronitens*
pseudopumicatus Le Moult, 1912; hyb *Chrysocarabus splendens* × *auronitens*
~*rufofemoratus* Barthe, 1924; hyb *Chrysocarabus splendens* × *auronitens*
~*rugosus* Le Moult, 1912, nec Fabricius, 1792; hyb *Chrysocarabus splendens* × *auronitens*
salvanerensis Raynaud, 1970; hyb *Chrysocarabus splendens* × *auronitens*
vacheri Basilewsky, 1931; nom.pro *rufofemoratus* Barthe; hyb *Chrysocarabus splendens* × *auronitens*
vulcanus Le Moult, 1912; hyb *Chrysocarabus splendens* × *auronitens*
annae Raynaud, 1936; hyb *Chrysocarabus lineatus* × *auronitens*
lorenzoi Raynaud, 1968; hyb *Chrysocarabus lineatus* × *auronitens*
arraizensis Raynaud, 1938; hyb *Chrysocarabus lineatus* × *splendens*
bartheensis Nicolas, 1923; hyb *Chrysocarabus lineatus* × *splendens*
jeannae Raynaud, 1936; hyb *Chrysocarabus lineatus* × *splendens*
portoi Raynaud, 1968; hyb *Chrysocarabus lineatus* × *splendens*

MEGODONTUS

deubeli Reitter, 1896; hyb *Megodontus violaceus* × *planicollis*
?*seriatus* Motschulsky, 1850; ?hyb *Megodontus exaratus* × *aurolimbatus*

MEGODONTUS/CHRYSOCARABUS

mouthiezi Darnand & Poussin, 1982; hyb *Megodontus violaceus* × *Chrysocarabus auronitens*

MACROTHORAX

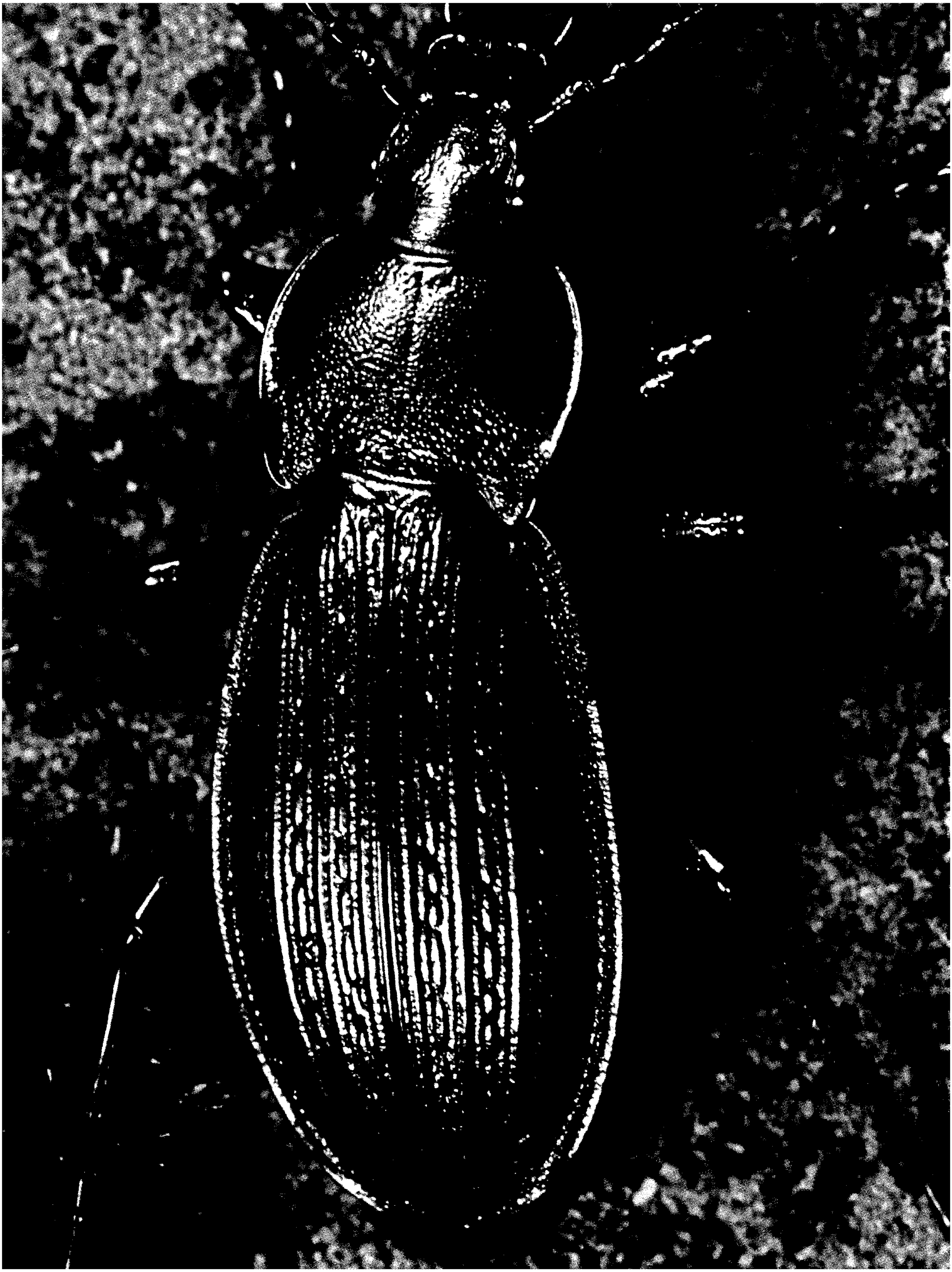
olcesei Putzeys, 1872; hyb *Macrothorax rugosus* × *morbillosus*

PROCRUSTES/MEGODONTUS

Born (1908) in Deuve (1994): hyb *Procrustes coriaceus* × *Megodontus violaceus*

PROCERUS/PROCRUSTES

hyb *Procerus gigas* × *Procrustes coriaceus* (Depoli, 1935)



Chapter 3 Key to the adults

A. Casale & O. L. Kryzhanovskij

3.1. INTRODUCTION

Many authors have studied the systematics and phylogeny of the genus *Carabus* Linnaeus, 1758, among them a number of noted scientists. However, the elaboration of this subject is still far from a final conclusion. Primarily, the subdivision of this extensive and polymorphous taxonomic complex into subordinate taxa of subgeneric rank is a major subject of discussion (see Deuve, 1994).

A number of independent genera have been established within the limits of *Carabus* (*s. lato*) during first half of the 19th century, for example *Procrustes* Bonelli, 1810; *Tribax* Fischer von Waldheim, 1822; *Cechenus* Fischer von Waldheim, 1822; *Procerus* Dejean, 1826; *Megodontus* Solier, 1848.

C. G. Thomson (1875) re-united the larger part of the numerous groups into the single genus *Carabus* (L.) C. G. Thomson in a way that remained relatively unchanged until now. A considerable number of subgenera has been subsequently established (Géhin, 1876, 1885; Morawitz, 1886; Seidlitz, 1887, etc.), but their mutual relationships were not studied. Reitter (1896) published the first, fairly complete, key to the Palaearctic subgenera and species of *Carabus*. He distinguished a large number of new (sometimes polyphyletic) subgenera and combined all subgenera into several large groups (**Carabi carabogenici, C. multistriati, C. tribacogenici, C. cechenogenici, C. procrustogenici**) mainly on the basis of their chaetotaxy and general appearance.

At the same time, A. Semenov-Tian-Shanskij (1896, 1898) described a series of subgenera mostly from Central and Eastern Asia and attempted the use of zoogeographic criteria in addition to morphological ones. The French entomologist G. de Lapouge (1905-1908 etc.) published a series of papers in which he made the first attempt to use larval characters for the classification of *Carabus*. He correctly outlined the three main groups into which the genus *Carabus* may be subdivided by larval characters. He also offered a new system within the Carabini, in which he subdivided *Carabus* (*s. lato*) into a large number of genera, and summarised this system in three volumes of 'Genera Insectorum' (1929-1932). Some of his 'genera' represented a fairly heterogenous mixture of remote species, but others have recently been re-evaluated as natural groups.

Breuning (1932-1937) published an extensive 'Monographie der Gattung Carabus' and summarised most taxonomic information on this group up until then. He regarded *Carabus* as a single genus with a complicate multi-step hierarchy of taxa including two large supra-subgeneric groups (**Carabi brevimandibulares** and **Carabi longimandibulares**), 20 subgenera, 68 sections and about 500 species. He interpreted the majority of species as polytypical systems hierarchically subdivided into subspecies, nationes and morphae. Many of Breuning's groups of subgeneric rank were evidently artificial: for example, in his subgenera *Tribax* and *Cechenus* and the sections *Eucarabus* and especially *Trachycarabus*, he united heterogenous assemblages of species. The extent of species and their dismemberment into subspecies and nationes considered by this author also aroused serious objections in many cases. Moreover, his multi-step infraspecific classification is not in agreement with the International Code of Zoological Nomenclature. However, in spite of the disadvantages mentioned above, Breuning's monograph is untill now, the most important summary in which all species and subspecies of *Carabus* known at the beginning of the 1930's were included and keyed.

In his 'Faune de France', Jeannel (1941-1942) considered 41 species of *Carabus* (*s. lato*) living in that country. He subdivided them into 11 genera, following mainly the classification of Vacher de Lapouge; his concept of species was fairly well-grounded in most cases.

Several important papers for the non-European fauna were published later (Kryzhanovskij, 1953; Ishikawa, 1973, 1978, 1985; Lafer, 1989). Ishikawa used the structure of the endophallus, already described in pioneering contributions by Meurgues & Ledoux (1966) and Sturani (1967), as the basic diagnostic character for a new classification of *Carabus* (*s. lato*), dividing it into a large number of genera. Some of his propositions are now generally accepted, others remain disputable, for example the unification of the Caucasian *Lipaster* with the subgenus *Morphocarabus*.

Recently, Deuve (1991, 1994) proposed a new scheme of an infrageneric classification of *Carabus* (*s. lato*), which is in many aspects similar to the classification by Ishikawa but contains several new proposals. In the first group, *Eucarabus* was united within the subgenus *Carabus* with

◄ ***C. monilis*** Fabricius. The Netherlands. Photo by Th. Heijerman.

the *granulatus*-complex, the E. Asiatic spp. related to *C. yunnanus* and *C. vigil* and several species from North America and the Canary Islands. The subgenus was then added to the new group **Digitulati** together with the E. Asiatic subgenera *Ohomopterus*, *Isiocarabus* and the Mediterranean *Eurycarabus*. The second group, comprising *Morphocarabus* (including *Trachycarabus*), in combination with the W. Asiatic *Lipaster* and *Mimocarabus*, the Central Asiatic *Cryptocarabus*, *Ophiocarabus* and *Cyclocarabus*, was linked to the group **Lipastromorphi**. This classification, although based on the endophallic structures and other important features, is not always confirmed by the larval, molecular, and some adult characters. Deuve (1994) attributed the other subgenera to five main subdivisions: **Spinulati**, **Digitulati**, **Lipastromorphi**, **Archicarabomorphi**, and **Lobifera**. A quite different, but basically similar classification has been proposed more recently (Deuve, 1997). Deuve has also treated many species in an extremely broad sense (for example, such complicated superspecies-groups as *C. monilis*, *C. sibiricus*, *C. violaceus*, some *Procerus* etc.) and has recently (1994) united quite distinct subgenera, such as *Chaetocarabus* and *Heterocarabus*. Although some opinions by Deuve can be disputed, his work is an excellent base for any future work on this genus.

It is important to mention the two detailed and well-considered checklists by Březina (1994, 1999), based on the works of Deuve (1994) and Imura (1996) respectively, and thus rather different in supraspecific classification. Although some opinions of this author are not accepted here, such as the conservation of monotypic subgenera for *C. alysidotus*, *C. glabratus* etc., it is a reliable base for all *Carabus* workers, particularly with respect to geographical information (including type-localities) on several taxa. The work of Březina (1999) was taken as a basis for the checklist in the present work. It was therefore modified according to the system that was made by Casale & Kryzkanowskij (see: Turin *et al.*, 1993) providing in the first place a nomenclatorial outlook to other systems. A comprehensive, but carefully elaborated and very useful list of the carabids of the world, including *Carabus* was published by Lorenz (1998). For the Russian Plain and the eastern Palearctic territories, the checklist for Russia and adjacent countries (former Soviet Union: Kryzhanovskij *et al.*, 1995) is indispensable.

Many important contributions to the phylogeny of *Carabus*, nowadays, come from molecular reseach (see Prüser, 1996 and Chapter 7)

Certain important papers have been published on the European *Carabus*, among them studies on the species of the Iberian Peninsula (Jeanne, 1965, 1972, 1974 etc.), Italy (Casale *et al.*, 1982), concerning the infraspecific taxonomy of some polytypical complexes, i.e. *C. creutzeri* F. (Mandl, 1967), *C. violaceus* and related species (Cleu, 1965, 1966, 1969; Mandl, 1960, 1962, 1985 and others). Sturani (1962) published important papers on the biology and life cycles of *Carabus*, mainly concerning European species. Cavazzuti (1989) published an interesting monograph of the subgenus *Procerus* (treated as a distinct genus).

The larvae of *Carabus* were intensively studied, among others, by Vacher de Lapouge (1905, 1908, 1929-32), Sturani (1947, 1962, 1963), Raynaud (1976) and Hůrka (1971b), who thoroughly described the major part of Central-European species, and many others. Recently, important keys were published by Arndt (1985, 1991a). Makarov is working on European and non-European groups and he has used characters of chaetotaxy for constructing the scheme of interrelations between the most significant subgenera (Turin *et al.*, 1993).

We conclude that *Carabus* should be considered a single large monophyletic genus with a very complex infrageneric structure including several large groups of suprasubgeneric rank and a great number of subgenera. Some of the subgenera are mono- or oligotypic, but many others include several subordinate species-group complexes or superspecies.

In view of the preceding arguments, a more or less traditional and rather pragmatic classification for the European subgenera will be presented here, listed approximately in a way that follows the important existing monographs.

The classification of European *Carabus* is generally well described and accepted with the majority of the subgenera included in the keys forming fairly natural groups. However, some groups need some further explanation:

1) The subgenera *Morphocarabus* Géhin, 1885, *Trachycarabus* Géhin, 1885 and *Eucarabus* Géhin, 1885, are closely related, and have therefore (partly) been combined in one key.

2) The old subgenus *Carabus* (sensu Breuning) is subdivided into three different subgenera:

a) *Carabus* (*s.str.*) for *C. granulatus* L. and *C. menetriesi* Humm.

b) *Limnocarabus* Géhin, 1876 for *C. clatratus* L.

c) *Tachypus* Weber, 1801 (= *Autocarabus* Seidlitz, 1887), which is rather homogenous, including *C. auratus* L., *C. cancellatus* Ill., *C. vagans* Ol. and excluding *C. obsoletus* Sturm.

3) Subgenera *Hygrocarabus* C. G. Thomson, 1875, *Ctenocarabus* C. G. Thomson, 1875 and *Rhabdotocarabus* Seidlitz, 1887 seem to be related and possibly deserve to be united (see Deuve, 1994; but also see Chapter 7, *Phylogeny*).

4) The same holds for *Chrysocarabus* and *Chrysotribax* (united in the present work), and for *Megodontus* and *Pachycranion* (see Deuve, 1994).

These and other taxonomic points will be discussed in the treatment of the subgenera.

The taxonomy in the species-group level is not clear for many European groups, especially in the polytypic complexes of *Morphocarabus* (*C. monilis* F. and related species, *C. comptus* Dej.) and in the superspecies *C. (Megodontus) violaceus* L. The status of 'good' taxa (i.e. valid, biological species, reproductively isolated from the relatives), for example in *Chrysocarabus*, *Orinocarabus*, *Chaetocarabus*, *Procerus* etc. needs to be ascertained.

The infraspecific taxonomic relationships of many European species are often complex. An almost countless number of subspecies, nationes, morphae, varieties and other infraspecific taxa have been described within *C. cancellatus*, *C. auratus*, *C. scheidleri*, *C. arvensis*, *C. auronitens* and many other widely distributed species. Some subjectivity is almost inevitable during the first stages of studies concerning such polytypical species, but many have been thoroughly revised since Breuning (1932-1937). For instance, the investigations of Bonadona (1973) and Casale & Cavazzuti (1975) may be mentioned. These authors revised *C. (Chrysocarabus) solieri* Dej., and arranged two dozens of available subspecific names into four to five natural and reliably distinguishable subspecies, which from a genetical point of view, could be reduced further to two or three (Rasplus *et al.*, 2000).

Much work still has to be done to improve our knowledge, especially for variable species with a large distribution. A combination of faunistic, ecological and genetic studies, covering different parts of the species ranges is needed to accomplish this.

Regional faunistic studies are necessary to improve our knowledge about distributions, especially for the countries of Southeastern and Eastern Europe. In contrast, the British Isles, Fennoscandia, Belgium, the Netherlands, most of Germany, Austria, Switzerland, France, Italy and the Iberian Peninsula have been extremely well investigated.

The numbering of subgenera and species follows the European checklist of *Carabus* by Turin *et al.* (1993). If modifications to this list have been made, this has been discussed in the appropriate couplet. The enumeration of taxa in this paper has been limited to the subspecific level and corresponds with the Chapters 2 (*Checklist*) and 5 (*Species accounts*). Nevertheless, the most studied subspecies and also some other infraspecific names, have been mentioned and discussed, to allow an optimal connection with other works on *Carabus*. Moreover, subspecies provide important information about (geographic) variation, which often is also indispensable for proper identification.

3.2. KEY TO THE SUBGENERA

Morphological characters, diagnostic features and limits of the genus, have been extensively illustrated by Deuve (1994).

The present key is a pragmatic one, written only for identification of European species.

The characters used are, for the most part, based on evident and easily accesible features. Although some subgenera have been combined for practical reasons, this key comprises 31 subgenera as described in the checklist by Turin *et al.* (1993), and their numbering follows that checklist as much as possible. Modifications, mainly resulting from the latest developments in *Carabus* taxonomy, have been worked out in the present checklist (Chapter 2) and the key below. Also the important checklists by Deuve (1994) and Březina (1994, 1999) are taken into account.

1 (54). Pronotum with marginal setiferous pores, sometimes medial pores missing but basal ones always present.
2 (29). Mandibles short and wide, their inner edge almost straight but strongly curved inward before apex (Fig. 3.1a). The 2nd antennal segment of larvae glabrous, their nasale usually with 2-7 denticles, the lateral denticles often distinct – ('Carabi brevimandibulares').
3 (4). Apex of protibiae protruding externally in finger-like process (Fig. 3.1c). 3rd antennal segment depressed and carinate (Fig. 3.1e) .... 07. ***Hemicarabus*** (p. 203).
4 (3). Protibiae without external process at apex (Fig. 3.1d). 3rd antennal segment not depressed.
5 (10). Apical segment of palpi distinctly dilated (Fig. 3.1g). Tooth of mentum very long, with distinct margin.
6 (7). Penultimate segment of labial palpi with 3 or more setae. Apical segment of palpi not strongly widened, triangular in male .... 10. ***Mesocarabus*** (p. 207).

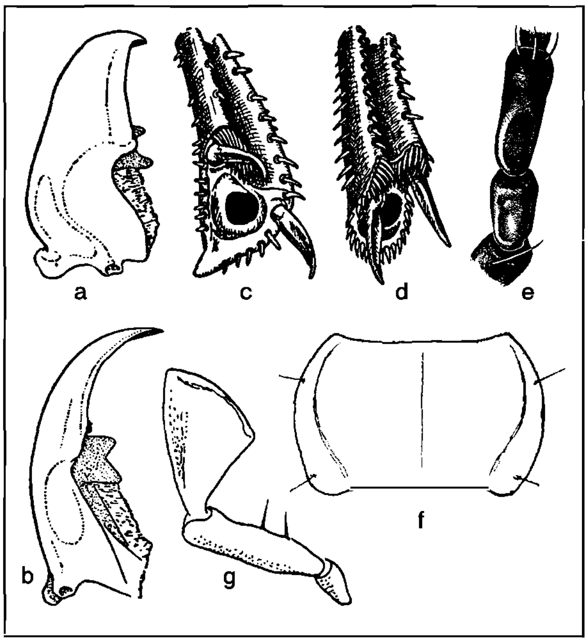


Fig. 3.1. Details of genus *Carabus* (a-e – after Sturani, 1962). a – Mandible of 'Carabi brevimandibulari'; b – The same of 'Carabi longimandibulari'; c – *C. (Hemicarabus) nitens*, apex of protibia; d – *C. (Carabus) cancellatus*, apex of protibia; e – *C. (H.) nitens*, 1th-3rd antennal segments; g – *C. (Tomocarabus) convexus*, labial palpus; f – *C. (Eurycarabus) faminii*, pronotum.

7 (6). Penultimate segment of labial palpi with 2, rarely with 3 setae. Apical segment of palpi strongly widened, more in male.

8 (9). Pronotum transverse, its sides widened and bent upwards. (Fig. 3.1f), submentum transversely thickened. Aedeagus characterised by a peculiar morphology, sinuous and widened before the apex (in Europe, only in Sardinia and Sicily) .... **14. *Eurycarabus*** (p. 233).

9 (8). Pronotum less transverse, its sides narrow, with narrow margin. Elytral sculpture heptaploid or minutely granulate. Submentum not thickened, except in *C. marginalis*, aedeagus regularly arcuate, of normal shape .... **13. *Tomocarabus*** (p. 228).

10 (5) Apical segment of palpi feebly dilated. Tooth of mentum without a clear margin.

11 (12) Submentum transversely thickened. Elytral sculpture triploid or pentaploid. Body rather short and wide .... **06. *Archicarabus*** (p. 196).

12 (11). Submentum not transversely thickened.

13 (20). Elytra with distinct, usually deep preapical emargination (stronger in females); epipleurae interrupted before apex. Elytral sculpture triploid or with primary keels only.

14 (17). Pronotum with 2 marginal setae at each side.

15 (16). Primary intervals interrupted by large and usually metallic foveae; secondary ones keel-shaped .... **01. *Limnocarabus*** (p. 155).

16 (15). Primary intervals keel-shaped, wide, more or less depressed, the others reduced .... **05 *Tachypus*** (part.) (= *Autocarabus* auct.) (p. 191).

17 (14). Pronotum with 3-6 marginal setae at each side.

18 (19). Metepisterna as long as wide. Elytra rather convex .... **05. *Tachypus*** (part.) (= *Autocarabus* auct.) (p. 191).

19 (18). Metepisterna much longer than wide. Elytra depressed .... **03. *Carabus*** (*s.str.*) (p. 178).

20 (13). Elytra not or feebly emarginate near apex, epipleurae not interrupted. Elytral sculpture variable.

21 (22). Elytra with sharp primary keels, the other intervals form very fine granulation .... **09. *Aulonocarabus*** (p. 207).

22 (21). Elytra with triploid or heptaploid, rarely pentaploid sculpture or confuse, consisting not only of primary keels.

23 (24). Elytra with triploid, or confuse, grater-like sculpture, reduced to rows of granulate series .... **02$^{\mathrm{I}}$. *Morphocarabus*** (part.) + **02$^{\mathrm{II}}$. *Trachycarabus*** + **04. *Eucarabus*** (p. 157).

24 (23). Elytral sculpture heptaploid or pentaploid (tripoloid in *C. latreilleanus* only).

25 (26). Sides of pronotum widely emarginate and more or less turned upwards, especially in the basal part. Abdominal sterna with, or without (in Iberian species), ventral furrows .... **12. *Oreocarabus*** (p. 221).

26 (25). Sides of pronotum narrowly margined over the whole length. Abdominal sterna normally without ventral furrows

27 (28). Elytra with regular triploid or heptaploid sculpture (less regular only in *carinthiacus*). Legs rather long. – Species from the mountains of C. Europe (Alps, Carpathians) .... **11. *Orinocarabus*** (p. 212).

28 (27). Elytra with confused heptaploid or pentaploid sculpture. Legs short. – Species of the taiga and tundra zones of N.E. Europe and Siberia (also for *C. truncaticollis*) .... **08. *Diocarabus*** (p. 205).

29 (2). Mandibles long and usually narrow, sickle-shaped, curved along whole inner edge (Fig. 3.1b), rarely feebly curved, but in that case head dilated with small labrum which is narrower than clypeus at base. 2nd antennal segment of larvae with 2-7 setae in apical part; their nasale usually with 1-2 medial denticles and 2 smaller lateral ones – ('Carabi longimandibulares').

30 (31). Labrum small, partly covered by the clypeus and narrower than the clypeus at base. Macrocephalic species with the head strongly thickened, mandibles stout, feebly curved .... **25. *Iniopachys*** (p. 264).

31 (30). Labrum normal, wider than base of clypeus.

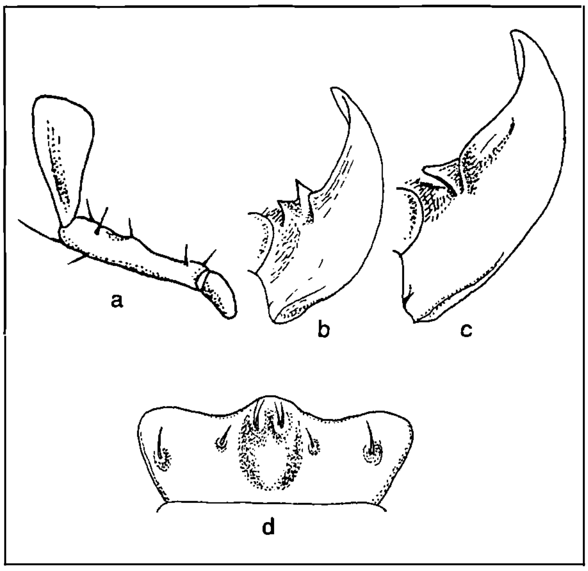


Fig. 3.2. Details of genus *Carabus*.
a – *C. (Heterocarabus) marietti*, labial palpus; b – *C. (Megodontus) germarii*, right mandible; c – *C. (Pachycranion) schoenherri*, right mandible; d – *C. (Procrustes) coriaceus*, labrum.

32 (35). The 4th antennal segment pubescent in distal part.

33 (34). Subapical segment of labial palpi with 4-7 setae, the apical seta horizontally inserted near apex (Fig. 3.2a). Elytral intervals homodynamous, the primary intervals with small, metallic punctures ... . **21. *Heterocarabus*** (p. 250).

34 (33). Subapical segment of labial palpi with 2-3 setae, without horizontal seta at apex. Elytral sculpture (in single European species) consisting of rows of primary tubercles, distinct secondary keels, and more or less reduced tertiary intervals .... **22. *Sphodristrocarabus*** (p. 251).

35 (32). The 3th antennal segment glabrous except few tactile distal setae.

36 (47). Submentum with setiferous pores.

37 (44). Penultimate segment of labial palpi with 2 setae. Elytra not depressed.

38 (39). The apical segments of all palpi strongly dilated, in males axe-shaped (trapezoid). Dorsal surface brilliantly metallic. Elytra with larger primary foveae .... **26 (+27). *Chrysocarabus*** (part.) (p. 265).

39 (38). The apical segments of all palpi slightly triangularly dilated. Upper side duller (except in *Chrysocarabus*, but in this case the primary foveae are very small).

40 (43). Humeral margin of elytra distinctly serrated. Abdominal sterna with setiferous pores.

41 (42). Ventral furrows sharp and unbroken. Primary intervals keel-shaped. Legs mostly reddish-brown .... **16. *Ctenocarabus*** (p. 238).

42 (41). Ventral furrows at most slightly marked laterally. Primary intervals interrupted by large concolorous foveae. Legs black .... **18. *Hygrocarabus*** (p. 239).

43 (40). Humeral margin of elytra smooth. Abdominal sterna without pores. Primary intervals keel-shaped .... **17. *Rhabdotocarabus*** (p. 238).

44 (37). Penultimate segment of labial palpi multisetose. Elytra more or less depressed.

45 (46). The apical segments of all palpi in both sexes strongly dilated, in males axe-shaped (trapezoid). Penultimate segment of maxillary palps with some apical setae. Elytral intervals more or less convex, often repeatedly interrupted, primary foveae small .... **19. *Chaetocarabus*** (p. 241).

46 (45). The apical segments of palpi in both sexes slightly triangularly dilated; penultimate segment of maxillary palpi without apical setae. Elytral intervals flattened, the primary ones with large, normally metallic foveae .... **20. *Platycarabus*** (p. 245).

47 (36). Submentum without setiferous pores.

48 (51). Labial palpi multisetose.

49 (50). Head not thickened, antennae relatively long, mandibles strongly curved, basal tooth of right mandible bidentate (Fig. 3.2b) .... **23. *Megodontus*** (p. 251).

50 (49). Head more or less thickened, antennae rather short, mandibles feebly curved, basal tooth of right mandible unidentate or blunt (Fig. 3.2c) .. .. **24. *Pachycranion*** (p. 262).

51 (48). Labial palpi bisetose.

52 (53). Abdominal sterna with setiferous pores. Primary intervals keel-shaped or all elytral surface uniformly granulated or smooth .... **26. *Chrysocarabus*** (part.) (p. 265).

53 (52). Abdominal setiferous pores absent. Primary intervals of elytra interrupted, the secondary ones keel-shaped .... **28. *Macrothorax*** (part., see also couplet 58) (p. 274).

54 (1). Pronotum without marginal setiferous pores.

55 (56). Mandibles short and wide (see couplet 2: brevimandibulares). Body stout, convex, black .... **15. *Pachystus*** (p. 234).

56 (55). Mandibles long, curved – (see couplet 31: longimandibulares).

57 (62). Labrum normal, bilobed. Dorsal surface or variable colour.

58 (59). Elytra with regular sculpture: primary intervals interrupted and forming rows of tubercles, the secondary ones keel-shaped .... **28. *Macrothorax*** (part.) (p. 274).

59 (58). Elytra without regular intervals.

60 (61). Elytra almost smooth, only minutely granulated. Protarsi in male with 3 dilated segments, with ventral pad of adhesive setae .... **29. *Lamprostus*** (p. 276).

61 (60). Elytra with rough tubercles not forming regular rows. Protarsi in male not dilated, without ventral pad of adhesive setae .... **31. *Procerus*** (p. 280).

62 (57). Labrum trilobate (Fig. 3.2d). Dorsal surface dull black .... **30. *Procrustes*** (p. 277).

01. Subgenus Limnocarabus Géhin, 1876

Type species *C. clatratus* Linnaeus, 1761.

Relatively large species, slightly depressed. Pronotum transverse subquadrangular, sides feebly sinuate before hind angles, with deep basal foveae and two marginal setae on each side. Elytra wide with crenulated humeral edge and strong preapical emargination; sculpture triploid, primary intervals forming rows of links interrupted by rather large usually metallic foveae, secondary intervals more or less keel-shaped, tertiary intervals usually minutely granulated, sometimes reduced. Aedeagus voluminous with tooth-shaped sclerite in the endophallus (this structure brings *Limnocarabus* together with E. Asiatic subgenus *Apotomopterus* which is sharply distinguished by other characters).

The subgenus includes one species with transpalaearctic range, but some authors regard *maaki* Morawitz, 1862, from the Far East of Russia, N. China, Korea and N. Japan as a distinct species.

1 (1). The only European species. Dorsally more or less shiny, dark-bronze to black with greenish of bronze lustre, primary foveae coppery, brassy, or green. 25-36 mm (in E. Asia to 38 mm). Wings dimorphic, some specimens are able to fly. – Temperate zone of Eurasia. Strongly hygrophilous, lives along shores of rivers and lakes (E. Europe), but mainly in marshes and bogs; found also in salt marshes on clayish soil (Netherlands, S. Europe and Kazakhstan), sometimes at high altitude (up to 2000 m in E.Anatolia). .... **01.001. *C. (Limnocarabus) clatratus*** Linnaeus, 1761 (p. 155).

Divided into several subspecies:

a) subsp. *clatratus* Linnaeus, 1761 – Body medium sized (26-32 mm), elytra moderately convex, primary foveae large and numerous, usually coppery, links of keels between them rather short and flattened, dorsal side moderately shiny, bronze- or greenish-black. – Europe except N. and S. parts: Belgium, the Netherlands, Germany, N. Switzerland, Czechia, Poland, Lithuania, Byelorussia, N. Ukraine, W. Russia: provinces of Smolensk, Bryansk, Kaluga, Moscow, Riasan, N. and E. Russia to C. Siberia and Kazakhstan.

b) subsp. *jansoni* Kraatz, 1890 – Small (22-27 mm, rarely to 20 mm), more shiny, elytra relatively convex, sculpture and colour as in the nominate subspecies, primary foveae usually larger and brighter; 1st segment of antenna and femora rarely red. Body stout. Margins of pronotum markedly rounded, elytra short. Dorsal surface mostly metallic greenish. – British Isles (see Kryzhanovskij *et al.*, 1995, p. 42, note 29).

c) subsp. *auraniensis* J. Muller, 1902 (= *epirensis* Purkyně, 1928) – Large (28-36 mm, rarely to 23 mm), flattened; hind angles of pronotum wide, rounded; primary foveae small, secondary keels stronger, tertiary ones forming small granules. Colour dark, mostly black. Apical lobe of aedeagus acute. – S. Austria, Hungary, S. Slovakia, Balkan states (in Greece only in N. parts), Moldova, S. Ukraine. In the east of the range there is a transition zone to *stygius*, and in the west (Adriatic coast of Italy) to subsp. *antonellii*.

d) subsp. *antonellii* Luigioni, 1921 – Related to *auraniensis*, but elytra more convex and shorter, the primary metallic foveae larger and the sides of pronotum more sinuous, hind angles forming longer lobes. Apical lobe of aedeagus wider and curved beneath. – N. and C. Italy from Piedmont to Lazio. The specimens from the Adriatic coast (Venezia, Ravenna), attributed normally to *antonellii* (Casale *et al.*, 1982), are transitional to *auraniensis*.

e) subsp. *arelatensis* Vacher de Lapouge, 1903 – Similar to *antonellii*, but elytra comparatively shorter, primary foveae often not metallic. 25-31 mm. – S. France (regions of Narbonne, Montpellier, Camargue).

(Probably not European: subsp. *stygius* Ganglbauer, 1890) – Large (30-36 mm) and dark, elytra more parallel-sided than in other subspecies, primary foveae small and shallow, secondary keels relatively less convex, the tertiary ones form distinct rows of tubercles (especially in basal part). – Form of Transcaucasus and Asia Minor, only marginally a European subspecies. Russia: Rostov province, Kalmykia; in E. Caucasus transitional to ssp. *aurianensis* and in N. Caucasus to ssp. *clatratus*. Mostly in slightly salty soils).

02^{I}. Subgenus Morphocarabus Géhin, 1885

Type species *C. monilis* Fabricius, 1792

+

02^{II}. Subgenus Trachycarabus Géhin, 1885

Type species *C. scabriusculus*, Olivier, 1795

+

04. Subgenus Eucarabus Géhin, 1885

Type species *C. ulrichii* Germar, 1824

This complex of 3 separate subgenera is the largest among the European *Carabus*. In all, the species are rather variable in structure and appearance. Many authors have subdivided them into two subgenera: *Morphocarabus* Géhin, 1885: XVIII (type species: *C. monilis* F.) and *Eucarabus* Géhin, 1885: XXI (type species: *C. ulrichii* Germar), principally on the basis of endophallic structures and larval characters. For several reasons we have re-established the subgenus *Trachycarabus* Géhin, 1885. However, the taxa within this complex are joined by a series of intermediate forms and it is difficult to separate them in a simple key. So here they are dealt with together, with the proper subgenus name given for each species. Furthermore, *Trachycarabus* has been demonstrated to be a polyphyletic group by Ishikawa (1978), and it is often treated as a synonym of *Morphocarabus* (Deuve, 1994). Březina (1994, 1999), however, retained *Trachycarabus* as a distinct subgenus for *C. besseri*, *C. coriaceipennis*, *C. estreicheri*, *C. latreillei* (*s. lato*), *C. mandibularis*, *C. planarius*, *C. planus*, *C. scabriusculus* and *C. sibiricus* (*s. lato*: including *bosphoranus*, *errans* and *haeres*).

These subgenera have been dealt with in one key for many reasons stemming from both practical and taxonomical points of view (see discussion below). *C. cristoforii* Spence has been included, although it is noted as belonging to **05. *Autocarabus*** in the checklist of Turin *et al.* (1993). The position of *C. cristoforii* in *Tachypus* (= *Autocarabus*) has been accepted by Březina (1994, 1999), although Zaballos & Jeanne (1994) have attributed it to *Tmesicarabus* Reitter, 1896.

Moreover, several other subgenera have been proposed: *Eutelocarabus* Géhin, 1885 (for *C. arvensis*), *Xystrocarabus* Reitter, 1896 (for *C. catenulatus* and *C. parreyssi*), *Loxocarabus* Reitter, 1896 (for *C. obsoletus*), *Apostocarabus* Reitter, 1896 (for *C. odoratus*), *Pancarabus* Reitter, 1886 (for *C. æruginosus*), *Basilicocarabus* Vacher de Lapouge, 1931 (for *C. regalis*), and several others. According to us, all these names are superfluous.

Deuve (1991) united *Eucarabus* (*ulrichii*, *arvensis*, *stscheglowi* etc.) with *Carabus* (*s.str.*) and placed it into his supra-subgeneric group 'Digitulati'. Makarov (in: Turin *et al.*, 1993) proposed to exclude *C. obsoletus* from *Morphocarabus* and unite it in *Autocarabus* with *C. cancellatus* and *C. auratus* on the basis of larval characters. Březina (1994) finally ascribed to *Eucarabus* the species: *C. arvensis*, *C. catenulatus*, *C. cumanus*, *C. deyrollei*, *C. italicus*, *C. obsoletus*, *C. parreyssii*, *C. stscheglowi*, and *C. ulrichii*. Zaballos & Jeanne (1994) listed *C. deyrollei* in *Eutelocarabus* Géhin, 1885.

Body moderately to strongly convex, never distinctly depressed or stretched. Mandibles short, antennae in males with middle segments swollen laterally at apex or simple. Submentum with setiferous pores, not transversely thickened, the labial palpi bi-, or very rarely trisetose. Pronotum usually with 3-5, more rarely with only 2 lateral setae. Elytra with or without very slight subapical excision, with triploid or confuse, grater-like sculpture; several supplementary intervals may be developed on the outher side of 3rd primary interval, sometimes 1-2 additional primary ones are included. Abdominal furrows absent or faint. Upper side often metallic or with metallic lustre. Many species, for example *C. arvensis*, *C. ulrichii*, *C. obsoletus*, and most members of *C. monilis*-complex, are extremely variable in colour: brassy, coppery-red, green, blue, violet or black with or without metallic tint; the margins often differ from the discs of pronotum and elytra; colour of head and pronotum sometimes strongly contrasting with that of the elytra.

1 (48). Pronotum mostly with 3-5 marginal setae on each side, rarely with only two setae, in which case the elytral intervals are convex and not forming grater-like granulation. Dorsal surface mostly metallic polychromous. (**Morphocarabus** Géhin + **Eucarabus** Géhin).

2 (43). Pronotum with 3 or more lateral setae.

3 (12). All elytral intervals more or less uniformly and densely transversely wrinkled.

4 (5). Hind angles of pronotum short, widely rounded, extending slightly beyond the basal side. Elytra slightly convex, with prominent shoulders. Middle antennal segments in male swollen laterally at apex. Colour extremely variable, almost always metallic. 13-25 mm (Aedeagus: Fig. 3.3a). – Distributed throughout N. and C. Europe and Siberia to Sakhalin, N. China and N. Japan. Mostly in open forests, in the S. in mountains. ....**04.001. *C. (Eucarabus) arvensis*** Herbst, 1784 (*arcensis* auct.) (see note in Chapter 5, p. 182).

A number of rather distinct subspecies, six of them in Europe.

a) subsp. *arvensis* Herbst, 1784 – Secondary keels of elytra less convex than the primary rows of tubercles; all intervals rather uniform in width and convexity, slightly to moderately transversely wrinkled. Microsculpture of elytra moderately strong, fairly shiny, colour variable. 16-23 mm (in the mountains of C. Europe to 14 mm). – Austria (except the Alps), Germany (except its S.W. parts), N. Czechia, Poland, Fennoscandia, Baltic States, N. and C. Russia. In the E. of Volga populations hind angles of pronotum with very short lobes (*baschkiricus* Breuning, 1932); they form the transition to the Siberian subsp. *conciliator* Fischer von Walheim, 1822.

b) subsp. *noricus* Sokolar, 1910 – Similar to preceding form, size small (13-17 mm), rather short and wide, sculpture rougher, colour duller. Populations inhabit Jura, N. and E. Alps to S.E. Austria and N.E. Italy, mountains of Czechia. Mostly above 1800 m.

c) subsp. *carpathus* Born, 1902 – Different from the nominate form by the strongly transversely wrinkled intervals, rather dull upper surface and smaller size (14-18 mm). – Carpathian Mts. of Slovakia, S. Poland, Romania, Ukraine; also in the lowlands of Ukraine to Kharkov province.

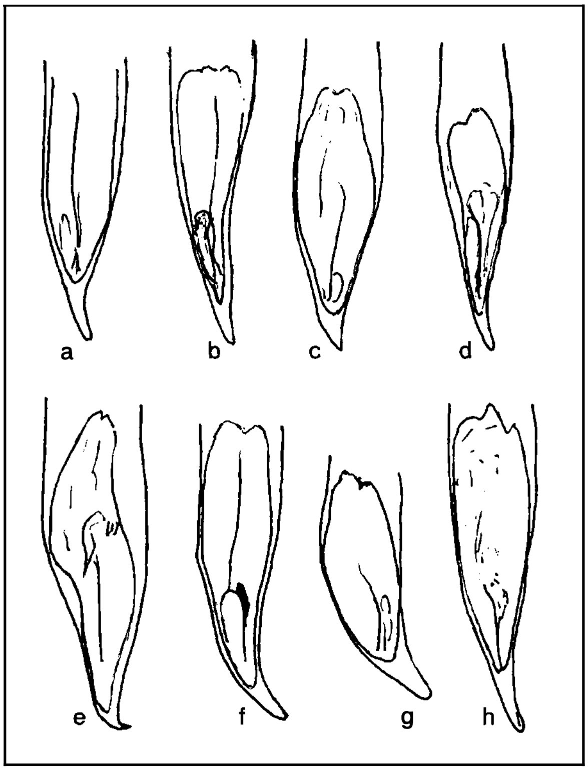


Fig. 3.3. Details of subgenus *Eucarabus* (aedeagus). a – *C. (E.) arvensis*; b – *C. (E.) deyrollei*; c – *C. (E.) parreyssii*; d – *C. (E.) stscheglowi*; e – *C. (E.) catenulatus*; f – *C. (E.) obsoletus*; g – *C. (E.) italicus*; h – *C. (E.) ulrichii*.

d) subsp. *venetianus* Bernau, 1914 – Similar to *carpathus* in the roughly sculptured dull elytra with short and wide primary tubercles, and in size (17-19 mm), but isolated geographically: S.E. Alps in N.E. Italy (Alpi and Prealpi Venete, Venezia Tridentina) and S.W. Slovenia.

e) subsp. *sylvaticus* Dejean, 1826 – All intervals only slightly wrinkled, secondary ones often smooth, keel-shaped, more convex than the primary rows of tubercles, upper surface with indistinct microsculpture, shiny. 17-25 mm. – British Isles, N. and E. France, Belgium, Netherlands, S.W. Germany, W. Switzerland. In the mountains of S.E. France, several isolated populations have been described as distinct subspecies (*jarrigei* Colas, 1971; *thebaudi* Colas, 1971). Quite distinct from Cévennes have been described as *costalis*.

5 (4). Hind angles of pronotum longer, lobe-shaped.

6 (7). Antennae and palpi very thin, with middle segments in male simple. Aedeagus strongly narrowed apically (Fig. 3.3b). Upper side shiny, colour variable. 15-20 mm – N. Portugal, N.W. Spain. .... **04.003b. *C. (Eucarabus) deyrollei*** Gory, 1839 (p. 186).

7 (6). Antennae and palpi of normal shape, middle segments of antennae in male swollen laterally at apex. Aedeagus moderately narrowed apically, its apex of various shape.

8 (9). General shape ovate, wide and stocky, pronotum strongly transverse (W/L more 1.6), its sides regularly rounded. Upper side slightly shiny. Aedeagus apically rounded (Fig. 3.3c). Colour variable, usually blue, greenish or violet. 18-32 mm. – N.W. part of Balkan Peninsula: Croatia, Bosnia, Hercegovina. .... **04.006. *C. (Eucarabus) parreyssii*** Palliardi,1825 (p. 188).

Two rather distinct subspecies:

a) subsp. *parreyssii* Palliardi, 1825 (= *gattereri* Géhin, 1882) – Smaller (18-26 mm) and very wide. Colour more variable. – Croatia, Bosnia, N. Hercegovina, E-Serbia: see (ssp.) *tippmannianus* in the *Checklist*.

b) subsp. *plassensis* Born, 1907 – Larger (25-32 mm), relatively elongate. Colour mostly dark blue or purplish blue, other varieties are fairly rare. – Bosnia: Bihac, Drenovac, Prenj Planina; Hercegovina: Plasa, vicinities of Mostar.

9 (8). Habitus elongate-ovate, pronotum moderately transverse (W/L= 1.4-1.5). Aedeagus of other form (Fig. 3.3d,e).

10(11). Antennae relatively short, just reaching the base of the pronotum. Smaller: 15-22 mm. Colour variable, margins usually brighter, contrasting with the rest of upper side. Apex of aedeagus narrow, acutely pointed (Fig. 3.3d). – N.E. Ukraine, the foothills of Crimea, E. Russia, S.W. Siberia. The S. part of forest zone and the forest-steppe, mostly in deciduous and mixed forests. .... **04.007. *C. (Eucarabus) stscheglowi*** Mannerheim, 1827 (p. 189).

11 (10). Antennae of normal length, reaching the basal quarter of the elytra, 5-8th segments in male swollen laterally at apex. Larger: 22-35 mm, usually more than 28 mm. Moderately shiny above, usually blue, violet or bluish-black, sometimes cupreous or green, margins violet, purple, reddish-cupreous or green. Aedeagus wide, hooked at apex (Fig. 3.3e). – N.E. Italy, S.E. Austria, N.W. part of Balkan Peninsula. In the forests from lowland to subalpine zone. .... **04.002. *C. (Eucarabus) catenulatus*** Scopoli, 1763 (p. 185). (= *catenatus* Panzer, 1805).

Two subspecies:

a) subsp. *catenulatus* Scopoli, 1763 – Elytra moderately wide, convex, their intervals distinctly transversely wrinkled. 28-34 mm (subalpine forms up to 22 mm, frequently cupreous-green: *rattii* Mandl). – N.C. to N.E. Italy (to the W. to the Como lake), S. Switzerland (Tessin), Slovenia, Croatia (except its Adriatic part), Bosnia, Hercegovina.

b) subsp. *fontanellae* Reitter, 1896 – Elytra wider, rather flattened, their intervals feebly wrinkled, slightly distinct from the typical form. 30-35 mm. – Croatia: Mts. Velebit, Dalmatian shore and its islands.

12 (3). All elytral intervals not transversely wrinkled, at most slightly granulate; if tertiary intervals wrinkled, then the secondary ones smooth and convex.

13 (14). Hind angles of pronotum forming rather long, acutely pointed lobes, strongly bent downwards. Elytral intervals almost smooth, flat or slightly convex, primary foveae usually small and shallow. Colour extremely variable: bluish-black, blue, golden-green or coppery-red, dull or shiny; pronotum and elytra sometimes of different colours. Aedeagus (Fig. 3.3f) 17-30 mm. – Carpathians and adjacent mountain groups from Moravia and Tatra to N. Serbia, from foothills and valleys to alpine zone, especially in forests. .... **04.005. *C. (Eucarabus) obsoletus*** Sturm, 1815 (p. 187).

Several subspecies have been described, although not recognised by some authors:

a) subsp. *obsoletus* Sturm, 1815 – Elongate-ovate; pronotum with longer and acute lobes of hind angles. Elytral intervals flat or scarcely convex, primary foveae rather indistinct; the external space of the 3rd primary interval irregularly granulated. 22-30 mm. – Mountains of Moravia, Tatra, Beskides, N. Carpathians from Slovakia to Bukovina and N. Moldova.

b) subsp. *uhligi* Vacher de Lapouge, 1908 (= *mallaszianus* Breuning, 1932) – Similar to preceding, but much smaller (19-23 mm), elytra somewhat wider and more convex. Colour black, purplish-blue or green. – E. Carpathians: Ceahleu, Caliman, Rareul, subalpine and alpine zones.

c) subsp. *prunneri* Mallasz, 1901 – Similar to nominate form, but hind angles of pronotum wider and 1-2 intervals visible on the outside of 3rd primary interval; primary foveae shallow but distinct. Upper side mostly green, coppery-red or two-coloured. 24-28 mm. – Romania: N.E. Transylvania and N. Moldova.

d) subsp. *fossulifer* Fleischer, 1893 (= *nagyagensis* Seidl.) – Body rather narrow, primary intervals interrupted by large shallow foveae, secondary ones faintly convex. 21-26 mm – Romania: W. Transylvania: Cluj, Aiud, Hunedoara, Bihar Mts.

e) subsp. *carpathicus* Palliardi, 1825 – Hind angles of pronotum rather short. Elytra relatively shorter and more rounded on sides, all intervals distinctly convex, 2-3 intervals are visible on the outside of the 3rd primary one, primary foveae moderately large. 17-27 mm. – Romania: S. Transylvania; Serbia: Vojvodina (Banat). This form has been described from larger individuals from the lower mountain zone; small specimens (17-20 mm) from the subalpine zone of Vojvodina are named *euchromus* Palliardi, 1825.

14 (13). Hind angles of pronotum slightly protruding behind its base, or longer but rounded at apex and not bent downwards.

15 (18). Base of pronotum almost straight, hind angles slightly surpassing the level of its base.

16 (17). Sides of pronotum narrowly margined, not bent upwards. General shape elongated, elytral intervals uniformly convex, all interrupted usually in the rows of more or less long links. Colour variable, in the nominate subspecies usually black or brownish-violet with margins of pronotum and elytra and primary foveae shiny: green, golden, coppery-red. Femora sometimes red. 20-30 mm (in Europe less than 26 mm). – Polar Ural; widely distributed through Siberia to the Pacific and N. Sakhalin, N. Mongolia, N. China, and N. Korea. Several subspecies, mainly in E. Asia. European individuals belong to the nominate form, or to the recently described subsp. *dshvangi* Menshikov & Gorbunov, 1997 .... **02.011. *C. (Morphocarabus) hummeli*** Fischer von Waldheim, 1823 (p. 166).

17 (16). Sides of pronotum more widely margined and feebly bent upwards. Elytra convex, their sculpture similar to that of the preceding species. Upper side shiny, coppery-brown, reddish-cupreous, brownish-violet or dark-blue, margins often another colour, legs black with reddish-brown tibiae; antennae also reddish-brown. 17-23 mm. – E. Russia, W. and C. Siberia to Baikal and Lena, mostly in forests. .... **02.010. *C. (Morphocarabus) henningi*** Fischer von Waldheim, 1817 (p. 165).

Three subspecies in Europe, one of them described recently.

a) subsp. *henningi* Fischer von Waldheim, 1817 – 17-22 mm. E. European Russia, Urals.

b) subsp. *oviformis* Beheim & Breuning, 1943 – Polar Ural, Vorkuta. Tooth in mentum shorter of same length as the lateral lobes. Elytral intervals interrupted into short links.

c) subsp. *peczoricus* Obydov, 2000 – Republic Komi, Kosiyu River mouth (Pechora Rivers basin). Differing from *oviformis* by tooth in mentum longer than the leteral lobes. Elytral sculpture smoother, secondary and tertiairy intervals integrated or interrupted into long links. Apical lamella of aedeagus longer and narrower.

18 (15). Hind angles of pronotum forming distinct rounded lobes.

19 (24). Pronotum with hind angles moderately short, feebly turned behind its base.

20 (21). All elytral intervals more or less uniform, primary ones interrupted by scanty foveae, the others also interrupted and usually granulated, rarely smooth. Colour of upper surface variable, in Europe mostly brassy or bronzed-brown, rather shiny. 19-28 mm. – E. part or European Russia, Siberia in the E. to the Lena and Lake Baikal; N. Mongolia. Mostly in taiga zone in light forests, meadows and cultivated lands. .... **02.017. *C. (Morphocarabus) regalis*** Fischer von Waldheim, 1822 (p. 171).

21 (20). The tertiary intervals of elytra fainter than the primary and secondary ones; primary intervals forming distinct rows of tubercles.

22 (23). Small: 13-16 mm. Middle segments of antennae in male simple. Tertiary intervals reduced. Colour of upper side variable; 1st antennal segment and femora sometimes red. – Pyrenees of France and Spain; above 1800 m. Included in the subgenus *Autocarabus* by Deuve (1991, 1994) and Březina (1994, 1999). .... **04.003a. *C. (Eucarabus) cristoforii*** Spence, 1821 (p. 186).

23 (22). Larger: always more than 20 mm. Elytral intervals usually strongly convex, especially the secondary ones; primary intervals interrupted into

short tubercles; tertiary ones wrinkled and granulated, sometimes very reduced. Colour variable, antennae and legs always black. Aedeagus (Fig. 3.3h). 20-34 mm (usually more than 24 mm). – C. and S.E. Europe from S. Belgium, S.W. Germany and E. Austria to S. Poland, W. Ukraine, Serbia, Bulgaria. .... **04.008.** ***C. (Eucarabus) ulrichii*** Germar, 1824 (= *ullrichi* auct.) (p. 190).

Several infraspecific taxa; their discrimination is difficult in some cases and the infraspecific taxonomy needs further study. In the opinion of J. Tosevski (*in litt.*), *ulrichii ulrichii* (monochromatic) and *ulrichii fastuosus* (polychromatic) are the only valid subspecies.

a) subsp. *ulrichii* Germar, 1824 (incl. *sokolari* Born, 1904) – Body large (24-33 mm), stocky. Pronotum strongly transverse, almost twice as wide as long, hind angles short, widely rounded, side margin narrowly bent upwards. Tertiary intervals of elytra densely wrinkled. Colour bronzed-brown to reddish-cupreous, sometimes violet, blue or bluish-violet. – Not in Belgium and Luxemburg, although cited by Breuning, 1932; also not in the Netherlands, as cited in some works, e.g. Blumenthal in Freude *et al.*, 1976. S.W. Germany, S.E. Germany (Niederbayern, Sachsen), W., S. and E. Austria, Czechia, Slovakia, S. Poland, Romania (except in the S.), Moldova, W. Ukraine, Hungary, N.E. Croatia, N. Serbia.

b) subsp. *fastuosus* Palliardi, 1825 – Body narrower. Pronotum less than twice as wide as long, hind angles form longer lobes. Elytral sculpture similar to nominate form. Colour extremely variable, often blue-violet. 22-34 mm. – S.W. Romania (Banat). Specimens transitional to subsp. *arrogans* from S.W. Romania and Vojvodina with smooth elytral sculpture and very bright colour have been described as *superbus* Kraatz, 1878.

c) subsp. *rhilensis* Kraatz, 1876 (*stussineri* Géhin, 1885) – Related to the preceding subspecies, more shiny; elytral sculpture slightly less marked, tertiary intervals feebly wrinkled. Upper surface usually reddish-cupreous or green. 20-30 mm – S.E. Austria (Carinthia, transitional populations to subsp. *ulrichii* (*s.str.*)), Slovenia, Croatia, Bosnia. S. Serbia, Bulgaria.

d) subsp. *arrogans* Schaum, 1858 – Close to *fastuosus*. Strongly shiny above, tertiary intervals very reduced, primary and secondary slightly convex, the intervals not or very feebly wrinkled. Upper surface bicolorous: head and pronotum bright-green, elytra coppery- or golden-red. 27-34 mm – E. Serbia: Negotin, Majdanpek, Milanovac.

24 (19). Hind angles of pronotum lobate, rounded, strongly bent upwards behind its base.

25 (26). Basal foveae of pronotum deep, elongated. Elytral sculpture similar to that in *C. ulrichii*. Wings reduced, rather long and wide; rudiments extending to the 1/2 length of the elytra. Upper side usually cupreous, sometimes with greenish to reddish lustre, margins and primary foveae brighter, usually greenish. Aedeagus (Fig. 3.3g) 16-27 mm. – Italy, from S. Alps to Campania and Abruzzi, absent in the Adriatic shore of the peninsula; Switzerland: Tessin. – Mainly in wet meadows or edges of canals and ditches, sometimes in marshes, bushes and wet forests. In lowlands, rarer in foothills and mountains up to 1000-1500 m. .... **04.004.** ***C. (Eucarabus) italicus*** Dejean, 1826 (p. 187).

Two rather distinct subspecies:

a) subsp. *italicus* Dejean, 1826 – Smaller (16-22 mm), more narrow and elongated. Tertiary intervals less convex than the secondary ones. Upper side brighter, metallic. – N. Italy.

b) subsp. *rostagnoi* Luigioni, 1904 – Larger (21-27 mm), wider and more plump. Tertiary intervals almost as convex as the secondary ones. Upper side duller, brownish-bronzed to bronzed-black, sometimes with greenish lustre. – C. and partly S. Italy, Toscana to Campania, rather rare.

26 (25). Basal foveae of pronotum shallow, round. Elytral sculpture mostly more uniform. Wings strongly reduced. .... (**C. monilis-species-group**):

Probably the most intricate group among all European *Carabus*. Highly numerous, mostly allopatric races but here and there also with cases of sympatry. All of them are similar in the structure of the aedeagus. Forming transitional populations in some areas but sharply differing in others. Many authors regard all of them as subspecies of one or two species. We prefer to treat them as a complex of 9 (following) species, divided into 2 groups (or superspecies).

27 (38). Elytra with 3 primary intervals, rarely with 4, but in that case all intervals either strongly flattened or convex but strongly and densely interrupted; differing from similarly sculptured *rothi* by the long lobes of hind angles of pronotum, and shape of the aedeagus. .... (**monilis-subspecies-group**).

28 (29). Elytra with regular rows of primary tubercles or chains of longer links; the other intervals not or scarcely interrupted; sides of pronotum regularly rounded, slightly bent upwards. Aedeagus rather wide, its apical lobe relatively short, widely rounded apically (Fig. 3.4a). Colour variable. 17-32 mm. – W. and partly C. Europe: British Isles, France (except the region bordering the mediterranean), Belgium, Netherlands, S.W. Germany, Switzerland, Italy (only in N.W. Alps). Other records refer to introduced individuals. .... **02.014.** ***C. (Morphocarabus) monilis*** Fabricius, 1792 (p. 168).

Many infraspecific forms have been described, most of them from S. France (see Deuve, 1994). We recall here the main subspecies (see note in Chapter 2, *Checklist*, p. 19):

a) subsp. *monilis* Fabricius, 1792 – Body always elongated and convex. Intervals slightly convex, rather feebly interrupted. Variable in colour and size (22-30 mm, usually less than 27 mm). – The major part of Europe.

b) subsp. *subpyrenaeus* Vacher de Lapouge, 1925 – Rather small (22-26 mm), narrow, green, rarely greenish-bronzed form. – N. slope of C. Pyrenees. Smallest polychromous specimens from Pic de Nore (Aude) were described as *norensis* Pham, 1977.

c) subsp. *alticola* Bellier, 1880 – Body short, slightly convex, usually bright-green, rarely blue or bronzed. Blackish specimens from Mt. Ventoux have been described as *ventusicus* Bellon & Tarrier, 1972. – Isolated form, living in the Prealps of the Provence (France).

d) subsp. *saouensis* Mandl, 1967 – Body wide, slightly convex; intervals very flattened, homodynamous, colour highly polychromous. – France, Drôme.

e) subsp. *consitus* Panzer, 1809 – Large (27-32 mm), tertiary intervals usually more or less reduced. – Lowland of W. Switzerland and E. France.

f) subsp. *schartowi* Heer, 1837 (= *taunicus* Heyden, 1871) – Very small (17-22 mm), narrow and convex, tertiary intervals more or less reduced. – High mountains of E. France (Vosges, Jura, Alps of Dauphine), W. Switzerland, S.W. Germany (Taunus, Vogelsberg). According to Deuve (1994), *sabaudus* is a synonym of *schartowi*.

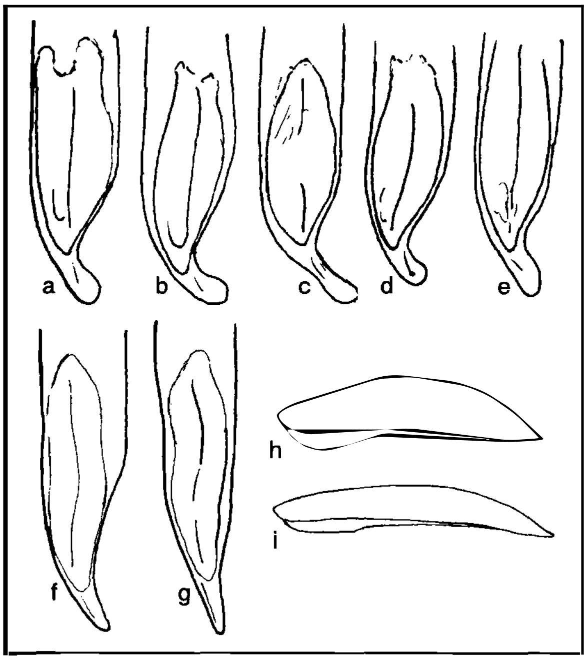


Fig. 3.4. Details of subgenus *Morphocarabus*.
a – *C. (M.) monilis*, aedeagus; b – *C. (M.) scheidleri*, aedeagus; **c** – *C. (M.) excellens*, aedeagus; d – *C. (M.) comptus*, aedeagus; **e** – *C. (M.) hampei*, aedeagus; f – *C. (M.) odoratus*, aedeagus; **g** – *C. (M.) karpinskii*, aedeagus; h – *C. (M.) odoratus*, side **view** of elytra; i – *C. (M.) karpinskii*, the same.

29 (28). Elytra only rarely with regular primary rows of tubercles or links, but in that case pronotum with the maximal width before the middle and its sides rather strongly bent upwards. Aedeagus narrower, its apical lobe longer (Fig. 3.4b).

30 (37). Elytral intervals moderately convex or flattened, all of them interrupted as a rule, or, more rarely, the primary ones only, but in that case sides of pronotum strongly bent upwards. Male antennae mostly laterally swollen at apex.

31 (36). Primary intervals not clearly different from the others.

32 (35). All intervals moderately to slightly convex or flattened.

33 (34). The 4th primary interval not developed, intervals moderately convex. Colour extremely variable, more often bluish-violet to greenish-black. 25-30 mm (rarely to 35 mm). – S. Germany (E. Bavaria), E. Austria, Czechia, W. Slovakia, S.W. Poland, W. Hungary. .... **02.021a. *C. (Morphocarabus) scheidleri*** Panzer, 1799 (p. 175).

Some subspecies:

a) subsp. *scheidleri* Panzer, 1799 – Body narrow and convex, intervals slightly convex, more feebly interrupted. Length 25-35 mm (usually less than 30 mm). Antennae of males distinctly laterally swollen at apex. – E. Bavaria, Czechia (incl. Moravia and Silesia), S. Poland, Austria (except true montane regions), W. Hungary. Mostly in open landscapes. Large (30-35 mm) dull-violet individuals occur in the forests of E. Austria (*floriani* Penecke, 1905).

b) subsp. *preysleri* Duftschmid, 1812 – Differs from *scheidleri* in the flattened elytral intervals. Antennal segments slightly swollen laterally at apex. – N.E. Austria. Probably, not subspecifically distinct from *scheidleri scheidleri*. Shorter and less convex form found in Slovakia and N. Hungary and described as *pseudopreyssleri* Breuning, 1932.

c) subsp. *helleri* Ganglbauer, 1892 – Differs from *scheidleri* (*s.str.*) in the narrower pronotum, shorter elytra and distinctly punctate elytral striae; elytral intervals moderately convex, often granulated or punctate. Colour variable. – Slovakia: Bratislava. Nitra, Trenczen, Moravia, part of Bohemia, N. Hungary, ?W. Ukraine.

d) subsp. *styriacus* Kraatz, 1887 (= *pannonicus* Csiki, 1906) – Similar to *scheidleri*, but smaller (25-30 mm), pronotum wide, transverse, its sides evenly rounded. Elytral intervals moderately convex, striae distinctly punctured. Colour variable. – S.E. Austria: Styria; N. Slovenia, W. Hungary.

34 (33). The 4th primary interval distinctly developed, intervals flattened to feebly convex. Antennae of males not laterally swollen at apex. Colour variable, usually rather dark: bluish-black, dark-blue, purplish-black or black, sometimes brassy. 26-32 mm. – The area of distribution stretches along N. Carpathians: E. Slovakia, W. Ukraine (provinces of Lviv, Ivano-Frankovsk, Uzhgorod, Tshernovtsy), northernmost Romania. Mostly in lowlands and foothills. – Individuals from the W. part of area (E. Slovakia, vicinity of Uzhgorod) were described as subsp. *ronayi* Csiki, 1906, differing by more convex elytral intervals. ....
.... **02.023a. *C. (Morphocarabus) zawadzkii*** Kraatz, 1854 (p. 177).

Note: 02.023b. *C. zherichini* Shilenkov, 1990 should be added here, because of a recent record within the European territory (see p. 178).

35 (32). Elytral intervals moderately to strongly converging, usually densely interrupted, sometimes the primary ones form series of links, the others almost unbroken. Colour very variable. Mostly large individuals (27-37 mm), smaller specimens (22-27 mm) can be found in the mountains of Bosnia and Hercegovina. – S.E. Austria, Slovenia, Croatia, W. and N. Serbia (including Vojvodina), Bosnia, Hercegovina, S.W. and C. Romania. Mostly in lowlands, here and there to subalpine zone. ....
.... **02.013. *C. (Morphocarabus) kollari*** Palliardi, 1825 (p. 167).

Several subspecies are known; infraspecific taxonomy very intricate:

a) subsp. *kollari* Palliardi, 1825 – Large and wide (32-37 mm). Usually 5-6, sometimes up to 8 external intervals on the 3rd primary ones, often present the 4th and sometimes the 5th primary intervals. Colour variable, the sides of pronotum and elytra often contrastingly coloured, but dark-blue individuals predominate. – W. Romania: Banat, Mehadia, Baie Herculeane, Krasowa, W. Valakhia.

b) subsp. *semetricus* Kraatz, 1878 – Smaller and narrower (28-32 mm). Elytral intervals more strongly interrupted. – S.W. Romania, N.E. Serbia (Negotin).

c) subsp. *illigeri* Dejean, 1826 – Narrow and elongated, all intervals strongly convex and densely interrupted. 27-36 mm. Usually blue, bluish-green or purplish-blue, rarely brassy. – Croatia, Bosnia.

d) subsp. *curtulus* Ganglbauer, 1892 (= *bjelasnisensis* Apfelbeck) – Small montane form, related to subsp. *illigeri*, length 22-27 mm, intervals often less convex. – Mountains of Bosnia and Hercegovina, W. Serbia.

e) subsp. *praecellens* Palliardi, 1825 – Similar to subsp. *illigeri*, very narrow, elongated and large (30-35 mm), pronotum more transverse; intervals less convex and less densely interrupted. Dark-blue or dark-violet, the sides brighter. – S.E. Austria, Slovenia, N.W. Croatia.

36 (31). Primary intervals forming regular rows of tubercles, clearly different from the other intervals, the tertiary ones more or less reduced. Extremely variable in size (18-38 mm) and in colour (often bicolorous). – Balkans: E. Serbia, N.E. Bosnia, Bulgaria (except in the S.). Mostly in foothills. ...
.... **02.021b. *C. (Morphocarabus) versicolor*** E. Frivaldszky, 1835 (p. 175).

Two subspecies (in the opinion of I. Tosevski (*unpublished*), each of them merits a specific state):

a) subsp. *versicolor* E. Frivaldszky, 1835 – Rather small (24-29 mm). Head and pronotum more roughly punctured, primary and secondary intervals strongly raised, the tertiary intervals flattened or absent. – Bulgaria (Stara Planina).

b) subsp. *simulator* Kraatz, 1876 – Very large (28-38 mm). Head and pronotum minutely punctured. Elytra with primary rows of links and secondary keels, the tertiary intervals more or less reduced, sometimes absent, rarely almost as high as the secondary ones. Colour extremely variable, often bicolorous. Several colour forms described. – N.E. Serbia: Maidanpek, Kucaina, Milanovac.

37 (30). All intervals of elytra strongly convex and usually densely interrupted, rarely the primary ones developed as longer rows, the others sparsely interrupted. Antennae of males not or feebly swollen laterally at apex. Apical lobe of aedeagus relatively long, sloped (Fig. 3.4c). Colour extremely variable, margins often contrasting with the general colour, femora often red. 22-28 mm. – S.E. Poland, N.E. Romania, Moldova, Ukraine (except the dry steppe and the Crimea), S.W. Russia (Kursk, Belgorod provinces). Mostly in forest-steppe, absent in the mountains. ....
.... **02.007. *C. (Morphocarabus) excellens*** Fabricius, 1798 (p. 162).

38 (27). Elytra with 4-5 primary intervals, all intervals very narrow, keel-shaped, only primary ones usually interrupted by small foveae; more rarely all intervals interrupted or the tertiary ones reduced, but in these cases body strongly elongated. Hind angles of pronotum form relatively short lobes. Aedeagus (Fig. 3.4d). Size (18-37 mm), colour variable. – Carpathian region. ....
.... (**rothi-subspecies group**).

39 (40). Elytra with 4 primary intervals. All intervals uniform. Colour usually black, at most with faint bluish or purplish tint, margins green, blue or violet; rarely upper side more bright in the S. of the area

– brassy, cupreous, green, golden-red. 18-24 mm. – S. Carpathians within the limits of Romania; data for N. Serbia (Vojvodina) are doubtful. Mostly in middle and upper mountain zones. .... **02.004. *C. (Morphocarabus) comptus*** Dejean, 1831 (p. 160).

40 (39). Elytra with 5 primary intervals, if only with 4, then the 4th distant from the edge.

41 (42). Intervals uniform, only primary ones usually interrupted by small pores but not forming tubercles, rarely tertiary intervals fainter. Upper side often with silky lustre, colour variable, from brassy to bluish-black, margins often brighter. Aedeagus (Fig. 3.4e). Size 25-37 mm (in alpine zone up to 20 mm). – S.E. part of Transcarpathian Ukraine, N.E. Hungary, Romania except the eastern provinces. From lowlands to alpine zone. .... **02.009. *C. (Morphocarabus) hampei*** Küster, 1846 (p. 164).

Two subspecies are rather distinct:

a) subsp. *hampei* Küster, 1846 – Body narrower and more elongated. 25-37 mm (usually 29-33 mm). Primary foveae small but distinct, may be present on other intervals. Colour very variable but usually rather bright, upper side often with silky lustre. – S.E. part of Transcarpathian Ukraine, Romania (except its eastern part). Mostly in lowlands and valleys. – Specimens from Beregovo with distinct lateral swelling at apex of antennae in males and reduced elytral intervals were described as *ormayi* Reitter, 1896; there is little difference.

b) subsp. *incompsus* Kraatz, 1880 – Differing from nominate subspecies by shorter and wider elytra with indistinct primary pores. Colour usually black with slight bluish or greenish lustre. 25-32 mm (in alpine zone up to 20 mm – *mehelyanus* Csiki, 1906). – C. Romania: Fogaras Mts., Rodnei Mts., Brasov, Azuga, Sinaia, from foothills to alpine zone.

42 (41). Primary and secondary intervals always densely interrupted, tertiary ones usually forming regular rows of tubercles. Colour usually brassy or reddish-cupreous, sometimes with greenish lustre, rarely blue or purple. 25-33 mm. – C. Romania: Targu-Muresh, Sibiu, upper and middle course of the Olt Valley. .... **02.018. *C. (Morphocarabus) rothi*** Dejean & Boisduval, 1829 (p. 172)

a) subsp. *rothi* Dejean & Boisduval, 1829 – Sculpture of elytron rough, irregular. Rodnei Mts., northern slopes.

b) subsp. *alutensis* Savulescu, 1972 – Sculpture regular, primary intervals catenulate, *cancellatus*-like. – Rodnei Mts., southern slopes.

43 (2). Pronotum with 2 lateral setae (one anterior, one basal).

44 (45). Mentum with tooth shorter than side lobes. Metepisterna shorter than wide. Black, only elytral margins often with metallic lustre; elytra sometimes reddish-brown with black margins (*aereus* Fischer, 1822). 22-28 mm. – The Urals, Siberia. Taiga and forest-tundra zones. .... **02.001. *C. (Morphocarabus) aeruginosus*** Fischer von Waldheim, 1822 (p. 157).

45 (44). Mentum with tooth as long as side lobes. Metepisterna as long as, or slightly longer than wide. Elytra less convex. Black, usually with purplish or greenish tint, sides of the pronotum and elytra and primary foveae purple, violet or green.

46 (47). Elytra moderately convex (Fig. 3.4h). Apical lobe of aedeagus more or less bent to the right (Fig. 3.4f). 15-24 mm. – Polar Ural, Siberia. In taiga and forest-tundra zones; in the S. in the alpine zone of mountains. .... **02.015. *C. (Morphocarabus) odoratus*** Motschulsky, 1844 (p. 170).

Several subspecies have been described. In Europe only one:

a) subsp. *septentrionalis* Breuning, 1932. – Body relatively short and wide, elytral intervals densely interrupted, moderately convex, striae punctured. Colour usually rather dark, black, sometimes with violet tint; the margins, primary foveae and often the points in striae purplish or dark-bronzed. 18-22 mm. Polar Ural.

47 (46). Elytra flattened (Fig. 3.4i). Apical lobe of aedeagus straight, acutely pointed (Fig. 3.4g). Pronotum subcordate. Upper side black with purplish tint. Sides of the pronotum, elytra and primary foveae purple, rarely green. 19-23 mm. – Endemic in S. Ural (loc. typ. Iremel Mt.); inhabiting the alpine zone above 1200 m. .... **02.012. *C. (Morphocarabus) karpinskii*** Kryzhanovskij & Matveev, 1993 (p. 167).

48 (1). Pronotum always with two marginal setae on each side (one anterior, one basal). Elytral intervals more or less depressed and forming grater-like granulations. Dorsal surface mostly black, sometimes with metallic lustre on sides (all: **Trachycarabus** auct., including **Mimocarabus**).

49 (50). Sides of pronotum narrowly bordered even in basal part. Black, elytra with slight bronzed or bluish tint and usually with wide brownish-red, violet or blue margin, femora sometimes red. 16-22 mm. – Forest-steppe and northern steppe zones from W. Ukraine and Moldova to W. Siberia and N.W. Kazakhstan, in the N. to Kaluga, Ryazan, S. parts of Kirov and Perm provinces; absent in dry steppes. Locally common. .... **02.006. *C. (Trachycarabus) estreicheri*** Fischer von Waldheim, 1822 (p. 161).

50 (49). Sides of pronotum widely bordered and turned upward at least basally.

51 (52). Segments of antennae in males simple, without knotted tubercles beneath. Pronotum almost as wide as elytra, its hind angles acutely protruded backward. Elytra with small primary foveae, the intervals flattened, rarely feebly convex, minutely tuberculate. Black, elytra often with faint greenish or bronzed lustre. Aedeagus with long acute apical lobe bent on left side (Fig. 3.5a). 22-30 mm. – Dry steppes of S. Ukraine (including the Crimea), Rostov province and the N. Caucasus, in the mountains to 1500 m. Rather variable in appearance and sculpture but not forming distinct geographical races. .... **02.016. *C. (Trachycarabus) perrini*** Dejean, 1831 (p. 170) (= *campestris* Fischer von Waldheim, 1822, = *planus* Géhin, 1855).

52 (51). Antennal segments in male with knotted tubercles beneath, before each tubercle with glabrous longitudinal line. Apical lobe of aedeagus sloped on right side.

53 (54). Head somewhat thickened. Antennal segments 1-4 and femora red. Upper side black, elytra shiny in males, dull in females, their margins with bluish or violet tint. Body fairly large and stout. Aedeagus (Fig. 3.5b). 26-32 mm. – Ukraine, west of Dnieper, Moldova, N.E. Romania, S.E. Poland. Mostly in forests-steppe landscapes, rather rare. .... **02.002. *C. (Trachycarabus) besseri*** Fischer von Waldheim, 1822 (p. 158).

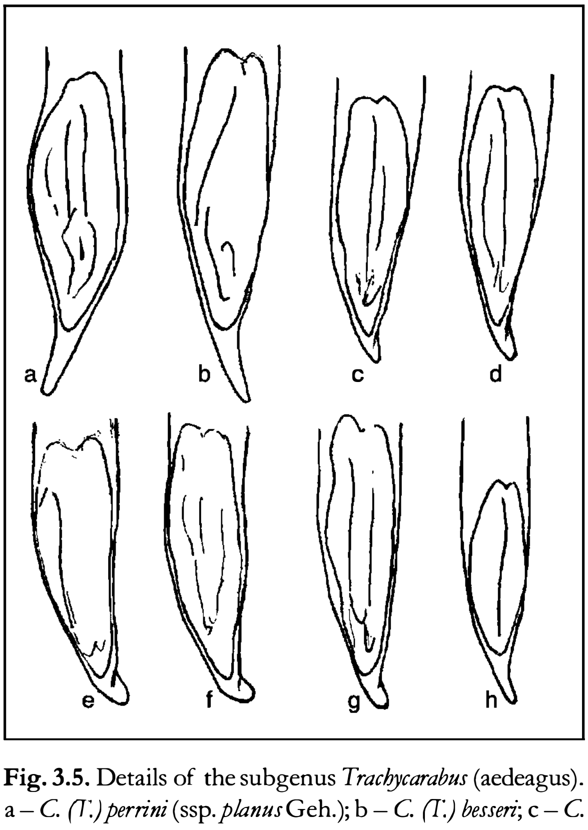


Fig. 3.5. Details of the subgenus *Trachycarabus* (aedeagus). a – *C. (T.) perrini* (ssp. *planus* Geh.); b – *C. (T.) besseri*; c – *C. (T.) haeres* ssp. *haeres*; d – *C. (T.) haeres* ssp. *fossulatus*; e – *C. (T.) errans*; f. *C. (T.) bosphoranus*; g – *C. (T.) sibiricus*; h – *C. (T.) scabriusculus*.

54 (53). Head not thickened, antennae and femora usually black, rarely the femora, very rarely the antennal base red.

55 (64). Elytra elongate-oval or almost parallel-sided at the middle, more than 1.6 times longer than wide, their striae minutely punctate, intervals nearly flat, densely granulate. Apical lobe of aedeagus short, usually rounded.

56 (59). Primary foveae large and conspicuous.

57 (58). Femora and the 1st antennal segment (rarely 2nd-4th segments also) red. Body elongate. 25-30 mm. – W. Ukraine: Lviv and Ternopol provinces. Very rare and insufficiently known, no recent records. .... **02.019. *C. (Trachycarabus) rybinskii*** Reitter, 1896 (p. 173).

58 (57). Body uniformly black, somewhat stouter. 22-28 mm. Aedeagus: Fig. 3.5c,d. – Forest-steppe and the N. part of steppe zone between Dnieper and Volga. .... **02.008. *C. (Trachycarabus) haeres*** Fischer von Waldheim, 1823 (p. 163).

Two distinct subspecies:

a) subsp. *haeres* Fischer von Waldheim, 1823 – Small: 22-26 mm Primary foveae moderately deep. Aedeagus: Fig. 3.5c. – The N.E. part of area: districts of Tula, Ryasan, Lipetzk, Voronezh, Saratov, E. part of Kursk.

b) subsp. *fossulatus* Dejean, 1826 – Larger: 25-28 mm. Primary foveae deeper and larger. Aedeagus: Fig. 3.5d. – The S.W. part of area: W. districts of Kursk province, provinces of Sumy, Kharkov, Tshernigov, Poltava, Kiev, Tsherkasy.

59 (56). Primary foveae smaller, sometimes indistinct. Colour uniformly black.

60 (63). Lateral borders of pronotum narrower, moderately bent upwards. Body slightly convex, elongate, elytra 1.60-1.67 times longer than wide.

61 (62). Larger and stouter; 25-32 mm (rarely up to 20 mm). Upper side slightly shiny. Primary foveae larger. Aedeagus: Fig. 3.5e. – Dry steppes of S. Ukraine, Rostov and Stavropol provinces, Kalmyk Republic; rather rare. .... **02.005. *C. (Trachycarabus) errans*** Fischer von Waldheim, 1823 (p. 160).

62 (61). Smaller and more slender: 20-25 mm (as exception up to 16 mm). Upper surface more shiny. Primary foveae very small. Aedeagus: Fig. 3.5f. –

Mountain steppes of Crimea (Jaila), mountain steppe and subalpine grasslands of N. Caucasus. Usually at altitude more than 1200 m. .... **02.003. *C. (Trachycarabus) bosphoranus*** Fischer von Waldheim, 1823 (p. 159).

63 (60). Lateral borders of pronotum strongly bent upwards. Body shorter and convex, elytra 1.55-1.59 times longer than wide. Upper surface shiny. Primary foveae usually small. Aedeagus: Fig. 3.5g. 20-24 mm. – Forest-steppe and grassland steppe, E. of the Volga: the provinces of Samara, Saratov, Orenburg, S. parts of Tatar and Bashkir Republics, Siberia to Yakutia and Irkutsk province, N.E. Kazakhstan, W. Mongolia. .... **02.022. *C. (Trachycarabus) sibiricus*** Fischer von Waldheim, 1822 (p. 176).

Several subspecies; only one in European Russia:

a) subsp. *karelini* Fischer von Waldheim, 1830 – Primary foveae somewhat larger than in Siberian forms. Steppes between Volga and S. Ural.

Note: Probably *C. kolosovi* Zinovjev, 1997 could be added here as a newly described species; however it is possible that it will be synonimised with 02.022 *C. sibiricus karelini* Fischer von Waldheim (Makarov, *pers. comm.*).

64 (55). Elytra short-oval, Length/Width = 1.50-1.58; striae distinctly punctate, intervals slightly convex, densely granulate, primary foveae shallow. Pronotum widely margined, sides strongly bent upwards, hind angles long and acute. Dorsal side black, sometimes with faint bronzed lustre. Aedeagus with rather long and narrow apical lobe (Fig. 3.5h). 14-25 mm. – C. and S.E. Europe from E. Austria, S. Czechia, Slovakia, S. Poland to Bosnia, Bulgaria, Ukraine and Don River. Mostly in forest-steppe zone and mountain grasslands. .... **02.020. *C. (Trachycarabus) scabriusculus*** Olivier, 1795 (p. 173).

Several subspecies with clinal transitions between them:

a) subsp. *scabriusculus* Olivier, 1795 – Middle-sized specimens (16-22 mm) with fairly flat, moderately tuberculate elytral intervals and slightly distinct primary foveae. Specimens with red femora (*erythropus* Fischer von Waldheim, 1822) are not rare in the Ukraine W. of Dnieper. – Inhabits the main part of the area: C. Europe, including Austria, Czechia, Slovakia, most part of Hungary, N. Romania, Moldova, Ukraine, except its easternmost provinces, Lipetsk and Voronezh provinces of Russia. Mostly in forest-steppe or meadow-steppe.

b) subsp. *inapertus* Motschulsky, 1850 – Somewhat larger (19-23 mm) and more oblong. Elytral intervals coarsely tuberculate; primary foveae more distinct. – E. Ukraine: Kharkov, Lugansk, Donetsk provinces; Russia – Rostov province. Records from the Crimea and Stavropol provinces are erroneous.

c) subsp. *lippii* Dejean, 1826 – The largest form (20-25 mm), sometimes with red femora. Primary foveae comparatively large and distinct, sculpture variable. – The most part of Romania especially its W. and C. territories, S.E. Hungary, Moldova.

d) subsp. *bulgarus* Vacher de Lapouge, 1908 – Elytral intervals rather convex, very coarsely tuberculate, primary foveae indistinct. 18-24 mm. – Balkan Peninsula, except its W. part: S. Romania, Serbia, Bosnia, N. Macedonia, Bulgaria, European Turkey, mostly in the foothills.

03. Subgenus Carabus (*s.str.*)

Type species *C. granulatus* Linnaeus, 1758

Characterised by medium-sized (16-30 mm), elongated body. Mandibles short; preapical segment of labial palpi with 2 setae; submentum flat, with setiferous pores. Pronotum almost quadrangular, with short hind angles and 4-6 lateral setae (among them 3-5 medial ones). Elytral sculpture triploid, primary intervals broken into rows of tubercles; elytral sides distinctly excised at the preapical part (stronger in females), epipleurae abruptly ended before excision. Abdominal pores present. Protarsi in male with 4 dilated segments.

This subgenus is considered here in its narrowest sense, i.e. without *Limnocarabus* (*C. clatratus* L.) and *Tachypus* (*C. auratus* L., *C. cancellatus* Ill., *C. vagans* Dej.). Thus including two European species, *C. granulatus* L. and *C. menetriesi* Hummel (considering classification in this sense, three species from the Caucasus and Iran related to *C. granulatus*, and probably *C. vanvolxeni* Putzeys from Japan, could be included in this subgenus).

1 (2). Antennae long, in male reaching almost to middle of elytra. Pronotum densely and finely wrinkled and punctured. First secondary interval separated from the suture, rarely joined with it in the apical part. Primary intervals forming rows of more or less long tubercles, secondary ones developed as smooth keels, rarely wrinkled or apically interrupted into short granulations; the tertiary ones usually transformed into rows of more or less distinct granulations, but sometimes inconspicuous absent. Wings usually reduced, sometimes fully developed. Upper side usually feebly shiny, dark bronzed or brassy, sometimes almost black with bronzed or greenish lustre, the primary foveae and margins often brighter; femora sometimes red. 17-30 mm (in Europe less than 27 mm, small individuals reaching a mere 13-15 mm). – Distributed throughout Europe and N. Asia from Ireland and N. Spain to E. Siberia, N. China and Japan, in the north to the N. limits of

forest zone, in the S. to N. Spain, S. Italy, Greece, Anatolia, the N. Caucasus, S.E. Kazakhstan, region of Beijing. Introduced into N. America. Hygrophilous species, lives mostly in lowlands or foothills, wet forests, meadows, along shores; hibernates mostly under bark. ....
.......................**03.001. *C. (Carabus) granulatus*** Linnaeus, 1758 (p. 178).

Many subspecies have been described. Breuning considered *leander* Kraatz, 1878, from N. slope of the Caucasus, and *corticalis* Motschulsky, 1846, from E. Transcaucasia, to be subspecies of *granulatus*, but we are inclined to attribute to them the status of distinct species both on morphological and ecological grounds. – In Europe 7 subspecies:

a) subsp. *granulatus* Linnaeus, 1758 – Body rather narrow. Elytral sculpture moderately strong, secondary intervals keel-shaped, usually smooth, tertiary ones forming less distinct rows of granulations, colour mostly bronzed, sometimes with greenish or cupreous lustre, femora black, sometimes red. 17-23 mm. – Inhabits most of Europe from Scotland, Norway, N. Russia (Murmansk, Arkhangelsk provinces) to N. Spain, S. France (except lowlands of Provence), Switzerland, Croatia, N. Bosnia, Bulgaria, S. Ukraine. In W. England transitional populations to subsp. *hibernicus*, in S. Alps to subsp. *interstitialis*.

b) subsp. *hibernicus* Lindroth, 1956 – Colour almost constantly metallic brassy or greenish. Elytral sculpture smooth, primary tubercles as well as secondary keels, slightly elevated, surface pronouncedly dull. – Ireland.

c) subsp. *interstitialis* Duftschmid, 1812 – Body wider, on the average larger. Primary and secondary intervals less convex, tertiary ones distinct, transformed into rows of granules. Colour black or bronzed-black almost without metallic lustre. – Italy, Corsica, W. part of Balkan Peninsula from Dalmatia to Albania.

d) subsp. *aetolicus* Schaum 1857 – N. Greece, Hercegovina. Small, rather convex, dark specimens from Greece have been described as *aetolicus*. Large individuals from Albania have been described as *miridita* Apfelbeck, 1901. Local forms with these characters have recently also been discovered in S. Italy (Monzini & Angelini, 1997). The forms that were mentioned by Casale *et al.* (1982) as 'forms close to the Albanese populations': blackish without bronze lustre, tertiary intervals complete and regular, not granulated; pronotum with basal angles more prominent from S.E. Italy (Puglia and Basilicata) should also be attributed to *aetolicus*. Specimens similar to *miridita* Apfelbeck can be found in Corsica (*corsicus* Born).

h) subsp. *calabricus* Spettoli & Vigna Taglianti, 2001 – Montane populations from Calabria (Serre Calabre). – Body slender, convex. Small size (16.5-21.5 mm).

e) subsp. *crimeensis* Breuning, 1933 – Rather distinct subspecies. Larger (19-24 mm) and wider individuals with less convex primary intervals and finely granulate tertiary ones. Colour bright cupreous. – Foothills and mountains of the Crimea.

Note: The following two subspecies have been regarded non-European by Březina (1999). However, since the notes on these taxa were written by O.L. Kryzhanovskij in the original manuscript, we mention them here to prevent them from being overlooked for Europe, until European Russian material has been examined.

f) subsp. *parallelus* Faldermann, 1835 – Secondary ridges strongly convex, mostly higher than primary tubercles; tertiary intervals distinctly reduced. Metepisterna distinctly longer than wide. Colour brownish-cupreous, rarely greenish of bronzed-black. 17-22 mm. – Russia: Lower Volga, N. Caucasus, in lowlands and foothills.

g) subsp. *duarius* Fischer von Waldheim, 1844 – Somewhat more convex than the typical form, elytral sculpture sharper, primary tubercles rather short, rounded, secondary keels strongly convex (but the 4th not distinct), tertiary intervals mostly reduced, roughly granulate. Upper side bronzed or greenish. – E. part of the European Russia (Samara, Orenburg provinces, S. Ural); W. and C. Siberia (in forest-steppe and taiga zones), Kazakhstan, N.W. Mongolia.

2 (1). Antennae short, slightly surpassing the basal side of pronotum. Pronotum sparsely punctured at middle. First secondary interval joined with suture, either at the middle or in first half of the elytra; primary intervals forming rows of short rounded tubercles, the tertiary ones almost completely reduced to sparse granulation. Rudiments of wings very short. Upper surface dark-bronzed with silky lustre, legs always black. 18-24 mm. – N.E. Europe and the westernmost part of Siberia, isolated populations in the mountains of C. Europe and ?W. Bulgaria. Lives mostly in *Sphagnum*-bogs. ....
.......................**03.002. *C. (Carabus) menetriesi*** Hummel, 1827 (p. 181).

Two subspecies are known:

a) subsp. *menetriesi* Hummel, 1827 – Rather wide and flat, elytra with projecting shoulders and parallel sides stronger than in other subspecies. – The main part of species area: N. and C. parts of European Russia (to the S. part of the taiga zone), W. Siberia (Tyumen province), N.E. Ukraine, Baltic States, Poland, N.W. Slovakia. In general fairly rare.

b) subsp. *pacholei* Sokolar, 1911 – More convex, the greatest width of elytra at the middle, shoulders rounded. – C. Europe: S.+ N.E. Czechia, Saxony, Mecklenburg-Vorpommern, E. and S.E. Bavaria, E. and N. Austria, scattered occurrences, rare and most probably endangered.

Note: The record of a single female from S.W. Bulgaria (Belasica planina) attributed to a probably undescribed subspecies (Gueorgueiv & Gueorguiev, 1995), seems to be highly questionable regarding the overall distribution area of the species.

05. Subgenus Tachypus Weber 1801
(Autocarabus Seidlitz, 1887 and auct.)
Type species *C. auratus* Linnaeus, 1761.

Characterised by short mandibles, bisetose labial palpi, apical segments of palpi not dilated, rather strong preapical excision of elytra, elytral sculpture triploid or keeled, short metepisterna, medium-sized, convex body and usually metallic dorsal surface. Contains 3 species, treated below. Some authors also include *C. cristoforii* Spence from C. Pyrenees (Březina, 1994; Deuve, 1991, 1994; Turin *et al.*, 1993) and *C. obsoletus* Sturm from Carpathians (see: Deuve, 1991, 1994, 1999; Turin *et al.*, 1993), which in the present work have been included in the *Morphocarabus/Eucarabus* key. Further study is needed, but phylogenetical/molecular studies support the present choice (Arndt, *in litt.*).

1 (2). Elytra with wide convex or flattened primary keels, without other distinct intervals. Dorsal surface usually gold-green, sometimes olive-green, coppery, bluish-green, blue, rarely black with greenish or bronzed lustre, margins of pronotum and elytra sometimes coppery-red; Segments 1-4 of antennae, palpi (except basal segment) and legs usually reddish-yellow, tarsi and sometimes femora infuscated. 17-30 mm. – W. and C. Europe from W. France and N.E. Spain to N. Germany and W. Poland; in the S. to S.E. France, N. Switzerland, Austria, Czechia; in Poland it spreads eastward. Absent in British Isles, Fennoscandia and in the S. of Alps and Carpathians. Introduced into the U.S.A. (New England)............... .... **05.001. *C. (Tachypus) auratus*** Linnaeus, 1761 (p. 191).

A very large number of subspecies were described, especially from France, but most of them were based on slightly differentiated populations:

a) subsp. *auratus* Linnaeus, 1761 – Body elongated, primary keels moderately to strongly convex. Colour mostly green to golden-green, margins mostly coppery-red, femora almost always reddish-yellow. 22-27 mm (rarely 19-22 or 27-30 mm). – Inhabits the major part of the species range except S. France. Lives mainly in open landscapes.

b) subsp. *lasserrei* Doué, 1855 – Body elongated, mostly large (22-30 mm) but small individuals (17-22 mm) are known from Margeride Mts (S.W. France). Primary keels strongly flattened, dorsal side shiny, colour variable, pronotum usually green or bluish-green, elytra green or olive-green, margins of elytra and pronotum narrowly reddish or coppery-red, femora often dark. – S.W. and C. France, in the N. to Loire. Specimens from Pyrenees on French (*pseudolotharingus* Barthe, 1921) and Spanish side (*navarricus* Vacher de Lapouge, 1924) probably refer to this subspecies.

c) subsp. *lotharingus* Dejean, 1826 – Hind angles of pronotum very short, scarcely extended beyond base. Body short and wide, pronotum strongly transverse, elytral keels flattened, coppery or bronzed, their background olive-green, femora usually dark. 21-28 mm. – C. part of S. France in the 'Zone de l'olivier' from Roussillon to Provence (was described erroneously from Metz).

d) subsp. *honnoratii* Dejean, 1826 – Body slender, elytra oval with strongly flattened keels, pronotum cordate. Mostly light- or dark green, sometimes with strong coppery tint, olive-green, more rarely blue, violet or black, the antennae and legs sometimes entirely black. 20-27 mm. – S.E. France (Basses-Alpes, Vaucluse). Some specimens from Mt. Ventoux (*nicolasi* Chobaut, 1897) are black with bluish lustre and yellow legs.

2 (1). Elytra with primary rows of links and secondary (also frequently tertiary) keels; the last ones, usually slighter than secondary ones and wrinkled or granulated, sometimes completely reduced.

3 (4). Basal segments of antennae not flattened and without edging. Body oval, rather wide and stout, on the average less convex. Tertiary intervals mostly less convex than secondary keels, often forming rows of small tubercles. Aedeagus more narrowed apically, with apex more rounded (Fig. 3.6a). Dorsal side almost always bronzed or brassy with greenish lustre in the margins of pronotum and elytra, appendages black, very rarely 1st antennal segment and femora brownish-red. 18-28 mm (usually 15-25 mm). – S.E. France (Basses-Alpes, Vaucluse, Alpes-Maritimes); N.W. Italy (W. Liguria). Mainly in plains, near marshes and foothills. .... **05.004. *C. (Tachypus) vagans*** Olivier, 1795 (p. 196).

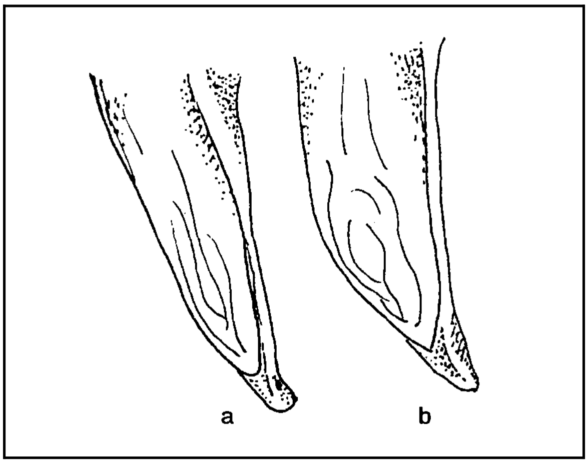


Fig. 3.6. The details of subgenus *Tachypus* (aedeagus). a – *C. (T.) vagans*; b – *C. (T.) cancellatus*.

4 (3). Segments 1-4 of antennae slightly but distinctly flattened basally when seen from above, the segments 2-3 with evident edging. Tertiary intervals mostly interrupted or more or less reduced, always less strong than secondary ones. Aedeagus less narrowed apically but acute at apex (Fig. 3.6b). Extremely variable in size (18-33 mm), sculpture and colour, but coppery or bronzed dorsal surface usual; 1st antennal segment black ('nigrobasal') or red ('rufobasal'), femora black ('nigrofemoral') or red ('rufofemoral'); their colour is important for discriminating infraspecific forms. – The range of the species stretches from W. France and N.W. Spain throughout C. and N. Europe to E. Siberia (Lena River, Baikal), but missing in the British Isles, most part of Iberian Peninsula, S. Italy, Greece, the Caucasus, etc., northern limit of range approximately follows 62° N. Lives in open landscapes (including fields and meadows) and in deciduous forests, from plains to middle mountain belts. .... **05.002. *C. (Tachypus) cancellatus*** Illiger, 1798 (p. 193).

The geographical and individual variability of this species is extremely high. It has resulted in the description of very many infraspecific taxa. Breuning (1932-1937) listed 10 subspecies and more than 70 'nationes' and 'morphae'. Although 210 names are enumerated by Deuve (1991), we believe that the real number of subspecies does not exceed 8-10; the majority of the described forms do not merit valid names. Especially intricate is the nomenclature of the forms in the S.E. part of Central Europe. The infraspecific taxonomy of *C. cancellatus* needs revision. Eight subspecies are discussed below. The terms 'rufobasal' and 'nigrobasal' refer to the basal segment(s) of the antennae.

a) subsp. *cancellatus* Illiger, 1798 – Rufobasal, nigro- or rufofemoral. Elytral sculpture varies from moderately feeble to strong. Length 19-28 mm (mostly 22-27 mm). Colour variable, mostly coppery or bronzed, but some populations have dark dorsal sides (to black without metallic lustre). – All E. and N. parts of species range: Germany (except the W. part), Fennoscandia, Baltic states, Poland, Byelorussia, most of Ukraine, Russia in the E. to the C. Siberia. We include in the nominate subspecies, the races *tuberculatus* Dejean, 1826 (rufofemoral, loc. typ. Warsaw) and *sulinensis* Born, 1902 (nigrofemoral, loc. typ. Sulin in N.E. Romania). Many authors, especially Kolbe (1913) and Breuning (1932-1937), attached too great importance to the colour of the femora, as this character is extremely variable in this large area, although nigrofemoral populations prevail in S. and W. parts and rufofemoral ones in the N. and E. parts; mixed populations for this character live in C. of European Russia and N.E. Ukraine. Only rufofemoral forms inhabit the Urals and Siberia. Green, blue or black individuals predominate in C. and S. Byelorussia (*conspersus* Vacher de Lapouge, 1902).

b) subsp. *emarginatus* Duftschmid, 1812 – Nigrobasal, nigrofemoral. Body more or less elongated, feebly convex. Pronotum relatively large with long lobe-shaped hind angles. Primary and secondary intervals rather feebly convex, the tertiary ones forming distinct wrinkled keels or rows of tubercles, shoulders slightly serrate to smooth. Size (21-33 mm) and colour very variable, mostly cupreous or brassy, often with greenish lustre, sometimes shiny green (*dahli* Schaum), rarely bluish-green or violet; small individuals (21-24 mm) mostly in montane districts. – N. Italy (in the S. to Florence), S.E. Switzerland (Tessin), Austria, Slovenia, Croatia.

c) subsp. *corpulentus* Kraatz, 1880 – Nigrobasal, nigrofemoral, medium sized (20-28 mm). Body wide and stout, flattened. Elytral sculpture moderately strong, tertiary intervals indistinct, shoulders feebly serrate or smooth. Colour mostly coppery-brown, sometimes with greenish lustre or dark olive-green. – Croatia: Dalmatian coastal region.

d) subsp. *alessiensis* Apfelbeck, 1901 – Nigrobasal, nigrofemoral, rather large (25-30 mm), elongated, moderately convex. Shoulders strongly serrate. Elytral sculpture rough, primary and secondary intervals strongly convex, the tertiary ones manifested as rows of granules or densely transversely wrinkled. Head, pronotum and margins of elytra bluish or reddish-violet, elytra dull reddish- or brownish-coppery. – N. Albania; one of the most distinct subspecies.

e) subsp. *intermedius* Dejean, 1826 – Nigrobasal, nigrofemoral, elongated. Pronotum large, cordate, with long hind angles. Elytra with moderately convex primary and secondary intervals, the tertiary ones slight, the background smooth or minutely granulate. Colour mostly cupreous, rarely golden greenish. Length usually 22-27 mm, in mountains to 19 mm. – S.E. Europe from S.E. Austria (Klagenfurt) and S.W. Hungary to Slovenia, Bosnia and Bulgaria (except the southernmost districts). Very large form (26-32 mm) living in C. Bosnia and S. Croatia and having smooth or feebly granulate background of elytra, was described as *maximus* Haury, 1880; such specimens have been found also in Hercegovina, and with *aurosplendens*, they could form a distinct subspecies. Large, elongate specimens with very reduced tertiary intervals and bright, metallic-cupreous or golden-reddish body surface, from moist lowland in Slovenia, Croatia and N. Bosnia, have been described as *aurosplendens* Born, 1910.

f) subsp. *graniger* Palliardi, 1825 – Nigrobasal, nigrofemoral. Size variable (22-31 mm). Pronotum with moderately short lobes of hind angles. Primary and secondary intervals strongly convex, the tertiary ones reduced, the background of elytra minutely to roughly granulate. Colour mostly rather dull, coppery to bronzed-brown, rarely green or black with metallic lustre. – Serbia (including Vojvodina), W. and C. Romania.

g) subsp. *carinatus* Charpentier, 1825 – Rufobasal, nigrofemoral. Body wide and compact. Primary rows feebly convex, secondary keels elevated, tertiary intervals reduced. Length 19-30 mm, medium-sized individuals most common. Colour mostly cupreous or green. – France, N.W. Spain (to Galicia), Belgium, S. Netherlands, W. Germany, N.W. Switzerland. Several local forms are known; the name *progressivus* Kolbe, 1912, is applied to populations, intermediate between *carinatus* and *cancellatus* (*s.str.*) and living in the N.E. part of subspecies range.

h) subsp. *tibiscinus* Csiki, 1905 – Rufobasal, nigrofemoral, moderately elongated, rather feebly convex. Elytral sculpture strong, tertiary intervals reduced, shoulders usually distinctly serrate. Colour cupreous to bronzed-black, margins sometimes purplish, green individuals are very rare. 20-27 mm, rarely up to 30 mm. – E. Austria, Hungary, S.Slovakia, N.W. Romania, Transcarpathian Ukraine. This subspecies is the intermediate form between western (*intermedius*, *graniger*) and north-eastern races (*cancellatus s.str.* and related forms).

06. Subgenus Archicarabus Seidlitz, 1887

Type species *C. nemoralis* O. Müller, 1764

Note: *C. alysidotus* has been retained by Březina in the monotypic subgenus *Rhipocarabus* near *Archicarabus*.

Submentum transversely swollen. Elytral sculpture more or less homodynamous, triploid to pentaploid. Pronotum almost square, body short, moderately convex, side margins of prothorax with 2-3 lateral setae. Penultimate segment of labial palpi with 2, rarely 3 or 4 setae. Upper surface almost always with metallic lustre at least at the sides of pronotum and of the elytral base. 7-8 species in Europe and several species in the Caucasus and S.W. Asia; the taxonomic status of some forms from Turkey is not completely clear. Mostly mesophilous, one species (*alysidotus*) is hygro-mesophilous; they prey mostly on earthworms and insect larvae.

1 (2). Antennae thick and short, hardly exceeding the base of elytra, hind angles of pronotum very short, broadly rounded. Elytral sculpture triploid, primary and secondary ridges forming rows of tubercles. Wings comparatively well-developed. Upper side brownish-coppery or brassy with golden-red, purple, or green reflections. 20-24 mm. – S. France, N.W. and C. Italy, in swamps and damp meadows, sometimes in forests (up to 1000 m). .... **06.001. *C. (Archicarabus) alysidotus*** Illiger, 1798 (p. 196).

Two subspecies:

a) subsp. *alysidotus* Illiger, 1798 – Body broader: width of elytra 8-9.5 mm. – Italy: coastal regions of Tyrrhenian Sea between 41° and 44° N from Alpes Maritimes to Lazio, Toscana (absent from Liguria) and Campania, also Abruzzo and points in Adriatic coast.

b) subsp. *stagnalisaequalis* Vacher de Lapouge, 1916 – Slightly distinct from *alysidotus* (*s.str.*), or synonym of it (Deuve, 1994). Body narrower: width of elytra 7-8 mm, colour mostly dull. – S. France from Alpes Martimes to Hérault, more common in Camargue.

2 (1). Antennae thin, of normal length, if shorter, then the hind angles of pronotum forming acute, triangular lobes. Wings strongly reduced.

3 (10). Abdominal furrows slight, broadly interrupted in the middle or absent.

4 (5). Metepisterna somewhat shorter than their width. Elytral intervals almost always triploid, strongly convex, rarely tertiary intervals doubled; primary ones forming rows of tubercles interrupted by small foveae. Aedeagus: Fig. 3.7a. Black, the sides of pronotum and elytra rather dull, slightly metallic. 18-27 mm. – S.E. Europe mostly at foothills and mountains to 2000 m; in forests and open areas. .... **06.003. *C. (Archicarabus) montivagus*** Palliardi, 1825 (p. 198).

Two rather distinct subspecies and several forms of unclear status:

a) subsp. *montivagus* Palliardi, 1825 – Elytral intervals regular, rather strongly convex, rarely tertiary ones doubled. Sides of pronotum usually duller. 22-27 mm. – E. part of range: S. Slovakia, Hungary, W. and S. Romania, Serbia, Macedonia, Bulgaria, N.E. Greece (Rhodopes). Introduced in N.E. Italy (Trento).

b) subsp. *vellepiticus* Hampe, 1850 – Elytral intervals more irregular, often strongly interrupted, moderately con-

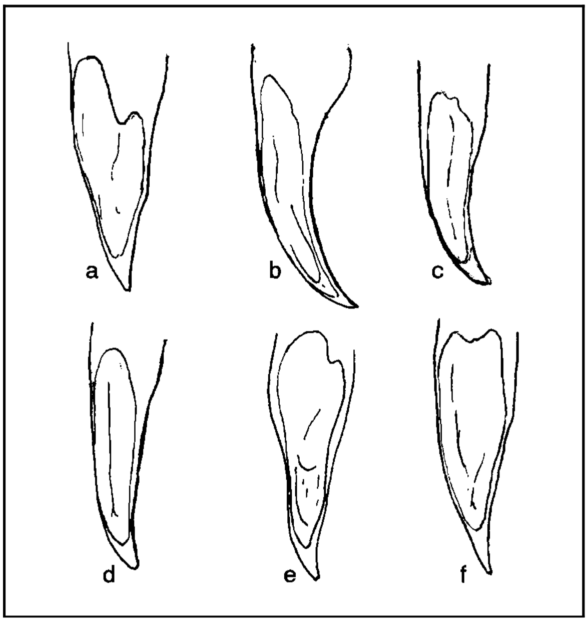


Fig. 3.7. Details of subgenus *Archicarabus* (aedeagus). a – *C. (A.) montivagus*; b – *C. (A.) nemoralis*; c – *C. (A.) pseudomonticola*; d – *C. (A.) monticola*; e – *C. (A.) steuartii*; f – *C. (A.) wiedemanni*.

vex. Upper surface moderately shiny. 20-25 mm, rarely up to 27 mm. – In Slovenia, Croatia, Bosnia and Hercegovina, Montenegro, N. Albania, N.W. Greece (Epirus).

5 (4). Metepisterna as long or slightly longer than their width. Tertiary and sometimes secondary intervals redoubled forming thin granulae, primary ones slightly prominent, not forming regular rows of tubercles, primary foveae more evident.

6 (9). Pronotum almost always with 3 lateral setae. Hind angles longer and more curved.

7 (8). Aedeagus strongly curved, its apex acute (Fig. 3.7b). Larger: 18-28 mm, usually more than 20 mm. Upper surface bronzed-black or bronzed-brown with pronounced metallic lustre, sometimes brightly metallic. – Europe, except the high N., the steppe zone and Mediterranean landscapes, extending eastward to the Urals. Introduced into N. America (where it is widely distributed) and S.E. Kazakhstan. .... **06.004.** ***C. (Archicarabus) nemoralis*** O.F. Müller, 1764 (p. 199).

Several subspecies have been described, but the geographic variations are clinal at most parts of the species ranges. Only two subspecies are considered here:

a) subsp. *nemoralis* O.F. Müller, 1764 – The wing rudiments short (less than 3 times longer than wide). Upper surface bronzed-black with violet or blue margins of pronotum and elytra. – In most part of the range, except its extreme S.W.

b) subsp. *prasinotinctus* Heyden, 1880 (*pascuorum* Vacher de Lapouge, 1908) – The wing rudiments long (more than 4 times as long as wide). Upper surface, especially elytra, more vividly coloured: violet, green, golden-bronzed, rarely blue. Antennae somewhat longer, granulation of elytra usually stronger and regular. – S.W. France (Massif Central, Pyrenees and their foot-hills, valley of Garonne); N. Spain.

8 (7). Aedeagus less curved, its apex not so acute (Fig. 3.7c). Smaller: 14-21 mm, usually less than 19 mm. The wing rudiments long (as in *nemoralis prasinotinctus*, see above). Colour usually greenish-bronzed with green or violet margins, less shiny than in *prasinotinctus*. – S.W. France. – Pyrénées-Orientales: Canigou, Albères; NE Spain: N. Catalonia. .... **06.005.** ***C. (Archicarabus) pseudomonticola*** Vacher de Lapouge, 1908 (p. 201).

9 (6). Pronotum always with 2 lateral setae, hind angles shorter and more rounded. Aedeagus slightly curved (Fig. 3.7d). Upper surface usually brownish black, only sides with metallic, green or blue-violet lustre. 16-26 mm. – S.E. France and N.W. Italy: W. Alps and Ligurian Apennines at the altitudes 200-2000 m, in forests and alpine meadows. Several subspecies described, but both Jeannel (1941) and Casale *et al.* (1982) regarded the species as a monotypical one. Rather characteristic forms constitute the most southern populations from the French Maritime Alps (*maritimensis* Born, 1923, with large depressed specimens with distinct sculpture) and from the Italian Ligurian Alps at high altitude, up to 1200-1500 m (*liguricus* Born, 1898, with small, convex, shiny specimens). .... **06.002.** ***C. (Archicarabus) monticola*** Dejean, 1826 (p. 197).

10 (3). Abdominal furrows completely and strongly cut.

11 (12). Hind angles of pronotum widely rounded. Elytral intervals convex, wrinkled. Brown to brownish-black, shiny, sides of pronotum and elytra with bluish or greenish lustre. 20-33 mm. – Endemic in Italy from Piedmont to N. Sicily, absent in the N.E. Euryzonal species, from sea level up to 2000 m. Highly variable but Casale *et al.* (1982) regarded it as a monotypical species.. .. .. **06.006.** ***C. (Archicarabus) rossii*** Dejean, 1826 (p. 201).

12 (11). Hind angles of pronotum long, triangular. Elytra intervals slightly convex, granulate.

13 (14). Side-margins of pronotum strongly turned up before hind angles. Aedeagus with apical moderately narrow lobe (Fig. 3.7e). Black, slightly shiny, elytra sometimes with bronzed lustre, margins often bluish-green, bluish or reddish-violet. 18-22 mm. – N. Portugal, N.W. Spain. Mostly in forests. .... **06.007.** ***C. (Archicarabus) steuartii*** Deyrolle, 1852 (p. 202).

14 (13). The side-margins of pronotum slightly turned up before hind angles. Aedeagus with apical lobe acute and very narrow (Fig. 3.7f). Black, rather dull, side margins of pronotum and elytra mostly with violet or green tint. 17-27 mm. – E. Bulgaria, European and Asiatic Turkey to Ankara and Baiburt. Mostly in dry forests and bushes. Several subspecies, but only the nominate one in Europe (*burgassiensis* Apfelbeck, 1904, is merely a 'morpha'). ....**06.008.** ***C. (Archicarabus) wiedemanni*** Ménétries, 1836 (p. 202).

07. Subgenus Hemicarabus Géhin, 1876

Type species *C. nitens* Linnaeus, 1758

Small, stout, often polychromous, moderately convex species. Head normal. Mandibles short, dorsally with traces of transversal wrinkles. The 2nd and basal part of 3rd antennal segments depressed, with external carina. Palpi short and thin, terminal segments slightly enlarged; labial ones with 2 setae, submentum with gular setae, not swollen. Pronotum rather small, with lateral setae, its hind angles slightly protruding. Elytra oval, moderately convex, humeral angles with 2-3 small but distinct denticles, sculpture triploid, more or less modified, the primary intervals are strongest. Legs short and stout, the apex of protibiae protruded externally in finger-like process.

The structure of mandibles and antennae is similar to that of several Calosomatini, and the shape of the protibiae resembles that of the Australian *Pamborus*. A homogenous group, 4-5 species: 1 in N. and C. Europe, 2-3 in Siberia to Korea and N. Japan, 1 in N. America. Some authors also include here the Nearctic – N.E.Asian *C. maeander* Fischer von Waldheim, 1822, but Deuve (1994) retained it in the monotypic subgenus *Homoeocarabus* Reitter, 1896.

1 (1). Head and pronotum golden-red, elytra metallic-green, with black primary carinae and red or purple lateral borders. Rarely pronotum green, or elytra coppery-brown, or all upper surface black with bronzed lustre; sometimes (mostly in the N.) the carinae are interrupted, especially apically. 13-18 mm. – N. and C. Europe from Atlantic coast to W. Siberia and from Scotland and N. Fennoscandia to W. France, Austria, Carpathian Mts., N. Ukraine. In humid meadows and marshes, in N.W. Europe especially in moist heathland with *Erica*, but also on sandy soil of (coastal as well as inland) dunes and in pine forests. No valid subspecies; many local forms have been described in the literature. .... **07.001. *C. (Hemicarabus) nitens*** Linnaeus, 1758 (p. 203).

08. Subgenus Diocarabus Reitter, 1896
Type species *C. loschnikovii* Fischer von Waldheim, 1823

Body small to medium-sized (14-21 mm) with rather short appendages; colour black or metallic, legs often reddish. Mandibles short; labial palpi bisetose, apical segments of palpi not dilated. Pronotum with 3-5 (rarely 2) lateral setae on each side. Elytra convex, their sculpture penta- or heptaploid, usually more or less irregular, primary foveae evident, each of them often interruped by three adjacent intervals.

About 10 species, mostly in C. and E. Siberia to Sakhalin; one of them has a circumarctic range. – In N.E. Europe 2 species living in taiga and tundra zones. Body short. Pronotum with very rough wrinkles.

1 (2). Elytral sculpture irregular, pentaploid, sometimes transitional to heptaploid. Middle antennal segments in males not laterally swollen at apex. Dorsal surface slightly shiny, dull-brown with metallic lustre, margins and primary foveae purplish or coppery-red or green, tibiae, tarsi, sometimes the antennal basis and femora rufous. 15-18 mm. – N.E. of European Russia (in S.W. to Kirov), Siberia to Baikal. In the forests, more often in lower and middle mountain belts. .... **08.001. *C. (Diocarabus) loschnikovii*** Fischer von Waldheim, 1823 (p. 205).

2 (1). Body more elongate, moderately convex. Pronotum densely and strongly punctured, basal part somewhat wrinkled. Elytra with heptaploid sculpture, the primary and adjacent quaternary intervals usually regular, the others often forming more or less irregular granulations. Middle antennal segments in males laterally swollen at apex. Colour of dorsal surface variable: green, coppery-red, brassy or black, primary foveae usually same colour; base of antennae, tibiae, tarsi and sometimes mandibles and femora reddish. 16-21 mm. – N.E. European Russia, N. Siberia and northernmost Alaska and Canada, forest-tundra and southern tundra belts (this species was erroneously included in the next subgenus: 09. *Aulonocarabus* by Turin *et al.*, 1993; see also under *Aulonocarabus*). .... **08.002. *C. (Diocarabus) truncaticollis*** Eschscholtz, 1833 (p. 206).

European specimens are mostly attributed to the subsp. *polaris* Poppius, 1905 (Březina, 1994); these Siberian, Euro-Asian specimens are distinct from N. American specimens in the less convex elytra and more regular sculpture.

09. Subgenus Aulonocarabus Reitter, 1896
Type species *C. canaliculatus* Adams, 1812

Note: this subgenus includes about 12 species, mostly living in forests of temperate E. Asia. Deuve (1991) united them with the representatives of subgenus *Leptocarabus* Géhin, 1876 from Japan, and some authors refer to this group also the circumpolar tundra dweller *C. truncaticollis* Eschsch., in the present keys included in the subgenus *Diocarabus* (see also: Deuve, 1994).

Only one species reaches the easternmost part of Europe. It differs from the other European *Carabus* by the combination of short mandibles, very faible subapical emargination of elytra and sharp primary keels.

1 (1). Black without metallic lustre, elytra often brown, moderately shiny. Head normal with convex eyes, Segments 5-9 of antennae at apex in males laterally swollen beneath. Sides of pronotum (in the European subspecies) feebly sinuate before hind angles, forming short rounded lobes. 22-30 mm. – Russia: Urals, Siberia to the Far East; N. Mongolia, N.E. China, N. Korea. Several subspe-

cies, among them only nominate one (described above) reaches Europe. It lives in taiga forests. .. .. **09.001. *C. (Aulonocarabus) canaliculatus*** Adams, 1812 (p. 207).

10. Subgenus Mesocarabus C. G. Thomson, 1875

Type species *C. catenulatus* Duftschmid, 1812,
nec Scopoli, 1763 = *C. problematicus* Herbst, 1786

Head of normal shape, or thickened, highly macrocephalic (in Iberian species); mandibles short, with deep scrobae; apical segment of palpi slightly dilated in both sexes; penultimate segment of labial palpi multisetose. Setae of submentum present. Pronotum from subquadrate to transverse, with sides widened, more or less bent upwards; basal angles prominent; two lateral setae (one anterior, one basal) present at each side. Elytra ovate to elongate ovate, convex, with highly reduced apical sinuation; elytral sculpture of triploid or heptaploid type; primary intervals catenulate, sometimes in rows of tubercles; intermediate costae smooth or broken, sometimes highly reduced; quaternary intervals often reduced to small granulations, or absent. Abdominal sterna with transversal furrows, with or without setiferous pore. The male tarsi with four basal segments dilated.

The name *Mesocarabus*, adopted in this work, is in agreement with the recent catalogues of Deuve (1994) and Březina (1994, 1999). Zaballos & Jeanne (1994) maintained *Hadrocarabus*, as in Jeannel (1941) and Casale *et al.* (1982). There are four European species (see below, concerning the specific or subspecific status of *C. lusitanicus* and *C. macrocephalus*), and one species in N. Morocco. Some of them are forest dwellers or montane elements (some subspecies of *C. lusitanicus*, *macrocephalus* and *riffensis*); others (*C. problematicus* and *dufourii*) are rather eurytopic, from lowland to high altitudes, often in dry environments; *C. problematicus* has a wide distribution and an exceptional ability to colonize different environments, from sub-mediterranean scrub to boreal territories.

1 (4). Head not, or slightly thickened. Colour mostly blue-violet to greenish-blue or blackish. Elytral sculpture with quaternary intervals rudimentary, or lacking.

2 (3). Pronotum strongly transverse, almost twice as wide as long; sides bent upwards. Elytral sculpture of triploid type, all intervals granulate, only the primary distinctly interrupted by small punctures. Dorsal surface bluish to bluish-black, sides of elytra bluish to violet. 24-28 mm. – Iberian Peninsula S. of Guadalquivir (Andalusia) from Atlantic coast to Sierra-Nevada, from sea level up to 2500 m. .... **10.001 *C. (Mesocarabus) dufourii*** Dejean & Boisduval, 1829 (p. 207).

3 (2). Pronotum subquadrate to moderately transverse, at least 1.6 times wider than long. Elytra with primary intervals catenulate, the intermediate ones more or less reduced or granulated. Dorsal surface mostly black to bronzed, bluish-violet, bluish-black to greenish, 18-32 mm. – Widespread in C. and N. Europe, from E. Spain in the W., to Poland in the E. In the N., its distribution reaches Iceland (only *Carabus*-species) and Murmansk district; in the S. to the Alps and N.W. Italy. .... **10.004 *C. (Mesocarabus) problematicus*** Herbst, 1786 (p. 210).

In lowland and montane forests and pastures, from sea level up to 2500 m, often in rather dry environments. *C. problematicus* is morphologically rather homogeneous in its large range of distribution, its ability to adapt to different ecological conditions greatly limiting the forming of isolated populations. Nevertheless, dozens of infraspecific forms (subspecies, 'nationes', 'morphae', etc. from slight colour variations, small montane specimens, inconstant variability of elytral sculpture and shape of the pronotum) have been described. Examples of bad and incorrect uses of infraspecific names has been criticised by Jeannel (1941) and Casale *et al.* (1982). Also the keys of Breuning (1932-1936) are quite useless for *C. problematicus*. Here we state, with Březina (1994, partim), that only 8 subspecies should be maintained at this moment:

a) subsp. *problematicus* Herbst, 1786 – Pronotum from subquadrate to transverse, with sides slightly narrowed posteriorly and slightly bent upwards. Elytral sculpture broken, scabrous; quaternary intervals fully reduced to faintly indicated rows of granulations. Dorsal surface mostly bluish-black, sides of pronotum and elytra blue to violet. – S. and E. Germany, Austria, Switzerland, S.E. France, N. Italy, Alps, Moravia, Slovakia.

b) subsp. *planiusculus* Géhin, 1885 – Elytral sculpture regular, normally smooth, not granulated; quaternary intervals fully reduced; dorsal surface from blue-violet to greenish or blackish. 20-30 mm. – W. Europe, from N. Spain (Pyrenees, Navarra and Catalonian chain: five subspecies described for this area! See Chapter 2), to C. and W. France.

c) subsp. *inflatus* Kraatz, 1878 – Head large and slightly thickened; pronotum highly transverse, more than 1.5 times wider than long, with sides bent upwards. Elytra wide and convex; secondary and tertiary costae regular and smooth. Dorsal surface blue-blackish, with violet sides. Often large: 26-32 mm. – S.E. France (Provence), Maritime- and Ligurian Alps, N. Apennines, S. Piedmont (Langhe). Transitional populations from *problematicus* (*s.str.*) to *inflatus* Kraatz, living in the W. Alps of Piedmont, have been described as *dellabeffae* Breuning, 1933.

d) subsp. *harcyniae* Sturm, 1815 (= *wockei* Born, 1898) – Intervals convex, the primary ones more distinct, the intermediate confused, granulated. Dorsal surface blackish blue. Size rather large (24-30 mm). – British Isles, S. and C. Norway, Sweden, N. and C. France, Benelux, Denmark, N. and C. Germany, Bohemia, N. Poland.

e) subsp. *strandi* Born, 1926 – Slightly distinct from *wockei*, for the intervals less convex, flattened. – N. and E. Scandinavia, Kola Peninsula.

f) subsp. *feroensis* Vacher de Lapouge, 1910 – Distinct in the very narrow body, the elytral intervals highly broken, granulated. The dorsal surface bronzed to greenish. – Faeroes, Hebrides, Shetland and Orkney Isles. Known as fossil in the Faeroes, referred to either the sub-boreal or subatlantic period, before the colonisation by humans.

g) subsp. *islandicus* Lindroth, 1968 – Black, normally with pronounced metallic reflection along the sides of pronotum and elytra, which are green, golden, copper or brass. Elytral sculpture strong, the primary intervals always more distinct from the others, usuallly broader as well as more convex. Head narrow in proportion to the thorax. Small size: 20-24 mm. – Iceland.

(h) subsp. *relictus* Hellén, 1934 – Known from only one specimen from the Hogland island in the bay of Finland (introduced?).

4 (1). Head large, strongly thickened. Elytral sculpture of heptaploid type, with quaternary intervals more or less distinct. Rather variable, for instance in colour and size: *C. macrocephalus*-complex. Unlike *C. problematicus*, variable in its range of distribution, this complex of species, semispecies, subspecies and local races, represents many highly distinct forms in a rather small area. One species (*C. riffensis* Fairmaire, 1872) is endemic to N. Morocco in the Rif-massif. The other taxa, for which recent authors do not agree in attributing a specific or subspecific status to some taxa (Deuve 1994; Březina 1994; Zaballos & Jeanne 1994), are present in the Iberian Peninsula and Pyrenees. We retain two distinct species (which are, more correctly, two main semispecies: hybrid zones exist among them, and natural hybrids are known between *C. lusitanicus* and *C. macrocephalus* in areas of parapatry).

5 (6). Body short to elongate-ovate, the elytra ovate and convex. Pronotum with sides regularly arcuated, not or slightly sinuous; basal angles rather short, wide and rounded. Aedeagus stout, slightly narrowed in the apical part. 20-34 mm. – All of the Iberian Peninsula, except the N. part. In foothills to fields at high altitude, mostly in rather dry scrubland and forests. .... **10.002 *C. (Mesocarabus) lusitanicus*** Fabricius, 1801 (p. 208).

Several subspecies, for which a major revision is necessary, have been described, often in isolated massifs (Sierras) and mountain chains:

a) subsp. *lusitanicus* Fabricius, 1801 – Pronotum densely rugoso-punctate, with sides slightly bent upwards and basal angles shorter obtuse. Elytral sculpture strong; primary intervals catenulate in rows of tubercles. Elytra wide and short; dorsal surface metallic bronze, sides of pronotum and elytra often green. – Coastal area between Coimbra and Lisboa to Extremadura.

b) subsp. *schaumi* Gaubil, 1849 – Pronotum with fine and scattered punctures and lateral margins more bent upwards. Elytral sculpture distinct but flattened, the primary intervals catenulate, in rows of smaller tubercles. Dorsal surface dark brownish to cupreous-green or green-blackish, the sides narrowly blue-green. – Spain, Central Montane System to C.W. Portugal.

c) subsp. *bolivari* Breuning, 1926 – Pronotum with large and deep punctures. Elytral sculpture strong, but primary intervals catenulate, not in rows of tubercles; primary foveae large, striae deeply punctate. – Spain, Central Montane System: Sierra de Béjar. The characters to distinguish *fuentei* Breuning, 1926, from the Sierra de Gata and Peña de Francia, seem variable.

d) subsp. *brevis* Dejean, 1826 – Body stout, elytra very short and wide. Pronotum with small, fine punctures. Elytral sculpture regular, the primary intervals catenulate, the primary foveae small, the striae slightly punctate. Dorsal surface brownish-green to black, sides green to violet. 20-25 mm. – Spain, Central Montane System: Sierra da Avila and S. de Guadarrama regions.

e) subsp. *complanatus* Dejean, 1826 – Slightly distinct from *brevis* for the dorsal surface green to brownish-bronzed, lateral margin green. – Spain, N. Meseta, Zaragoza, Soria and Burgos regions.

f) subsp. *molossoides* Lassalle, 1984 – General features as in *brevis*, but the primary foveae larger and deeper, head in the females very large and thickened, shoulders more prominent. Dorsal surface bluish-black. Large size, 25-32 mm. – Spain, Central Montane System, W. and C. Sierra de Gredos, Tras la Sierra mountains.

g) subsp. *helluo* Dejean, 1826 – Body short, elytra convex, sculpture slightly flattened; primary punctures very small. Pronotum with small punctures. Dorsal surface bluish-black to brownish-bronzed or greenish. Sides blue-greenish. – Spain, N. Iberian and S. Iberian chains, E. Baetic chain.

h) subsp. *castilianus* Dejean, 1826 – Body elongate-ovate. Sides of pronotum not sinuate, the basal angles obtuse. Elytral sculpture with all intervals broken in granulations. Dorsal surface brownish-bronzed, sides metallic green. – Meseta region of Salamanca.

i) subsp. *egesippei* LaFerté-Sénectère, 1847 – General features as in *castilianus*, but elytral intervals more or less convex, not granulated. Dorsal surface bluish-black, sides green to blue-violet. – Mountains of N. Portugal.

j) subsp. *antiquus* Dejean, 1826 – Body ovate, short. Pronotum posteriorly narrowed, with basal angles short, rounded. Elytral sculpture like *lusitanicus* (*s.str.*), strong, the primary intervals wider than the other, broken in rows of tubercles; primary punctures large and deep. Dorsal surface brownish-bronzed to green. – S. Portugal and S.W. Spain, N.E. to Salor and Zapaton rivers.

k) subsp. *albarracinus* Gangbauer, 1886 – General features as in *antiquus*, but primary intervals lower, not in rows of tubercles. Pronotum finely punctate. Dorsal surface highly shiny, bronzed-black to bluish-black. – Spain, Sierra de Albarracin and Sierra de Cuenca.

l) subsp. *latus* Dejean, 1826 – Ovate, short. Distinct from *albaracinus*, for the pronotum densely punctate, the primary intervals more convex, surface smooth. – Spain, S. Meseta, to the Sierra Morena, to E. to the Toledo and Cordoba regions.

m) subsp. *baguenai* Breuning, 1926 – Ovate, short. Pronotum finely punctate. Elytral sculpture with all intervals of the same size, primary intervals flattened, primary punctures very small, striae with smallest punctures. Dorsal surface bluish-black to black, sides blue to violet. – Spain, N. Baetic chains, Almeria and Granada regions.

n) subsp. *trabuccarius* Fairmaire, 1857 – General features as in *baguenai*, but pronotum more densely punctate, elytral intervals convex, elytral striae with distinct punctures. *C. problematicus*-like. – Spain, Catalunian chain, E. and C. Pyrenees. Very small specimens at high altitude, from Central Pyrenees (Ordesa, Cinca and Esera valleys) have been described as *trypalsi* Breuning, 1975.

6 (5). Body elongate to ovate-elongate, more slender than in subspecies of *lusitanicus*. Pronotum large, transverse, with sides arcuate, posteriorly bent upwards, and basal angles strongly prominent from the posterior side. Aedeagus elongate, highly narrowed in apical part. – N. Spain, from W. Galicia to the Sierra de Andia. France, W. Pyrenees in the subalpine and alpine zone, mostly from 1000 up to 2000 m. .... **10.003. *C. (Mesocarabus) macrocephalus*** Dejean, 1826 (p. 209).

The most evident subspecies are:

a) subsp. *macrocephalus* Dejean, 1826 – Elytra elongate-ovate; primary intervals catenulate, secondary intervals costate, normally more convex than the quaternary. Dorsal surface bronzed or cupreous-brown to metallic-greenish. – W., C. Cantabrian chain.

b) subsp. *macrocephaloides* Jeanne, 1972 – Elytra elongate-ovate, shorter and more convex than in *macrocephalus* (*s.str.*). Elytral sculpture more flattened, all intervals of the same size. Dorsal surface mostly bronzed-greenish, sides metallic green. – N.E. Spain, Sierra de Andia.

c) subsp. *cantabricus* Chevrolat, 1840 – Elytra elongate, narrow, more or less depressed. Elytral sculpture low, fine, regular; all intervals of the same size; primary punctures very small. Dorsal surface dull, bluish-black, the lateral margins violet. – Mountains of Galicia.

d) subsp. *asturicus* Born, 1925 – Some general features as in *macrocephalus* (*s.str.*): quaternary intervals reduced, primary punctures large, distinct. Elytra more elongate, or subparallel. Dorsal surface bluish-black to black-violet. – W. Cantabrian Mountains.

e) subsp. *joaquini* Breuning & Toulgoët, 1974 – Same general features as in *asturicus*, but elytra more narrowed to base and more convex. Dorsal surface bronzed-green to bluish-green. – S. side of W. Cantabrian Mountains.

f) subsp. *moroderi* Breuning, 1926 – Elongate-ovate, elytra convex. Pronotum wide, with sides arcuate and bent upwards. Sculpture regular, flattened, all intervals of same size. Primary intervals very small. Dorsal surface shiny, brownish-bronzed to black, sides green to bluish. – Spain, mountains of Léon.

This subspecies, and the following, are transitional forms to *lusitanicus* (the specific separation of the latter from *macrocephalus* by Zaballos and Jeanne (1994), therefore questionable).

g) subsp. *breuningi* Csiki, 1927 – Slightly distinct from *moroderi*. Elytral sculpture more convex, pronotum slightly narrowed towards base, dorsal surface duller, bronzed-green to dark-violet. – Spain, S. Galicia.

h) subsp. *barcelecoanus* Vacher de Lapouge, 1924 – According to Deuve (1994) and Březina (1999), *barcelecoanus* is markedly distinct from *macrocephalus* (*s.str.*). Characterised by narrow, elongate body and reduced sculpture – N.C. Spain (Santander to Pomplona), E. Cantabrian chain, W. Pyrenees on both sides.

11. Subgenus Orinocarabus Kraatz, 1878

Type species *Carabus sylvestris* Panzer, 1793

Mandibles short, with deep scribe. Palpi thin, elongate. Apical segment of palpi slightly dilated in both sexes; penultimate segment of labial palpi bisetose. Apex of antennae in the males mostly with some segments ventrally depressed and laterally swollen. Pronotum from subcordate to transverse, with sides not or slightly bent upwards; several (2-3 antero-mediane, 1 basal) lateral setae present on each side. Elytra from depressed to subconvex, with apical sinuation distinct; elytral sculpture of triploid (without quaternary intervals) to heptaploid type, all intervals low, the primary ones broken by more or less large, deep punctures, often also breaking the adjacent quaternary intervals. Abdominal sterna without transverse furrows, or with furrows reduced, vanishing in the middle. Four basal segments of male protarsi with ventral pad of lamellae.

In the narrow sense adopted here, so excluding the Asian and boreal species mostly attributed to this subgenus by Breuning (1932-1936), *Orinocarabus* is a homogeneous group of montane, small to medium-sized species, peculiarly distributed in C.E. Europe, and in the

Alpine chain. Deuve (1994) included *Orinocarabus* in *Oreocarabus* (see p. 41 in Chapter 2). In our opinion however, it seems difficult to group the European species, traditionally included in *Orinocarabus*, with for example very large, convex, black species, such as *C. (Oreocarabus) titanus* Breuning (from the forests of Southern China), on the basis of either morphological characters or geographical distribution. Furthermore, phylogenetic molecular studies (see Chapter 7 and Imura *et al.*, 1998), confirm the separation of *Orinocarabus* from *Oreocarabus*). We treat *Orinocarabus* as a monophyletic or paraphyletic unit. One species for which it could be possible to maintain a distinct subgenus (*Carpatophilus* Reitter, 1896), is *C. linnaei* Panzer, 1812, that Březina (1999) recently attributed to *Oreocarabus*. Furthermore, Imura (1998) has recently proposed the new subgenus *Cavazzutiocarabus* for *latreilleanus* Csiki, 1927, supported bu molecular and genital features, and apparently remote from the *Orinocarabus*-cluster.

In forests of C. and E. Europe, and at high altitudes (from 1500 to 3000 m) in the Alps. Several very similar species, which are difficult to identify on external features, highly characterised, however, by the morphology of the male genitalia (see Casale *et al.*, 1982). The (sub)specific status of some of them (*cenisius-fairmairei* complex) has to be confirmed.

1 (2). Head small; antennae very long, segments 5-9 slightly swollen laterally at apex in the male; pronotum narrow, with sides subsinuous and bent upwards. Elytra wide, ovate, flattened, with prominent shoulders. Sculpture of pentaploid type, i.e. five intervals between the primary ones. Legs long, fore femora with anterior furrow limited to the apical region. Dorsal surface cupreous-brown; head, pronotum and primary punctures metallic cupreous to greenish; tibiae and base of the antennae reddish. Aedeagus: Fig. 3.8. 16-21 mm. – C. and E. Europe, from Central Germany, Switzerland and Austria to the Carpathian Mts. to W. Ukraine; in Italy only in the E. Alps, from E. Lombardia to the Venetian Alps and Prealps. In *Fagus* and *Abies* forests, at 800-1500 m, to alpine meadows at 2000 m in the Italian Prealps.......... .... **11.011. *C. (Orinocarabus) linnaei*** Duftschmid, 1812 (= *linnei* Panzer, 1813) (p. 218).

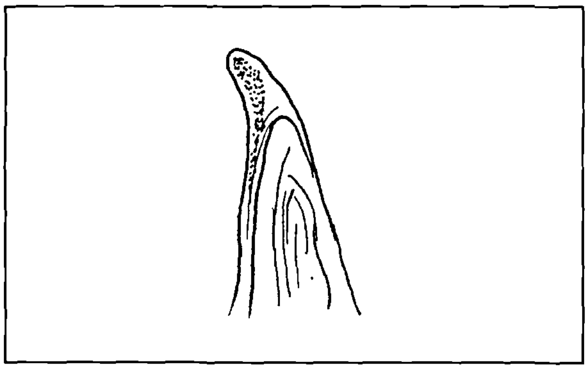


Fig. 3.8. Aedeagus of *C. (Orinocarabus) linnaei.*

2 (1). Head larger, more thickened. Pronotum from subquadrate to transverse, with sides not or slightly bent upwards. Elytral shape ovate to elongate-ovate, sometimes subparallel, from depressed to subconvex and with smooth shoulders. Sculpture of triploid to heptaploid type, i.e. three (*C. latreilleanus*) to seven intervals between the primary ones. Legs short and stouter; fore femora with anterior furrow not reduced. Dorsal surface of variable colour, mostly bronze to cupreous, greenish or blackish; tibiae and base of antennae mostly brown-blackish (except in some specimens of *C. sylvestris*).

3 (4). Segments from 5 (or 6) to 10 of male antennae swollen laterally at apex. Abdominal sterna with transverse furrows distinct at all sides. Aedeagus very long and thin, turned, with apex strongly dilated, dorsally protruded-serrated or axe-shaped (Fig. 3.9a-d). 18-24 mm. – Ligurian, Maritime and S. Cottian Alps. In montane landscapes, from 1700 to 3000 m............................... .... **11.012. *C. (Orinocarabus) putzeysianus*** Géhin, 1876 (p. 219).

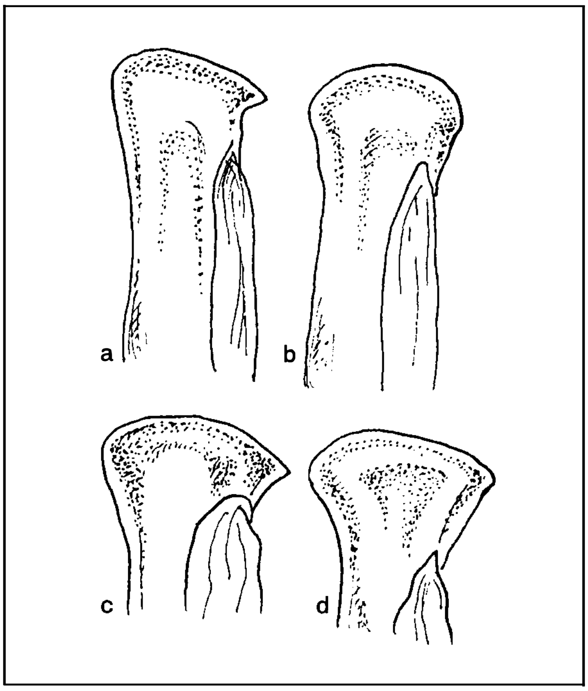


Fig. 3.9. Aedeagus of *C. (Orinocarabus) putzeysianus.*
a – *C. (O.) putzeysianus* ssp. *omensis*; *b* – *C. (O.) putzeysianus* ssp. *pedemontanus*; *c* – *C. (O.) putzeysianus* ssp. *putzeysianus* ; *d* – *C. (O.) putzeysianus* ssp. *germanae.*

Several subspecies have been characterised, mostly using the shape of the aedeagus:

a) subsp. *putzeysianus* Géhin, 1876 – Elytra subdepressed, ovate-elongate; primary foveae small. Surface often metallic-greenish. Aedeagus slightly turned, with apex widened and asymmetrical, rounded on the ventral side, toothed dorsally (Fig. 3.9c). – Ligurian and Maritime Alps, from the Roya Valley to Stura di Demonte Valley on the Italian side, and the Vallée de la Vésubie on the French side.

b) subsp. *raynaudianus* Deuve & Simard, 1977 – Body depressed, elytra wide, colour from bronze to cupreous green. External features closer to *putzeysianus* (*s.str.*), but characters of aedeagus more similar to that of subsp. *omensis*. – Maritime Alps: Colla Lunga area.

c) subsp. *germanae* Casale & Cavazzuti, 1976 – Similar to *putzeysianus* (*s.str.*) for external features, normally smaller, with dorsal surface bronze to cupreous-brownish. Aedeagus with apex symmetrically and strongly widened, axe-shaped (Fig. 3.9d). – Ligurian Alps: Mt. Saccarello, M. Fronté and Mt. Bertrand.

d) subsp. *omensis* Born, 1901 – Same characters as in *putzeysianus* (*s.str.*), bronze to greenish, often more convex. Aedeagus with apex slightly widened, rounded at the ventral side, toothed dorsally (Fig. 3.9a). – Maritime and Cottian Alps, from the Stura di Demonte Valley and the Maira Valley.

e) subsp. *pedemontanus* Ganglbauer, 1892 – Elytra shorter and more convex. Primary punctures large and deep. Dorsal surface mostly bronze to cupreous-brownish. Aedeagus very long, strongly turned, with apex symmetrically dilated, but rounded both on the dorsal and ventral sides (Fig. 3.9b). – Ligurian Alps, from Mt. Marguareis (Tenda Pass) to Pesio, Ellero and Corsaglia Valleys.

f) subsp. *bisioi* Cavazzuti & Meli, 1999 – Morphological features as in *putzeysianus putzeysianus*, but body more slender and depressed; pronotum smaller and narrower at base; integument more dull, colour dark greenish to blackish. Aedeagus similar to that of ssp. *omensis*, but apex much narrower, more rounded at the ventral side, the dorsal tooth more reduced in size. – Cottian Alps, Colle di Bellino and La Colletta, between the Maira an the Varaita Valleys, at high altitude (2750-3000 m). Sympatric with *C. (O.) faimairei pelvicus*.

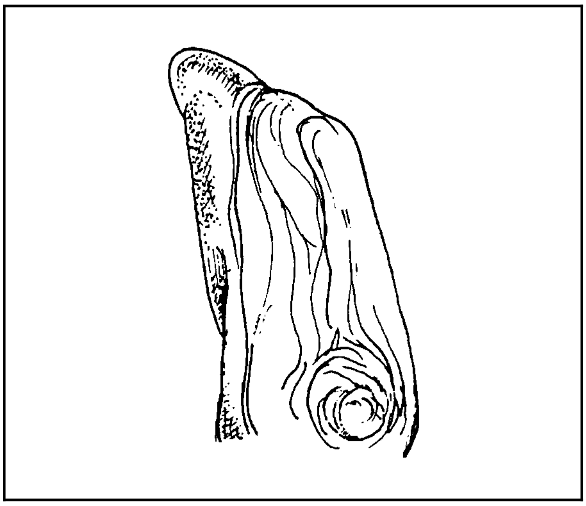


Fig. 3.10. Aedeagus of *C. (Orinocarabus) carinthiacus*.

4 (3). Segments of male antennae from 5 (or 6) to 8 (or 9 in *castanopterus* and *alpestris* from the C. and E. Alps) swollen laterally at apices, or almost simple in both sexes (*latreilleanus*). Abdominal sterna without transverse furrows. Aedeagus regularly arcuate, not or slightly dilated at apex.

5 (6). Body stout, ovate-elongate, convex. Elytral sculpture of heptaploid type; primary intervals catenulate, broken by small, concolorous, nonmetallic punctures. Intermediate intervals mostly confused, granulated. Dorsal surface black to blackish-bronze. Aedeagus large, stout; apex wide, short, widely rounded distally, depressed at the sides (Fig. 3.10). 18-24 mm. – E. Alps, in Italy from the Adige Valley to Friuli; S. Austria, Carinthia; N.W. Slovenia. Some isolated populations exist in the mountains of Bosnia. At altitudes, less than other *Orinocarabus*-species, mostly in high *Fagus* and *Picea* forests, from 1000 to 1500 m. .... **11.004. *C. (Orinocarabus) carinthiacus*** Sturm, 1815 (p. 214).

6 (5). Body usually less convex or depressed. Elytral sculpture regular, distinct, the intermediate intervals (except the quaternary ones if present) not granulated. Dorsal surface metallic, bronze to greenish or cupreous, less frequently blackish. Primary punctures concolorous to metallic. Aedeagus of different shape.

7 (8). Antennae simple in both sexes, in the male the median segments merely a little laterally swollen at apex. Pronotum wide at the base, with sides rounded and narrowed anteriorly. Elytra short, rather wide, strongly depressed; quaternary intervals fully reduced (triploid sculpture), primary punctures strongly emarginated at the anterior side, 'heart-shaped'. Dorsal surface polychromous, bronze to cupreous-red or -green, often two-coloured; the head, pronotum and primary punctures cupreous, the elytra greenish. Aedeagus strongly thickened in the medial part. Body slender, small: 13-18 mm. – An isolated species for which a distinct subgenus has been proposed: see above, discussion of *Orinocarabus*). Endemic to the Pennine and N.E. Grajan Alps, in the Monte Rosa Massif (both on the Italian and Swiss sides) and in the E. Gran Paradiso-Levanna Massif. From montane (1500 m) to high altitude alpine pas-

tures (2600-2800 m), near the snow. Sympatric in Mt. Rosa with *C. (O.) concolor*, and in Gran Paradiso with *C. (O.) heteromorphus*. ....
.... **11.010. *C. (Orinocarabus) latreilleanus*** Csiki, 1927 (p. 218).

8 (7). Male antennae with several segments depressed and notched ventrally. Pronotum more or less cordate and narrowed at the base, anteriorly. Elytra often more elongate and convex; quaternary intervals distinct (heptaploid sculpture), primary punctures rounded, foveolate, not emarginated at the anterior side.

9 (12). Apex of aedeagus very long and strongly arcuate on the ventral side, hooked (Fig. 3.11).

10 (11). Pronotum with sides slightly sinuate in the posterior half. Dorsal surface bronze with metallic cupreous-golden or greenish lustre, sometimes brownish to bronze-blackish. Apex of aedeagus widened slightly (Fig. 3.11a). Smaller size: 15-23 mm. – Pennine Alps, from Mt. Bianco Massif and Mt. Rosa Massif on both sides, east to Valgrande and the Tessin Alps; Swiss Alps in the N. to region of Berna. Alpine pastures from 1600 to 3000 m, exceptionally, also in montane forests at 1300-1500 m. Depressed, elongated specimens of the high Aosta Valley have been described as *bernhardinus* Kraatz, 1878; small high-altitude specimens from Mt. Rosa Massif have been described as *alpinus* Dejean, 1826; large specimens with widened pronotum from Biellese (Sessera and Sesia Valleys), have been described as *amplicollis* Kraatz, 1878. We believe these names to be synonyms of *concolor* (*s.str.*). However, *C. lepontinus* (see below) appeares to be specifically distinct on the basis of constantly differing features, such as the shape of the aedeagus and the lack of intermediate forms; this was recently confirmed by sympatric findings of *concolor* and *lepontinus*, in Val Grande (Lepontine Alps) (Vigna Taglianti *et al.*, 1998). ....
.... **11.007a. *C. (Orinocarabus) concolor*** Fabricius, 1792 (p. 216).

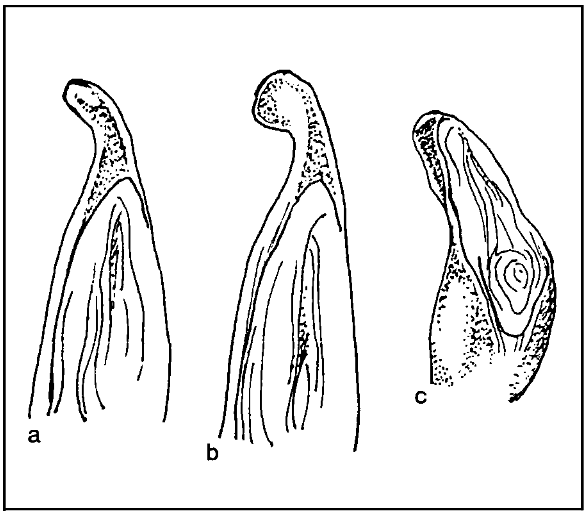


Fig. 3.11. Aedeagus of *C. (Orinocarabus) concolor* (a), *C. (O.) lepontinus* (b), and *C. (O.) heteromorphus* (c).

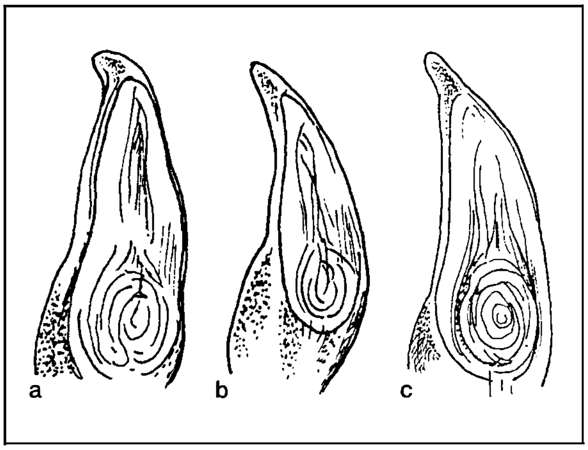


Fig. 3.12. Aedeagus of *C. (Orinocarabus) fairmairei* ssp. *fairmairei* (a), *C. (O.) cenisius* ssp. *cenisius* (b), and *C. (O.) alpestris* (c).

11 (10). Pronotum cordate, with sides distinctly sinuous in the basal half. Dorsal surface consistently darker, brownish to bronze-blackish. Apex of aedeagus turned and distinctly widened (Fig. 3.11b). Larger size: 20-25 mm. – W. Lepontine Alps, E. side of Toce Valley, Mt. Zeda, Mt. Limidario, Pizzo Marone, Cima Laurasca, Valgrande and Cannobina Valley. ....
.... **11.007b. *C. (Orinocarabus) lepontinus*** Born, 1908 (p. 216).

12 (9). Apex of aedeagus slightly arcuate, narrowed to rounded or obtusely truncated, not hook-shaped.

13 (14). Apex of aedeagus truncated (Fig. 3.11c). Antennal segments 5-9 swollen laterally at apex in the male. Elytral sculpture of heptaploid type, primary intervals catenulate; primary punctures breaking both the primary and the adjacent quaternary intervals. Dorsal surface bronze, to bronze-cupreous or bronze greenish, sides with metallic bronze, to greenish lustre. 17-22 mm. – N. Grajan Alps, in the Gran Paradiso Massif. In Levanna Massif substituted by the vicariant (and close) *C. (O.) cenisius* Kraatz, 1878. In alpine pastures from 1700-3000 m. W. Alps: *cenisius*-complex (see below). ....
..... **11.009. *C. (Orinocarabus) heteromorphus*** K. Daniel, 1896 (p. 217).

14 (13). Apex of aedeagus narrowed, or obtusely rounded, never truncated (Fig. 3.12).

15 (20). Apex of aedeagus more or less elongated, narrow and arcuate on the ventral side (Fig. 3.12).

16 (19). Apical half of aedeagus thickened, more or less sinuate on the ventral side, shortly narrowed only distally (Fig. 3.12a,b). W. Alps. .... ***cenisius***-complex.

17 (18). Body short, stout, wide, more depressed. Antennal segments from 6-8 swollen distally in the male. Apex of aedeagus distinctly turned to the right in dorsal view (Fig. 3.12.a). Dorsal surface bronzed to bronzed-green, less frequently cupreous, brownish, golden-greenish or bluish-black. 16-22 mm. – W. (Cottian) Alps. Italy: from Germanasca Valley to Maira Valley. France: Briançon and Queyras Alps. Alpine pastures from 1500-2800 m. .... **11.008. *C. (Orinocarabus) fairmairei*** C. G. Thomson, 1875 (p. 216).

Some subspecies have been described. On the other hand, we retain *heteromorphus, faimairei* and *cenisius* (see Casale *et al.*, 1982) as three semispecies that recent authors (see Deuve 1994) consider subspecies of a single species:

a) subsp. *fairmairei* C. G. Thomson, 1875 – Body more elongate. Primary punctures more numerous and rather superficial. Apex of aedeagus short, obtusely rounded distally. 18-22 mm. – Monviso Massif, high Pellice Valley.

b) subsp. *pelvicus* Cavazzuti, 1973 – Few primary punctures, large and deep. Apex of aedeagus more elongated and narrower. – High Varaita (Bellino) Valley and Maira Valley.

c) subsp. *stecki* Born, 1902 – Body very short, primary punctures numerous and very small. Small size: 16-19 mm. Apex of aedeagus rather long, depressed on the sides, and only slightly turned to the right. – Cottian Alps on the transalpine (French) side, in Italy in high Germanesca Valley and in Varaita (Chianale) Valley.

18 (17). Body elongate, more convex. Antennal segments 6-8 laterally swollen at apex in the male. Apex of aedeagus straight, not turned to the right and slightly on the ventral side (Fig. 3.12b). Dorsal surface bronzed or bronzed-green to cupreous-brown, less frequently greenish to bluish-black. 18-25 mm. – W. Alps, from N. Cottian Alps (Mt. Albergian) to Grajan Alps (Levanna Massif: in this area as southern vicariant of *C. heteromorphus*). On the French side, in the Haute-Maurienne, Haute Tarentoise and Vanoise. In alpine pastures from 1600 to 2700 m. .... **11.006. *C. (Orinocarabus) cenisius*** Kraatz, 1878 (p. 215).

Closely related to *C. (O.) faimairei* (see above). Some subspecies rather distinct:

a) subsp. *cenisius* Kraatz, 1878 – Body more elongated and slender. Pronotum narrowed to the base. Apex of aedeagus elongate and arcuate, narrower, sub-acuminate distally (Fig. 3.12b). – W. (N. Cottian) and Grajan Alps, both on the French and Italian sides. In Italy from Stura di Viù Valley to Mocenisio and Dora Riparia (Susa) Valley. *Note*: specimens from Savoie (Iseran Massive) have been described as *iseranicus* Deuve & Simard, 1977; they could represent a transitional form (hybrid zone) to *heteromorphus*.

b) subsp. *ceresiacus* Born, 1896 – Apex of aedeagus less narrow, more stout and obtusely rounded distally. – Grajan Alps, from Stura di Lanzo to Lavanna Massif.

c) subsp. *fenestrellanus* Beuthin, 1899 – Body stouter and wider. Pronotum transverse. Aedeagus larger, with apex short and wide. – Cottian Alps, mountains from the right side of the Susa Valley to Chisone (Mt. Albergian) Valley.

19 (16). Apical half of aedeagus regularly arcuate and narrowed to the apex, which is elongate, a little depressed on the dorsal side, rounded distally (Fig. 3.12c). Body elongate-ovate. Antennal segments 5 (or 6) to 10 laterally swollen at apex in the male. Dorsal surface brownish-bronze to cupreous, bronzed-green, or blackish with bluish or greenish lustre. 16-21 mm. – E. Alps on both sides. From Dolomiti and Tyrol in the west, to Slovenia in the east. In alpine forests, mostly from 1700 to 2700 m, exceptionally at 1100 m in Slovenia (Planica). In some localities sympatric with *C. (O.) bertolinii*, or with *C. (O.) carinthiacus*. .... **11.002. *C. (Orinocarabus) alpestris*** Sturm, 1815 (p. 213).

Some subspecies rather distinct:

a) subsp. *alpestris* Sturm, 1815 – Body more elongate, narrow, sub-depressed. Pronotum narrowed to base, basal

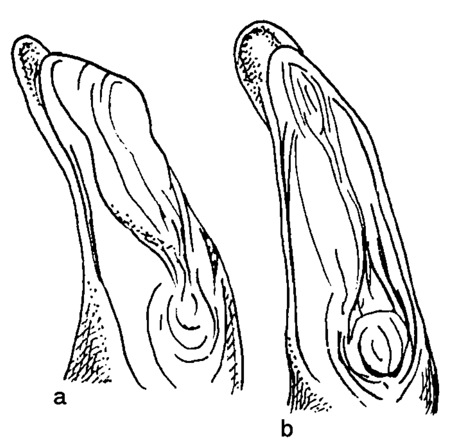


Fig. 3.13. Aedeagus of *C. (Orinocarabus) sylvestris* (a) and *C. (O.) bertolinii* (b).

angles acute and prominent. Aedeagus slightly arcuate, apex shorter, ventral side not thickened. – South and Central lower Austria to Styria.

b) subsp. *dolomitanus* Mandl, 1956 – Distinguished from *alpestris* (*s.str.*) by the shape of the aedeagus, with ventral side more thickened, convex. – E. Alps, Dolomites, east and central parts of the Pusteria Valley, Carnian and Julian Alps, N. Slovenia, Karawanke and Saviniche Alps.

c) subsp. *hoppei* Germar, 1824 – Body shorter, stouter and more convex. Pronotum slightly narrowed to base, basal angles shorter and obtuse. Aedeagus strongly arcuate, apex more elongate. – Austria: from Tyrol to Klagenfurt. Italy: Pusteria Valley, Aurina Valley and Vizze Valley.

20 (15). Apex of aedeagus blunt and rounded, or depressed at the sides, spatulate or blade-shaped and turned on the dorsal side (Fig. 3.13a,b).

21 (24). Apex of aedeagus very short, distally rounded. Antennal segments 5-9 laterally swollen at apex in the male.

22 (23). Apex of aedeagus very wide, rounded (Fig. 3.13a). Body short-ovate to elongate-ovate. Pronotum transverse, narrowed to the base, with lateral margins posteriorly a little bent upwards. Elytra more or less convex; primary intervals catenulate, primary punctures metallic. Dorsal surface variable in colour, brownish-bronze to cupreous-bronze, golden to cupreous-green or bluish-black; tibiae brownish-black to reddish. 19-29 mm. – C. Europe, from France (Vosges) and Switzerland (Jura) in the W., to Transylvania and Carpathian Ukraine in the east. Alpine chain on the northern side, in Italy only in some areas at the border with Switzerland and Austria. In some localities sympatric with *C. (O.) alpestris*. .... **11.013. *C. (Orinocarabus) sylvestris*** Panzer, 1796 (p. 220).

Some subspecies rather distinct:

a) subsp. *sylvestris* Panzer, 1793 – Apex of aedeagus slightly arcuate. Pronotum with basal angles prominent. Dorsal surface light cupreous to golden-brown or blackish (*nivosus* Heer, 1837). – From Vosges and Jura, Switzerland, C. Germany, eastward to Bohemia and Moravia, to the S. in Italy, in some localities of the C. Alps.

b) subsp. *kolbi* Breuning, 1927 – Apex of aedeagus a little sinuous. Pronotum with dense, large punctures and basal angles very prominent to the basal side; elytra slightly convex. Dorsal surface shiny. – E. Alps, S.E. Austria, Slovenia.

c) subsp. *redtenbacheri* Géhin, 1876 – Distinguished from *kolbi* by the basal angles of pronotum being short, slightly pronounced of the basal side. Dorsal surface more smooth. – S.E. Austria.

d) subsp. *transylvanicus* Dejean, 1826 – Characterised by the pronotum having small and scattered punctures, the elytra very convex; dorsal surface highly metallic shiny. – Carpathian Mountains, to S. Poland, Slovakia, Ukraine and Romania.

e) subsp. *haberfelneri* Ganglbauer, 1892 – Apex of aedeagus strongly arcuate, widened. Pronotum with sides bent upwards and basal foveae deep. – S.E. Germany (Bavaria), N. and C. Austria.

23 (22). Apex of aedeagus narrow, subconical (Fig. 3.13b). Body elongate-ovate, sometimes parallel-shaped, rather convex. Pronotum transverse, with sides slightly sinuous in the basal half. Elytral sculpture as in *sylvestris*. Dorsal surface bronze-brownish to cupreous or greenish, sometimes bicoloured; primary punctures bronzed to green or bluish. Tibiae always brownish-black. 16-21 mm. – Trentino (Dolomiti), Veneto (Belluno), and Friuli Prealps. Specimens from the last localities, with a wide base of pronotum and elytra more depressed along the suture have been described as *cavallensis* Bernau, 1914. Alpine pastures, from 1600 to 2900 m. .... **11.003. *C. (Orinocarabus) bertolinii*** Kraatz, 1878 (p. 213).

24 (21). Apex of aedeagus elongated, blade shaped or spatulate (Fig. 3.14). Antennal segments 5-9 (or 10) laterally swollen at apex in the male. Dorsal surface minimally variable, dark, bronze-brownish to bronze-greenish (*castanopterus*-complex).

25 (26). Apex of aedeagus a little narrowed, spatulate (Fig. 3.14a). Antennal segments 5-10 laterally swollen at apex in the male. Pronotum densely rugoso-punctate. Elytra rather convex; elytral sculpture heptaploid, all intervals slightly convex; primary

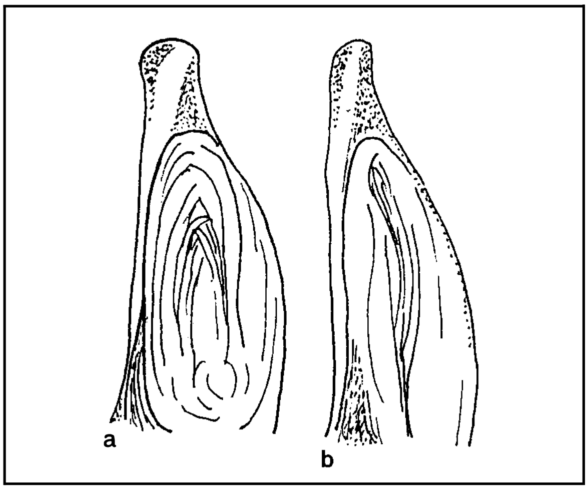


Fig. 3.14. Aedeagus of *C. (Orinocarabus) castanopterus* (a) and *C. (O.) adamellicola* (b).

punctures small and deep. Dorsal surface bronze to bronze-blackish, sometimes the sides of elytra with greenish lustre. 18-22 mm. – Endemic to the C. Alps on the S. side; E. Lepontine Alps (Tessin Alps), Orobian (Bergamascan) Alps, Valtellina, E. to Valcamonica Valley. Alpine pastures, 1600 to 2500 m. ....
.... **11.005 *C. (Orinocarabus) castanopterus*** A & G.B. Villa, 1833 (p. 214).

26 (25). Aedeagus shorter and more slender than in *castanopterus*, blade-shaped and a little turned to the dorsal side (Fig. 3.14b). General features and colour as in *castanopterus*, angles of the pronotum more prominent, the primary intervals of the elytra more distinct, with primary punctures larger, breaking three contiguous intervals; 17-21 mm. – Endemic to the C.E. Italian Prealps, Adamello and Brenta massifs, from Brescia (Oglio Valley) to Adige Valley. In limestone massifs, from 1600 to 2500 m. ....
.... **11.001 *C. (Orinocarabus) adamellicola*** Ganglbauer, 1904 (p. 212).

12. Subgenus Oreocarabus Géhin, 1876.

Type species *Carabus errans* Gory, 1839, not Fischer, 1823
(= *amplipennis* Vacher de Lapouge, 1924)

Male antennal segments 6 to 8 strongly depressed at the base and swollen distally and apical segment of maxillary palpi slightly widened in the male; penultimate segment of labial palpi bisetose, sometimes trisetose. Sides of pronotum widely margined and more or less bent upwards, particulary at the basal part; two lateral (one anterior, one basal) setae on each side. Elytra ovate, more or less convex, normally with sides widened and bent upwards; elytral sculpture of homodynamous, heptaploid type, with primary foveae extended sometimes to the contiguous interstriae, or granulated, confused, without distinct intervals. Abdominal sterna with, or without transverse furrows.

A wide, but (in the present limitation to European species) rather homogeneous subgenus. Deuve (1994) included in *Oreocarabus* the species that were (and here are) attributed to *Orinocarabus*. Furthermore, Březina (1994) maintained some species in distinct, often monotypic, subgenera, e.g.: *Phricocarabus* Reitter, 1896 for *C. glabratus* Paykull, 1790, but later (1999) he treated again *Oreocarabus* as a wide subgenus, and attributed also *linnaei* to it, which species is included here in *Orinocarabus*. We think that *Oreocarabus*, in the rather narrow sense adopted here, is a monophyletic (although, perhaps, paraphyletic) unit.

1 (6). Abdominal sterna with distinct, deep and complete transverse furrows.

2 (3). Elytra smooth with very reduced, almost indistinct, finely granulate intervals; primary foveae lacking or reduced to small, concolorous points. Dorsal surface uniformly black, shiny to sericeous; elytra strongly convex. 22-34 mm. – N. and C. Europe, from E. European Russia and W. Siberia to E. France and N.W. Italy (in Toscana to the S.); N. England, Fennoscandia. In bushes and open country, from lowlands to montane forests and pastures at 1200-1800 m. ....
.... **12.003. *C. (Oreocarabus) glabratus*** Paykull, 1790 (p. 223).

Morphologically rather homogeneous through its distribution. Some subspecies can be distinguished:

a) subsp. *glabratus* Paykull, 1790 – Elytra finely granulated, dorsal surface shiny. 26-34 mm. – C. and N. Europe, W. Siberia.

b) subsp. *extensus* Kraatz, 1885 – Dorsal surface more shiny than in the nominate subspecies. Body more elongate, pronotum cordate, sides deeply sinuous. – Carpathian Mountains.

c) subsp. *lapponicus* Born, 1909 – Body short: 22-26 mm. Dorsal surface dull, sericeous. – Lapponia to the Kola Peninsula.

d) subsp. *gibbosus* Heyden, 1866 – Body short, as in *lapponicus*. Dorsal surface very shiny. – E. montane form of Austria, Balkans and Transylvania.

e) subsp. *latior* Born, 1895 – Large size: 25-32 mm. Pronotum very transverse, elytra dull, with slight bluish reflections. Further investigations demonstrated that this southern form, cited as a synonym of *glabratus glabratus* by Casale *et al.* (1982), merits a subspecefic rank. – N. and C. Italy (from the Alps to Tuscania).

3 (2). Elytra with regular, finely costate intervals; primary foveae metallic, distinct. Dorsal surface brownish to blue-blackish or greenish, not so shiny. Elytra depressed. *C. hortensis*-complex: two semispecies are recognised, *hortensis* and *preslii*, treated here as distinct species (see Casale *et al.*, 1982), but listed by several authors (see Deuve, 1994) with subspecific rank.

4 (5). Pronotum with sides slightly bent upwards posteriorly; body elongate, convex; dorsal surface dark brownish to cupreous or greenish, elytra with large metallic cupreous or greenish primary foveae. Aedeagus with apex sharply acuminate. 23-30 mm. – N. and C. Europe; Alps; Balkan Peninsula to parts of Bosnia, Montenegro and Macedonia. In bushes and open country, from lowlands to montane forests. ....
.... **12.005. *C. (Oreocarabus) hortensis*** Linnaeus, 1758 (p. 225).

5 (4). Pronotum with sides strongly bent upwards posteriorly; body ovate, shorter and more flattened; dorsal surface bluish-black to bluish-violet, sometimes with greenish lustre; primary foveae small, metallic green, blue or violet. Aedeagus short, obtuse at apex. 22-27 mm. – W. Balkans: from Albania to Pelopponesos, S. Dalmatian coast, including Dalmatian and Ionian islands; S. Apennines (from Campania to Aspromonte). A typical transadriatic-transionic element. From mediterranean bushes along the coasts, to montane forests. .... **12.006. *C. (Oreocarabus) preslii*** Dejean & Boisduval, 1830 (p. 227).

Two main subspecies can be recognised:

a) subsp. *preslii* Dejean, 1830 – Pronotum with basal angles short, wide and obtuse. Primary foveae small, breaking only the primary intervals. – Greece, Pelopponesos. A distinct form was described from the Panakhaion Massif, S.W. of Patra ((ssp.) *pecoudellus* Deuve, 1998).

b) subsp. *neumeyeri* Schaum, 1856 – Pronotum with basal angles long, acuminate. Primary foveae normally larger, often breaking two contiguous intervals. – Adriatic coast, from Montenegro to Croatian coast, N. and C. Greece. Italy: S. Apennines (Campania, Basilicata, Calabria). According to Deuve (1994), the (ssp.) *herzegowinensis* from Bosnia-Herzegovina, and (ssp.) *jonicus*, from Kerkyra, S. Albania and Pyndos (*pindicus*), seem to be distinct from both *preslii* (*s.str.*) and *neumeyeri*.

6 (1). Abdominal sterna with transverse furrows more or less interrupted in the middle, or completely lacking. *C. amplipennis*-complex. A taxonomically difficult group of Iberian species and subspecies. Deuve (1994) and Březina (1994) recognised three species (two of them polytypical). Zaballos and Jeanne (1994) also listed *getschmanni* and *pseudosteuarti* as distinct species. In absence of a revision of these taxa we have adopted here the traditional treatment.

7 (8). Abdominal furrows sharp but interrupted in the middle. Dorsal surface dark brownish, sides of pronotum cupreous to bluish, sides of elytra metallic green or bluish. Body relatively short and wide; pronotum with angles arcuate, not sharply sinuous; elytral sculpture regular, fine; primary points very small, concolorous, nonmetallic, 20-25 mm. – Spain: Central Montane System, from Sierra de Gata to Sierra de Guadarrama; Hyberian chain, N.W. of the Sierra de la Demanda; N. Baetican chains. In bushes and forests. .... **12.004. *C. (Oreocarabus) guadarramus*** LaFerté-Sénectère, 1847 (p. 225).

8 (7). Abdominal furrows lacking.

9 (10). Pronotum cordate, strongly narrowed to the base, with basal angles acute, strongly prominent; antennae simple in both sexes. Elytra elongate-ovate; sculpture regular, the primary foveae evident. Dorsal surface cupreous to blue-blackish. 18-24 mm. – Spain: Central Montane System. In scrub and forests. .... **12.002. *C. (Oreocarabus) ghilianii*** LaFerté-Sénectère, 1847 (p. 222).

Two quite distinct subspecies:

a) subsp. *ghilianii* LaFerté-Sénectère, 1847 – Dorsal surface brownish to cupreous red; sides of pronotum and of elytra cupreous red, the primary foveae metallic green to cupreous red (*C. hortensis*-like). – Sierra da Guadarrama.

b) subsp. *negrei* Breuning, 1966 – Dorsal surface blackish, primary foveae concolorous; sides of pronotum and elytra bluish. – Sierra de Gredos and Sierra de Béjar.

10 (9). Pronotum transverse, not or slightly narrowed to the base, with basal angles wide, lobate, obtuse, less prominent; antennal segments 5-8 (or 9) swollen at apex in the male. Elytra short ovate; sculpture more variable. Dorsal surface bronzed-blackish to violet. 18-25 mm. – Spain: Cantabrian Mountains and Central Montane System: Sierra de Bussaco, de Lousa and de Estrella. .... **12.001 (+007). *C. (Oreocarabus) amplipennis*** Vacher de Lapouge, 1924 (p. 221).

Some well characterised subspecies are recognised:

a) subsp. *amplipennis* Vacher de Lapouge, 1924 – Dorsal surface brownish, often with bronzed lustre; sides of pronotum and lateral margins of elytra bluish to green. Sculpture regular, intervals low, the primary foveae very small. 20-24 mm. – W. Cantabrian Mountains.

b) subsp. *getschmanni* Vacher de Lapouge, 1924 – Distinguished by the reduced size (18-22 mm). Body more elongate, elytra narrower, often with parallel sides. – C. and E. Cantabrian Mountains, E. to the Sierra de Andia.

c) subsp. *pseudosteuarti* Vacher de Lapouge, 1924 – (listed as species (12.007) in Turin *et al.*, 1993). Highly distinctive by the wide, ovate elytra, and particularly by the strong, costate elytral sculpture, with quaternary intervals often reduced and the primary ones catenulate, with large foveae, breaking three contiguous intervals. Dorsal surface blackish, sides of pronotum and lateral margins of elytra bluish to violet. – Portugal: Sierra d'Estrella, Cea, Bussaco.

13. Subgenus Tomocarabus Reitter, 1896

Type-species *Carabus* convexus Fabricius, 1775

Differing from the other 'brevimandibulares' *Carabus* by the strongly dilated apical segment of maxillary palpi. Body relatively broad, head small, labial palpi with 2 setae, elytral sculpture heptaploid, homodynamous.

Eight to nine Eurasiatic species, four of them in Europe (1 doubtful).

1 (2). Submentum swollen transversely. Elytra moderately convex, surface minutely granulate, primary foveae small, indistinct. Hind angles of pronotum short, triangular. Upper surface moderately shiny, black with reddish or purplish lustre, sides of pronotum and elytra brightly shiny, gold-green, inside often with narrow golden-yellow or -red border. 20-26 mm. – Poland, Romania, Byelorussia, N. Ukraine, Russia, in the N. almost to 54° N, and eastward to Middle Ural and S.W. Siberia. In deciduous or pine forests, mostly in forest-steppe zone. .... **13.004. C. (Tomocarabus) marginalis** Fabricius, 1794 (p. 232).

2 (1). Submentum not swollen transversely. Metallic lustre of the sides of elytra narrower, not so contrasting with the dark surface.

3 (6). Hind angles of pronotum forming long triangular lobes.

4 (5). Aedeagus with apical lobe broader, rounded. Elytra wide, rather convex, with thin quaternary sculpture, often forming rows of tubercles. Black, more or less shiny, side margins of pronotum and elytra blue, green or violet, sometimes the whole upper surface with bluish or greenish tint. 14-23 mm. – Most of Europe to 60° N (absent however from the British Isles, N.W. France and most part of Iberian Peninsula), in the S. to N. Sicily and S. Greece; Turkey, the Caucasus, W. Siberia to Altai and N. Kazakhstan. Mostly in deciduous and pine forests, parks and gardens; mountains up to 2200 m. .... **13.003. C. (Tomocarabus) convexus** Fabricius, 1775 (p. 229).

Many infraspecific forms were described, some of them merit to be maintained as distinct subspecies:

a) subsp. *convexus* Fabricius, 1775 – Elytral sculpture regular, intervals not interrupted. Upper surface moderately to strongly shiny, black with blue or green margins of pronotum and elytra, rarely uniformly bluish or greenish (mostly in populations of peninsular Italy, described as *paganettii* Born, 1905). Small, slender specimens from Romania, S.E. Bulgaria and N.E. Greece are known as *gracilior* Géhin, 1885. 15-20 mm. – Inhabits the greatest part of species range.

b) subsp. *pyrenaeicola* Csiki, 1927 – Elytral sculpture coarser, somewhat interrupted or transversely wrinkled, the primary foveae more distinct. 15-18 mm. – Pyrenees.

c) subsp. *dilatatus* Dejean, 1826 – Elytral sculpture irregular, granulate, more confused at sides and apex, striae distinctly punctate, primary foveae larger; pronotum strongly punctate. 17-23 mm. – S.E. Austria, N.E. Italy, whole Balkan Peninsula except S. Greece.

d) subsp. *moreanus* Reitter, 1896 – Elytral intervals as in subsp. *dilatatus* but more flattened and shiny; between every 2 primary intervals, only 5 distinct ridges. 17-20 mm. – S. Greece: Peloponnesos, island Euboea.

5 (4). Aedeagus with apical lobe narrowed and pointed. Elytra elongate, less convex, their sculpture as in *convexus*. Black, margins of pronotum and elytra with bluish lustre. 17 mm. – Described by a single male from Romania: Varatec (surely described after an aberrant specimen of *convexus*) and thus to be removed from all lists! .... (13.001. *C. (Tomocarabus) antipai* Panin, 1942) (p. 228)

6 (3). Hind angles of pronotum short, obtuse, rounded. Body convex, stout. Elytral sculpture consisting of more or less regular rows of tubercles. Black, unicolorous, shiny. 21-25 mm. – Ukraine, Lower Volga, N. Caucasus, S.W. Siberia, Kazakhstan. It was described from Moldova (Bendery) but probably extinct there. – Typical steppe species, threatened and supplanted by agricultural methods, such as ploughing. In the mountains up to 1000 m. .... **13.002. C. (Tomocarabus) bessarabicus** Fischer von Waldheim, 1823 (p. 228).

Two subspecies:

a) subsp. *bessarabicus* Fischer von Waldheim, 1823 – Elytra oval with coarser sculpture, primary foveae distinct. – Steppes of Ukraine including the Crimea. Extinct in the major area of its former distribution.

b) subsp. *concretus* Fischer von Waldheim, 1823 – Elytra more elongate, with more delicate sculpture; primary foveae often hardly visible. – N. Caucasus, Lower Volga, S.W. Siberia, Kazakhstan.

14. Subgenus Eurycarabus Géhin, 1885

Type species *C. faminii* Dejean, 1826

Body relatively short and wide, ovate, medium to small sized; colour (in European taxa) blackish, sides of elytra with metallic lustre. Apical segment of palpi slender, slightly dilated (*genei*) or very dilated in the male (*faminii*); penultimate segment of maxillary palpi from bisetose to multisetose. Pronotum very wide, transverse, with margins more or less bent upwards; two lateral (one anterior, one basal) setae. Elytra wide, convex (*faminii*) to subdepressed (*genei*); shoulders rounded. Elytral sculpture of triploid type: primary intervals costate (*genei*) or fused in a wide intermediate smooth area, in which intervals and striae are hardly distinguishable (*faminii*). Abdominal sterna with transversal furrows and setiferous pores. Protibiae often sulcate with outer apical angle more or less prominent. Male protarsi with four basal segments dilated. Aedeagus of peculiar shape, with apical region strongly turned to the right, widened and depressed; parameres very short and wide.

Three species of the S.W. Mediterranean area (Maghreb and the largest Tyrrhenian islands: Sicily, Sardinia and Corse). Mostly in open country and in mediterranean scrub areas, but also in mountain forests and in high altitude pastures. Polyphagous, normally active in autumn-winter, but also in spring and summer when humidity is favourable.

Note: The present key has been constructed for European species. Several North African subspecies, belonging to *faminii* and to the W. Maghrebinian *favieri* Faimaire, 1859, may present peculiar features (for example, polychromous dorsal surface). The three species of *Nesaeocarabus* living in the Canary Islands (not included in the present volume) seem to be related to *Eurycarabus* in the light of the analysis of larval characters and molecular data (Prüser *et al.*, 1998).

1 (2). Apical segment of palpi narrower and slender. Elytra depressed; secondary and tertiary intervals distinct. Dorsal surface brownish-black, rather dull, mostly sides of elytra metallic green to bluish. Aedoeagus: Fig. 3.15a. 22-27 mm. – Sardinia (also in several small islands near Sardinia), Corsica. Mostly in open country, sometimes in scrub, from sea level up to 1200 (1500) m. ....
.... **14.002. *C. (Eurycarabus) genei*** Gené, 1939 (p. 233).

2 (1). Apical segment of palpi strongly widened, the maxillary ones are axe-shaped in the male. Elytra convex; secondary and tertiary intervals reduced, fused in a single intermediate, smooth zone. Dorsal surface black, shiny, the lateral margins of elytra purple-violet to golden-green. Aedoeagus: Fig. 3.15b. 19-23 mm. – W. and S. Sicily (the typical form; some highly distinct subspecies in Tunesia and Algeria). In open countries, mediterranean scrub or dry forests, never in montane forests (in Sicily); active mostly in winter (from November to January). ....
.... **14.001. *C. (Eurycarabus) faminii*** Dejean, 1826 (p. 233).

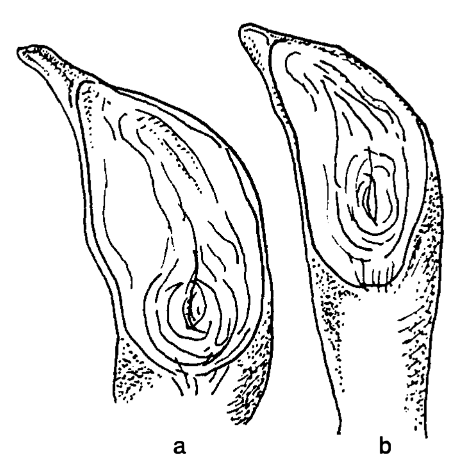


Fig. 3.15. Aedeagus of *C. (Orinocarabus) genei* (a) and *C. (O.) faminii* (b).

15. Subgenus Pachystus Motschulsky, 1865

Type species *C. hungaricus* Fabricius, 1801

Mandibles short and broad. Penultimate segment of labial palpi multisetose, apical segment slightly enlarged. Submentum normally with setae (rarely missing). Pronotum without lateral setae. Elytra with triploid or heptaploid sculpture or with irregular granulation. Abdominal furrows present. Body stout and convex, black without metallic lustre. – Rather xerophilous group living mostly in steppe landscapes of Eurasia. In Europe 4 species.

1 (4). Hind angles of pronotum short, rounded, not lobate.

2 (3). Hind angles of pronotum not exceeding the basal margin. Elytra strongly convex, uniformly finely granulate, primary foveae small, indistinct. 23-32 mm. – S. and E. parts of Balkan Peninsula, Turkey. ....
.... **15.003. *C. (Pachystus) graecus*** Dejean, 1826 (p. 236).

Two subspecies:

a) subsp. *graecus* Dejean, 1826 – Middle antennal segments in male simple or slightly swollen laterally at apex. Granulae of elytra flattened. 23-27 mm. – Greece, S. Albania.

b) subsp. *morio* Mannerheim, 1830 – Middle antennal segments in male swollen beneath. Granulae of elytra coarse, somewhat wrinkled. 23-32 mm. – E. part of Balkan Peninsula from S.E. Romania to Macedonia and Turkey to Ankara and Baiburt.

3 (2). Hind angles of pronotum extending slightly beyond the basal margin. Elytra with fine distinct granulation in more or less regular rows (probably an insular subspecies of *C. graecus* Dej.) – Greece: Sporades, Creta. ....
.... **15.005. *C. (Pachystus) trojanus*** Dejean, 1826 (p. 237).

4 (1). Hind angles of pronotum lobate, more or less triangular.

5 (8). Tibiae black. Head not or slightly thickened.

6 (7). Elytra almost smooth, shiny, minutely granulate, with rows of large and deep primary and

secondary foveae sometimes with irregular points between them. 24-30 mm. – S. Italy and Balkan Peninsula, in dry montane grasslands higher than 1000 m. A true transadriatic species. .... **15.001. *C. (Pachystus) cavernosus*** E. Frivaldszky, 1837 (p. 234).

Two geographically isolated subspecies:

a) subsp. *cavernosus* E. Frivaldszky, 1837 – Elytral surface pointed between the rows of foveae, with traces of visible intervals. – Bosnia, Hercegovina, Montenegro, Serbia, Macedonia, Albania, Bulgaria.

b) subsp. *variolatus* O. G. Costa, 1839 – Elytral surface not or only sporadically pointed between the rows of foveae, without traces of visible intervals. – C. Italy: Abruzzi, Gran Sasso, Velino, Greco and Sibillini Mts.

7 (6). Elytra more or less dull, distinctly granulate, with traces of intervals and with rows of shallow (often hardly visible) primary foveae (in one subspecies with large foveae). 23-34 mm. – Steppes of C. and E. Europe and the Caucasus. .... **15.004. *C. (Pachystus) hungaricus*** Fabricius, 1792 (p. 236).

Three rather distinct subspecies (some other described forms have infra-subspecific rank):

a) subsp. *hungaricus* Fabricius, 1792 – Comparatively small (23-28 mm), more shiny, with small elytral foveae and smoothed granules. – E. Austria, S. Moravia, S. Slovakia, Hungary, W. Romania, W. Bulgaria.

b) subsp. *mingens* Quensel, 1806 – Larger (27-34 mm), elytra densely granulate, rather dull, primary foveae small and shallow. – Crimea, the N. Caucasus, Middle and Lower Volga region, in lowlands and mountain steppes up to 1800 m.

c) subsp. *scythus* Motschulsky, 1847 – Larger (30-33 mm), rather dull with large primary and small secondary foveae. – Occurred in XIX century in the steppes between Dniester and Don, almost extinct now, surviving in some nature reserves of E. Ukraine.

8 (5). Tibiae and sometimes tarsi reddish-brown. Head distinctly thickened. Elytra rather shiny, with rows of large and deep primary and often also secondary foveae. 24-30 mm. – In Europe only in the steppes of S.E. Urals. Siberia (to Jakutsk and Transbaikalia), N. and C. Kazakhstan. .... **15.002. *C. (Pachystus) cribellatus*** Adams, 1812 (= *perforatus* Dejean, 1826) (p. 235).

16. Subgenus Ctenocarabus C. G. Thomson, 1875

Type species *C. galicianus* Gory, 1839

Body elongate, slender. Palpi long and thin; apical segment of palpi slightly dilated in the male; penultimate segment of labial palpi bisetose. Antennae rather long. Pronotum small, subquadrate-cordate; two lateral (one anterior one basal) setae. Elytra ovate-elongate; disc convex in the male, depressed in the female; humeral margins serrate. Elytral sculpture of costate type: primary intervals keel-shaped, intermediate intervals granulated, broken, only in the secondary ones low (flat) but distinct. Abdominal sterna with sharp, unbroken transverse furrows and with setiferous pores. Legs very long and thin; three basal segments of protarsi with pad of lamellae in the male. One highly hygrophilous species from N. Iberian Peninsula. A subgenus closely related to *Hygrocarabus* and to the following *Rhabdotocarabus*.

1 (1). Dorsal surface black, shiny-sericeous, femora reddish-yellow. 18-28 mm. – N.W. Spain and N. Portugal. Mostly near streams, in which it dives and hunts. .... **16.001. *C. (Ctenocarabus) galicianus*** Gory, 1839 (p. 238).

17. Subgenus Rhabdotocarabus Seidlitz, 1887

Type species *C. melancholicus* Fabricius, 1798

Note: *Ctenocarabus* and *Rhabdotocarabus* are so close (also for the larval characters), that Deuve (1994) and Březina (1999) believe that they cannot be separated. We maintain in this paper a provisional and traditional separation.

Same general features as in *Ctenocarabus*, only distinguished by the humeral margin of elytra being smooth, rather than serrated and the abdominal sterna without pores. One species in the Iberian Peninsula and N. Morocco.

1 (1). Body ovate to ovate-elongate, convex. Dorsal surface bronze-blackish to cupreous-bronze; dorsal surface dull to moderately shiny. Pronotum non-cordate, widened to base, with sides bent upwards in the posterior half and basal angles strongly prominent. Elytral sculpture of costate type: primary intervals keel shaped; intermediate intervals strongly reduced, granulated, only the secondary intervals slightly distinct. 20-30 mm. – Iberian Peninsula, except S.E. Spain; Pyrenees; N. Morocco. Hygrophilous, near marshes and streams, able to hunt under water; from the lowlands (sea level) up to 2000 m. .... **17.001. *C. (Rhabdotocarabus) melancholicus*** Fabricius, 1798 (p. 238).

Two European subspecies are recognised (subsp. *melancholicus* Fabricius, 1978 in N. Africa: Morocco).

a) subsp. *submeridionalis* Breuning, 1975 – Elytra elongate-ovate; dorsal surface bronze-blackish, dull. Primary intervals less convex, secondary garanulated but distinct.

Normally larger size (25-30 mm). – Only in S. Portugal and S. Spain, from Cadiz to Almeria.

b) subsp. *costatus* Germar, 1824 – Elytra short, more convex; dorsal surface cupreous to cupreous-bronzed, rather shiny. Primary intervals keel-shaped, secondary fully reduced. Normally smaller (20-25 mm). – Rest of Iberian Peninsula, Pyrenees. Deuve (*in litt.*) believes that the populations from the Caceres province (*dehesicola* Garcia-Paris & Paris, 1996), are markedly distinct and merit a status of subspecies.

18. Subgenus Hygrocarabus C. G. Thomson, 1875

Type species *C. variolosus* Fabricius, 1787

Mandibles moderately long with deep scrobae. Antennae fairly short. Palpi thin and long, the apical segment feebly dilated, subapical segment of labial palpi bisetose. Mentum with one seta. Pronotum transversal, subcordate, with 2 lateral setae. Elytra ovate, convex, deeply emarginate at apex (more in the female), its humeral margin serrate; primary intervals carinate, interrupted by large foveae, other intervals in form of irregular rows of tubercles. Abdominal furrows slightly developed or absent; abdominal pores present. Three basal segments of protarsi in the male dilated. Body black, slightly shiny above, rarely with feeble bronze lustre.

Two closely related species in Europe (often regarded as subspecies of one species). They are strongly hygrophilous, living on the banks of rivers and streams, in forests, mostly in foothills and mountains. They readily dive and stay submerged for 20-30 minutes, hunting for aquatic molluscs, worms, Crustacea (*Gammarus*), larvae of aquatic insects and small Amphibia. Jeannel (1941) reported specimens of *C. variolosus* mating in deep water in the Bihar Mountains.

1 (2). Aedeagus strongly narrowed, subacuminate apically (Fig. 3.16a). Body relatively broad. Primary fovea shallow, secondary intervals evident. 26-33 mm. – W. part of C. Europe: E. France, Switzerland, Austria, Germany (mostly in the W. and S.), N.E. Italy (only near Trieste), W. Hungary, Slovenia, Croatia, Bosnia-Hercegovina. .... **18.001. *C. (Hygrocarabus) nodulosus*** Creutzer, 1799 (p. 239).

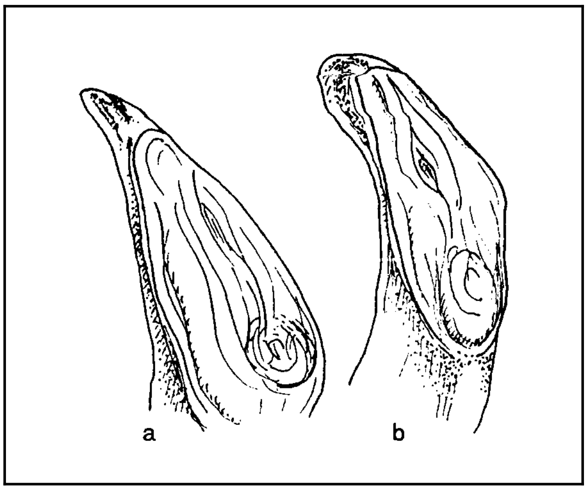


Fig. 3.16. Aedeagus of *C. (Hygrocarabus) nodulosus* (a) and *C. (H.) variolosus* (b).

2 (1). Aedeagus slightly narrowed apically, broadly rounded, depressed (Fig. 3.16b). Body relatively narrow and slender. Primary foveae deeper, secondary intervals reduced or evanescent. 22-30 mm. – Eastern part of Europe: Czechia, Slovakia, S. Poland, Ukrainian Carpathians, Moldova, Romania, Bulgaria, E. Serbia. .... **18.002. *C. (Hygrocarabus) variolosus*** Fabricius, 1787 (p. 240).

19. Subgenus Chaetocarabus C. G. Thomson, 1875

Type species *C. intricatus* Linnaeus, 1761

Medium to large sized species, elongated, depressed with more widened, ovate elytra in the females, and very long legs; upperside uniformly bluish-violet to bluish-green to blackish, in *arcadicus* with head, pronotum and sides of elytra metallic golden-red to golden-green.

Mandibles very long, without external scrobae; antennae very long. Apical segment of labial palpi very wide, rugose, dorsally sulcate along the external margin; penultimate segment multisetose. Penultimate segment of maxillary palpi peculiarly with some apical setae. Pronotum cordate, rugose; 2-3 marginal setae on each side. Elytral sculpture of regular triploid type, or confused vermicular granulated with primary intervals interrupted by rather superficial points. Abdominal segments with transverse furrows and pores. Three to four segments in the male protarsi with ventral pad of spatulate setae.

Comprising two species in the opinion of several authors (i.e. Březina 1994, 1999). We think, however, that some southern taxa merit a specific status, so that the subgenus *Chaetocarabus* consists here of five species, or, more correctly, of two 'superspecies', *intricatus* (with the semispecies *intricatus*, and *lefebvrei*), and *arcadicus* (with the semispecies *arcadicus*, *merlini* and *kruepen*). Furthermore, the Apennine and Sicilian forms (*lefebvrei s. lato*) seem more closely related to the forms of the southern Balkans of *intricatus* (*macedonicus* and *weiratheri*), than to the alpine and C.-European populations of the same species.

1 (4). Fourth tarsal segment in the male protarsi with distinct ventral pad of spatulate setae. First interval of elytron not or poorly distinct from the suture. Colour constantly blue-violet or blue-blackish, at least with green lustre.

2 (3). Body elongate, narrow, rather depressed. Pronotum cordate with sides strongly sinuous, the basal

angles long and acuminate. Elytral intervals more irregularly broken, the tertiary intervals normally reduced. 24-36 mm. – Europe, from the Pyrenees and N. Italy to Poland; Balkan Peninsula to the S. (Bulgaria, N. Greece); Belgium, C. Germany to the N. with isolated (mostly or recently extinct) populations in S. England, the Netherlands and S. Sweden. A forest-dwelling species, from the lowland to montane forests. ....
.... **19.002. *C. (Chaetocarabus) intricatus*** Linnaeus, 1761 (p. 242).

Rather homogeneous in its wide rage of distribution. Some populations from southern Balkans, such as *macedonicus* Jurecek, 1928, *starensis* Born, 1918, *subrhodopensis* Blumenthal, 1976 and *weiratheri* Breuning, 1932, are mainly distinguished by the reduced size and more regular sculpture; they merit probably a subspecific status.

3 (2). Body relatively short, elytra convex. Pronotum wider, with sides gently sinuous, basal angles short, obtusely rounded. Elytral intervals more regularly interrupted, more convex, intervals always evident. 20-36 mm. – C. and S. Apennines chain, N. Sicily. ....
.... **19.004. *C. (Chaetocarabus) lefebvrei*** Dejean, 1826 (p. 244).

Two subspecies have been recognised:

a) subsp. *lefebvrei* Dejean, 1826 – Pronotum more transverse, slightly narrowed to the base. Elytral sculpture homodynamous, all intervals normally of the same size; primary points small and scarcely deep. Dorsal surface bluish-black with sides blue-violet. – Sicily, Calabria (Aspromonte).

b) subsp. *bayardi* Solier, 1835 – Pronotum more narrow towards the base, with sides deeply sinuous. Elytral sculpture normally with primary and sometimes secondary intervals convex; primary points larger and deeper. Dorsal surface blue to violet to greenish-blue, sides violet or green; dorsal surface more shiny. – C. and S. Apennines. Small, montane specimens from Sila have been described as *silaensis* Haury, 1881.

4 (1). Fourth tarsal segment in male protarsi with ventral pad of spatulate setae reduced or absent. Elytra with 1st interval distinct and well separated from the suture. Colour bluish-black or strongly bicolorous, the head and pronotum metallic golden-red, the elytra blue-violet with wide, golden margins (*arcadicus*-complex).

5 (6). Dorsal surface bicolorous, the head, pronotum and lateral margins of elytra cupreous to golden-red, the disc of elytra blue-violet. Elytral sculpture triploid regular, disc of pronotum almost smooth. – A magnificent species, endemic in Greece, from Pyndos in the N.W. to Olympus in the E. and C. Greece (Parnassos, Elikon) in the S., mainly in pine forests, from 600 to 1800 m.
.... **19.001. *C. (Chaetocarabus) arcadicus*** Gistel, 1850 (p. 241).

6 (5). Dorsal surface uniformly blackish-blue, at least with metallic lustre on the shoulders, sides of elytra and/or epipleurae. Elytral sculpture more confused, vermiculate; disc of pronotum transversally rugulose.

7 (8). Pronotum cordate, strongly widened in the anterior half, narrowed to the base, sides deeply sinuous, the basal angles acute, prominent. Lateral margins of elytra slightly bent upwards. 30-40 mm. – S. Greece, mountains of the Pelopponesos Peninsula. Mainly in pine forests, in montane pastures up to 2000 m. ....
.... **19.005. *C. (Chaetocarabus) merlini*** Schaum, 1861 (p. 245).

8 (7). Pronotum hardly widened in the anterior half, slightly narrowed to the base, sides shortly or not sinuous, the basal angles rounded, obtuse, scarcely prominent. Lateral margins of elytra strongly bent upwards. 28-30 mm. – E. Greece, Ossa and Pelio Massifs. In *Pinus*-, *Castanea*- and *Fagus*-forests. ....
.... **19.003. *C. (Chaetocarabus) kruеperi*** Reitter, 1896 (p. 244).

20. Subgenus Platycarabus Morawitz, 1886
Type species *C. depressus* Bonelli, 1811

Body highly depressed, with elytra more or less flattened; dorsal surface smooth, polished, elytral sculpture of triploid type; primary foveae normally distinct, metallic. Mandibles long with deep scrobae; apical segment of palpi slightly dilated, penultimate segment of labial palpi multisetose. Pronotum cordate, transverse or cychrisised, with one or more antero-marginal setae (normally none in *cychroides*); basal setae normally absent (present in *cychroides*). Abdominal sterna without transverse furrows. Protarsi in the male with four segments with ventral pad of setae.

A homogeneous subgenus (Casale *et al.*, 1998), including forest-dwelling as well as montane species, highly specialised to a helicophagous diet, with consequently strong modifications (cychrisised or macrocephalic head respectively) in two species.

Note: the type species of *Platycarabus* has correctly been indicated as *depressus* by Deuve (1994) and incorrectly as *irregularis* by Jeannel (1941). The name *depressus* Bonelli, 1811, substituted by *bonellii* Dejean, 1826, for reasons of homonymy (Casale *et al.* 1982; Turin *et al.*, 1993), has to be maintained in the opinion of Deuve (1991, 1994), Březina (1999) and by us as 'nomen conservandum'.

1 (2). Highly macrocephalic species, with head large, very wide and thickened; basal segments of antennae reddish; outer sides of mandibles thickened, the left one with a prominent obtuse ridge. 21-30 mm. – C. and E. Europe, mainly in montane forests. .... **20.005. *C. (Platycarabus) irregularis*** Fabricius, 1792 (p. 248).

Three main subspecies can be maintained:

a) subsp. *irregularis* Fabricius, 1792 – Legs concolorous blackish. Medium sized (20-26 mm). Head moderately thickened. Dorsal surface more shiny, primary foveae and sides of elytra normally metallic green or cupreous. – S. Belgium, N.E. France, C. and S. Germany, Switzerland, C., S. and W. Austria, Czechia, Hungary, N.E. Italy.

b) subsp. *bucephalus* Kraatz, 1879 (= *ramanus* Sokolar, 1909) – Differing from *montandoni* by the strongly thickened head, highly macrocephalic, and for the darker, less shiny dorsal surface. 21-30 mm. – Dinaric chain and Balkan Peninsula, from Slovenia, Serbia, Croatia to S. Bosnia. Blackish specimens from E. Slovenia have been described as *hayeki* Kobmann, 1925.

c) subsp. *montandoni* Buysson, 1882 – Differing from both preceding subspecies mainly in legs being completely or partially (tibiae) red or reddish-brown. – Carpathian Mountains of Slowakia, Romania and W. Ukraine.

2 (1). Head of normal size, or small and narrow. Mandibles not thickened, without outer ridge.

3 (4). Head very elongate, cychrisised; pronotum narrow anteriorly, with basal seta and normally without anterior seta; elytra less depressed, widened in the females. – Italy, helicophagous species, in alpine areas at high altitude (2000-2400 m) in the Cottian Alps (Mt. Orsiera-Rocciavré, Mt. Albergian). With the more famous *C. olympiae*, it is one of the most localised *Carabus*-species in Europe. .... **20.003. *C. (Platycarabus) cychroides*** Baudi di Selve, 1860 (p. 247).

4 (3). Head of normal shape. Pronotum with one or more antero-marginal setae and without basal seta. Elytra wider, very depressed.

5 (6). First antennal segment thickened and short, always reddish. Pronotum scarcely narrowed to the base. Elytra less flattened, often metallic cupreous or greenish, with distinct metallic primary foveae. Small species, 18-24 mm. – C. and E. Europe: N. side of the C. and E. Alps, Carpathian Mountains and Tatra. In montane forests up to the alpine zone (2500 m). .... **20.004. *C. (Platycarabus) fabricii*** Duftschmid, 1812 (p. 248).

Three more or less distinct and geographically isolated subspecies can be recognised:

a) subsp. *fabricii* Duftschmid, 1812 – Elytra elongate, moderately ovate. Primary foveae small, less deep and more scattered. – C. and E. Alps, Czechia (only old records from Beskydy Mts.), Switzerland, Austria and N.E. Italy, eastward to the Tatra. Rather variable through its distribution: for a list of described forms, see Březina (1999).

b) subsp. *koralpicus* Sokolar, 1910 – Distinguished from *malachiticus*, by the shorter elytra being more ovate, widened at the sides. – Austria, southern vicariant of the typical form.

c) subsp. *malachiticus* C. G. Thomson, 1875 – Distinct by the larger, deeper and more dense primary foveae of elytra; upperside normally highly metallic green or bluish-green. – Tatra and Carpathian Mountains of S. Poland, Slovakia, Ukraine and Romania. Specimens from W. Ukraine (Gorgany Mts.) have been described as *ucrainicus* Lazorko, 1951.

6 (5). First antennal segment elongate, reddish or blackish. Pronotum cordate, strongly narrowed at the base. Elytra very flattened.

7 (8). First antennal segment narrow and slender at the base, distally thickened, club-shaped. Disc of pronotum smooth or with scattered punctures. 18-22 mm. – Alpine chain, on the N. and S. sides, from Ligurian Alps to Carinthia. Montane forests and alpine zone, from 800 to 2600 m. .... **20.001. *C. (Platycarabus) depressus*** Bonelli, 1810 (= *bonellii* Dejean, 1828; see notes above and Chapter 5, p. 245).

Rather variable, but only two subspecies well characterised:

a) subsp. *depressus* Bonelli, 1810 – Primary foveae distinct and rather large. Upper surface cupreous to greenish or brownish, less metallic shiny. – From W. (Cottian) Alps (Monviso) to E. Alps.

b) subsp. *lucens* Schaum, 1857 – Primary foveae very reduced, small, or virtually absent. Upper surface highly shiny, smooth, normally metallic cupreous to black greenish. – W. Alps, from Monviso Massif, S. to the Ligurian Alps.

8 (7). First antennal segment sub-cylindrical, regularly and only scarcely thickened at apex. Disc of pronotum with dense punctures. Size very variable: 18-35 mm. – C. and E. Prealps and Alps on the S. side, from Italy (Lombardia) to E. Austria (Carinthia), W. Croatia and Slovenia. In montane scrub and forest above 300 m up to the alpine zone (2000-2300 m). .... **20.002. *C. (Platycarabus) creutzeri*** Fabricius, 1801 (p. 246).

A highly variable species, of which almost 30 infraspecific forms were described so far. Only some of them, belonging to two main 'semispecies' (*creutzeri s.str.* and *kircheri*), merit a subspecific status:

a) subsp. *creutzeri* Fabricius, 1801 – Pronotum relatively wide; elytra strongly depressed, with all interstriae flattened and primary foveae very small. Dorsal surface dark, blackish, at least with cupreous, purple or violet lustre. Tibiae normally brownish, less frequently reddish. *Note*: *viridimicans* Kraatz, attributed by Breuning (1932-1936) to the *kircheri*-complex, is recognised as an extreme form of *creutzeri creutzeri* by Casale *et al.* (1982). 22-30 mm. – N.E. Italy (Venezia Giulia) to W. Slovenia and S. Austria.

b) subsp. *heros* Vacher de Lapouge, 1924 – Distinguished from the latter by the larger size and more elongate, less ovate elytra. 28-35 mm. – Carinthia, N. Slovenia.

c) subsp. *humilis* Bernau, 1911 – Small, short montane form, with elytra largely widened at the sides. 22-27 mm. – Croatia, along the N. Dalmatian chains.

d) subsp. *kircheri* Germar, 1824 – Pronotum narrow; elytra elongate-ovate, less depressed, with the intervals more distinct and the primary foveae more dense and larger. Dorsal surface lighter, normally with bronzed-cupreous or greenish metallic lustre; basal segments of antennae normally reddish, tibiae reddish or reddish-brown, less frequently blackish. 18-25 mm. – C. and C.E. Alps and Prealps. Western vicariant of *creutzeri* (*s.str.*).

e) subsp. *baldensis* Schaum, 1857 – Distinguished by the widened pronotum, the more rounded and more depressed elytra, larger primary foveae and metallic green, golden or cupreous colour (sometimes *fabricii*-like). – Italy (Veneto and W. Trentino), southern and eastern vicariant of *kircheri* in the mountains east of the Garda Lake.

21. Subgenus Heterocarabus Morawitz, 1886

Type species *C. marietti* De Cristoforis et Jan, 1837

Note: the endophallic features and other characters make *Heterocarabus* so close to *Chaetocarabus*, that Deuve (1994) synonymised the two subgenera.

Mandibles long, evenly curved. Antennae with 1st segment long, basally thin, then thickened; the 3rd and 4th segments pubescent apically. Penultimate segment of labial palpi multisetose with horizontal apical seta (Fig. 3.2a). Maxillary palpi with apical segments dilated, especially in the male. Pronotum with 4-5 lateral setae. Elytra with regularly punctured striae and moderately convex intervals; primary foveae small. Upper surface brightly metallic. Two or more species in the forests of Turkey, one of them also in Europe.

1 (1). Upper surface, epipleurae, pro- and mesosternum coppery-red to coppery-brown, sometimes with violet tint, borders of pronotum and elytra golden or cupreous-red, more shiny. 19-23 mm. – S.E. Bulgaria. N. part of European and N.W. part of Asiatic Turkey, in forests. ....**21.001. *C. (Heterocarabus) marietti*** De Cristoforis et Jan, 1837 (p. 250).

22. Subgenus Sphodristocarabus Géhin, 1885

Type species *C. adamsi* Adams, 1817

Mandibles long, narrow, evenly curved, their scrobae short. First antennal segment normal, the 3rd segment pubescent distally. Penultimate segment of labial palpi normally with 2-3 setae. Submentum without setae. Pronotum with 3-4 lateral setae. Elytral sculpture triploid, regular or more or less confused, granulate. Upper surface shiny, usually metallic. Protarsi in male with 4 dilated tarsomeres. About 15 species in Turkey and the Caucasus; one of them was reported from the Ural.

1 (1). Body rather elongate. Pronotum coarsely punctured, punctures often fused or wrinkled. Elytral primary intervals forming rows of short tubercles, secondary and tertiary ones usually transversely fused. Upper surface dark-blue to golden-red. 22-27 mm. – W. Caucasus in the limits of Krasnodar region and Abkhasia. Lives in forests of lower and middle zone. .... **22.001. *C. (Sphodristocarabus) varians*** Fischer von Waldheim, 1823 (p. 251).

Several subspecies have been described. We support the opinion of Březina (1999) who treats the European representative as a subspecies of *C. (S.) varians* Fischer: *varians janthinus* Ganglbauer, has dark-blue to violet upper surface and rather coarse elytral sculpture. It inhabits the N. part of species area (in the S. to Sotchi and Krasnaja Poliana). One specimen was found in the S. Ural (surely occasionally imported).

23. Subgenus Megodontus Solier, 1848

Type species *C. caelatus* Fabricius, 1801

Aulacocarabus Géhin, 1876

Mandibles long and rather narrow, curved uniformly. Penultimate segment of labial palpi multisetose; apical segment moderately dilated (in females) to axe-shaped (in males); tooth of mentum longer than lateral lobes, usually narrow and acute, sometimes dilated and bent downwards; submentum without pores. Pronotum more or less cordate, with lateral setae. Elytral sculpture triploid, sometimes uniformly granulated, primary and secondary intervals sometimes carinate. Male protarsi with 4, rarely 3 dilated segments.

More than 15 species, among them 9-10 in Europe, mostly living in forests. *C.(M.) violaceus* and related subspecies, form a complex of taxonomically extremely difficult, allopatric or parapatric taxa. It has been treated here as a superspecies consisting of 4 species (or 'semispecies'), genetically not strictly isolated and capable of generating hybrid populations. Březina

(1994) listed them all as subspecies of *C. violaceus* and Deuve (1994) divided them into two species: *violaceus* and *germarii*. The species *C. septemcarinatus* that has been included in the European checklist of *Carabus* (Turin *et al.*, 1993), is strictly out of the geographic limits of the present keys. It has, however, been introduced into the Crimea region.

1 (2). Elytra with primary and secondary keels; tertiary intervals disrupted into granules or wrinkles or reduced. Tooth of the mentum wide, somewhat bent downwards. Upper side blue or violet, margins of pronotum and elytra sometimes reddish-violet, or elytra green with purplish margins, suture and keels black. 22-34 mm. – The N. Caucasus from the Black Sea to C. Daghestan, mostly in forests up to an altitude of 2000-2200 m, also in gardens and shelter belts, fairly common. During last decades expanded its area northwards, reaching the Rostov province, occasionally introduced individuals have been found in Vitebsk regions and in the S. Ural. Several geographic races are known, but only the nominate subspecies has been found in Europe. .... **23.004. *C. (Megodontus) exaratus*** Quensel, 1806 (p. 254).

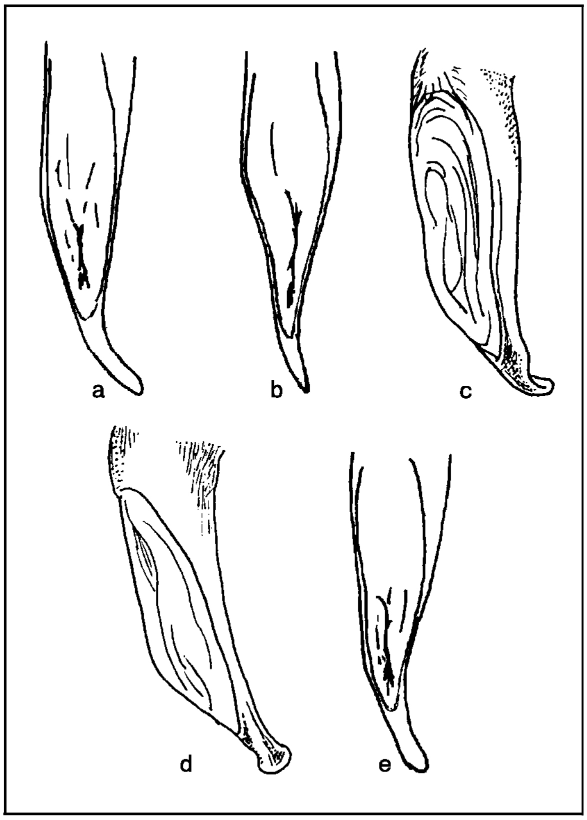


Fig. 3.17. Aedeagus of *C. (Megodontus) violaceus* ssp. *purpurascens* (a), *C. (M.) germarii* ssp. *germarii* (b), *C. (M.) germarii* ssp. *fiorii* (c), *C. (M.) violaceus* ssp. *picenus* (d), and *C. (M.) violaceus* ssp. *volffii* (e).

2 (1). Elytra without distinct keels. Tooth of the mentum narrower, usually flat, apically acute.

3 (16). First elytral interval not fused with suture in the whole of its length, separated by a fine stria at least in basal part, or all intervals more or less flattened, smoothed out or finely granulate.

4 (13). Pronotum usually rather wide at the basal side. Elytral sculpture more or less smoothed out (complex of *C. violaceus*).

Discrimination of species is difficult within this complex and based mainly on the elytral sculpture. Some hybrid populations are complicated, especially in the areas where two or more taxa live together. Mandl (1985a,b) published important papers on the Balkan forms of this group.

5 (8). Apex of aedeagus narrow (Fig. 3.17a).

6 (7). Apex of aedeagus long, strongly curved, not button-shaped, the apical orifice narrow (Fig. 3.17a). Elytral sculpture consisting of 15 more or less convex intervals, rarely they are finely granulate, striae punctate. Body usually elongate, length 24-38 mm (exceptionally from 18 mm). – N. Spain, France, Belgium, Netherlands, W. Germany, N. Switzerland, W. Austria. .... **23.010. *C. (Megodontus) violaceus*** Linnaeus, 1758 *partim*, concerning the subspecies near *purpurascens* Fabricius, 1787 (= *purpurascens* subspecies-group) (p. 261).

Includes about 7 geographical races:

p) subsp. *aurichalceus* Kraatz, 1879 – Fairly small (25-30 mm), elongated and narrow. Dorsal surface shiny, brassy brownish-cupreous, reddish-cupreous or golden-green, margins golden-green to golden-red. – N. Spain: mountains of Asturia (prov. Bilbao, Santander). – Small (18-24 mm) alpine specimens from Picos de Europe Mt. in Asturia have been described as *europae* Breuning, 1935. It differs by the shorter and more stocky build. Coloured as in *aurichalceus*.

q) subsp. *asturiensis* Born, 1925 – Related to preceding, differs by the dorsal side shiny blue-green, rarely black with intensive greenish lustre. – Asturia: prov. Oviedo – Los Cabos. – From this region another form has been described (*lugensis* Breuning, 1972).

r) subsp. *muelleri* Haury, 1878 – Largest form (30-38 mm; sometimes up to 40 mm) wide and robust, pronotum trapeziform, narrowed forwardly, rarely basally. Elytral intervals very regular, smooth or minutely granulate. Black with reddish-violet or greenish tint, margins light-purple. – N.E. Spain (prov. Barcelona, Lerida, Gerona). Population from S. France, related to *muelleri*, with the pronotum distinctly narrowed towards the basis, are known as (ssp.) *baeterrensis* Vacher de Lapouge, 1901. Race *provincialis* Born, 1903 is closely related to *baeterrensis*, it is of the same length but wider, coloured as *muelleri*, elytral intervals are slightly granulate. – S.E. France: dep. Gard, Vaucluse, Basses-Alpes, Isère, in the middle forest zone.

s) subsp. *pseudofulgens* Born, 1905 – Similar to *muelleri* but smaller (28-33 mm), narrower, pronotum narrowed basally. Upper side black with slight greenish or bluish lustre, the margins blue, violet or green. – N. and S. foothills of Pyrenees in Spain (to prov. Santander, Burgos, Zaragoza) and France (to dep. Gironde and Aude).

t) subsp. *fulgens* Charpentier, 1825 – Rather small (25-30 mm), elongate and convex, pronotum more densely and roughly punctured than in other races. Greenish-black with green margins or dark-bronzed with brassy or golden-red margins. – W. and C. Pyrenees of France and Spain, in upper forest and alpine zones.

u) subsp. *purpurascens* Fabricius, 1787 (incl. *pseudopurpurascens* Breuning, 1935). – Narrow and elongate, length usually 27-33 mm, sometimes up to 23 mm. Elytral sculpture regular, intervals uniformly convex, smooth or minutely granulate; tertiary ones are sometimes not so regular, may have been disrupted into rows of tubercles. Colour variable, rather shiny, usually black to purplish-black with violet, purple, more rarely golden-red or golden-green margins. – N. and C. France, Belgium, Netherlands, W. Germany, N.W. Austria, N.W. Switzerland, mostly in lowlands. The populations from E. France, Germany, Austria have more strongly punctured elytral striae, the sides of intervals are serrate. Some authors (Jeannel, 1941) treat this form as subsp. *crenatus* Sturm, 1815.

v) subsp. *mixtus* Géhin, 1876 – The most distinct subspecies. Rather small (24-29 mm), stocky and convex. Black, the margins of elytra metallic green or violet. Elytra very roughly granulate, granulae often arranged linearly, primary and sometimes secondary intervals outlined more distinctly. Aedeagus is of typical *purpurascens* structure. – S.W. France: dep. Isère, Drôme, locally in upper forest and subalpine zones.

7 (6). Apex of aedeagus shorter, apex button-shaped, slightly curved; apical orifice very wide; it is rather variable in different geographical forms (Fig. 3.17b,c). Size strongly variable (22-37 mm). Elytra from rather dull, roughly granulate with outlined primary and sometimes secondary intervals to very shiny, finely and evenly granulate. Upper side black, often with slight bluish, green or purple tint, margins mostly violet, rarely green or blue. – Area is disrupted: Alps from Savoie to Slavonia and from N. Apennines to N. Tirol and W. Hungary (to Buda Mts); the second fragment of area in S. Bosnia, Hercegovina and Montenegro. Living from lower forest belt up to the alpine zone. .... **23.005. *C. (Megodontus) germarii*** Sturm, 1815 (see notes in Chapter 5, p. 255 and Lorenz, 1998).

About 10 subspecies are known. They are listed from west to east:

a) subsp. *fiorii* Born, 1901 (incl. *pedemontanensis* Breuning, 1935) – Differs from the other subspecies by the comparatively short and very slightly curved apical lobe of aedeagus (Fig. 3.17c). Length 28-36 mm. Body relatively wide and feebly convex. Elytral sculpture more or less roughly or finely granulate, the granulae often forming rows; primary and not infrequently secondary intervals may be outlined. Black, mostly with slight bluish or reddish tint (more distinct in alpine forms: *pedemontanensis*), margins purplish-red or blue. – Italy: Piedmont, Alps to Mt. Generoso, N. Apennines of Liguria and Padanian plain; France: Savoie (Chamonix) and Haute Savoie; Switzerland: Tessin. Mostly in middle forest zone, rarely in lowland.

b) subsp. *savinicus* Hammer, 1906 – Apical lobe of aedeagus longer than in preceding subspecies, slightly turned. Length 22-32 mm, body comparatively elongate and convex. Elytral sculpture rather roughly granulate, the granulae partly disposed into rows, the primary and sometimes secondary intervals are often outlined, upper side rather shiny, mostly black, more seldom with bluish or reddish tint, margins purplish-red or (in the N. of the subspecies area) green. – Switzerland: Tessin southward of St. Gothard, Italy: Orobie, Lessinian, Venetian and Julian Alps, Dolomites (partly); Mts. of Slovenia; Austria: Carinthia, Karawanks, Dobratsch. Mostly at middle and upper forest belts and alpine zone. A small (22-26 mm), very narrow form of *savinicus* from Tessin, Trentino and Venetian Alps has been described as *rombonensis* Bernau, 1911, it has still more roughly sculptured elytra with strong purple tint. Some authors, including Casale *et al.* (1982), united subsp. *savinicus* with *germarii* (*s.str.*) but their differences are fairly appreciable.

c) subsp. *germarii* Sturm, 1815 – Apical lobe of aedeagus more long and distinctly turned (Fig. 3.17b). Body large (30-37 mm), moderately convex. The hind angles of pronotum longer than in preceding forms, more acute. Elytra finely granulate, often the primary intervals and sometimes the secondary ones outlined as the lines. Fairly strongly shiny, black, sometimes with bluish or reddish tint, margins purple or violet, rarely steel-blue or green. – Italy: environments of Venezia, Trieste, Trentino; Austria: Steiermark (Lichtenwald), Slovenia: Krain (loc. typ.), Dravgrad, environments of Ljubljana. Living in lowlands and valleys.

d) subsp. *exasperatus* Duftschmid, 1812 (= *obliquus* Breuning, 1935, nec C. G. Thomson, 1875) – Aedeagus as in *germarii* Sturm. Body somewhat smaller (24-33 mm), more or less elongate and convex. The hind angles of pronotum shorter. Elytral sculpture finely and uniformly granulate, seldom with vestiges of rows. Upper side fairly shiny, black, rarely with bluish or reddish tint, margins purple or violet. – Inhabits the N.E. part of the species' range: Slovenia, N. Croatia, E. Austria (Lower Austria, Styria, Burgenland), W. Hungary, Czechia (Brno), Slovakia (Bratislava). Occurs sympatrically with *C. violaceus*. Several local forms have been described from this territory, but they do not deserve a subspecific status.

e) subsp. *styriensis* Breuning, 1932 (= *laevigatus* Dejean, 1826 praeocc.) – Similar to *exasperatus*, but elytra still more finely granulate and shiny. Black, margins continuously blue or green. 26-33 mm. – Austria (Oberösterreich, Steiermark, Carinthia, Tirol). – From valleys to upper forest belt and sometimes in alpine zone. Probably, according to Blumenthal (in Freude, 1976), and Březina (1999), a mere synonym of *neesi*.

f) subsp. *neesi* Hoppe & Hornschuch, 1825 – Body small (22-27 mm), short, convex. Elytra extremely finely granulate, without traces of intervals; black, margins green, blue, rarely violet or brassy. – Alps of W. Austria, Switzerland (Graubünden) and N. Italy (Alto Adige, Dolomiti). Always in alpine zone.

g) subsp. *scordiscus* Vacher de Lapouge, 1901 – Body relatively large (27-32 mm), elongate. Elytra roughly granulate, granules mostly arranged in lines. Aedeagus with apical lobe long, narrow and somewhat turned. – Upper side black, rarely with bluish or reddish tint, margins violet to red. Similar to geographically remote *savinicus*. – S. Bosnia, Hercegovina; in middle forest zone. – Very large (31-35 mm) and narrow individuals have been described as *igmanensis* Eidam, 1927.

h) subsp. *vlasuljensis* Apfelbeck, 1894 – Small (22-27 mm) alpine race. Sculpture is variable, granulae disordered or arranged in linear rows; colour extremely diverse: green, brown-cupreous, brassy, blue or violet, margins mostly of the same colour but lighter. – Bosnia (Volujak, Magli, Treskavica), Hercegovina (Plasa Planina), N. Montenegro. According to Březina (1999), the preceding (*scordiscus*) and the following (*prenjus*) taxa are mere synonyms of *vlasuljensis*.

i) subsp. *prenjus* Eidam, 1927 – Very small (22-24 mm) high-alpine specimens from Prenj-Planina (Hercegovina), narrow and convex, upper side brownish-black with dark violet tint, elytral sculpture varied as in *vlasuljensis*. Mandl (1985b) considered this form a distinct subspecies, but other authors have doubts about its status.

8 (5). Apex of aedeagus wider, not pointed (Fig. 3.17d,e).

9 (10). Apical lobe of aedeagus somewhat spatulate distally (Fig. 3.17d). Upper side bright blue or violet, sometimes with reddish tint. – Italy and the S. part of Balkan Peninsula. .... **23.010. *C. (Megodontus) violaceus*** Linnaeus, 1758; (partim: concerning the subspecies near *picenus* Villa) (*C. violaceus* subspecies-group) (p. 258, 259).

Subspecific division of this species is not elaborated sufficiently but the races from Italy and Balkan Peninsula differ distinctly from each other. The taxonomy of the Balkan forms is extremely complicated. At the moment it is not possible to separate *picenus* Villa at specific level from *violaceus* L.

(SUB COMPLEX I)

a) subsp. *picenus* A. & G.B. Villa, 1838 – Wide, rather short and moderately convex. Elytral sculpture roughly tuberculate, the tubercles often linear, primary and secondary intervals more or less distinct, the tertiary ones usually redoubled or broken into irregular tubercles. Colour very bright, purple-red, reddish-cupreous or green, margins intensively light-purple or green-blue. Aedeagus: Fig. 3.17d. 26-32 mm, rarely (in high mountains) up to 20 mm. – France, Maritime Alps, Italy from Ligurian Alps to the S. of the Peninsula, absent in the plain of Po and to the N of it; not in Sicily. From the lowlands to the montane forests, also in the alpine zone. Small (20-25 mm), montane and extremely polychromous individuals from Abruzzi have been described as subsp. *bruschii* Tarrier, 1974. Casale *et al.* (1982) excluded that this form represents a distinct subspecies.

b) subsp. *bartoni* Mařan, 1930 – Rather narrow, elongate and convex. Elytra with uniformly granulate intervals, the striae strongly punctured. Black with purple tint, the margins reddish-cupreous. 26-31 mm. – S.W. Bulgaria: Sandanski, Begovica, the spurs of Pirin Mts, Mt. Slavianka (= Alibotus), near the frontier of Greece. Mostly at altitudes 1000-1600 m. Very small individuals (22 mm) with golden-green margins from the alpine zone of Pirin have been described as *pirinensis* Mandl, 1985. We consider it a variety of *bartoni*. Subsp. *letellieri* Blumenthal, 1976, from Pangaeon Mt., seems to be a synonym of *bartoni* or *dryas*.

c) subsp. *marani* Štěrba, 1945 – Sculpture and colour similar to *bartoni*. According to Březina 1999, *bartoni* and *marani* are mere synonyms of m) subsp. *dryas*. Small (20-22 mm). – Alpine race from S.W. Macedonia between Bitola and Ohrid lake (Jablanica, Golesnica, Peristeri, Popova Sapka, 1800-2500 m).

d) subsp. *rilvensis* Kolbe, 1887 – Convex, granulate intervals and deep strongly punctured striae, primary foveae rather distinct. Description based on one male, labelled 'Rumelia' but named by Rila-Mts. – W. Bulgaria. Another form of *violaceus*-complex occurs in Rila-Mts., that is n) subsp. *skombrosensis* Eidam, 1925. It is quite different from *rilvensis*. The specimens similar to holotype of *rilvensis* were collected later in S.W. Bulgaria (Kostenec, Chamkuria, Kozhukh-Planina); they are 24-26 mm long, elongate, black with greenish tint and bright-green margins. Mandl (1985a) supposed that the typus of *rilvensis* either was labelled erroneously, or, if it really comes from Rila Mts., it is a hybrid form between *violaceus* subsp. *skombrosensis* and *picenus* subsp. *bartoni*.

10 (9). Aedeagus apically sloped, feebly rounded (Fig 3.17e). Upper surface usually rather dull.

11 (12). Head normal, eyes moderately convex. The elytral sculpture is extremely variable: uniformly granulate or with more or less distinct primary and secondary rows. Colour also is strongly varied. Length 20-35 mm. – N., C. and S.E. Europe, lives in forests and open country, from lowland up to the alpine zone. .... **23.010. *C. (Megodontus) violaceus*** Linnaeus, 1758; (partim: *C. violaceus* subspecies-group) (p. 258).

A large number of subspecies have been described. The infraspecific taxonomy is very intricate especially in the Balkan Peninsula. Mandl revised the Fennoscandian forms (1962) and the Balkanian ones (1985a, b). Many named forms are of doubtful status: (SUB-COMPLEX II)

e) subsp. *violaceus* Linnaeus, 1758 – Rather large (26-33 mm), moderately convex, feebly shiny. Elytral sculpture usually finely and irregularly granulate, rarely (in the W. part of area) granulae form rows. Black, sometimes with bluish or reddish tint, margins purple or violet. – The nominate subspecies inhabits southernmost Sweden, Denmark, the most part of N. European lowland from river Weser to W. Poland, in the S. to N. Bavaria and Czechia.

f) subsp. *candisatus* Duftschmid, 1812 – Similar to *violaceus* (*s.str.*) but the margins are bluish-violet or blue. – Such populations inhabit E. Austria and S.W. Czechia. Real differences between *violaceus* (*s.str.*) and *candisatus* need to be thoroughly studied.

g) subsp. *salisburgensis* Kraatz, 1879 (= *meyeri* Born, 1898) – Related to preceding subspecies, but elytra more roughly granulate, body smaller (23-28 mm), rather stocky and convex, margins are mostly purple or violet. – S. Germany, N. Switzerland, W. Austria, here and there in Jura and N. foothills of Alps. Very small (20-23 mm) individuals from alpine zone of Austria (Vorarlberg) and Switzerland (Simmentaler Alps) with almost smooth elytral sculpture, have been described as *muellerianus* Born, 1902.

h) subsp. *sollicitans* Hartert, 1907 – Similar to *salisburgensis* and united with it by several authors. Elytra almost smooth with minute granulae, which are distributed quite irregularly or joined into three faint longitudinal rows. Dull-black with faint violet tint, margins mostly purple or blue, sometimes greenish or golden. 20-30 mm. – British Isles; rather common. The population from the S. coast of England have more roughly granulate elytra with more distinct intervals. A markedly isolated population, relict in Raasay island (Scotland), characterised by stout specimens with metallic blue-green margins of the elytra, has been described as *browni* Deuve, 1999.

i) subsp. *ottonis* Csiki, 1909 – Related to *violaceus* (*s.str.*), but on average smaller (22-26 mm), elytra more finely granulated, more shiny, black with purple or violet margins. – Most part of Fennoscandia (except the northernmost parts and high mountains). More narrow specimens from S. Finland have been described as *lindbergi* Burkhard, 1921; individuals from Karelian isthmus with rather broad elytra, more cordate pronotum and bluish margins, as *carelicus* Hellen, 1934. Finally, a form very similar to *carelicus* was collected from the moors of Lüneburger Heide (N.W. Germany) and has been described as *blumenthali* Blumenthal, 1961. This population belongs probably to *violaceus* (*s.str.*). All these forms are similar to *ottonis* and probably do not deserve the subspecific rank.

j) subsp. *lindrothi* Silfverberg, 1977 (= *arcticus* Sparre-Schneider, 1888). Small form (17-24 mm) having finely granulated, very shiny, almost polished elytra with blue or green margins. – Mountains and extreme N. of Norway, Sweden and Finnish Lapland and the Murmansk province of Russia. This subspecies probably derived from the populations which survived the last glaciation in the refugia of the Norway coast.

k) subsp. *volffii* Dejean, 1826 (= *wolffi*, auct.) – Similar to *violaceus* (*s.str.*) but more finely sculptured and more strongly shiny, granulae of elytra not arranged into rows. Colour black, sometimes with reddish, bluish or greenish tint, margins are mostly violet or purple in the N. of the area and blue or green in the S. Aedeagus: Fig. 3.17e. – N.W., C., S.W. Romania (Banat), E. Hungary, S.E. Slovakia.

l) subsp. *azurescens* Dejean, 1826 – Body elongate, moderately convex, slightly shiny. Elytral sculpture roughly granulate, rather irregular but often forming rows, especially on primary intervals; striae finely punctured. Black sometimes with reddish tint, margins purple red, rarely golden or violet. 27-33 mm. – Croatia, Bosnia, Hercegovina, W. and N.E. Serbia, Montenegro, N. Albania. High-mountain individuals from Montenegro are somewhat smaller (25-28 mm) and coloured more brightly – blue or green with purple-red, violet or green margins. They have been described as *zabljakensis* Eidam, 1927 and *durmitorus* Mandl, 1985.

m) subsp. *dryas* Gistel, 1857 (= *merditanus* Apfelbeck, 1918) – Small alpine form related to *azurescens*, more vividly coloured: blackish or greenish, margins bright purple or green, sometimes the sides of pronotum violet, and of elytra green. 23-26 mm. – N.C. Albania, Macedonia, N.E. Greece (Thessaloniki region).

n) subsp. *skombrosensis* Eidam, 1927 (= *balcanicus* Vacher de Lapouge, 1902, nec Born, 1899) – Similar to *azurescens*, somewhat smaller (25-29 mm), secondary and tertiary intervals usually redoubled, striae not punctured. Coloured as *azurescens*. – Bulgaria: Stara Planina, vicinities of Sofia, Rila. According to Březina (1999), this taxon is probably a synonym of d) subsp. *rilvensis* Kolbe, 1887.

o) subsp. *andrzejuscii* Fischer von Waldheim, 1823 – Similar to *volffii*, but brightly coloured: pronotum usually bluish with purple-red margins, elytra with reddish or bluish tint, margins bright cupreous or golden-red. Elytra densely granulate, granulae more rough than in *volffii*: 27-33 mm. – C.E. Poland, C.W. Russia, N.E. Slovakia, N. Romania, Ukraine, Baltic states, mostly in lowlands and foothills. This subspecies may be considered the aggregate of populations intermediate (and possibly hybrid) between *violaceus* subsp. *volffii* Dejean and *aurolimbatus* Dejean.

12 (11). Head rather narrow, eyes strongly convex. Body elongate, slightly convex, small (20-26 mm). Elytra uniformly granulate, usually without distinct intervals (rarely they are traceable in Siberian specimens). Upper side dull, always with purplish tint; the margins of pronotum violaceous or purple, margins of elytra vividly golden-red or golden-green. – E. part of European Russia (except the

taiga and dry steppes), forest steppe zone of W. and C. Siberia (to Krasnoyarsk) and N. Kazakhstan (Kokshetau), mountains of the N. Caucasus (up to 2000 m), mostly in open landscapes. Very invariable morphologically, no local races. .... **23.001. *C. (Megodontus) aurolimbatus*** Dejean & Boisduval, 1829 (p. 251).

Many authors united this form with *C. violaceus* as its subspecies, but the Russian entomologists (Jakobson, 1905; Semenov-Tian-Shanskij, 1898) considered it a distinct species. K. Makarov (*in litt.*) corroborated recently the last opinion on the basis of larval characters.

13 (4). Pronotum strongly cordate, its basis narrow. Elytra coarsely sculptured.

14 (15). Body narrow, elongate, rather depressed. Pronotum relatively small, densely and finely punctured. Elytra with rounded shoulders, sculpture consists of 14-15 uniformly convex, laterally and apically granulated intervals, the primary ones sometimes slightly broader than the others, striae coarsely punctured. Protarsi with 4 dilated segments. Upper side black, moderately shiny, usually with faint bluish tint, the margins of pronotum and elytra mostly violet, purple or green. 21-30 mm. – Locally in the upper forest and alpine zones (usually above 1500 m) of S. Carpathians in Romania. .... **23.007. *C. (Megodontus) planicollis*** Kuester, 1846 (p. 257).

(Ssp.) *verae* Csiki, 1905, was described after rather slightly sculptured and more shiny individuals, from S.E. Carpathians; apparently it does not deserve the subspecific rank. *C. deubeli* Reitter, 1896 from Transylvania is probably a hybrid of *planicollis* and *violaceus volffii* Dej.; a single specimen is known.

15 (14). Body elongate but more massive, pronotum relatively large. Elytral intervals interrupted by wrinkles into more or less long tubercles which are usually fused on each sides, striae roughly punctate. Head slightly widened, wrinkled from above. Pronotum roughly punctured and wrinkled. Upper surface slightly shiny, bluish-black, blue, violet, green, rarely black without tint, margins brighter, violet or green. Protarsi in male usually with 4 dilated segments, but the adhesive sole of the 4th segment is sometimes reduced. 22-37 mm, mostly longer than 26 mm. – W. part of Balkan Peninsula: from S.W. Slovenia to N. Albania and N.W. Macedonia, absent at Adriatic shore. Mostly at middle and upper forest belts up to alpine zone. .... **23.003. *C. (Megodontus) croaticus*** Dejean, 1826 (p. 253).

Many geographical races have been described. About 7 or 8 of them are generally considered subspecies (Kratschmer & Drovenik, 1977) but some names are probably superfluous:

a) subsp. *croaticus* Dejean, 1826 (incl. *frankenbergeri* Obenberger, 1914) – Elytral sculpture very rough and strongly disrupted. Pronotum and margins of elytra blue or violet, elytral disc dark blue or greenish-blue. Adhesive sole of 4th protarsal segment in male fully developed. 26-37 mm. – Krain, S.W. Slovenia, Croatia, C.N. Bosnia.

b) subsp. *bosnicus* Apfelbeck, 1890 (incl. *kobingeri* Apfelbeck, 1904) – Similar to preceding, narrower and more depressed, elytral sculpture more regular, primary foveae distinct. Pronotum and elytra mostly bluish-violet. 26-32 mm. – C.N. Bosnia: mountains near Foinica, Travnik, Kresov etc. Purplish-black form with narrow violet margins from Bosnia (Ostrelj, etc.) have been described as *pretneri* Kratschmer et Drovenik, 1977.

c) subsp. *zepcensis* Reitter, 1902 – Body rather wide, convex. Elytral sculpture moderately rough. Elytra blue or violet. Adhesive sole of 4th protarsal segment in male sometimes reduced. 24-35 mm. – E. Bosnia, C.W. Serbia.

d) subsp. *durmitorensis* Apfelbeck, 1904 – Small (22-26 mm), very narrow, elongated, elytral sculpture regular, feebly disrupted. Black or pronotum and margins of elytra (rarely the elytral disc also) dark bluish-violet or greenish. Adhesive sole of 4th male protarsal segment more or less reduced. – Isolated mountainous race from Montenegro (Mt. Durmitor). See note below!

e) subsp. *ljubetensis* Apfelbeck, 1918 – Narrow and elongated, 25-30 mm. Pronotum rather sparsely punctured, sculpture of elytra fairly regular (as in *kobingeri*). Pronotum and margins of pronotum violet, disc of elytra dark bluish or greenish. – Mountains of S. Kosovo, N.W. Macedonia, N.E. Albania, S.E. Montenegro.

f) subsp. *babinjensis* Apfelbeck, 1919 – Similar to preceding subspecies, still more elongated. – Local race from the high altitudes of N. Albania (Babinje-Planina). The latter two taxa possibly do not deserve a subspecifical rank, and should be included in *durmitorensis* (see Březina, 1999).

16 (3). First elytral interval fused with suture over all its length. All intervals distinct, uniformly developed.

17 (18). Smaller (26-31 mm). Protarsi in male with 4 dilated segments.– Oblong-ovate, more elongated in male, moderately shiny, blue or violet, elytral margins violet or purple. Pronotum with narrow margins and wrinkled sculpture. Elytral sculpture consist of 14 uniformly convex intervals, the primary ones with small pores, striae roughly punctured. – Strictly endemic to the mountains of the Crimea. Mostly in the beech and oak forests. .... **23.006. *C. (Megodontus) gyllenhali*** Fischer von Waldheim, 1827 (= *dejeani* Fischer von Waldheim, 1823, nec Fischer von Waldheim, 1822) (p. 256).

18 (17). Larger (26-45 mm, usually longer than 33 mm). Protarsi in male with 3 dilated segments. – Body narrow, head feebly dilated, antennae long. Pronotum subcordate, roughly sculptured, with rather long hind angles. Elytra moderately convex, with 15 uniformly convex intervals, all of them interrupted into more or less long tubercles, often fused by sides; striae with deep and large punctures. – N.E. Italy, S.E. Austria and the western parts of Balkan Peninsula to Montenegro and N. Albania. Lives from the sea level up to 2200 m, mostly inhabiting the middle forest zone. .... **23.002. *C. (Megodontus) caelatus*** Fabricius, 1801 (p. 252).

Several geographical races. Four among them have been regarded as subspecies:

a) subsp. *caelatus* Fabricius, 1801 – Elytral sculpture strongly irregular, densely interrupted, granulated, primary foveae feebly distinct or almost missing. Body more convex, upper side black, at most with faint bluish or greenish tint. 32-45 mm. – S.E. Austria, N.E. Italy (Friuli), N.W. and C. Slovenia, N. Croatia to Zagreb.

b) subsp. *schreiberi* Kraatz, 1877 – Body form and elytral sculpture similar to preceding subspecies. Upper side vividly blue or violet, rarely black with metallic margins or green. 26-34 mm. – Widely distributed from the Alpi Giulie and Trieste in Italy through S. Slovenia and N.W. Croatia.

c) subsp. *dalmatinus* Duftschmid, 1812 – Elytral sculpture more regular, linear, primary foveae distinct. Body broader and more depressed. Upper side almost always blue or violet. 31-45 mm. – Croatia, W. Bosnia, Hercegovina, Montenegro and N. Albania. Mostly along sea-shores and islands, but also mountains to middle forest zone. Large specimens with depressed greenish elytra, from the coasts in S. Croatian and Montenegro, have been described as *procerus* Reitter, 1885.

d) subsp. *sarajevoensis* Apfelbeck, 1890 – Close to subsp. *caelatus* (*s.str.*) and sometimes treated as its synomym (see: Deuve, 1994, who maintains the southern forms of *caelatus* as distinct subspecies). Elytral sculpture densely interrupted, primary punctures almost indistict. Elytra very convex, ovate; upperside metallic greenish to golden-green or purple. Large size in forest populations (30-40 mm: *metalkanus* Apfelbeck, 1919, *grmecensis* Born, 1910), small specimens in alpine forms (26-30 mm: *volujakianus* Apfelbeck, 1894; *malissorum* Apfelbeck, 1919). – S. Croatia, Bosnia-Herzegovina, Montenegro, Kossovo, E. Albania, in mountains (replaced along sea-shores by *dalmatinus*). *Note*: it seems that the distribution areas of the subspecies *dalmatinus* and *sarajevoensis* overlap in some parts of the coastal chains, which makes it probable that they are ecologically separated in one or another way.

24. Subgenus Pachycranion Solier, 1848

Type species *C. schoenherri* Fischer von Waldheim, 1822

Head more or less thickened, antennae rather short, 4th segment without pubescence, only with apical tactile setae. Mandibles rather long, usually feebly curved, the basal tooth of right mandible unidentate or blunt. Subapical segment of labial palpi multisetose; the tooth of mentum broad, more or less dilated, swollen, longer than lateral lobes (Fig. 3.18); submentum without setae. Pronotum with lateral setae. Elytra convex with triploid sculpture, more or less modified.

Closely related to *Megodontus* and possibly its synonym (see Deuve, 1994; Březina 1994, 1999). About 5 species in Siberia, two of them in the E. parts of European Russia also.

1 (2). Large and stout (27-33 mm); appendages black. Head strongly thickened, mandibles long, blunted apically, the basal teeth of mandibles rectangular (Fig. 3.2c). Pronotum about 1.8 times as broad as long, hind angles short, rounded, slightly bent downwards. Elytra strongly convex, with 14 uniformly thin intervals, the striae roughly punctured; the broad irregularly wrinkled space disposed laterally of the 14th interval. Protarsi in male with 3 dilated segments. Upper surface dull, head and pronotum violet, blue, black with violet margins, rarely entirely black; elytra reddish-brown to yellowish-brown with blue, violet or green margins, rarely entirely violet; antennae, legs and underside black. – E. part of European Russia from Nizhnii Novgorod, Penza and Saratov provinces to Urals; W. and C. Siberia to Irkutsk; in the N. to the middle taiga zone. – In coniferous and mixed forests, preys mostly on molluscs. .... **24.002. *C. (Pachycranion) schoenherri*** Fischer von Waldheim, 1822 (p. 263).

2 (1). Small (17-21 mm), appendages partly red, head slightly thickened, mandibles fairly short, normally curved, their basal teeth unidentate. Pronotum about 1.6 times as wide as long, subcordate, hind angles triangular, rounded apically, disc roughly punctured and wrinkled. Elytra convex, suture and primary intervals carinate, smooth, the rest of sur-

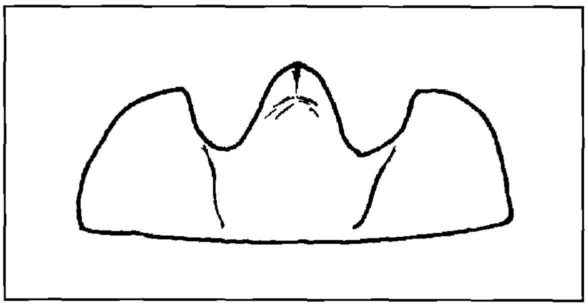


Fig. 3.18. Tooth of mentum of *C. (Pachycranion) schoenherri*.

face minutely tuberculate and transversely wrinkled. Protarsi in male with 4 dilated segments. Upper surface moderately shiny; head and pronotum coppery-red, pronotum with golden-red or green margins, elytra bright green with golden or red margins, carinae black, pro- and meso-episterna and epipleure violet or green, 1-4th antennal segments, basal segments of palpi, and legs brownish-red, the rest of the underside black. – N.E. of European Russia and N. Siberia to Jenissei river, in forest-tundra and southern tundra belts; also in alpine zone of Altai and Saian Mts. .... **24.001. *C. (Pachycranion) ermaki*** Lutshnik, 1924. (= *amoenus* Chaudoir, 1852, nec auct.) (p. 262).

Recently a new subspecies was described from N. Russia (Republic of Komi, Usa, Lek-Rogovaia):

subsp. *laetensis* Obydov, 2000 differing from the nominate subspecies by a broader and flatter pronotum. Pronotum with shorter hind angles and the elytral striae wider and coarser; primary intervals less prominent. Fourth segment of the male tarsi less dilated and colouration more dull. Body longer and more robust.

25. Subgenus Iniopachys Solier, 1848.

Type species *C. pyrenaeus* Audinet-Serville, 1821.

A peculiar subgenus, including two macrocephalic species, with the same general habitus as in the Caucasian *Cechenochilus*. Deuve (1998) demonstrated from study of the mandibles, sculpture and a natural hybrid (*C. pyrenaeus* x *C. punctatoauratus*), that *Iniopachys* is probably closely related to the *Chrysocarabus*/*Chrysotribax*-complex.

Head large and thickened, with sides almost parallel, without an evident narrowing at the neck. Labrum short, deeply emarginate and bilobed at the anterior side, dorsally incavate; suture with the clypeus very thin, unarticulated. Eyes prominent. Apical segment of palpi moderately dilated; penultimate segment of labial palpi bisetose. Pronotum strongly transverse; anterior margin deeply incavate and thickened; fore and basal angles acute, prominent; two (one anterior, one basal) setae on each side. Elytra short, depressed, without apical sinuation; sculpture normally confused, the interstriae often interrupted or granulated, the primary intervals finely catenulate, indicated by rows of small primary pores. Legs short; four segments of male protarsi with ventral pad of setae. Small size: 15-26 mm. Two montane species, of the Pyrenees and Cantabrian mountains respectively.

1 (2). Pronotum with sides scarcely sinuous and bent upwards, fore and basal angles short, scarcely prominent. Shoulders more apparent, lateral margins of elytra less widened. 15-26 mm. – Pyrenees, both on the French and Iberian sides, in the alpine zone. .... **25.002. *C. (Iniopachys) pyrenaeus*** Serville, 1821 (p. 264).

Deuve (1994) agreed that two main 'strong' subspecies can be distinguished. Some other local forms ('nationes'), will be treated under the subspecies *pyrenaeus* (*s.str.*) or as questionable subspecies (ssp.).

a) subsp. *pyrenaeus* Serville, 1821 – Interstriae more or less granulated, confused; primary intervals more convex than the others. – The typical *pyrenaeus* (= *ignitus* Reitter,1896), from the C. Pyrenees, have a rather bright reddish-bronzed dorsal surface, with regularly punctated elytra; *cerdanus* Vacher de Lapouge, 1924, described from the Maladetta Massif from small specimens, and present also in the E. Pyrenees (Andorra, Carlitte and Puigmal), have a brownish-violet or bluish dorsal surface with sides of pronotum violet. More distinct are the populations from W. Pyrenees, described as *cephalicus* Csiki, 1927 (= *cephalotes* Nicolas, 1919) and *occidentalis* Jeanne, 1969, characterised by larger head, more thickened; generally by the larger size, and the dorsal surface including the disc of pronotum, metallic purple, reddish or golden green (for the variations of *pyrenaeus* see Deuve (1994, p. 219).

b) subsp. *costulus* Géhin, 1885 – Well characterised by two well-developed retinacular teeth of the left mandible, and by the more ovate and convex elytra, with all interstriae regular, distinct, the primary ones more convex, costate; dorsal surface blackish-violet or blue-violet. Often large size (to 26 mm). – Locally in the Aude, Canigou Massif (small specimens from Pic du Madres, have been described as 'natio' *madresensis* Mollard, 1996).

c) subsp. *jeanneli* Deuve, 1994 – From Spain, Port de Vénasque, is blackish, with bluish or greenish lustre on the elytra; *vallierensis* Colas, 1965, from Montvallier Massif, present the disc of the elytra often with more distinct greenish, purple or violet lustre.

2 (1). Pronotum with sides strongly sinuous and bent upwards; fore and basal angles long, acute and prominent. Shoulders more rounded. Margins of elytra widened. 15-26 mm. – N. Spain, Cantabrian chain. Alpine zone, up to 1800 m .... **25.001. *C. (Iniopachys) auriculatus*** Putzeys, 1872 (p. 264).

At least two distinct subspecies:

a) subsp. *auriculatus* Putzeys, 1872 – Normally larger (17-26 mm), head wider and more thickened. Elytra more elongate, shiny; disc and lateral margins green or bronzed green. C. Cantabrian chain: Picos d'Europa Massif.

b) subsp. *ubinensis* Puissegur, 1955 – Normally smaller (15-20 mm), the head narrower and less thickened. Elytra shorter, more dull, with variable colour, disc greenish, bluish, cupreous or dark purple, lateral margins green. W. Cantabrian chain: Peña Ubiña Massif.

The status of ssp. *ornizensis* Meyer, 1998 is questionable.

26. Subgenus **Chrysocarabus** C. G. Thomson, 1875
Type species *C. auronitens* Fabricius, 1792

incl.

(27. Subgenus **Chrysotribax** Reitter, 1896)
Type species *C. hispanus* Fabricius, 1792

Body elongate, elytra convex or sub-convex; integument shiny metallic, highly polychromous. Mandibles long. Apical segment of palpi moderately to strongly dilated (*hispanus*, *rutilans*) in the male. Penultimate segment of labial palpi bisetose; submentum without setae. Pronotum normally elongate-cordate, narrower than elytra; basal angles prominent; two (one anterior, one basal) setae present. Elytral sculpture of homodynamous, triploid type, finely costate (*olympiae*), or only with the primary intervals costate, or fully reduced, smooth, sometimes with primary foveae large and distinct (*rutilans*). Abdominal sterna with or without transverse furrows; abdominal pores present. Legs long, protarsi in the male with three or four segments with ventral pad of setae.

Chrysotribax, including two magnificent species from S. France and N.E. Spain, has been considered synonymic with *Chrysocarabus* by some authors (see Deuve 1991, 1994; not Březina, 1999). This assumption is correct, because different species of *Chrysocarabus* and *Chrysotribax* interbreed regularly, both in nature and in the laboratory, resulting in perfectly developed hybrids (some of them described as distinct species). Furthermore, a closer relationship of *splendens* with *rutilans*, based on characterisation by DNA-sequencing, demonstrates that *Chrysotribax* is a polyphyletic unit (Prüser, 1996). For these reasons, in the present key, we have united *Chrysocarabus* with *Chrysotribax*. The species have been re-numbered successively as 26.006 and 26.007 (compare Turin *et al.*, 1993).

1 (4). Apical segments of all palpi strongly dilated, axe-shaped in the males. Primary intervals not more evident than the others. Large species (26-38 mm).

2 (3). Head and pronotum densely punctate. Elytra with all intervals interrupted, densely granulate, the primary foveae less distinct. Dorsal surface constantly bi-coloured, the head and pronotum bluish or bluish-green, the elytra golden-red or greenish-red with lateral margins metallic bluish. 26-38 mm. – S.W. France, in forests: Montagne Noire, C. Massif, Corbières, Cevennes, Drôme. .... **26.006 *C. (Chrysocarabus) hispanus*** Fabricius, 1787 (p. 272).

The species is very homogeneous through its distribution, only *latissimus* Vacher de Lapouge, 1910, from Montagne Noire, in which the 4th article of male protarsi is lacking the ventral lamellae, and *dromensis* Forel & Leplat, 1995 (formerly known as *boudeti* Beuthin, 1892; see Coulon *et al.*, 2000), isolated from the other populations in the E. side of the Rhône (Drôme, forêt de Saou), merit perhaps the status of distinct subspecies.

3 (2). Head and pronotum with scattered punctures. Body more convex. Elytral surface smooth, the primary foveae large and distinct. Dorsal surface uniformly metallic red-cupreous to golden-greenish, or, in two subspecies (*perignitus* and *opulentus*) strongly bicolorous, *hispanus*-like, the head and pronotum greenish or bluish, the elytra purple-red with bluish lateral margins. 28-38 mm. – S.W. France (Corbières and E. Pyrenees); N.E. Spain (Catalonia, C. Pyrenees). In forests, scrub, sometimes in open country at high altitude. .... **26.007 *C. (Chrysocarabus) rutilans*** Dejean, 1826 (p. 273).

Many infraspecific forms were described; only in Spain seven subspecies have been cited by Zaballos and Jeanne (1994). We agree with Deuve (1994), and believe that only three valid subspecies merit to be maintained:

a) subsp. *rutilans* Dejean, 1826 – Dorsal surface concolorous, cupreous red or greenish, elytra with large primary foveae along darker lines. – E. Pyrenees on both sides (French and Spanish), entire Cataloniain chain to the Ebro river region.

b) subsp. *perignitus* Reitter, 1896 – Dorsal surface bicolorous, the head and pronotum green, the elytra purple-red. – C. Pyrenees: Andorra and adjacent mountains on the Spanish and French sides.

c) subsp. *opulentus* Oberthür, 1898 – Similar to *perignitus*, but head and pronotum bluish-green or blue. Elytral sculpture more evident, the primary foveae more reduced. – Spain, C. Pyrenees: high basin of Noguera de Tor river.

4 (1). Apical segments of all palpi moderately dilated, triangular in males. If more dilated, axe-shaped, then the primary interals are more evident than the others, sometimes costate, and/or the size is smaller (18-38 mm).

5 (6). Elytra with all intervals of the same size, a little costate, and with all striae deeply punctate. Pronotum black with purple sides; elytra green, golden green, golden red or purple, with purple margins. Legs black. 28-36 mm. – An extremely local and magnificent species, endemic to the W. Alps (Piedmont: Biellese), in forests (Fagetalia) and alpine pastures, from 900 to 1600 m. .... **26.003 *C. (Chrysocarabus) olympiae*** Sella, 1855 (p. 270).

6 (5). Elytra without punctate striae; either the primary intervals are costate or the surface of the elytra is smooth and shiny.

7 (8). Protarsi in the male with only three dilated basal segments and with ventral pad of spatulate setae. Basal foveae of pronotum elongate and lin-

ear. Primary intervals strongly costate. Upper surface metallic green to golden green, blue-violet or blackish, lateral margins of elytra purple. 24-38 mm. – S.E. France, N.W. Italy (W. Alps, from Cottian to Ligurian Alps, N. Apennines). In deciduous forests in foothills to montane forests and alpine zone, from 200 to 2000 m. .... **26.004 C. *(Chrysocarabus) solieri*** Dejean, 1826 (p. 270).

Several infraspecific forms have been described; some of them merit subspecific status:

a) subsp. *solieri* Dejean, 1826 – Dorsal surface metallic green, golden green, purple or cupreous; sides of elytra golden-red to purple-violet; primary costae blackish, secondary and tertiary intervals of elytra confusely granulate. – W. Alps, from the Cottian to the Maritime Alps, and Basses Alpes near Digne, both on the Italian (Susa Valley, only) and the French sides.

b) subsp. *liguranus* Breuning, 1932 – Slightly different from *solieri* (*s. str.*) by the intermediate intervals more regular and reduced, almost smooth, with a shinier lustre. Size normally larger. 25-40 mm. – Ligurian Alps and N.W. (Ligurian) Apennines, S. Piedmont (Langhe region).

c) subsp. *clairi* Géhin, 1885 – Upperside green, or with slight traces of red lustre on the sides, or bluish, green-bluish to blue-violet. Intermediate intervals often in regular rows. 26-32 mm. Maritime Alps, mostly on the French side (in a wide area, with a hybrid zone with *solieri solieri*).

d) subsp. *bonnetianus* Colas, 1937 – Upperside dark violet, rather dull, only the sides of pronotum with bluish-violet to green-bluish lustre. Primary costae wide, low, the intermediate intervals in the form of regular, distinct rows. 26-34 mm. – S.E. France: Tanneron-Esterel Massif.

e) subsp. *bonadonai* Colas, 1948 – Distinguished from the latter by the smaller size (25-30 mm) and the less regular, granulate or reduced intermediate intervals. – France, Alps of the Provence and S. Maritime Alps.

8 (7). Protarsi in the male with four basal segments dilated and with a ventral pad of spatulate setae. Basal foveae of pronotum rounded, short.

9 (10). The apical segment of palpi slightly dilated (in females) to triangular (in males); antennal segments swollen laterally at apex in the male. Elytra very shiny, completely smooth or with slightly indicated primary intervals; dorsal surface metallic cupreous-red to golden-green, rarely purple-violet to blackish. – S.W. France and N. to E. Spain, Pyrenees. In lowland woods to montane forests, rarely in the alpine zone. .... **26.005. C. *(Chrysocarabus) splendens*** Olivier, 1791 (p. 271).

Morphologically rather homogeneous, only highly variable in colour and size. Although some forty infraspecific forms have been described, we agree with Deuve (1994) and Březina (1999), that none of them merit subspecific status. Some local populations, however, merit attention, for example the one that inhabits the Pic d'Arradoy (Atlantic Pyrenees), described as *arradoyensis* Legnet, 1975, constituted by constantly very large, green specimens.

10 (9). The apical segment of palpi in both sexes strongly dilated, in males axe-shaped; antennae simple in both sexes (*lineatus*) or sometimes swollen laterally at apex (some subspecies of *auronitens*), but in the last case, primary intervals evident and often distinctly costate.

11 (12). Body very elongate, elytra mostly depressed; antennae simple in both sexes. Antennae and femora always black or brownish. Apex of aedeagus slightly arcuate. Dorsal surface green, purple-reddish to bicolorous; primary intervals flattened to slightly costate. 20-35 mm. – W. Pyrenees and Cantabrian chain. In lowland woods to the alpine zone. .... **26.002. C. *(Chrysocarabus) lineatus*** Dejean, 1826 (p. 269).

Many infraspecific forms described: such as for *C. auronitens* (see below), two semispecies (*C. lineatus* and *C. lateralis*) belong to *lineatus* in the widest sense. They are retained by several authors (see Zaballos & Jeanne 1994) as distinct species.

a) subsp. *lineatus* Dejean, 1826 – Primary intervals distinct, narrow; interguments of elytra finely granulate. – C. Cantabrian chain.

b) subsp. *troberti* Kraatz, 1860 – Primary intervals reduced to fine metallic lines or fully evanescent; dorsal surface metallic, shiny, smooth, *C. splendens*-like. Dorsal surface green or cupreous-red. 26-30 mm. A local form *ursuius* Vacher de Lapouge, 1911 was described from Mt. Ursui, which slightly differs from the latter by its longer elytra and larger size: 30-35 mm. – W. Pyrenees, both on the French and Spanish sides.

c) subsp. *lateralis* Chevrolat, 1840 – Primary intervals distinct, sub-costate, convex, blackish; intermediate intervals in rows, finely granulate. 23-30 mm. – W. and C. Cantabrian chain, and Sierra de Estrella.

d) subsp. *leonensis* Born, 1918 – Distinguished from the latter by the smaller size and the shorter elytra (sometimes *C. nitens*-like): 19-22 mm. Dorsal surface often dark, violet to blackish. – Mountains of Leon.

e) subsp. *salmantinus* Bolivar, 1922 – Similar to *leonensis*, but the body flattened, the intermediate intervals more reduced and confused, dull, the upperside strongly bicolorous: head, pronotum and sides of elytra purple to metallic-red, the disc of elytra dark green to bluish-green. – Iberian central chains: Sierra de Gata, Sierra de Francia and Sierra de Bejar.

12 (11). Body ovate to ovate-elongate, normally more convex. Basal segments of antennae and femora red-

dish-yellow or dark-brownish, but in the latter case the antennae of male have the segments more or less laterally swollen at apex. Apex of aedeagus arcuate, narrowed. Dorsal surface metallic shiny to rather smooth, highly polychromous, the primary intervals roughly costate to slightly prominent. 18-34 mm. – C. Europe, from France (Pyrenees) in the W. to Poland and Romania in the E., Alpine chain in the S. and Germany in the N. Typical forest-dwelling species, both in deciduous and pine forests, more rare in the alpine zone. ....
.... **26.001. *C. (Chrysocarabus) auronitens*** Fabricius, 1792 (p. 265).

A subspecies-complex; more correctly, two semispecies, *auronitens* and *punctatoauratus*, are recognised as valid species by some authors. However, from a genetic standpoint, *punctatoauratus*, although geographically isolated (see map on p. 265), seems to be conspecific with *auronitens*:

a) subsp. *auronitens* Fabricius, 1792 – The most widespread subspecies in C. Europe, S.-wards to the W. Alps. Antennal segments in the male simple or only very slightly swollen laterally at apex; basal segments, femora and tibiae reddish-yellow. Highly polychromous. A dozen of forms, some of which merit in the opinion of several authors a subspecific status, have been based on the dorsal surface colour (normally with pronotum golden and elytra green in the typical *auronitens*, often red, violet, bronzed or black in northern populations), or on the smaller size in the high altitude populations. The most characteristic and notably, constant forms are *putzeysi* Mors, 1863, from the Belgian forests, for specimens with head and pronotum golden to cupreous-red and elytra blackish-violet to black, and *cupreonitens* Chevrolat, 1861, dark bronzed to bluish or violet, from the Calvados (France).

b) subsp. *costellatus* Géhin, 1882 (= *subfestivus* Obertür, 1884) – Similar to *auronitens* (*s.str.*) but tibiae black, primary costae very distinct and intermediate intervals rugoso-punctate. Dark forms more common in the northern populations. – C. and W. France: Auvergne, Bretagne.

c) subsp. *kraussi* Vacher de Lapouge, 1898 (= *intercostatus* Gredler, 1854) – Same characters as above, but tibiae black; dorsal surface constantly golden-green. Pronotum with sides slightly narrowed to the base; elytra wide and convex, primary intervals costate. – E. Alps.

d) subsp. *festivus* Dejean, 1826 – Tibiae black, as in *kraussi*. Pronotum highly cordate with sides narrowed and sinuous to the base, basal angles prominent; body more slender and depressed; primary intervals costate or (in typical *festivus*) reduced or almost lacking. Dorsal surface smooth and shiny. – S.W. France, Aude: Montagne Noire, Tarn.

e) subsp. *escheri* Palliardi, 1825 – Same characters as in *auronitens* (*s.str.*), but the body more elongate, pronotum narrower, the elytra less ovate, more depressed, narrowed at the base, widened in the apical third. Antennae very long, in the male reaching the middle of the elytra. Head and pronotum golden-reddish, elytra green or bluish-green, rarely bronze-blackish. – Carpathian Mountains to W. Ukraine and Romania.

f) subsp. *punctatoauratus* Germar, 1824 – The most isolated taxon of the *auronitens*-complex, treated as a distinct species by several authors. Antennomeres in the male swollen laterally at apex; basal segments of antennae and femora dark-reddish to black. Dorsal surface smooth, shiny, or more often with distinct points on primary intervals, all over the elytron. Primary intervals from costate to very reduced, flattened. Colour variable, from golden-green to golden-red or violet, less polychromous that in typical *auronitens*. – S.W. France, Pyrenees on both sides. Some local forms of *punctatoauratus* merit to be recognised as distinct subspecies (of a distinct species) in the opinion of several authors (see Deuve 1994; Zaballos & Jeanne, 1994 and Březina, 1999). These are:

punctatoauratus (*s.str.*), small sized (20-25 mm). Elytra ovate, convex; all surface of elytron confusely punctate. – E. Pyrenees.

montanus Géhin, 1882, wide, depressed specimens with pronotum slightly narrow to the base and primary points reduced. – C. and W. Pyrenees, both on French and Iberian sides.

farinesi Dejean, 1826, for specimens with primary intervals reduced to narrow, scarcely convex lines, so that the elytra are smoother, appearing highly metallic and polished, sometimes with primary points inconspicuous. Small size: 20-27 mm. – S.W. France: Ariège, Aude.

barthei Barthe, 1912, close to *farinesi*, but specimens of large size (25-34 mm), normally golden-green to cupreous-red, with elytral sculpture more evident and teguments less shiny. – S.W. France: Belesta forest and adjacent zones. Probably local form of *farinesi*.

canigouensis Schaefer, 1966, small (20-24 mm), depressed, more parallel-sized, montane specimens; primary points strongly impressed, intermediate intervals distinct, granulate; upperside cupreous, rather dull. – S.W. France, Canigou massif.

28. Subgenus Macrothorax Desmarest, 1850

Type species *C. aumonti* Lucas, 1849

Highly specialised species. Mediterranean (Tyrrhenian) subgenus consisting of three species (or four, if attributing a specific status to the Moroccan *C. aumonti* Lucas, 1849, a characteristic, cychrisised semispecies, which seems to have, however, a hybrid zone with *C. morbillosus*). A subgenus, close to *Macrothorax*, *Relictocarabus* Ledoux, 1984, has recently been described, for one species endemic to the High Atlas mountains.

Body elongate, medium to very large (25-40 mm). Head rather narrow, or cychrisised (in *C. aumonti*). Apical segment of palpi dilated, axe-shaped in the male; penultimate segment of labial palpi bisetose; submentum without setae. Pronotum subcordate, or narrowed anteriorly (in *aumonti*); marginal setae present or lacking. Elytra elongate-ovate, from depressed (*planatus*) to convex (*aumonti*), sometimes with apex mucronate; elytral sculpture of triploid type, with primary intervals catenulate, secondary and tertiary costate; the sculpture smooth in *aumonti*. Abdominal sterna with transverse furrows and without setiferous pores. All species are helicophagous, living in open country, mediterranean scrub or montane forest, also in cultivated land, from sea level up to 1500, sometimes 1800 m.

1 (2). Basal angles of the pronotum without setiferous pore. Body more or less convex; dorsal surface normally metallic polychromous, bronze, green to cupreous-red. 26-35 mm. – W. Mediterranean species, present in Maghreb (N. Algeria and N. Tunisia), S. part of the Iberian Peninsula, S. Italy (Calabria: Aspromonte), in the main Tyrrhenian islands (Baleares, Corsica, Sardinia, Sicily) and in several small islands near Sardinia and Sicily, Lampedusa, Malta. In S.E. France, C. Italy (Toscana) and probably introduced on several small islands. Eurytopic, more frequent in open country, also in cultivated land at low altitude, but in some areas frequent in mediterranean scrub and forest from sea level to about 1000 or1200 m. ... . **28.001. *C. (Macrothorax) morbillosus*** Fabricius, 1792 (p. 274).

Casale *et al.* (1982) included the populations of Corsica and Sardinia in subsp. *morbillosus* in the widest sense. Recently, Deuve (1994), limited the typical form to the W. Maghrebian populations, restoring the name *constantinus* for the E. Maghrebian and Corsico-Sardinian populations. Some subspecies are rather distinct:

a) subsp. *morbillosus* Fabricius, 1792 – Pronotum widened anteriorly, sides arcuate, slightly narrowed anteriorly side. Elytra elongate-ovate, subconvex. Elytral sculpture with primary intervals catenulate, convex, 4th secondary interval evident, complete, tertiary intervals reduced, broken in rows of granulations. Dorsal surface often darker and more polychromous, in some population green to blue-violet. – N. Algeria. Specimens introduced in S.E. France, probably from Kabylia, have been described as subsp. *cheminorum* Deuve, 1988.

b) subsp. *constantinus* Vacher de Lapouge, 1899 – Elytra more convex; intervals less convex, 4th secondary interval fully reduced, tertiary intervals granulated but more evident than in the typical form. Dorsal surface more constantly metallic bronze to reddish-cupreous. – N.E. Algeria, N. Tunisia, C. Italy (Toscana, introduced?), Sardinia, Corsica, Lampedusa. Specimens introduced to S.E. France, probably from Corsica, were described as *galloprovincialis* Vacher de Lapouge, 1910.

c) subsp. *alternans* Palliardi, 1825 – Body wider, elytra shorter and subdepressed. Pronotum narrowed anteriorly. Elytral surface flattened, the primary intervals slightly convex, secondary depressed, the tertiary reduced. Apex of aedeagus shorter, wider and more arcuate than in the typical form. – Sicily, Calabria (Aspromonte), Malta.

d) subsp. *macilentus* Vacher de Lapouge, 1899 – Pronotum narrowed anteriorly, sides slightly arcuate. Tertiary intervals highly reduced, elytron depressed. Dorsal surface normally dark cupreous, or greenish, the disc of pronotum often blackish. – S.E. Spain (Murcia, Catalonia); recently introduced in the region of Cadiz. Baleares (described as *balearicus* Vacher de Lapouge, 1913).

2 (1). Basal angles of the pronotum with setiferous pores.

3 (4). Body more elongate, highly depressed. Labium medially thickened, with median tooth shorter than the lateral lobes. Pronotum subquadrate to transverse, with sides slightly sinuous and bent upwards. Elytra long, flattened; sculpture of regular triploid type, the tertiary intervals broken, granulate. Dorsal surface shiny, brownish-black to black, at least with bluish or violet lustre on the sides of pronotum and elytra. 27-35 mm. – A very restricted, endemic species in N. Sicily (Madonie, Nebrodi). In montane *Fagus*-forests, from 1300 to 1700 m. .... **28.002. *C. (Macrothorax) planatus*** Chaudoir, 1843 (p. 275).

4 (3). Body stouter and more convex. Labium not thickened medially, with median tooth longer than the lateral lobes. Pronotum with sides only slightly bent upwards near the basal angles. Elytra more or less convex; sculpture of regular triploid type, the tertiary intervals complete or reduced. Dorsal surface duller, brownish-black to bronze, bluish, blue-violet or greenish. 20-36 mm. – C. and N. Morocco, Iberian Peninsula, S.W. France (Albères), introduced. .... **28.003. *C. (Macrothorax) rugosus*** Fabricius, 1775 (p. 275).

Many subspecies have been described; three main complexes can be recognised:

a) subsp. *rugosus* Fabricius, 1775 – (Only C. and N. Morocco).

b) subsp. *celtibericus* Germar, 1824 – Elytra very convex; primary and secondary intervals convex, tertiary reduced in rows of granulations. Dorsal surface brownish to brownish-violet, sometimes pronotum blue or green. – C. and N.W. Spain, C. and N. Portugal. Small, highly polychromous specimens from the Sierra de Gata, were described as *laufferi* Breuning, 1927; large specimens with very strong, convex elytral sculpture, from W.C. Spain, were described as *brannani* Schaufuss, 1871.

c) subsp. *boeticus* Deyrolle, 1852 – Elytra slightly convex; primary intervals narrow, flattened. Dorsal surface black to bluish-black, the sides often greenish. – S. Spain, from Andalusia to Catalonia and Guadalquivir Valley. S.W. France, introduced. Small specimens (22-24 mm) from Sierra de Segura, Sierra de Cazorla, Sierra del Pozo, Sierra de la Sagra and Sierra de Alcaraz, were described as *seguranus* Lauffer, 1905; large specimens with tertiary intervals complete or scarcely broken, from Catalonia, were described as *levantinus* Lauffer, 1905. Other local forms from Guadalquivir Valley, were described as *pseudobaeticus* Branes, 1985 (= *pseudoboeticus* Lasalle, 1986).

29. Subgenus Lamprostus Motschulsky, 1865

Type species *C. spinolai* Cristofori et Jan, 1937

Head large or thickened. Antennae fairly thick and short, apical segment of palpi slightly dilated, penultimate segment of labial palpi multisetose. Submentum without setae, labrum deeply bilobed. Pronotum without lateral setae, elytral sculpture triploid, homodynamous, intervals flattened, striae only minutely punctured, or elytral surface minutely granulate. Abdominal furrows present but reduced, male protarsi with 3 dilated segments. Related to *Procrustes* but different in the bilobed labrum. About 15 species, mostly in Anatolia to the Caucasus, N. Iran, Syria and Israel; especially numerous in Turkey. Only 1 species in S.E. Europe (E. part of the Balkan Peninsula).

1 (1). Large and stout, strongly convex. Black, slightly shiny, upper surface smooth, elytra minutely granulate, the margins of pronotum and elytra sometimes with greenish or bluish lustre. 32-37 mm. – S.E. Romania (Dobrudja), E. Bulgaria, European and widespread in Asiatic Turkey. In plains and foothills, rather xerophilous. .... **29.001. *C. (Lamprostus) torosus*** E. Frivaldszky, 1835 (p. 276).

Some subspecies; in Europe only the nominate subsp. *torosus* (*s.str.*); the other subspecies in the W., C. and S. part of Asiatic Turkey.

30. Subgenus Procrustes Bonelli, 1809

Type species *C. coriaceus* Linnaeus, 1758

Body from middle-sized to very large (23-55 mm), black, at most elytra rufous or the margins with slight metallic lustre. Head normal to moderately thickened. First antennal segment frequently without setae. Labrum trilobate (Fig. 3.2d). Mandibles long, the basal tooth of right mandible usually unidentate. Apical segments of palpi more or less dilated (more strongly in males); the penultimate segment of labial palpi multisetose; tooth of mentum thickened. Pronotum without lateral setae. Elytra sculpture more or less homodynamous, flat, frequently wrinkled. Abdominal furrows present; abdominal sterna without pores. Male protarsi with 3 dilated segments. About 10 species mostly in S.W. Asia, the E. mediterranean area, and the Caucasus. In Europe 2 species; they prey mostly on molluscs but also insects and earthworms.

1 (2). Sides of pronotum with wide borders and strongly bent upwards. Black, slightly shiny. Elytra moderately roughly tuberculate, without slides of intervals. 23-30 mm. – Greece: Isl. Creta. In the hills and mountains. .... **30.001. *C. (Procrustes) banoni*** Dejean & Boisduval, 1829 (p. 277).

2 (1). Sides of pronotum with narrow borders and slightly turned upwards. Black, dull to moderately shiny. Elytra roughly wrinkled to almost smooth. 26-42 mm. – Europe, except British Isles, N. Fennoscandia, and the Iberian Peninsula; in the E. to Jaroslavl, Moscow, Tula provinces, C. Ukraine; the islands of the Jonian and Aegean seas; to the S. in S. Italy, and Turkey (except N.E. districts). Mostly in broad-leafed quercetalia, mixed or pine forests, more rare in gardens and meadows. .... **30.002. *C. (Procrustes) coriaceus*** Linnaeus, 1758 (p. 277).

Many infraspecific forms have been described. Six of them possibly merit the subspecific rank, although their limits are not sharp in many cases.

a) subsp. *coriaceus* Linnaeus, 1758 – Large (35-42 mm, rarely to 28 mm) and stout, elytra dull, wrinkles irregular, moderately rough. – The N. and C. parts of species range; in the S. to S. France, Italy (also in Sicily; reported from Sardinia: introduced?), Slovenia, Serbia, middle Hungary, Czechia, N. slope of Carpathian Mts., C. Ukraine.

b) subsp. *rugifer* (Kraatz, 1877) – Similar to *coriaceus* (*s.str.*) but somewhat smaller (32-40 mm), elytra more shiny, wrinkles very rough. – Carpathian Mts. of Slovakia, Poland, Ukraine, Romania, also in the forests of Moldova and W. Ukraine.

c) subsp. *excavatus* Charpentier, 1825 – Smaller (28-37 mm) and especially narrower than *coriaceus* (*s.str.*). Hind angles of pronotum fairly long and acutely triangular. Elytra roughly but regularly sculptured. – N.E. Italy (Trieste), W. parts of Balkan Peninsula from Croatia to C. Albania, in the E. to W. Bosnia.

d) subsp. *mediterraneus* Born, 1906 – Somewhat larger than *excavatus* (30-38 mm), rather narrow. Hind angles of prothorax shorter, broadly triangular. Elytra with thin and shallow wrinkles. – S. Albania, W. Greece (Epyros), Ionian islands, S. Italy (Calabria, Puglia). A transadriatic-transionian element. All forms attributed to *joniensis* Breuning and to *florinensis* Vacher de Lapouge (see Chapter 2, *Checklist*, p. 68), are probably synonyms of *mediterraneus*.

e) subsp. *kindermanni* Waltl, 1838 – Rather small (28-35 mm). The sides of pronotum evenly rounded, somewhat turned upward, hind angles rather long, broadly rounded, elytra shallowly but distinctly wrinkled. – E. Bulgaria, European and the N.W. part of Asiatic Turkey.

f) subsp. *cerisyi* Dejean, 1826 – Small to rather large (26-38 mm). Elytra smooth with quite flat wrinkles or only with irregular punctures; primary foveae frequently distinct. – C. parts of Balkan Peninsula, from Serbia and S. Romania, through Macedonia, W. and C. Bulgaria to Greece (including Peloponnisos), islands of Archipelagos, W. and S.W. districts of Asiatic Turkey. Many local forms, especially in islands.

31. Subgenus Procerus Dejean, 1821
Type species *C. scabrosus* Fabricius, 1801
(nec Olivier, 1795 = *C. gigas* Creutzer, 1799)

Very large species. Mandibles long, strongly curved, acute, labrum bilobate. First antennal segment with seta. Apical segments of palpi strongly dilated, in males axe-shaped. Pronotum without marginal setae, abdominal furrows present. Protarsi in male not dilated. Upper surface of head and pronotum coarsely wrinkled, elytra with irregular rows of large tubercles. Body large and robust, length (in Europe) 36-60 mm, shiny above, black or metallic. From the revision of Cavazzuti (1989), it appears that there are 7 all together species in S.E. Europe and S.W. Asia (4 of them in Europe). In the checklists of Deuve (1994) and Březina (1994, 1999), only *C. gigas* (*s. lato*), *C. scabrosus* (*s. lato*) and *C. syriacus* have been maintained as valid species. Both adults and larvae are specialised mollusc-eaters.

1 (4). Body black, at most the margins of pronotum and elytra in humeral part with bluish tint.

2 (3). Pronotum strongly transverse, approximately 1.5 times as broad as long, front margin 1.4-1.5 times as narrow as than base. Elytra convex. 40-60 mm. – S.E. Austria, N.E. Italy, S.W. Romania, Balkan Peninsula except its S.E. part, probably Albania (but never cited) and N and C. Greece. Forests and scrub, also in gardens and parks, mostly on limestone soils. .... **31.002. *C. (Procerus) gigas*** Creutzer, 1799 (p. 280).

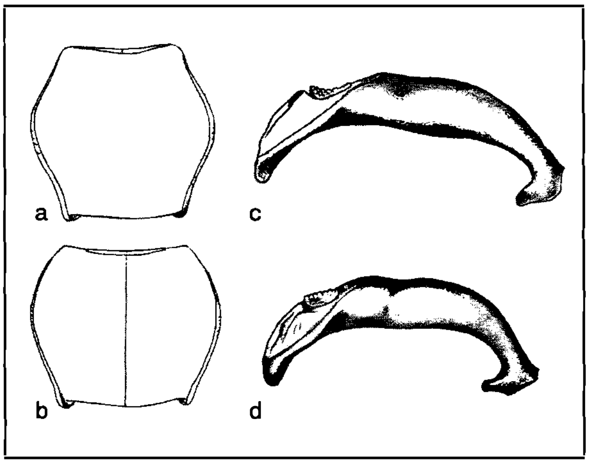


Fig. 3.19. The details of subgenus *Procerus* (after Cavazzuti, 1989). a – *scabrosus* (ssp. *culminicola*); b – *sommeri* (ssp. *sommeri*); c – *scabrosus* (ssp. *scabrosus*); d – *sommeri* (ssp. *bureschianus*).

In the opinion of Cavazzuti (1989), specimens from C. Greece and S. Macedonia, characterised by a smaller head and narrower pronotum, have to be attributed to the subspecies *parnassius* Kraatz-Koschlau, 1884, which would be a transitional form to *C. duponchelii*.

3 (2). Pronotum less transverse, strongly narrowed forward, front margin at 1.75-1.9 times narrower than base. Elytra more depressed. 36-53 mm. – S. Greece: Peloponnesos, from lowland forests up to 2000 m. Probably, an extreme southern subspecies of *C. gigas*. .... **31.001. *C. (Procerus) duponchelii*** (Dejean, 1831) (p. 280).

4 (1). The upper surface, epipleurae, and underside of thorax, metallic violet, blue, green or purplish-black, rarely black with metallic lustre.

5 (6). Pronotum almost hexagonal, anteriorly narrowed, its sides roundly obtuse-angled (Fig. 3.19a). External margin of mandible slightly curved. Aedeagus: Fig. 3.19c. Colour variable from dull-purple to green, length (in European specimens) 38-56 mm. – S.E. part of Balkan Peninsula, the Crimea, N.W. Asiatic Turkey................. .... **31.003. *C. (Procerus) scabrosus*** Olivier, 1795 (p. 281).

Several subspecies are known; two of them in Europe:

a) subsp. *scabrosus* Olivier, 1789 – Larger (47-56 mm) and more elongate. Upper surface usually violet, rarely bluish-violet or greenish-blue, sometimes bicolorous. – N. part of European Turkey and S.E. Bulgaria. Also in the Asian part of the Bosphorus.

b) subsp. *tauricus* Bonelli, 1810 – Smaller (38-48 mm), more short. Colour in the Crimean mountains usually violet or purplish-violet, sometimes almost black; at the S. shore of Peninsula mostly blue or green. – The Crimea except in steppe.

6 (5). Pronotum transverse to subcordate, sides more rounded (Fig. 3.19b). External margin of mandible evenly curved. Aedeagus: Fig. 3.19d. Colour mostly purplish-violet to violet. 25-60 mm. – S.E. part of Balkan Peninsula, Asiatic Turkey (C. and S.W. parts). .... **31.004. *C. (Procerus) sommeri*** Mannerheim, 1844 (p. 282).

Several subspecies are known, most of them in Asia Minor. In Europe one subspecies:

a) subsp. *bureschianus* Breuning, 1928 – Elongate, rather large (43-55 mm), dark violet to black-violet. – Bulgaria: C. Rhodope: Bačkovo, Čepelare, Asenovgrad; N.E. Greece: Xanthi region.

Chapter 4 Key to the larvae

E. Arndt & K. Makarov

4.1. INTRODUCTION

There is more information available on the larvae of the genus *Carabus* Linné than of most other coleopteran genera. Bengtsson (1927) and Lapouge (1905, 1908, 1929) were the first to describe the larvae of many *Carabus* species and the number of known larvae has increased dramatically in the second half of the 20th century. Major works included Sturani (1962) and Casale *et al.* (1982) for the Italian fauna, Hůrka (1971a) for the Central European fauna, and Raynaud (1975-76) who compiled the *Carabus* larvae worldwide. Arndt (1985) produced the first larval key of the European fauna, based on characters of the nasale region, head appendages and urogomphi. Recently, Makarov (1992) published a subgeneric key which used chaetotaxy in addition to other new characters. These characters enabled recognition of the larvae of most subgenera. However, a re-evaluation of previously described larvae was considered necessary to distinguish them at species level (see Arndt *et al.* 1994 and Makarov *et al.* 1991, 1993, 1994).

Today, the larvae of the majority of European *Carabus* species have been described. Although we have been able to examine the larvae of most species, we have not yet produced species keys for all subgenera. It has not been possible to produce keys for the larvae of *Mesocarabus* Thomson, *Orinocarabus* Kraatz, *Oreocarabus* Géhin, *Chaetocarabus* Thomson, and several species of *Eucarabus* Géhin, because some larvae were not available and/or the larvae of these taxa are very similar. Species keys to the larvae are also lacking for the two species of *Eurycarabus* Géhin, *Iniopachys* Solier and *Procrustes* Bonelli, the three species of *Macrothorax* Desmarest, the four species of *Procerus* Dejean (see Cavazzuti 1989 for this subgenus), and the five species of *Pachystus* Motschulsky. However, it is possible to distinguish the larvae of these groups because of the allopatric distribution of their species.

Characters of single species such as *C. (Ctenocarabus) galicianus* Gory and *C. (Iniopachys) pyrenaeus* Serville were taken from the literature (Andrade 1977; Raynaud 1965). The larva of the subgenus *Heterocarabus* Morawitz (only one species: *C. marietti* De Cristofori et Jan) is unknown. Using the key and the species' distribution, larvae of about 75% of the European fauna can be identified now (see Tab. 4.1).

The kwowledge of larvae can be helpful not only in ecological and faunistic studies but also in taxonomic and phylogenetic investigations (see Chapter 7). The larval morphology of two species from the European fauna contradicts the present taxonomy. *Carabus ermaki* Lutshnik differs markedly from *Pachycranion* Solier in the larval stage. Therefore, the subgenus *Carabulus* Lutshnik was accepted for this species by several authors (see Kryzhanovskij *et al.* 1995), however not followed in the present checklist (see Chapter 2). According to several authors (Shilenkov, 1993; Deuve, 1994; Březina, 1999), *Carabus truncaticollis* Eschscholtz should be placed in *Aulonocarabus* Reitter because of its larval and genital characters; here treated however in *Diocarabus* Reitter (compare Chapter 3).

4.2. LARVAL MORPHOLOGY

General habitus and colouration: Larva of campodeoid type, body subparallel (Fig. 4.1). Sclerites markedly sclerotised, brown to black, sometimes with blue metallic lustre or reddish head capsule, IX tergite.

Head capsule: Sides of head capsule more or less rounded, six stemmata present (Fig. 4.2), antenna four-segmented with a very small sensorial appendage on segment III. Cervical groove lacking, coronal suture short or lacking. First instar larva with 1-3 pairs of egg bursters in the posterior part of frontale. Nasale more or less protruding, of variable shape, ventral side of nasale with a single tooth (hypodon) in part visible from dorsal side; adnasale straight or protruding (see also Appendices 4.1-4.2). Gular suture complete. Labial palps with two palpomeres, ligula flat. Maxilla consisting of two-segmented cardo, stout stipes, large lacinia, two-segmented galea, four-segmented maxillary palps (including palpifer). Mandible with distinct retinaculum and penicillus.

Thorax: Pronotum (Fig. 4.3) larger than meso- and metanotum, with median suture present; meso- and metathorax (Fig. 4.4) with median suture and anterior keel. Legs five-segmented (coxa, trochanter, femur, tibia, tarsus), tarsus with two subequal claws. Mesothorax with large stigma.

◀ Larva of *C. putzeysianus omensis* Born. Italy, Cottian Alps (C. Valcavera). Photo by A. Vigna Taglianti

Table 4.1. Review of possible determination of larvae of European *Carabus* species (direct by key to the larvae or indirect by allopatric distribution).

Subgenus	Total No. of species	No. of species which can be distinguished		Number of species indistinguishable
		with the key	by allopatric distribution	
01 *Limnocarabus*	1 species only			–
02^{I} *Morphocarabus* 02^{II} *Trachycarabus*	23	15	3	5
03 *Carabus s.str.*	2	2		–
04 *Eucarabus*	8	4	1	3
05 *Tachypus*	4	2		2
06 *Archicarabus*	8	2	6	–
07 *Hemicarabus*	1 species only			–
08 *Diocarabus*	1 species only			–
09 *Aulonocarabus*	2			–
10 *Mesocarabus*	4		1	3
11 *Orinocarabus*	13	1	3	9
12 *Oreocarabus*	8	3	3	2
13 *Tomocarabus*	4	3		1
14 *Eurycarabus*	2		2	–
15 *Pachystus*	5	2	3	–
17 *Rhabdotocarabus* (incl. 16 *Ctenocarabus*)	2	(2)	2	–
18 *Hygrocarabus*	2		2	–
19 *Chaetocarabus*	5		3	2
20 *Platycarabus*	5	5		–
21 *Heterocarabus*	1 species only			1
08 *Diocarabus*	1 species only			–
23 *Megodontus*	10	3	1	6
24 *Pachycranion* (incl. *Carabulus*)	2	2		–
25 *Iniopachys*	2		2	–
26+27 *Chrysocarabus* (= *Chrysotribax*)	7	5	2	–
28 *Macrothorax*	3	2	1	–
29 *Lamprostus*	1 species only			–
30 *Procrustes*	2		2	–
31 *Procerus*	4		?4	–
Total Number	**132**			**34**

Note: The genera have been numbered and named in agreement with the present *Checklist* (Chapter 2). Some subgenera have been combined in the *Key to the adults*, but have been treated separately in *Checklist* (Chapter 2) and *Species accounts* (Chapter 5) e.g. 02^{I} *Morphocarabus* and 02^{II} *Trachycarabus* (see notes on pp. 16, 78 and 157).

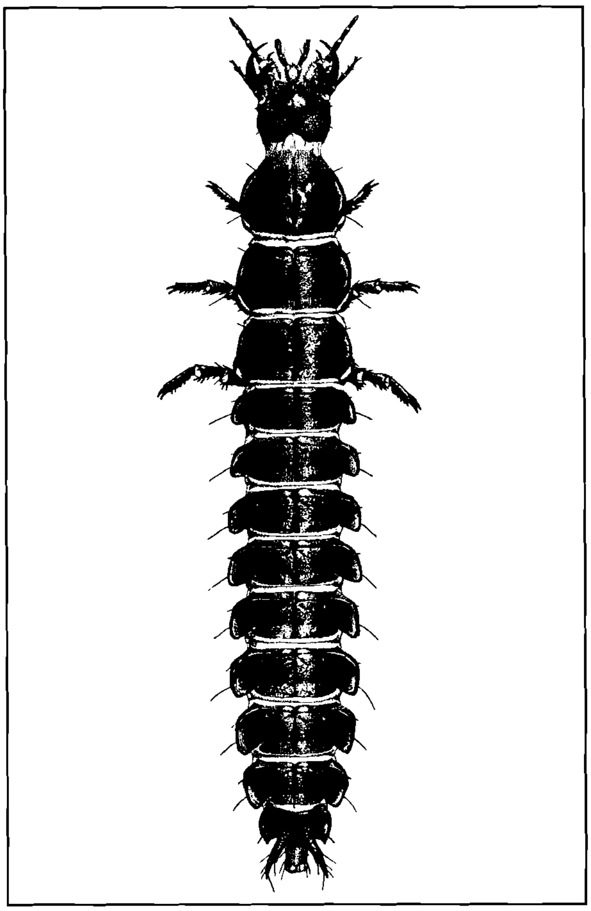


Fig. 4.1. Habitus (*C. exaratus*).

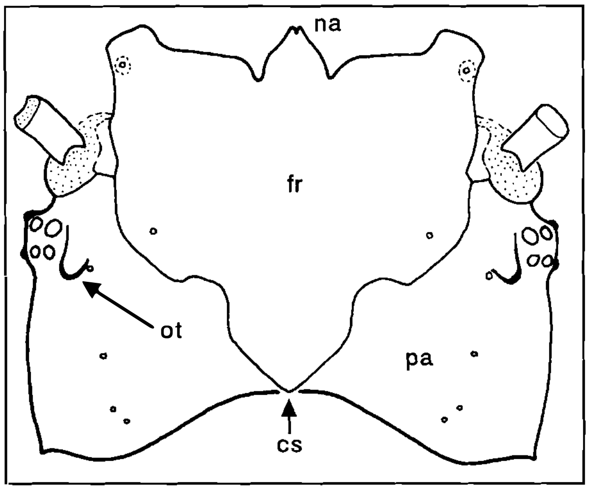


Fig. 4.2. Head capsule (*C. olympiae*). cs – rudiment of coronal suture; fr – frontale, na – nasale region, ot – supraocular tubercle, pa – dorsal side of epicranium (parietale).

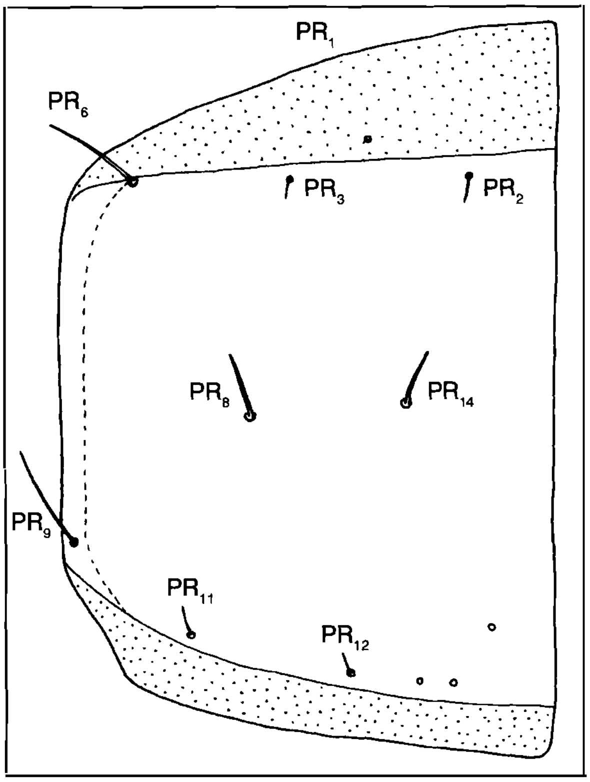


Fig. 4.3. Left half of pronotum with chaetotaxy (after Bousquet & Goulet 1984 and Makarov 1992).

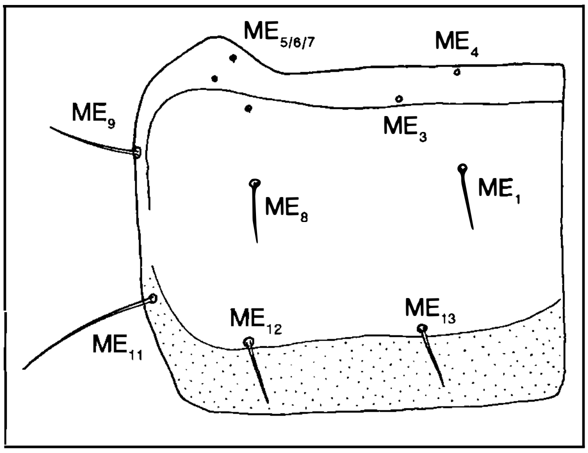


Fig. 4.4. Left half of mesonotum with chaetotaxy (after Bousquet & Goulet 1984 and Makarov 1992).

Abdomen: Eight subequal segments, segment IX smaller with urogomphi dorsoposteriorly, segment X (pygopod) conical, placed ventrally to segment IX. Abdominal segments I-VIII laterally with epipleurite, hypopleurite, ventrally with mediosternite, laterosternite (=coxal lobe) and sternellum (Fig. 4.5). Ventral sclerites in part fused. Segments I-VIII with a stigma each between tergite and epipleurite anteriorly. Tergites (Fig. 4.6) with anterior keel and median suture. Urogomphi fused with tergite IX, comparatively short, with pointed apex and usually 1-2 sharp horns dorsally and/or laterally (Fig. 4.7, see also Appendix 4.2).

Chaetotaxy: Setae and pores of the ground plan pattern present as described in Bousquet & Goulet (1984),

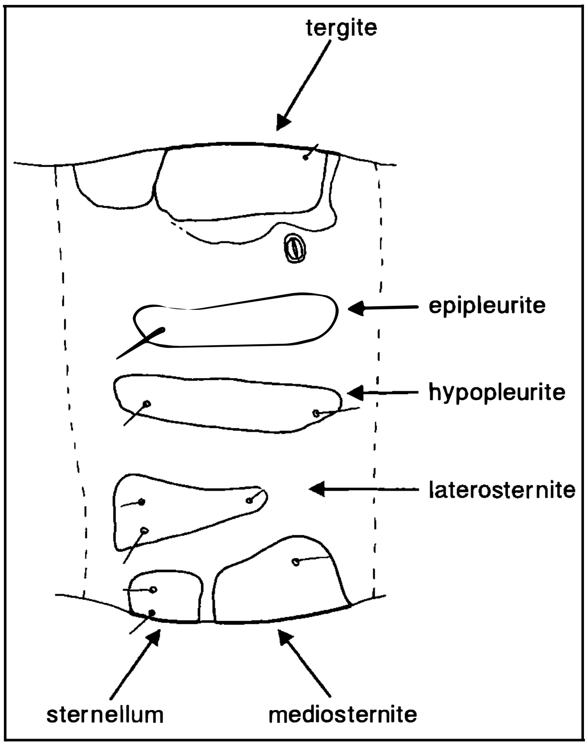


Fig. 4.5. Abdominal segment III, lateral view.

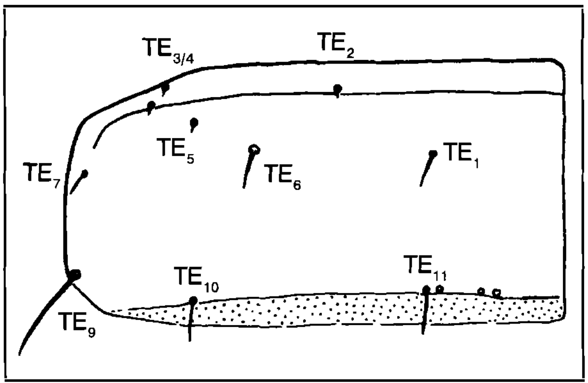


Fig. 4.6. Left half of tergite I with chaetotaxy (after Bousquet & Goulet 1984 and Makarov 1992).

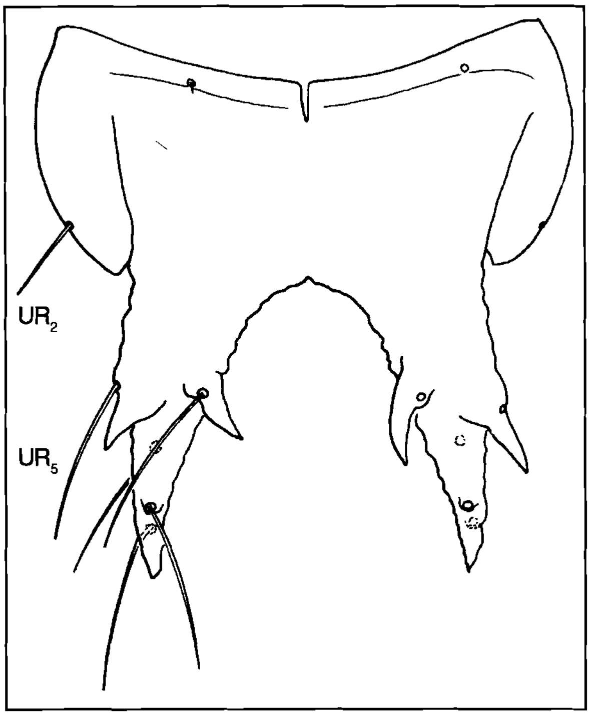


Fig. 4.7. Abdominal tergite IX and urogomphi with seta UR$_2$ and UR$_5$ (see also appendix 4.2).

except the following: PA$_{4,5,6,8,10}$ on parietale, PR$_{4,5,7,10}$ on pronotum, ME$_{2,10}$ on meso- and metanotum, TE$_8$, on tergite I-VIII, UR$_3$ on tergite IX which are all pore-like or lacking. Reduction of further setae (e.g. FR$_{8,9}$, PR$_{16,17}$, ME$_8$, TE$_{1,6,7}$) may occur in some species. Additional setae not present in the ground plan, however a large number of pores present on nearly all sclerites which complicates the homologization of pores and reduced setae.

Contrary to most other Carabidae, second and third instar larvae of *Carabus* do not have a set of secondary setae as described by Bousquet (1985) other than a higher number of bristles on the ventral side of the tarsi, additional setae on the ventrites and pleurites.

Note: A more detailed description of structures is given by Makarov (1992). In Appendices 4.1-4.2 nasale and urogomphi of different instar stages of several European species are presented.

4.3. KEY TO THE SECOND AND THIRD INSTAR LARVAE

4.3.1. Key to the European subgenera

(excluding *Heterocarabus* Morawitz)

All European *Carabus* species have three larval instars. The first instar is distinguished from the second and third instar by having egg bursters (only visible after clearing of larvae in KOH), a slightly different shape of nasale region and urogomphi, and fewer setae on ventral side of the tarsi. All characters used in the key concern the character state of the second and third instars. However, characters were selected in a way that also allows the determination of first instar larvae in most cases.

1 Antennomere II apically without setae 2
– Antennomere II apically with one or more setae 22
2 Nasale transverse or consisting of four teeth, not rostrum-like; adnasale sloped (cf. Figs 4.8a,b). Posterolateral angles of abdominal tergites extended or not extended. Urogomphi in most species not long and slender 3

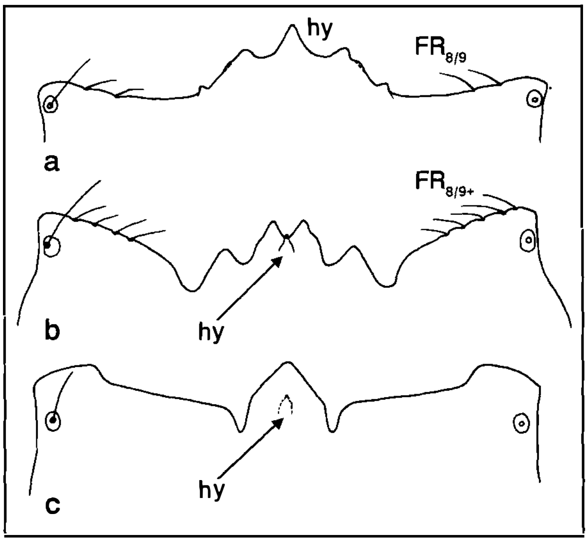


Fig. 4.8. Nasale and adnasale with position of most important setae ($FR_{8,9}$ and duplicated setae $FR_{8,9+}$) and hypodon (hy).
a – *C. granulatus*, b – *C. glabratus*, c – *C. coriaceus*.

– Nasale rostrum-like, lacking teeth; adnasale nearly horizontal (cf. Fig. 4.8c). Postero-lateral angles of abdominal tergites with extended lobes. Urogomphi long and slender with two horns (see App. 4.2: 40) .... 19. *Chaetocarabus* Thomson
(The other species of the subgenus can be identified by geographical exclusion: see table 4.1)

3 Cutting edge of mandible apically of retinaculum simple, not sloped (Fig. 4.9a); retinaculum with or without accessory tooth. Nasale not consisting of four distinct teeth; hypodon large, well-developed, usually building a medial tooth (Fig. 4.8a, see also App. 4.1: 24-25); setae $FR_{8,9}$ present or reduced, never duplicated. (Archeocarabi sensu Bengtsson, 1927) 4

– Cutting edge of mandible apically of retinaculum sloped (Fig. 4.9b), retinaculum always without accessory tooth. Nasale with four distinct teeth; hypodon small, usually not visible from dorsal view; setae $FR_{8,9}$ always present, in some cases duplicated (Fig. 4.8b, see also App. 4.1: 25, 38) 9

4 Urogomphi with two large horns, coarsely granulate (App. 4.2: 24). Setae ME_1 and ME_8 on mesonotum and metanotum present (cf. Fig. 4.4) .... 01. *Limnocarabus* Géhin (C. *clatratus* Linné)

– Horns of urogomphi smaller, less granulate. At least one of the setae ME_1 or ME_8 on mesonotum and metanotum reduced 5

5 Seta TE_9 present in posterolateral angles of abdominal tergites (Fig. 4.6). Mandibular retinaculum with accessory tooth, if absent, then labial palpomere II with only one sensorial area apically 6

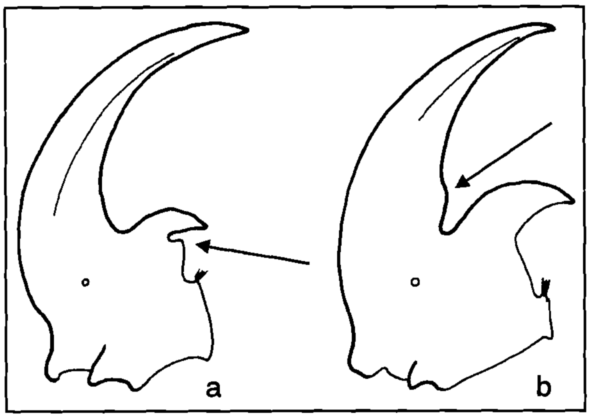


Fig. 4.9. Mandible, left side, dorsal view.
a – *C. scheidleri*, arrow shows an accessory tooth of retinaculum; cutting edge of mandible apically of retinaculum is simple, b – *C. problematicus*, arrow shows a sloped cutting edge; base of retinaculum without accessory tooth.

– Seta TE_9 lacking (cf. Fig. 4.6). Mandibular retinaculum without accessory tooth; second labial palpomere with two sensorial areas on divided apex .... 06. *Archicarabus* Seidlitz
Most of the species can be distinguished by their distribution. The larvae of the two widespread species are distinguished as follows:
A – Apex of urogomphi rounded, dorsal setae of urogomphi short (App. 4.2: 17) .... C. (*Archicarabus*) *montivagus* Palliardi
B – Apex of urogomphi acute, dorsal setae of urogomphi longer (App. 4.2: 16) .... C. (*Archicarabus*) *nemoralis* O. Müller

6 Posterior angles of abdominal mediosternites I-VIII without setae (as in Fig. 4.5), pygopod mesoventrally with 1-2 pairs of setae .... 02^{I} *Morphocarabus* Géhin + 02^{II} *Trachycarabus* Géhin (p. 132)

– Posterior angles of abdominal mediosternites I-VIII with at least one seta, pygopod mesoventrally with more than two pairs of setae 7

7 Labial palpomere II wide or slender, with two in part rather small sensorial areas on apex. Labial palpomere I dorsoapically with 0-2 setae, lateral group of setae on mediosternite (cf. Fig. 4.5) with two setae 8

– Labial palpomere II slender, with one sensorial area on apex. Labial palpomere I dorsoapically with 1-3 setae, lateral group of setae on mediosternite (cf. Fig. 4.5) with 3-4 setae .... 03. *Carabus s.str.*
A – Retinaculum without accessory tooth. Species widespread, not restricted to fen habitats........................... .... *C. (Carabus s.str.) granulatus* Linné

B – Retinaculum with accessory tooth (cf. Fig. 4.9a). Species only in fen habitats. .... *C. (Carabus s.str.) menetriesi* Hummel

8 Labial palpomere I dorsoapically without setae. Supraocular tubercle strongly protruding; teeth of urogomphi forked (App. 4.2: 23) .... 05. *Tachypus* Weber

A – Ventral side of epicranium with two long setae. Abdominal tergites I-VII with setae TE$_{7,9}$ (cf. Fig. 4.6) lacking. Laterosternite, inner sternite and largest part of hypopleurite with transverse meshed microsculpture. Teeth of nasale not turned to outer sides; hypodon large and distinct (App. 4.1: 23) .... *C. (Tachypus) cancellatus* Illiger

B – Ventral side of epicranium with three long setae. Abdominal tergites I-VII with setae TE$_{7,9}$ (Fig. 4.6) present. Hypopleurite completely, and parts of the laterosternite and inner sternites with distinct granulate microsculpture. Teeth of nasale turned outwards; hypodon not distinct from dorsal side (App. 4.1: 10) ... . *C. (Tachypus) auratus* Linné

– Labial palpomere I dorsoapically with one long and 2-3 medium-sized setae. Supraocular tubercle indistinct, teeth of urogomphi of another shape (App. 4.2: 13, 21) .... 04. *Eucarabus* Géhin (p. 134)

9 (3) Seta TE$_7$ absent (cf. Fig. 4.6). Labial palpomere II with apex not divided. Inner side of retinaculum with small and less distinctive sinuation. Seta UR$_2$ on abdominal tergite IX (cf. Fig. 4.7) very long, nearly as long as tergite, and placed almost in the posterior angles of tergite. Urogomphi long and thin (App. 4.2: 39) 10

– Seta TE$_7$ small but present (Fig. 4.6). Labial palpomere II with divided apex. Inner side of retinaculum equally rounded without any sinuation. Seta UR$_2$ much shorter as tergite IX and often shifted anteriorly. Urogomphi shorter and stout. (Metacarabi sensu Bengtsson, 1927) 11

10 Anterior margin of frontale between nasale and adnasale angles not equally sinuated, adnasale region straighter, angles acute, turned outside. Seta TE$_9$ present (cf. Fig. 4.6). .... 17. *Rhabdotocarabus* Seidlitz (*C. melancholicus* Fabricius) (Larvae at least in part with seta on antennomere II, see couplet 22)

– Anterior margin of frontale between nasale and adnasale angles equally sinuated; angles not turned outside. Seta TE$_9$ absent (cf. Fig. 4.6, see also App. 4.1: 39) .... 18. *Hygrocarabus* Thompson (?and *Ctenocarabus* Thomson)

A – Nasale wider, hypodon distinctive. Species distributed in Czech Republic, Slovakia, Western Ukraine, Hungary, Romania .... *C. variolosus* Fabricius

B – Nasale slender, hypodon less distinctive. Species distributed in Germany, the Alps, Western Balkan .... *C. nodulosus* Creutzer (The larva of *C. galicianus* Gory meets probably the same characters like those of *Hygrocarabus* species. *C. galicianus* is restricted to the Western Iberian peninsula.)

11 Seta TE$_9$ present in posterolateral angles of abdominal tergites I-VIII (Fig. 4.6). Labial palpomere I without setae. Urogomphi longer than tergite IX, strongly granulate .... 07. *Hemicarabus* Géhin (*C. nitens* Linné)

– Seta TE$_9$ absent in posterolateral angles of abdominal tergites I-VIII (cf. Fig. 4.6). Labial palpomere I with setae dorsoapically. Urogomphi shorter, less granulate 12

12 Anterior margin of adnasale with two setae FR$_{8,9}$ (cf. Fig. 4.8a) 13

– Anterior margin of adnasale with 3-8 setae including FR$_{89}$ (Fig. 4.8b) 16

13 Urogomphi with one large horn dorsally, lateral horn completely lacking; tergite IX and urogomphi equally fine punctate. Labial palpomere I with two small setae dorsoapically .... 14. *Eurycarabus* Géhin (Two species of which the larvae cannot be distinguished: *C. faminii* Dejean on Sicily and *C. genei* Gene on Corsica and Sardinia)

– Urogomphi with two large horns, lateral horn distinctive; urogomphi more or less coarsely granulate, much more granulate than tergite IX. Labial palpomere I with 1-5 setae dorsoapically 14

14 Labial palpomere I with one seta dorsoapically 15

– Labial palpomere I with 3-5 setae dorsoapically .... 09. *Aulonocarabus* Reitter (*C. canaliculatus* Adams)

15 Seta UR$_2$ in apical angle of tergite IX; urogomphi stout and more granulate (App. 4.2: 27) .... 08. *Diocarabus* Lapouge (part., *C. truncaticollis* Eschscholtz)

– Seta UR$_2$ (cf. Fig. 4.7) in posterior third of lateral margin of tergite IX, distinctly removed from the angles; urogomphi more slender and less granulate (App. 4.2: 32) .... 11. *Orinocarabus* Kraatz part (excl. *C. linnaei* Panzer)

16 (12) Urogomphi with two large and distinct horns (cf. Fig. 4.7) 17

– Dorsal horn of urogomphi present, large; lateral horn reduced, indistinctive or completely absent 18

17 Labial palpomere I with one seta dorsoapically. First segment of maxillary palpomere without any setae dorsally. Horns of urogomphi of the same size. Seta UR$_2$ (cf. Fig. 4.7) on tergite IX in the posterior third of the lateral margin (App. 4.2: 31) .... 11. *Orinocarabus* Kraatz (*C. linnaei* Panzer)

– Labial palpomere I with 3-5 setae dorsoapically. First segment of maxillary palpomere with some very small setae dorsally. Lateral horn of urogomphi smaller than dorsal horn. Seta UR$_2$ (cf. Fig. 4.7) on tergite IX shifted to the median third of the lateral margin (App. 4.2: 30) .... 10. *Mesocarabus* Thomson

18 Labial palpomere I without seta or with one seta dorsoapically. Setae TE$_{10,11}$ (cf. Fig. 4.6) on abdominal tergites I-VIII long, nearly as long as tergites; sternellum with only one seta, inner seta (ST$_3$) reduced. .... 12. *Oreocarabus* Géhin, part. (*C. glabratus* Paykull)

– Labial palpomere I with 3-5 setae dorsoapically. Setae TE$_{10,11}$ (cf. Fig. 4.6) short, not longer than 1/5 of tergal length, sternellum with two setae (ST$_{3,4}$) present. 19

19 Maxillary palpomere IV with one small sensorial area. Anterior margin of adnasale with 2-3, rarely on one side with 4-5 setae (cf. Fig. 4.8b, see also App. 4.1: 29) .... 12. *Oreocarabus* Géhin (excl. *C. glabratus* Paykull)

A – Mesoventrally on pygopod (group PY$_7$) with 4 setae .... *C. hortensis* Linné

B – Mesoventrally on pygopod (group PY$_7$) with about 8 setae .... *C. preslii* Dejean

(The larvae of the three Iberian species are unknown or not adequately described (see Tab. 4.1))

– Maxillary palpomere IV with two sensorial areas. Anterior margin of adnasale with 4-8 setae (cf. Fig. 4.8b) 20

20 Urogomphi relatively short and robust, slightly curved apically. Anterior part of laterosternite and hypopleurite without setae (cf. Fig. 4.5) .... 08. *Diocarabus* Lapouge (*C. loschnikovii* Fischer)

– Urogomphi longer, strongly curved apically. Anterior part of laterosternite (ST$_6$) and anterior part of hypopleurite with setae (cf. Fig. 4.5) 21

21 Hypodon distinctive visible between the median nasale teeth. Anterior margin of adnasale with 5-8 setae (cf. Fig. 4.8b, see also App. 4.1: 37, 38) .... 15. *Pachystus* Motschulsky

The species are distinguished by their allopatric distribution. The two most easterly distributed species can also be distinguished morphologically:

A – Hypodon larger, seta UR$_5$ on urogomphi (see Fig. 4.7) present... .... *C. cribellatus* Adams

B – Hypodon small, seta UR$_5$ usually absent .... *C. hungaricus* Fabricius

– Hypodon not visible from dorsal view. Anterior margin of adnasale with 4-6 setae .... 13. *Tomocarabus* Reitter

22 (1) Adnasale region not S-like sinuate, nearly straight (App. 4.1: 41) 23

– Adnasale region S-like sinuate (Fig. 4.8c) 24

23 Nasale with 4 distinct teeth (cf. Fig. 4.8b) .... 17. *Rhabdotocarabus* Seidlitz (*C. melancholicus* Fabricius)

– Nasale without teeth, rostrum-like (cf. Fig. 4.8c, see also App. 4.1: 41, 43) ....20. *Platycarabus* Morawitz (p. 134)

24 Lateral margin of abdominal tergites at most with two setae (TE$_{7,9}$, cf. Fig. 4.6). Sternella and laterosternites each with three setae or less. Dorsal surface of body without metallic lustre 25

– Lateral margin of abdominal tergites with 3-9 setae (incl. TE$_{7,9}$). Sternella and laterosternites each with more than four setae. Dorsal surface of body with metallic blue or blue-green lustre; larvae very large with head width >2.8 mm in first instar and >5.5 mm in third instar............ .... 31. *Procerus* Dejean

25 Laterosternite with three setae. Inner sternites of first abdominal segments separate or fused 26

– Laterosternite with only two setae. Inner sternites of first abdominal segments always fused 31

26 Antennomere II with only one apical seta. Sternellum with two single setae (ST$_{3,4}$). Nasale triangular, in part with small apical incision 27

– Antennomere II apically with 3-6 setae. Sternellum usually with a group of three setae. Nasale not triangular 28

27 Lateral tooth of urogomphi present, large. Mediosternite with two pairs of setae on each side .... 26.+27. *Chrysocarabus* Thomson (incl. *Chrysotribax* Reitter (p. 134)

– Lateral tooth of urogomphi reduced (App. 4.2: 45). Mediosternite with three pairs of setae on each side . ... 22. *Sphodristocarabus* Géhin (*varians* Fischer, = *C. janthinus* Gangelbauer)

28 Inner sternites of first abdominal segments separate, coronal suture reduced .... 25. *Iniopachys* Solier

(Differences between the larvae of *Iniopachys* could not be found. However, the two species are geographically separated.)

– Inner sternites fused, coronal suture distinct, on average not shorter than diameter of antennomere IV 29

29 Urogomphi coarsely granulate with a large lateral tooth (App. 4.2: 49). Setal group on outer side of stipes consisting of two long and 3-5 medium long setae .... 24. *Pachycranion* Solier part. (*C. schoenherri* Fischer)

– Urogomphi not distinctively granulate with lateral tooth small or absent. Setal group on outer side of stipes consisting of two long and 0-2 medium long setae. 30

30 Last maxillary palpomere considerably widened apically; setal group gMX on inner side of stipes divided in two parts: a row of setae on mesal margin and a field of equally distributed setae dorsally. Lateral group of setae on mediosternite (cf. Fig. 4.5) with at most two setae. Seta PR$_{14}$ present (Fig. 4.3). Galeomere I without setae. Labial palpomere I dorsoapically with one long and 2-4 medium long setae. Epipleurite and pleurite of prothorax with setae .... 23. *Megodontus* Solier (p. 135)

– Last maxillary palpomere slightly widened apically; setal group gMX on inner side of stipes not split into

two parts, consisting of one extended setal field. Lateral group of setae on mediosternite (cf. Fig. 4.5) with 2-3 setae. Seta PR$_{14}$ (cf. Fig. 4.3) lacking. Galeomere I with setae. Labial palpomere I dorsoapically with one long and one (rarely two) medium long setae. Epipleurites and pleurites of prothorax without setae. ..
.... 24. *Pachycranion* Solier part.
(= *Carabulus* Lutshnik; *C. ermaki* Lutshnik)

31 (25) Hypodon completely lacking*. Seta ME$_8$ lacking (cf. Fig. 4.4). Urogomphi longer than tergite IX, lateral horn ± distinct (App. 4.2: 51). Nasale more or less lancet-shaped. Setal group gMX on inner side of stipes divided into two parts, a row of setae on mesal margin and a field of equally distributed setae dorsally. Mediterranean species ....
.... 28. *Macrothorax* Desmarest

A – Nasale wider, not lancet-shaped. Lateral horn of urogomphi reduced, indistinctive ....
.... *C. rugosus* Fabricius

B – Nasale slender, lancet-shaped (App. 4.1: 51). Lateral horn of urogomphi distinct ....
.... *C. morbillosus* Fabricius

(The larva of *C. planatus* Chaudoir is unknown. It occurs only on Northern Sicily.)

– Hypodon present on ventral side of nasale*. Seta ME$_8$ present (cf. Fig. 4.4). Urogomphi not longer than tergite IX, lateral horn absent or shifted dorsobasally. Nasale wide, not lancet-shaped. Setal group gMX on inner side of stipes divided in two parts or not divided, equally distributed. Not restricted to Mediterranean ..
.... 32

* Only visible after clearing larvae in KOH.

32 Seta FR$_6$ in middle distance between FR$_4$ and FR$_7$ (cf. Fig. 4.10). Supraoculare tubercle strongly protruding (cf. Fig. 4.2). Urogomphi with dorsal tooth of normal shape, lateral tooth lacking (App. 4.2: 52). Setal group gMX on inner side of stipes at least in some species divided into two parts, a row of setae on mesal margin and a field of equally distributed setae dorsally ....
.... 30. *Procrustes* Bonelli
(Only the larva of *C. coriaceus* Linné is known. The second species, *C. banoni* Dejean, is restricted to Crete, where *C. coriaceus* does not occur.)

– Seta FR$_6$ nearby FR$_7$ (cf. Fig. 4.10). Supraoculare tubercle flat. Urogomphi of another shape. Setal group gMX on inner side of stipes not divided, equally distributed. ....
...29. *Lamprostus* Motschulsky (*C. torosus* Frivaldszky)

—

4.3.2. Key to selected subgenera

02$^{\mathrm{I}}$ *Morphocarabus* Géhin + 02$^{\mathrm{II}}$ *Trachycarabus* Géhin
(Eastern European species)

(Characters in part variable and species difficult to distinguish – this key should be regarded as preliminary.)

1 Ventral side of epicranium with two or less setae (PA$_{17}$, in part PA$_{16}$ lacking, cf. Fig. 4.11) and TE$_7$ (cf. Fig. 4.6) usually absent (TE$_7$ and three setae on ventral side of epicranium present in *C. odoratus* Motschulsky and *C. karpinskii* Kryzhanovskij et Matveev), teeth of urogomphi subequal, directed upwards (02$^{\mathrm{I}}$ *Morphocarabus* Géhin) 2

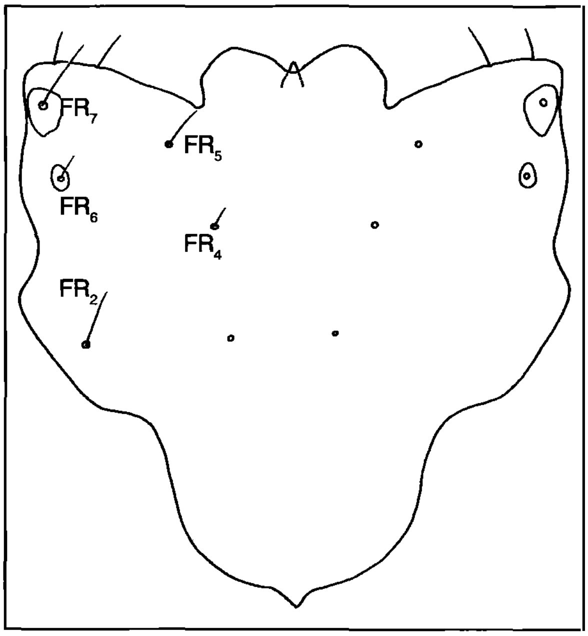


Fig. 4.10. Frontale with chaetotaxy (*C. auratus*).

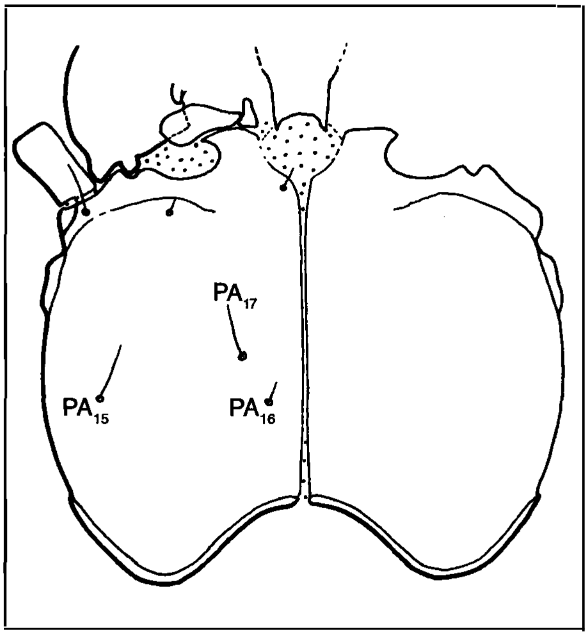


Fig. 4.11. Parietale ventral side with chaetotaxy.

– Ventral side of epicranium with three setae (Fig. 4.11, PA$_{16}$ somtimes pore-like, e.g. in *C. sibiricus*) and TE$_{7}$ (cf. Fig. 4.6) usually well developed (in *C. planus* seta TE$_{7}$ very small), dorsal tooth of urogomphi larger, directed obliquely inside (subgenus 02^{n} *Trachycarabus* Géhin) 9

2 Middle of ventral epicranium without setae (setae PA$_{16}$ and PA$_{17}$ always absent, only lateral PA$_{15}$ present, cf. Fig. 4.11). Urogomphi of last instar larvae not longer than tergite IX, tarsi of posterior legs as long as tibiae or longer than tibiae 3

– Ventral side of epicranium with three setae (setae PA$_{16}$ and PA$_{17}$ present, cf. Fig. 4.11). Urogomphi of last instar larvae longer than tergite IX, tarsi of posterior legs longer than tibiae (App. 4.2: 7) 8

3 Hypodon protruding distinctively over level of lateral teeth of nasale 4

– Hypodon small, not protruding over level of lateral teeth of nasale (App. 4.1: 2) .... *C. excellens* Fabricius

4 Lateroventral surface of coxae with 5-8 strong spines (gCO$_{7}$). Lateral teeth of nasale separated from adnasale region by small incision 5

– Lateroventral surface of coxae with 2-4 thin bristles (gCO$_{7}$). Lateral teeth of nasale not separated from adnasale region by a small incision 6

5 Galeomere I with accessory seta .... *C. hampei* Küster

– Galeomere I without accessory setae .... *C. hummeli* Fischer von Waldheim

6 Anterior seta of laterosternite (ST$_{6}$) present (cf. Fig. 4.5). Distal part of urogomphi short. Hypodon smaller, usually with pointed tip 7

– Anterior seta of laterosternite (ST$_{6}$) generally reduced (cf. Fig. 4.5). Urogomphi with elongate distal part. Hypodon well developed, in last instar larvae with broad roundish tip .... *C. aeruginosus* Fischer von Waldheim, *C. scheidleri* Panzer and *C. monilis* Fabricius (The three species differ geographically. Galeomere I dorsoapically usually with 3 or more setae in *C. scheidleri* and two or less setae in *C. monilis*. Posterior tarsi of both species longer than tibiae).

7 Labial palpomere I with 2-3 setae dorsoapically. The pair of setae on ligula (LA$_{6}$) divergent. Posterior part of hypopleurite (cf. Fig. 4.5) usually with accessory seta .... *C. regalis* Fischer von Waldheim

– Labial palpomere I with one (rarely two) seta dorsoapically. The pair of setae on ligula (LA$_{6}$) parallel. Posterior part of hypopleurite (cf. Fig. 4.5) without accessory seta .... *C. henningi* Fischer von Waldheim

8 Urogomphi robust, relatively short. Seta PA$_{16}$ at least 0.5 times as long as seta PA$_{17}$ (cf. Fig. 4.12) .... *C. odoratus* Motschulsky

– Urogomphi longer and slender. Length of seta PA$_{16}$ less than 0.5 times that of seta PA$_{17}$ (cf. Fig. 4.12) .... *C. karpinskii* Kryzhanovskij et Matveev

9 (2) Labial palpomere I with 1-2 setae dorsoapically 10

– Labial palpomere I with 3-4 setae dorsoapically 11

10 Nasale with short hypodon, much shorter than nasale teeth (App. 4.1: 14). Urogomphi with very short horn. South-East European distribution, not east of the Black Sea .... *C. scabriusculus* Olivier

– Nasale with long and distinct hypodon protruding inner nasale teeth (App. 4.1: 15). Urogomphi with large horns of normal size. Eastern European distribution, north and east of the Caspian Sea .... *C. sibiricus* Fischer von Waldheim

11 Hypodon not shorter than median teeth of nasale. Seta PA$_{17}$ very short (cf. Fig. 4.11) 12

– Hypodon distinctly shorter than median teeth of nasale. Seta PA$_{17}$ longer (cf. Fig. 4.11) 13

12 Epipleurites and pleurites of prothorax without setae. Trochantin mostly with one seta .... *C. haeres* Fischer von Waldheim

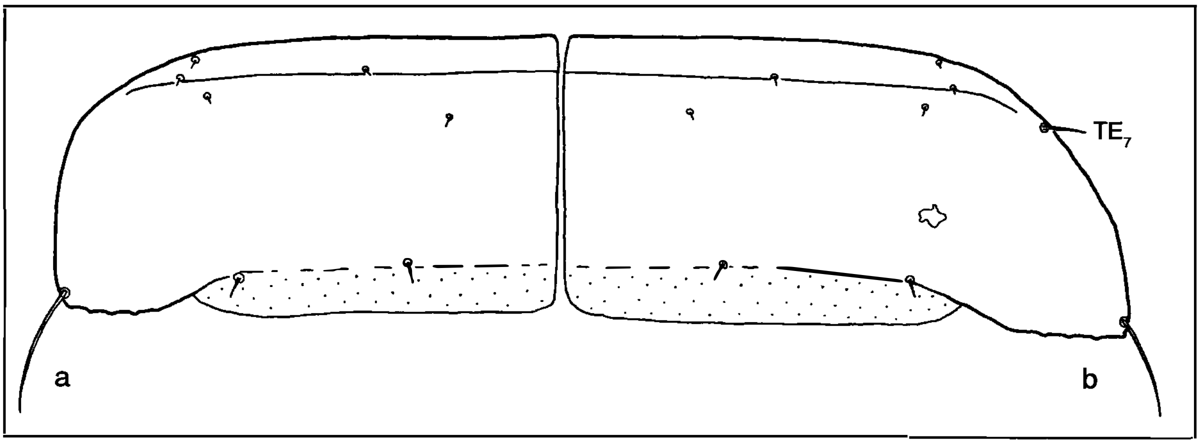


Fig. 4.12. Tergite I of *Platycarabus* species (a – *C. fabricii*, *C. irregularis*; b – *C. cychroides*, *C. depressus* = *bonelli*, *C. creutzeri*).

– Epipleurites and pleurites of prothorax with one seta. Trochantin with two setae. .... *C. besseri* Fischer von Waldheim

13 Seta PA_{17} longer (cf. Fig. 4.11) of moderate size. Pleurites of prothorax without setae .... *C. estreicheri* Fischer von Waldheim

– Seta PA_{17} (cf. Fig. 4.11) very long. Pleurites of prothorax with one seta 14

14 Pleurites of mesothorax and metathorax with one seta, epipleurites of prothorax with 1-2 setae .... *C. bosphoranus* Fischer von Waldheim

– Pleurites of mesothorax and metathorax with three setae, epipleurites of prothorax without setae .... *C. perrini* Géhin

04. *Eucarabus* Géhin

A key is available for four widespread species. A further species (*C. deyrollei* Gory) is distinguished by its allopatric distribution on the Iberian peninsula. Three in part sympatric species from Italy and the Balkan cannot be distinguished.

1 Hypodon relatively small; setae $FR_{3,4}$ close to each other. Epimeron of meso- and metathorax with more than 10 setae. Seta LA_6 on ligula divergent. .... 2 (Larvae of *C. obsoletus* Sturm will also probably key out here, with a distinct accessory tooth on nasale in contrast to *C. stscheglowi* and a robust granulate urogomphi in contrast to *C. arvensis*. But larvae were not available for comparison.)

– Hypodon very large, protruding as central tooth distinctly beyond the lateral teeth of nasale (cf. Fig. 4.8a, see also App. 4.1: 21); setae $FR_{3,4}$ distant from each other (cf. Fig. 4.10). Epimeron of meso- and metathorax with more than 2-8 setae. Seta LA_6 on ligula parallel .... *C. ulrichii* Germar

2 Retinaculum with small accessory tooth. Seta FR_5 long, extended to the median teeth of nasale. Hypopleurite with 1-2 setae anteriorly, mesosternite with 2 (rarely 1) setae laterally. Urogomphi slender, less granulate (App. 4.2: 18) .... *C. arvensis* Herbst

– Retinaculum without accessory tooth. Seta FR_5 shorter, not extended to the lateral teeth of nasale. Hypopleurite with 3-5 setae anteriorly, mesosternite with 3 (rarely 2) setae laterally. Urogomphi robust and granulate (App. 4.2: 20) .... *C. stscheglowi* Mannerheim

13. *Tomocarabus* Reitter

The larva of *C. antipai* Panin is unknown.

1 Two sensorial areas on last maxillary palpomere fused. Lateral horn of urogomphi and seta UR_5 completely lacking. Nasale in all instars wide .... *C. bessarabicus* Fischer

– Last maxillary palpomere with two distinctive sensorial areas. Lateral horn of urogomphi and seta UR_5 present. Nasale in first instar narrow 2

2 Seta FR_5 shifted laterally (cf. Fig. 4.10). Urogomphi robust, more granulate, with large lateral horn (App. 4.2: 36) .... *C. marginalis* Fabricius

– Seta FR_5 near to the nasale region, not shifted laterally (see Fig. 4.10). Urogomphi slender, sparsely granulate, with very small lateral horn (App. 4.2: 35) .... *C. convexus* Fabricius

20. *Platycarabus* Morawitz

1 Terebrum (cutting edge) of mandible serrate. Seta TE_7 on lateral margin of abdominal tergites present (Fig. 4.12b) .... *C. cychroides* Baudi

– Terebrum (cutting edge) of mandible smooth. Seta TE_7 on lateral margin of abdominal tergites present or lacking 2

2 Seta TE_7 on lateral margin of abdominal tergites present (Fig. 4.12b) 3

– Seta TE_7 on lateral margin of abdominal tergites lacking (Fig. 4.12a) 4

3 Apical sensorial area of last maxillary palpomere extended, kidney-shaped .... *C. depressus* Bonelli (= *C. bonellii* Dejean)

– Apical sensorial area of last maxillary palpomere not extended, round and small .... *C. creutzeri* Fabricius

4 Apical sensorial area of last maxillary palpomere extended, divided .... *C. fabricii* Panzer

– Apical sensorial area of last maxillary palpomere extended, round and small .... *C. irregularis* Fabricius

26.+27. *Chrysocarabus* Thomson (including *Chrysotribax* Reitter)

1 Supraocular tubercle strongly protruding, large (Fig. 4.2). Species restricted to the North-Western Italian Alps .... *C. olympiae* Sella

– Supraocular tubercle flat, little distinct. Other distribution 2

2 Labial palpomere I dorsoapically with one long and 1-2 short setae 3

– Labial palpomere I dorsoapically with one long and 3-4 short setae 4

3 Nasale with small incision apically. Species distributed in the North-Western Iberian peninsula .... *C. lineatus* Dejean

– Nasale without incision, pyramidal ....
A – Species distributed in the Pyrenees .... *C. splendens* Olivier

B – Species distributed in the South-Western parts of the Alps .... *C. solieri* Dejean

4 Nasale very wide and comparable flat (App. 4.1: 44) .. .. *C. auronitens* Fabricius

– Nasale less wide, protruding more strongly................
A – Species distributed in Southern France .... *C. hispanus* Fabricius
B – Species distributed in the South-Eastern Pyrenees .... *C. rutilans* Dejean

23. *Megodontus* Solier (Eastern European species)
(Characters sometimes variable and species difficult to distinguish. Some differences in shape of nasale and urogomphi see in App. 4.1: 46-48 and App. 4.2: 46-48)

1 Seta TE_7 well-developed (cf. Figs 4.6, 4.12b). Row of setae on inner margin of stipes consisting of uniformly very short setae. Seta FR_6 nearby FR_7 (cf. Fig. 4.12) 2

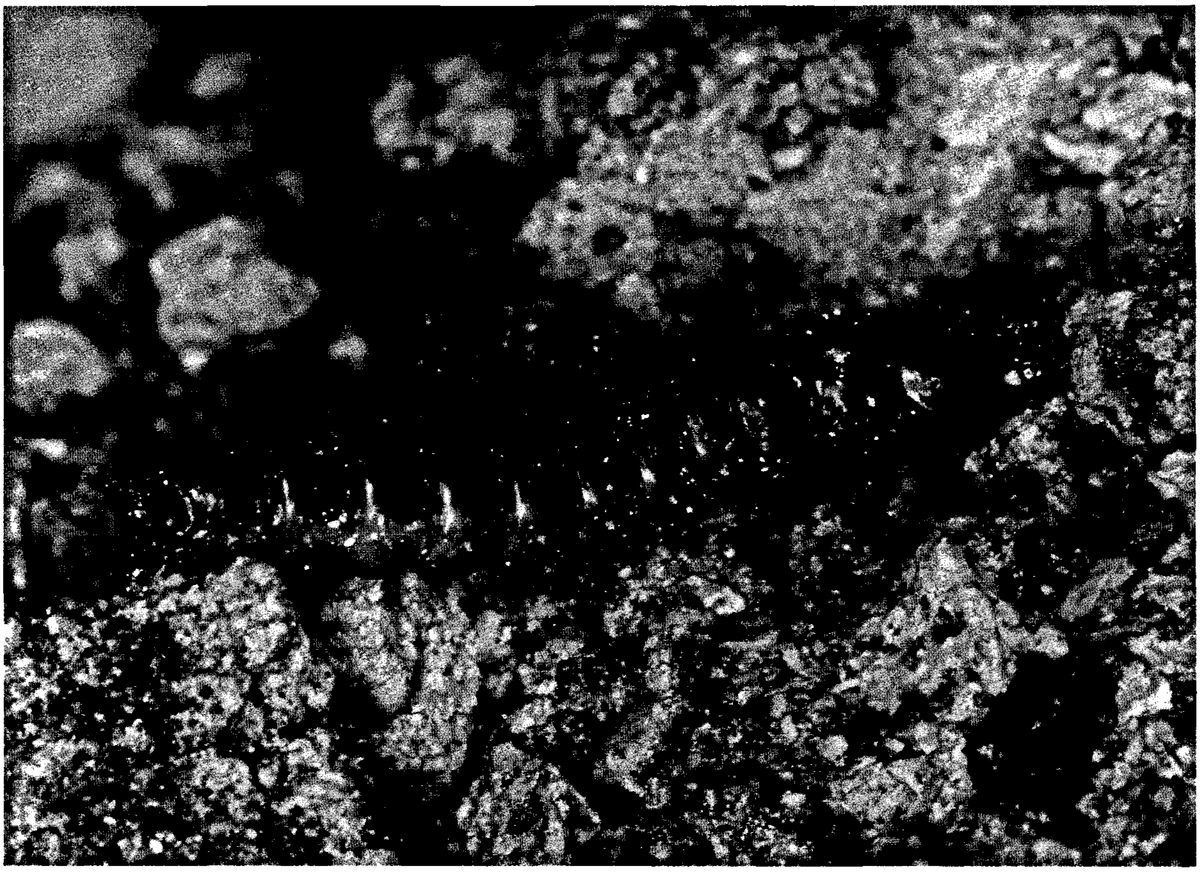
– Seta TE_7 lacking (cf. Fig. 4.12a). Row of setae on inner margin of stipes longer with the most apical setae still longer than those in the middle part. Seta FR_6 distant from FR_7 (cf. Fig. 4.10, see also App. 4.1: 46; 4.2: 46) .... *C. exaratus* Motschulsky

2 Pleurites of prothorax with two setae, pleurites of meso- and metathorax with 3-4 setae, epipleurites of prothorax with four setae, epipleurites of meso- and metathorax with five setae (App. 4.1: 47; 4.2: 47) .... *C. gyllenhali* Fischer von Waldheim

– Pleurites of prothorax, meso- and metathorax with two or less setae, epipleurites of prothorax with three or less setae, epipleurites of meso- and metathorax with less than four setae 3

3 Coronal suture reduced. Sternellum only with one seta. Incision of nasale tip inconspicuous. Dorsal surface of head dark pigmented .... *C. aurolimbatus* Dejean

– Coronal suture longer than diameter of antennomere IV. Sternellum with two setae. Anterior incision of nasale distinctive. Dorsal surface of head more or less red or reddish brown .... *C. violaceus* Linné, *C. violaceus purpurascens* Fabricius and *C. germarii (= exasperatus)* Sturm



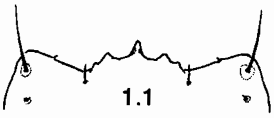
Larva of
C. rossii Born
Italy, Latium (Rome).
Photo by
A. Vigna Taglianti.

APPENDIX 4.1. Nasale of different stages of *Carabus* larvae

Sp.: The first numbers refer to the species and correspond with the numbering in Appendix 4.2 (Urogomphi).
Stages: The second number refers to the larval instar (14.3 means *Carabus scabriusculus*, third instar).

Sp.		Stages		
02^{I} Morphocarabus				
1	*aeruginosus*	1	2	3
2	*exellens*	1	2	3
3	*hampei*	1	2	3
4	*henningi*		2	3
5	*hummeli*	1		3
6	*karpinskii*	1	2	
7	*odoratus*	1	2	3
8	*regalis*	1	2	3
02^{II} Trachycarabus				
9	*besseri*	1	2	
10	*bosphoranus*	1		3
11	*estreicheri*			3
12	*haeres*	1	2	3
13	*perrini (= ssp. planus)*	1	2	3
14	*scabriusculus*	1	2	3
15	*sibiricus*	1	2	3
06 Archicarabus				
16	*montivagus*	1		3
17	*nemoralis*	1	2	3
04 Eucarabus				
18	*arvensis*	1	2	3
19	*cumanus* (N. Caucasus)	1	2	3
20	*stscheglowi*		2	3
21	*ulrichii*	1	2	3
03 Carabus				
22	*granulatus*	1	2	3
05 Tachypus				
23	*cancellatus*	1	2	3
01 Limnocarabus				
24	*clatratus*	1	2	3
07 Hemicarabus				
25	*nitens*	1	2	3
09 Aulonocarabus				
26	*canaliculatus*	1	2	3
08 Diocarabus				
27	*truncaticollis*	1	2	3
12 Oreocarabus				
28	*glabratus*	1	2	3
29	*hortensis*	1	2	3

Sp.		Stages		
10 Mesocarabus				
30	*problematicus*		2	
11 Orinocarabus				
31	*linnaei*	1		3
32	*sylvestris*		2	3
08 Diocarabus				
33	*loschnikovii*	1	2	3
13 Tomocarabus				
34	*bessarabicus*	1		3
35	*convexus*	1	2	3
36	*marginalis*	1	2	3
15 Pachystus				
37	*cribellatus*	1	2	3
38	*hungaricus*	1	2	3
18 Hygrocarabus				
39	*variolosus*	1	2	3
19 Chaetocarabus				
40	*intricatus*	1	2	3
20 Platycarabus				
41	*depressus*			3
42	*fabricii*			3
43	*irregularis*			3
26(+27) Chrysocarabus				
44	*auronitens*	1	2	3
22 Sphodristocarabus				
45	*varians (=janthinus)*	1	2	3
23 Megodontus				
46	*exaratus*	1	2	3
47	*gyllenhali*	1	2	
48	*violaceus*	1	2	3
24 Pachycranion				
49	*schoenherri*	1	2	3
50	*ermaki*	1	2	3
28 Macrothorax				
51	*morbillosus*			3
30 Procrustes				
52	*coriaceus*	1	2	3
29 Lamprostus				
53	*torosus*			3
31 Procerus				
54	*scabrosus*	1	2	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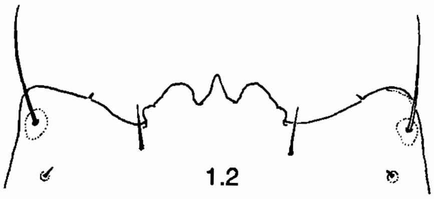
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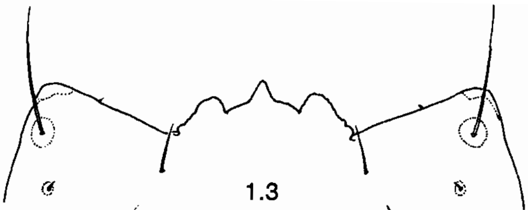
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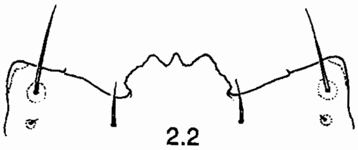
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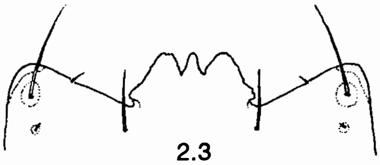
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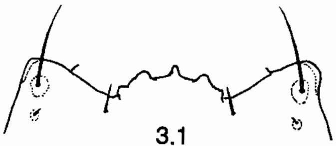
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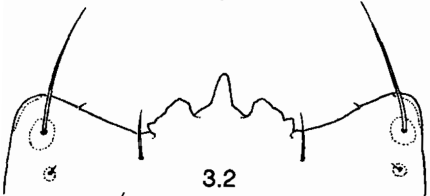
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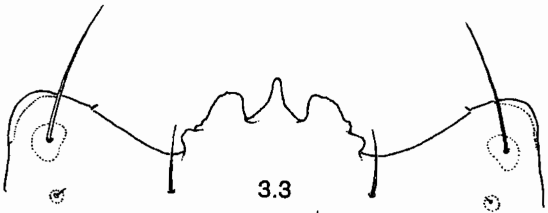
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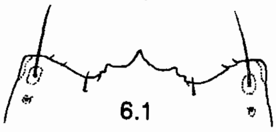
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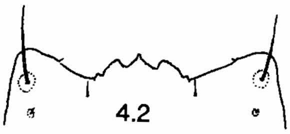
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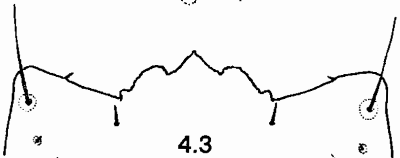
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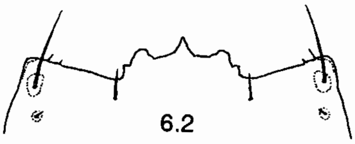
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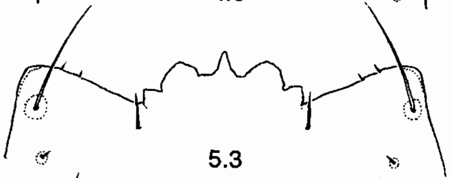
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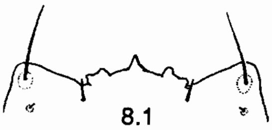
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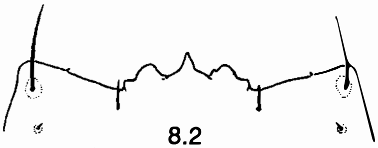
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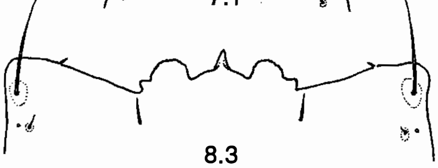
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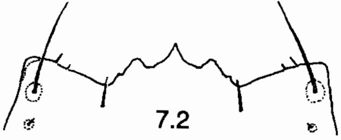
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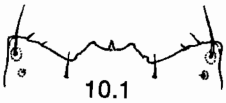
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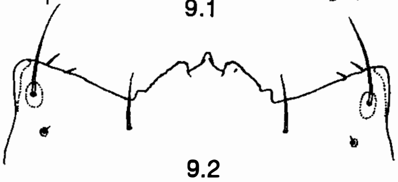
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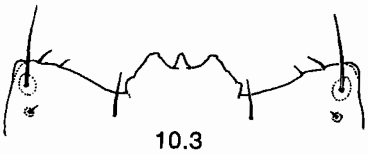
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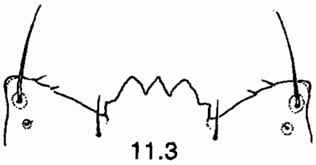
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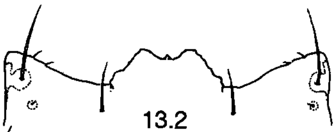
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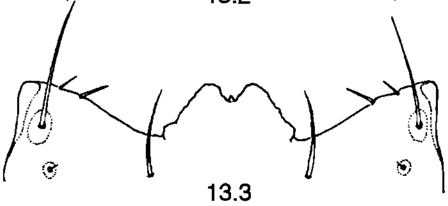
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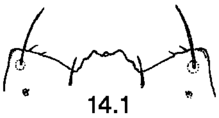
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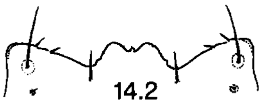
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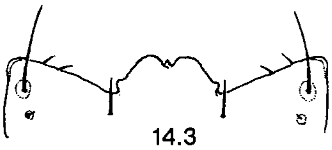
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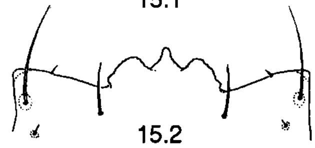
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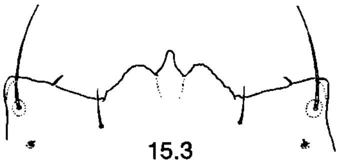
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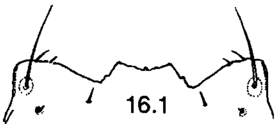
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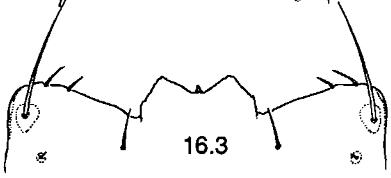
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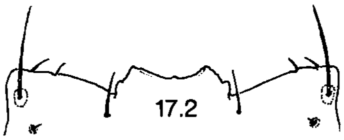
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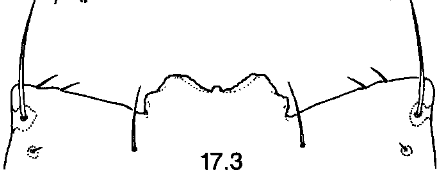
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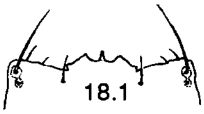
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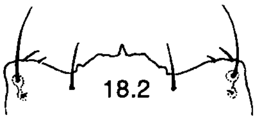
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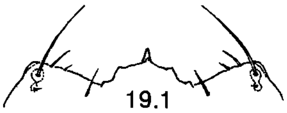
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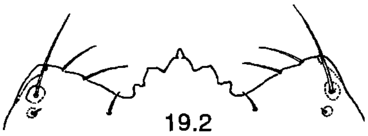
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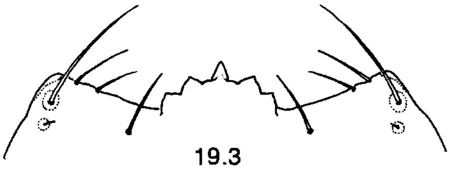
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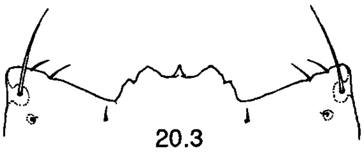
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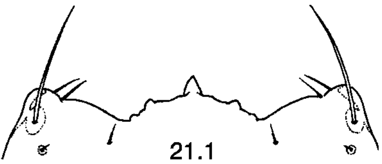
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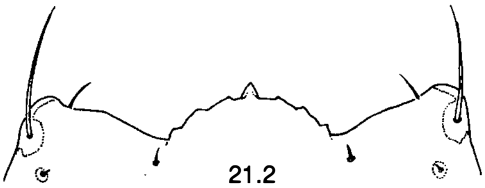
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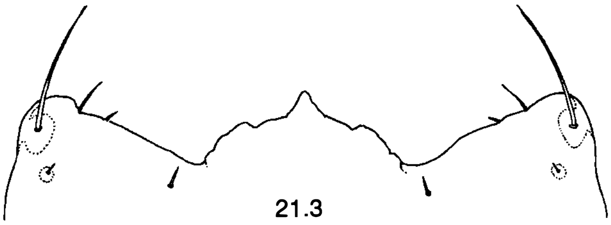
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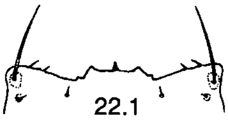
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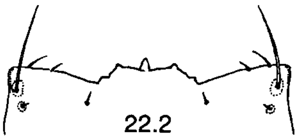
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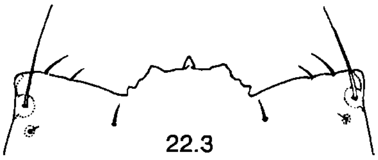
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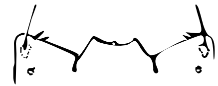

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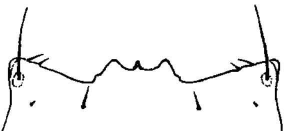

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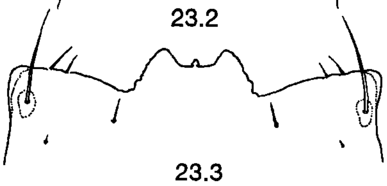

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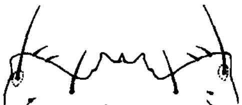

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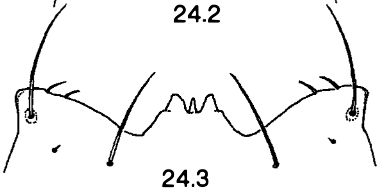

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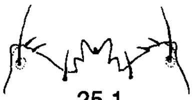

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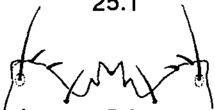

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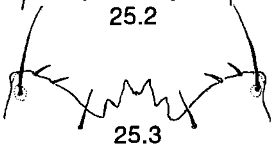

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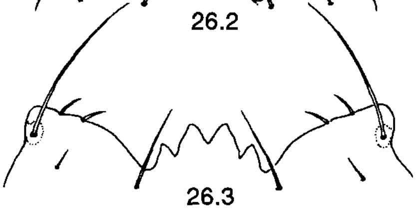

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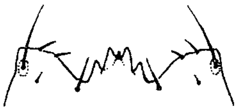

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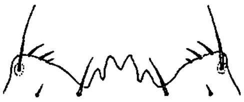

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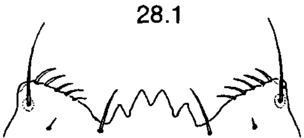

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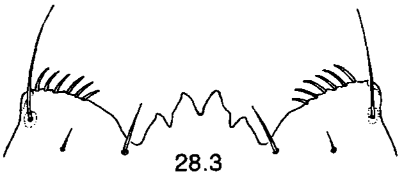

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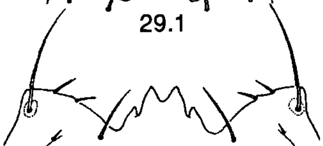

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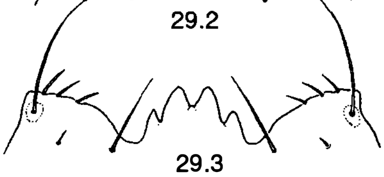

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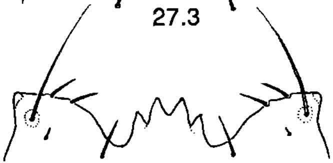

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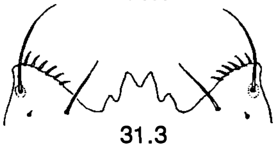

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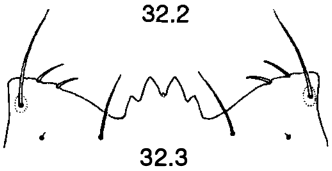

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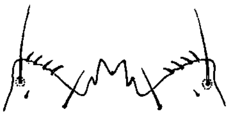

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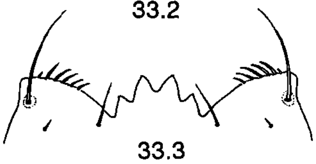

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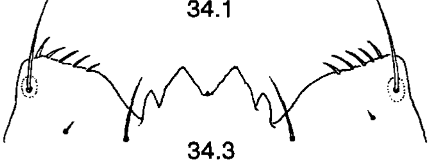

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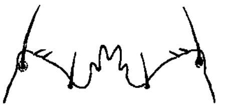

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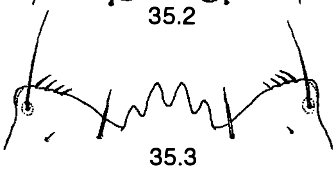

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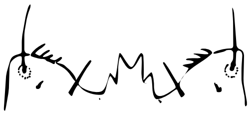
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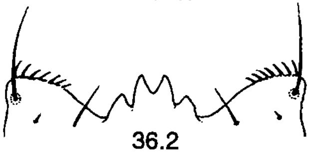
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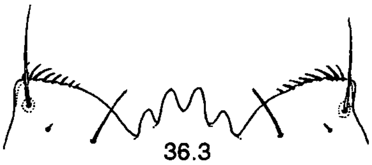
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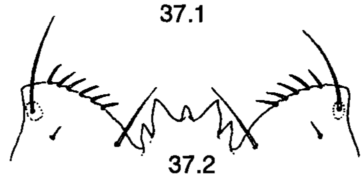
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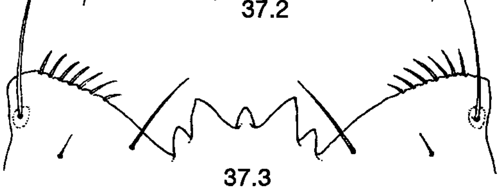
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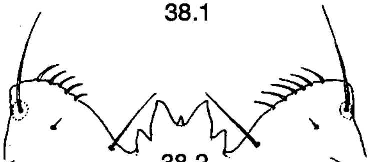
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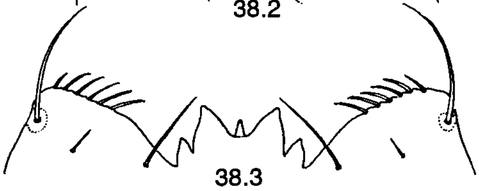
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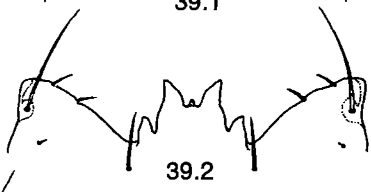
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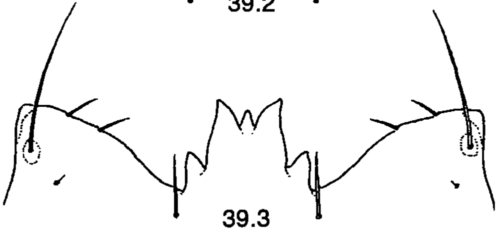
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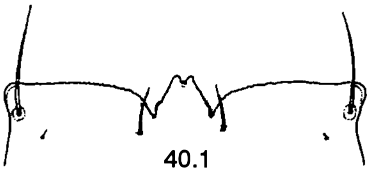
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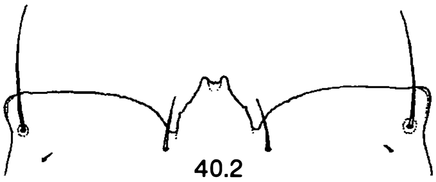
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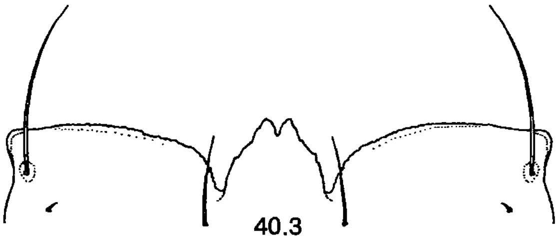
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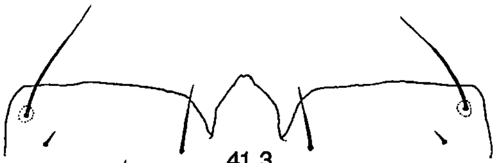
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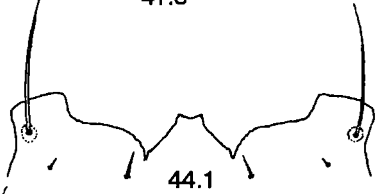
42.3


43.3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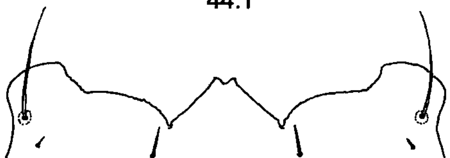
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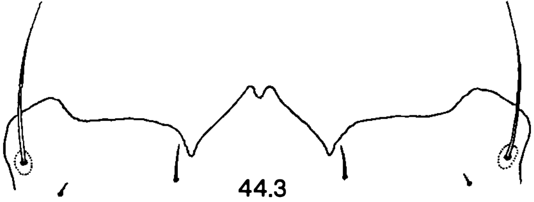
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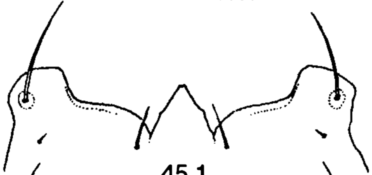
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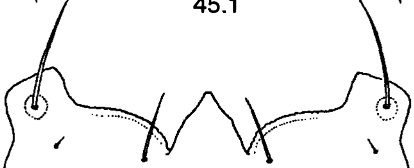
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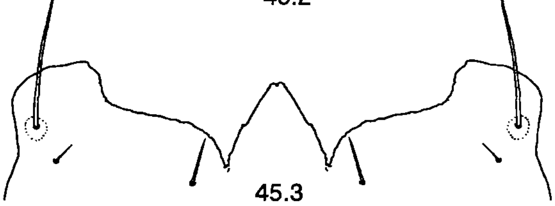
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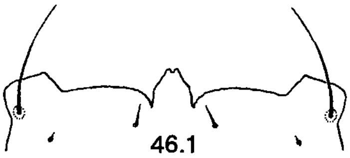
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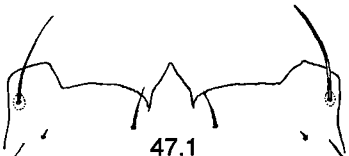
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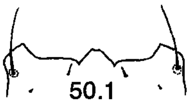
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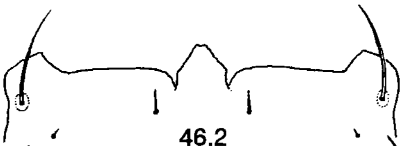
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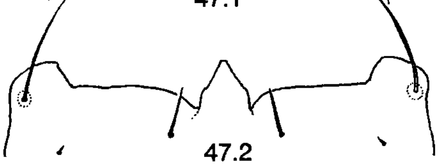
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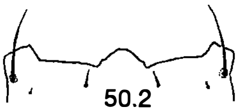
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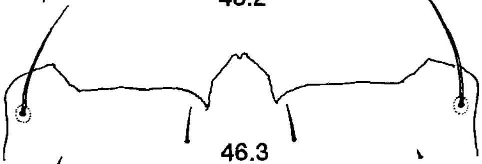
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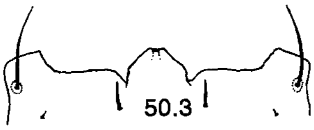
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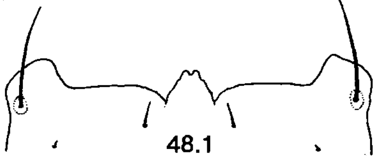
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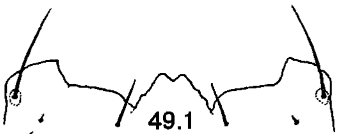
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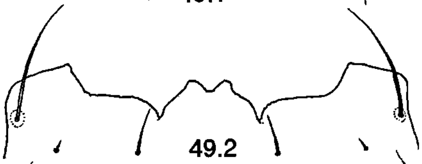
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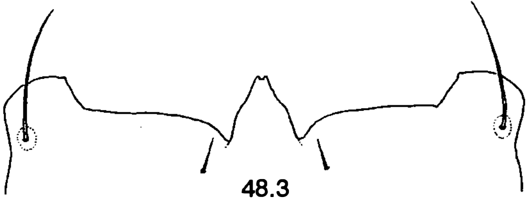
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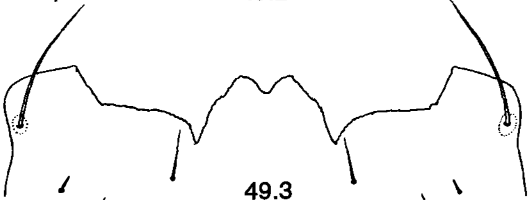
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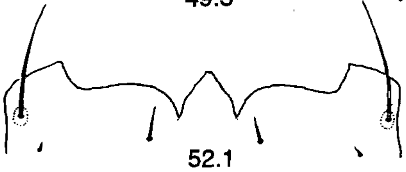
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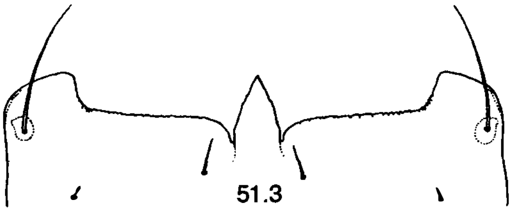
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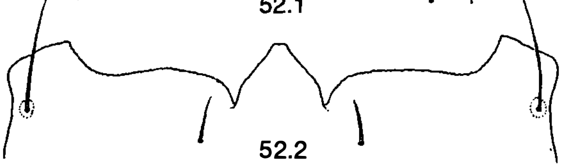
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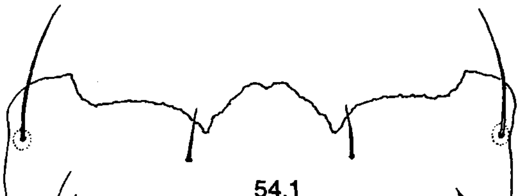
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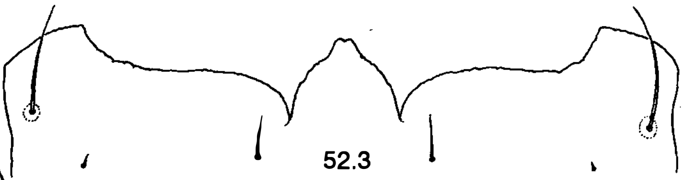
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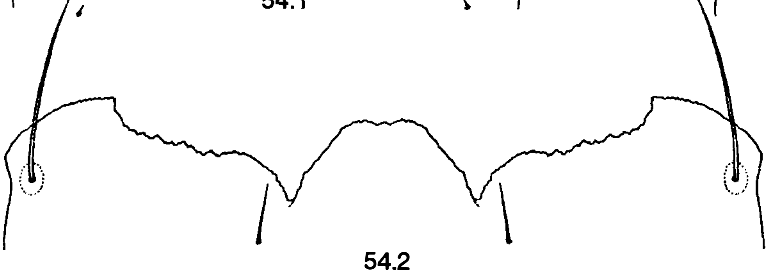
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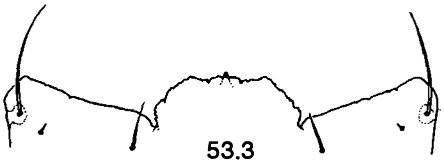
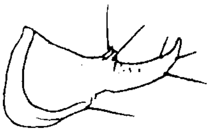

53.3

APPENDIX 4.2. Urogomphi of different stages of *Carabus* larvae

Sp.: The first numbers refer to the species and correspond with the numbering in Appendix 4.1 (Nasale).
Stages: The second number refers to the larval instar (14.3 means *Carabus scabriusculus*, third instar).

Sp.		Stages		
	02^{I} Morphocarabus			
1	*aeruginosus*	1	2	3
2	*exellens*	1	2	3
3	*hampei*	1	2	3
4	*henningi*		2	3
5	*hummeli*	1		3
6	*karpinskii*	1	2	
7	*odoratus*	1	2	3
8	*regalis*	1	2	3
	02^{II} Trachycarabus			
9	*besseri*	1	2	
10	*bosphoranus*	1		3
11	*estreicheri*			3
12	*haeres*	1		3
13	*perrini (= ssp. planus)*	1	2	3
14	*scabriusculus*	1	2	3
15	*sibiricus*	1	2	3
	06 Archicarabus			
16	*montivagus*	1		3
17	*nemoralis*	1	2	3
	04 Eucarabus			
18	*arvensis*	1	2	3
20	*stscheglowi*	1	2	
21	*ulrichii*	1	2	3
	03 Carabus			
22	*granulatus*	1	2	3
	05 Tachypus			
23	*cancellatus*	1	2	3
	01 Limnocarabus			
24	*clatratus*	1	2	3
	07 Hemicarabus			
25	*nitens*	1	2	3
	09 Aulonocarabus			
26	*canaliculatus*	1	2	3
	08 Diocarabus			
27	*truncaticollis*	1	2	3
	12 Oreocarabus			
28	*glabratus*	1	2	3
29	*hortensis*	1	2	3

Sp.		Stages		
	10 Mesocarabus			
30	*problematicus*			3
	11 Orinocarabus			
31	*linnaei*	1		3
32	*sylvestris*		2	3
	08 Diocarabus			
33	*loschnikovii*	1	2	3
	13 Tomocarabus			
34	*bessarabicus*	1	2	
35	*convexus*	1	2	3
36	*marginalis*	1	2	3
	15 Pachystus			
37	*cribellatus*	1	2	3
38	*hungaricus*	1	2	3
	18 Hygrocarabus			
39	*variolosus*	1	2	3
	19 Chaetocarabus			
40	*intricatus*	1	2	3
	20 Platycarabus			
41	*depressus*			3
42	*fabricii*			3
43	*irregularis*			3
	26(+27) Chrysocarabus			
44	*auronitens*	1	2	3
	22 Sphodristocarabus			
45	*varians (=janthinus)*	1	2	3
	23 Megodontus			
46	*exaratus*	1	2	3
47	*gyllenhali*	1	2	
48	*violaceus*	1	2	3
	24 Pachycranion			
49	*schoenherri*	1	2	3
50	*ermaki*	1	2	3
	28 Macrothorax			
51	*morbillosus*			3
	30 Procrustes			
52	*coriaceus*	1	2	3
	29 Lamprostus			
53	*torosus*			3
	31 Procerus			
54	*scabrosus*	1	2	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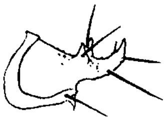
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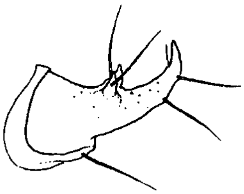
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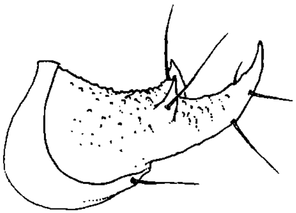
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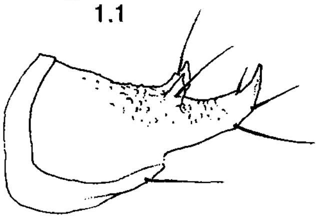
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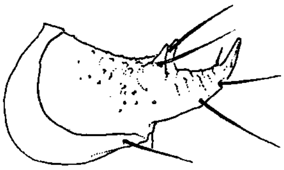
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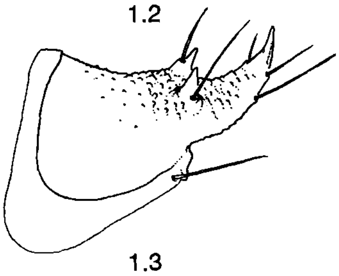
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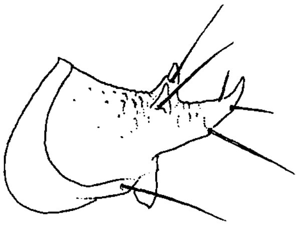
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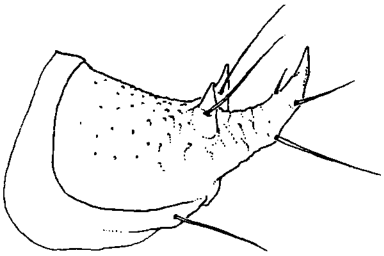
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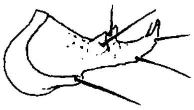
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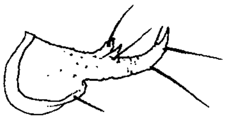
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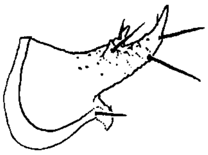
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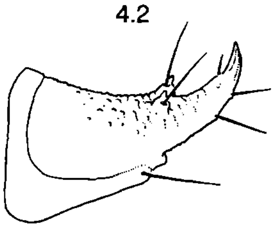
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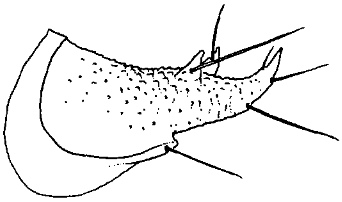
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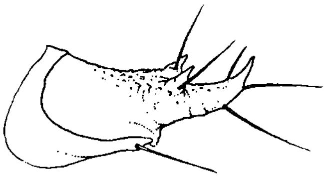
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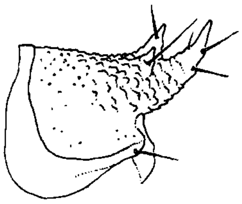
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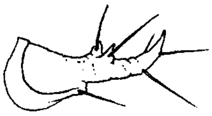
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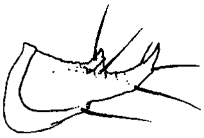
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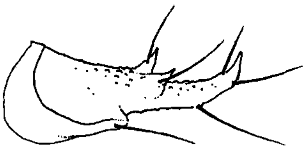
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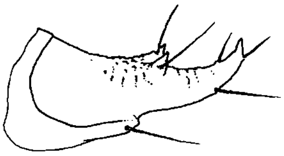
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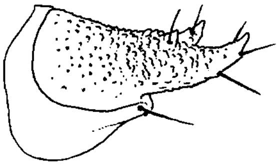
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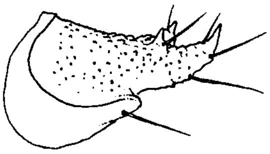
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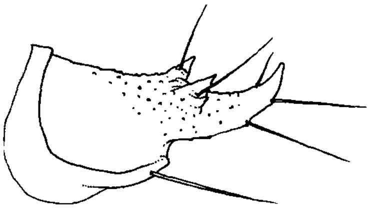
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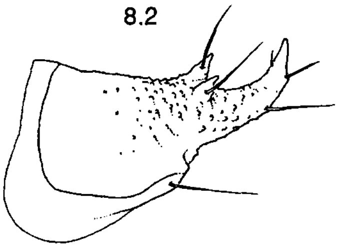
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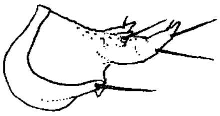
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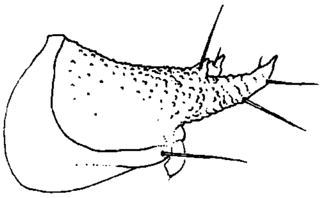
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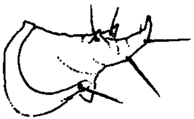
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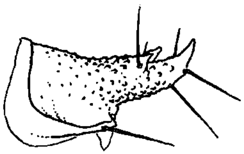
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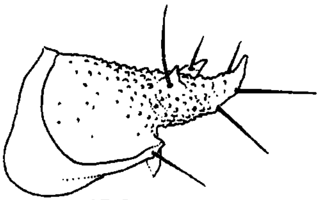
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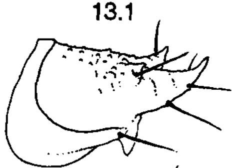
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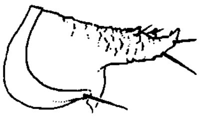
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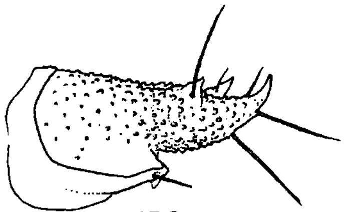
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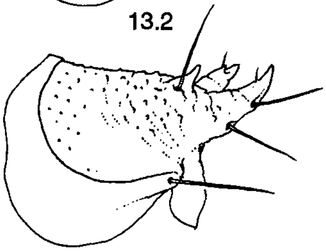
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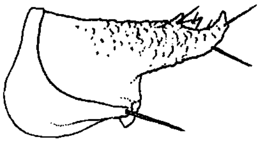
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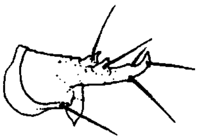
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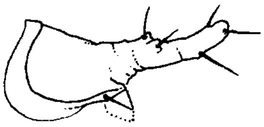
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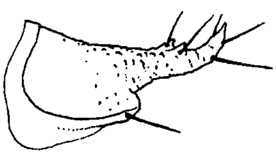
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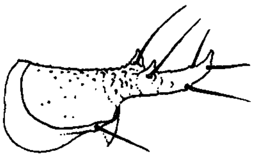
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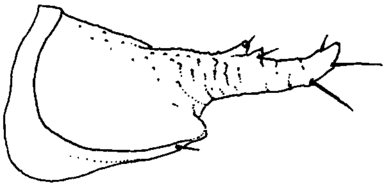
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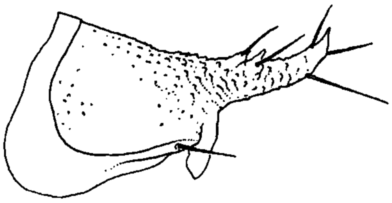
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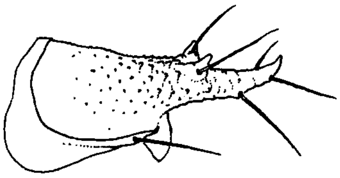
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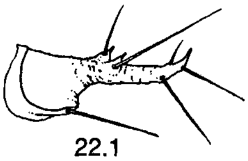
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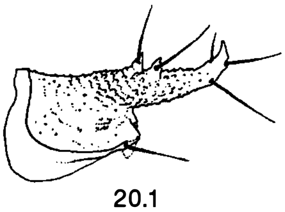
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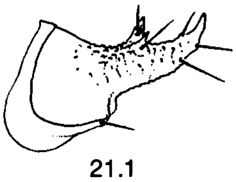
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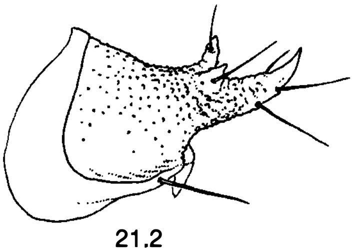
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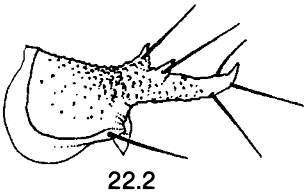
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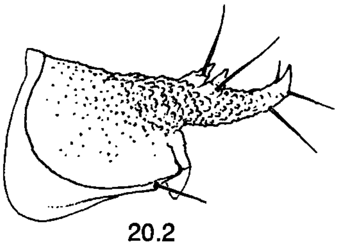
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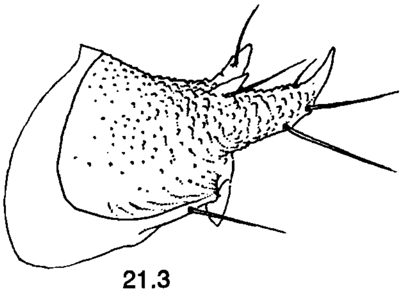
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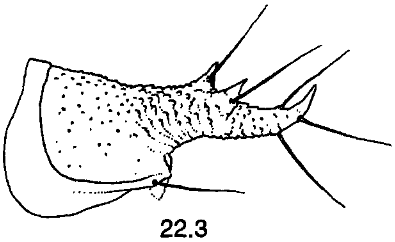
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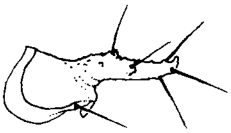
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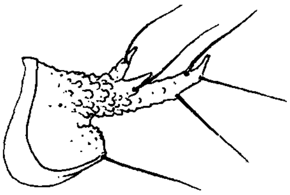
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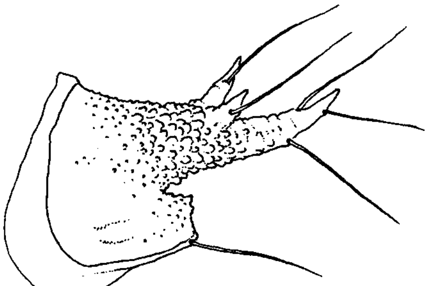
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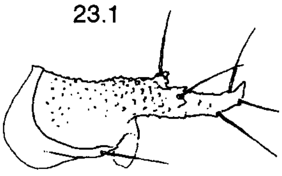
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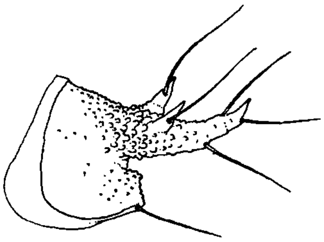
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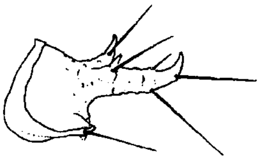
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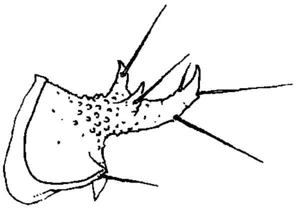
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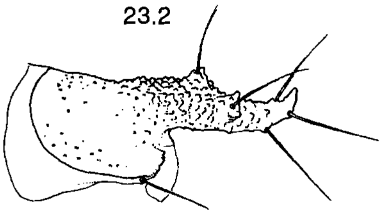
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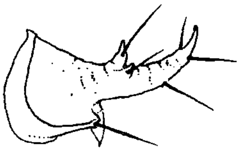
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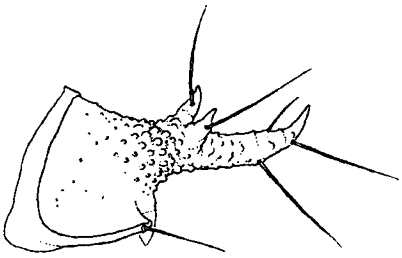
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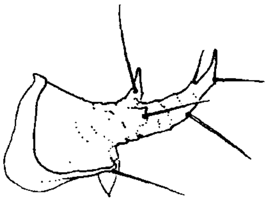
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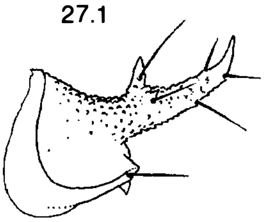
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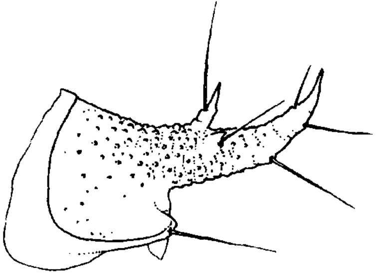
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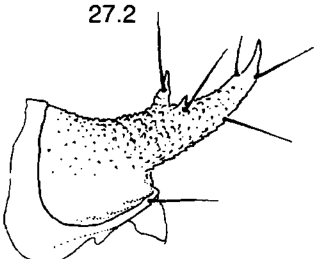
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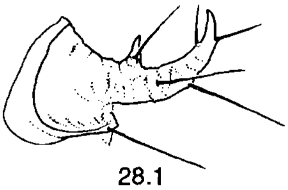
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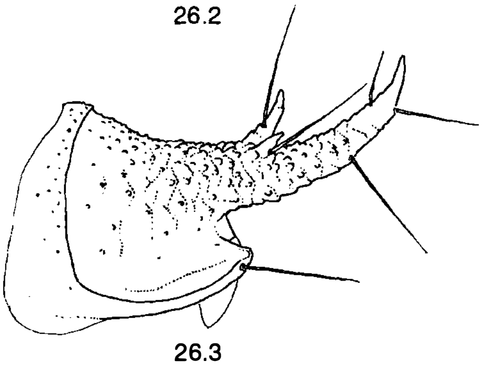
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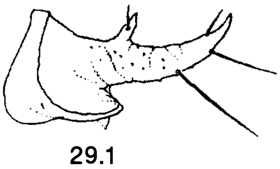
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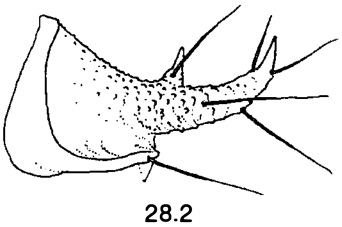
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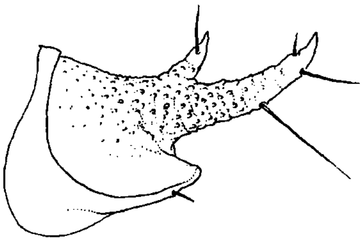
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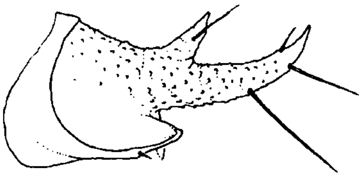
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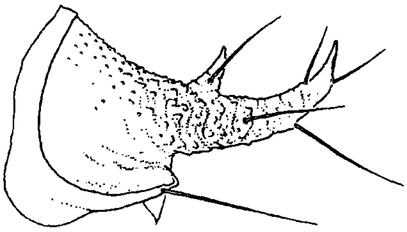
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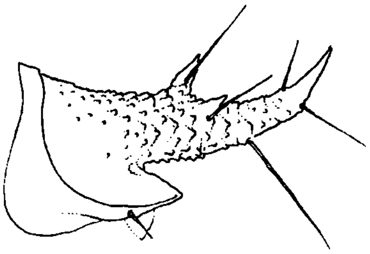

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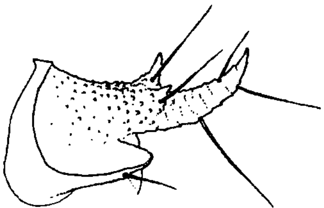

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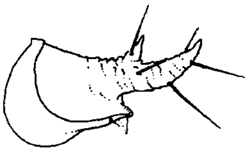

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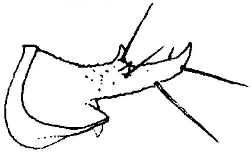

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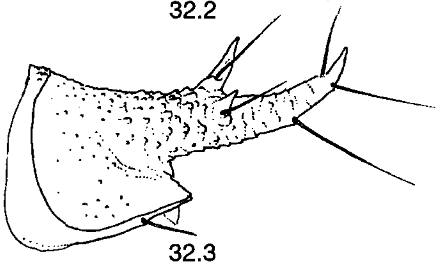

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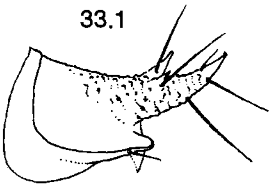

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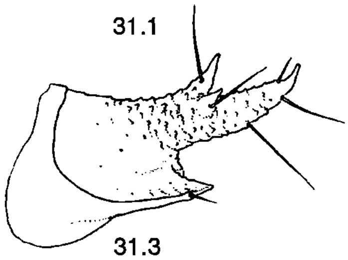

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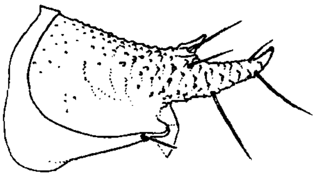

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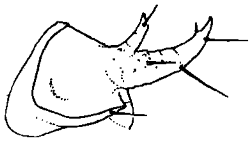

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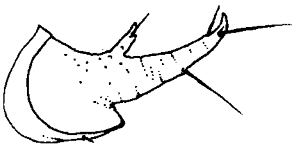

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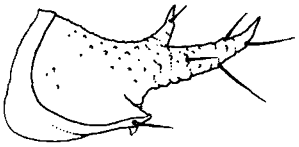

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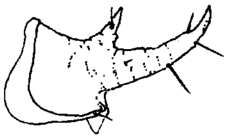

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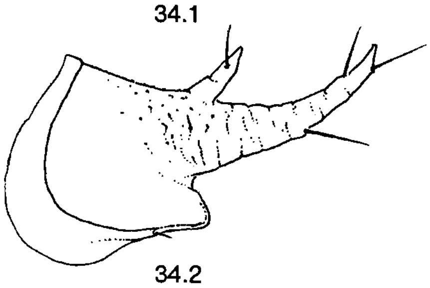

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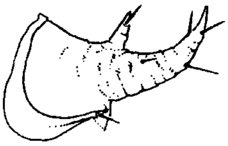

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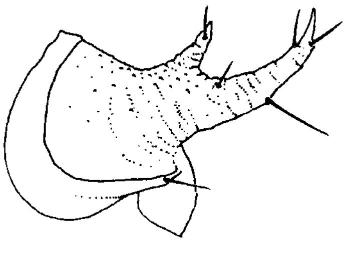

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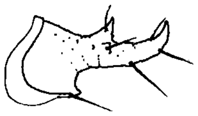

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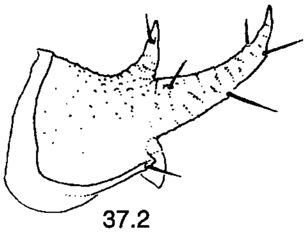

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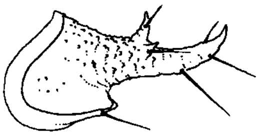

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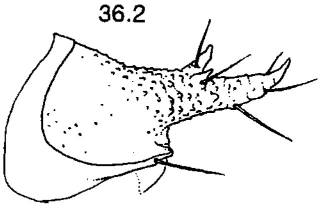

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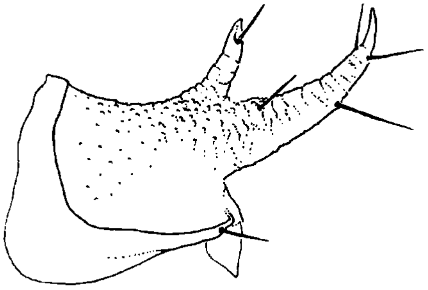

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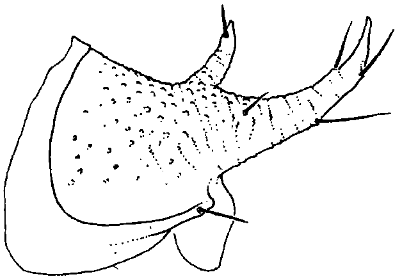

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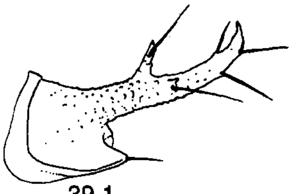
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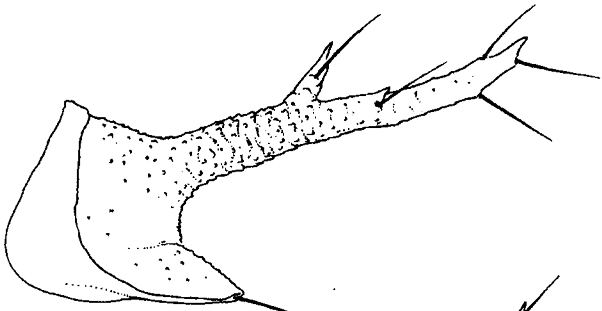
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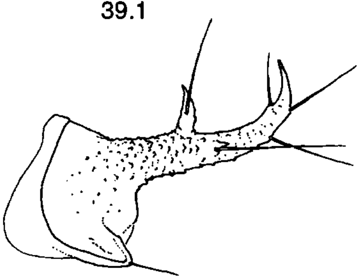
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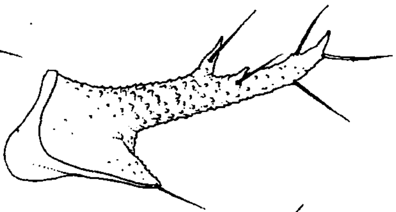
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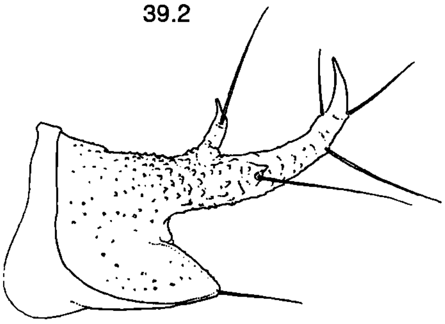
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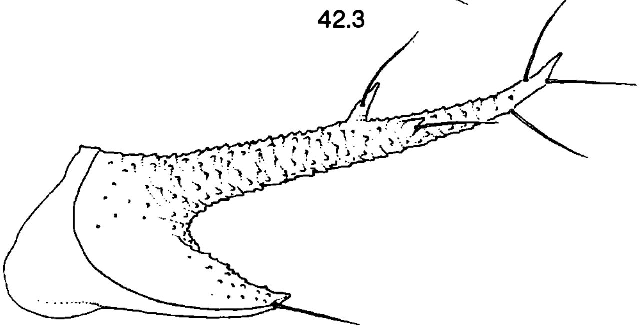
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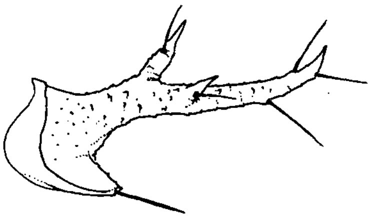
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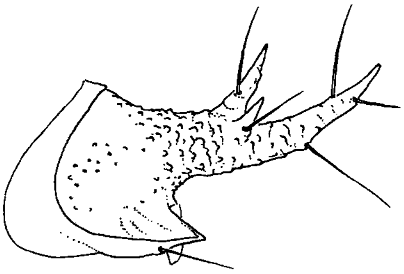
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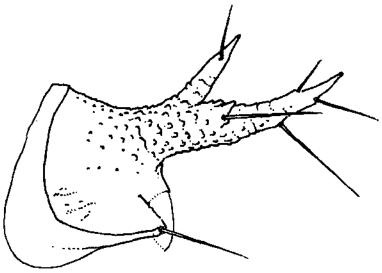
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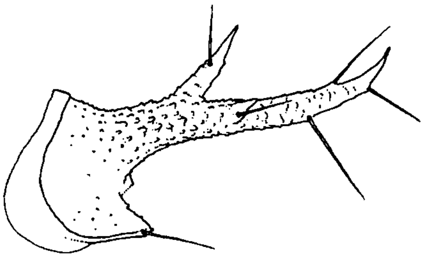
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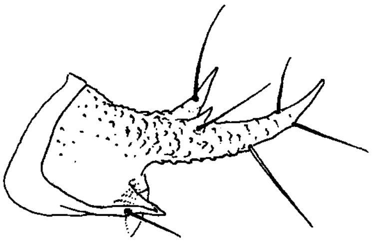
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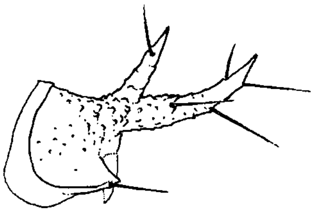
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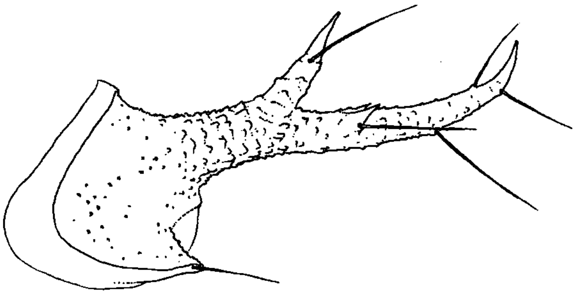
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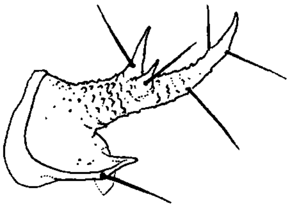
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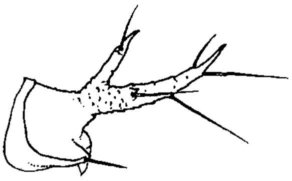
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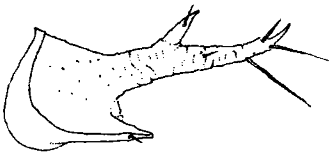
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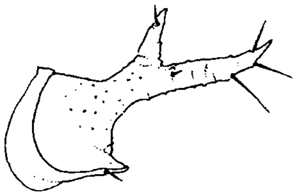
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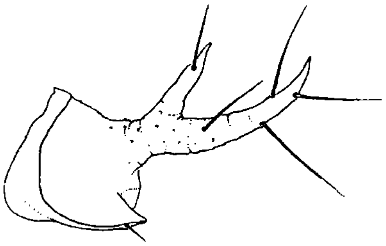
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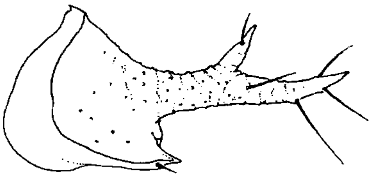
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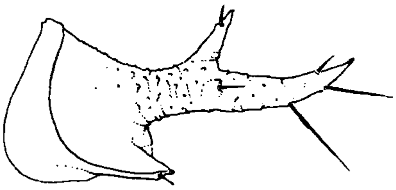
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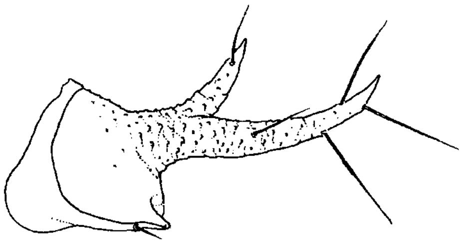
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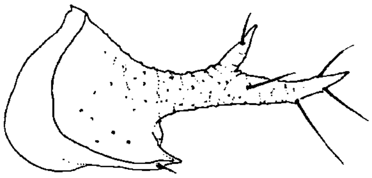
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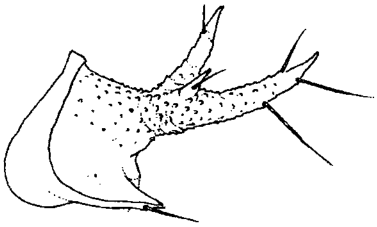
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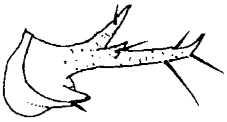
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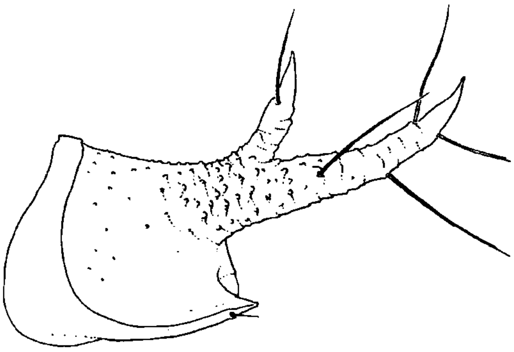
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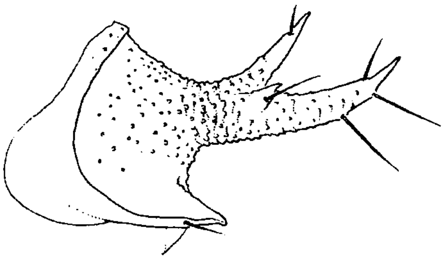
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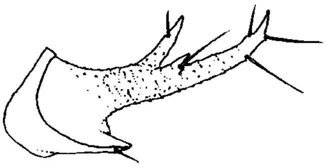
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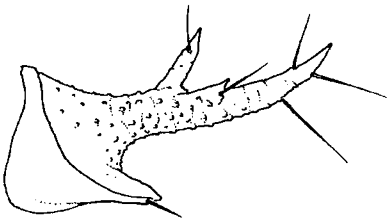
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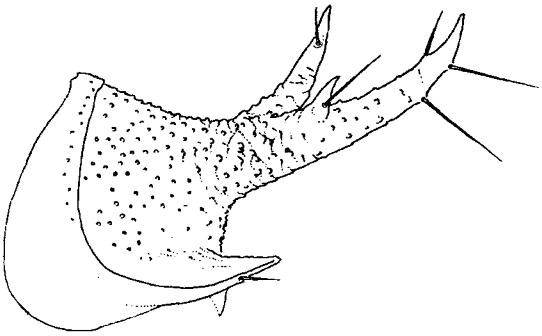
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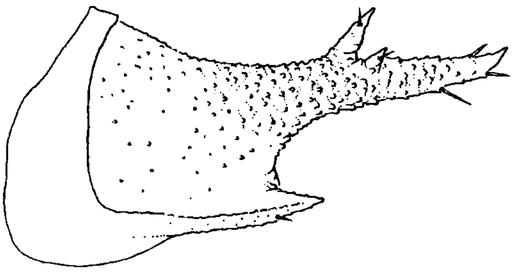
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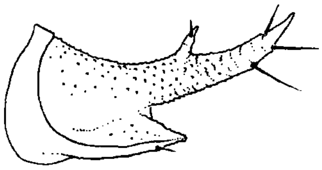

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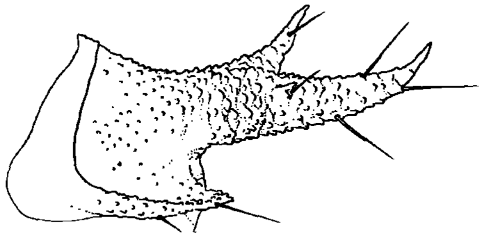

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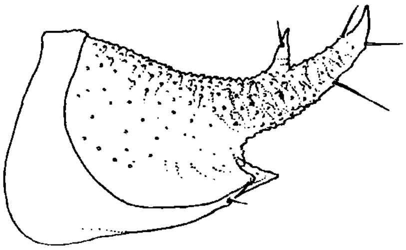

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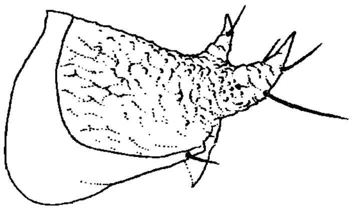

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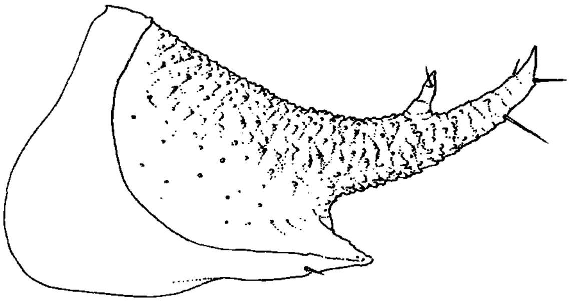

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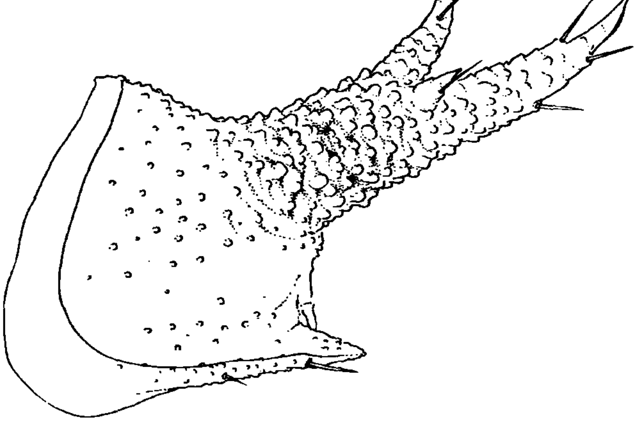

54.2

Chapter 5 Species accounts

H. Turin, L. Penev, A. Casale, E. Arndt, Th. Assmann,
K. Makarov, D. Mossakowski, Gy. Szél & F. Weber

5.1 INTRODUCTION

In this chapter, the most relevant basic information, known so far from the literature, as well as from original surveys and results from the present project, has been collected and compiled. In general a standard pattern has been followed, presenting the information in distinct sections. Exceptions to this have been made, if information for a certain section was poor or lacking.

References to the main sources used (often being important and significant compilations themselves), are listed below in section 5.2 (*General works*). For the section 'Range characteristics: Distribution in Europe', for instance, one and the same reference should have been repeated within each species description. Therefore, the main sources of information have been listed once in the beginning of this chapter. Only sources containing information, additional to these main works, have been referred to in the species' texts. The same applies to the section 'Subspecies' for which the data in general have been taken from the same sources.

References to literature in the sections **'Ecology'** and **'Biology'**, have been cited more in detail, because these sections have been compiled from various sources and because the amount and kind of information that is available, is quite heterogeneous. There are a few important basic works with respect to these sections, e.g. mainly the works of Casale *et al.* (1982), Cavazzuti (1989: on *Procerus*), Hůrka (1973) and Sturani (1962), and, for the section **'Food'**, Larochelle (1990). We will now briefly discuss the ordering of the information within the sections of this chapter.

Abbreviations used:

C. – Central (e.g.: C. Europe; in the C. parts)
E. – East, eastern (e.g.: E. Germany; to the E.; E. of...; E.-wards; E. distribution etc.).
N. – North, northern
S. – South, southern
W. – West, western
L1 etc– Larva, first instar, etc.
Mt(s).– Mountain, mountains

5.2 EXPLANATIONS TO THE SECTIONS IN THE SPECIES ACCOUNTS

Species number and name: The numbering refers to the *Checklist* (Chapter 2) and to the European checklist and atlas of Turin *et al.* (1993), which was used as framework for the present study. Within the subgenera, the species are listed alphabetically. The classification has been slightly modified with respect to the authoritative world lists of Deuve (1991, 1994) and Březina (1994, 1999). These modifications have been discussed in the first paragraph(s) of the respective genera in the *Key to the adults* (Chapter 3), and/or in the general introduction to the same chapter.

General literature: **Checklists and catalogues** – Only the most relevant checklists and catalogues have been mentioned, first of all the classical work of Breuning (1932-1937), that still serves as a basis for all subsequent studies on *Carabus*. Secondly, we cite the important and recent world lists of Deuve (1991, 1994) and Březina (1994, 1999, see also Chapter 2), as well as the list of Kleinfeld & Schütze (1999), that is particularly helpful for the numerous useful annotations concerning nomenclatorial and taxonomic matters. A reference has also been given to the comprehensive list of all carabids of the world by Lorenz (1998). A very important list for many species in Eastern Europe is that of Kryzhanovskij *et al.* (1995), covering the territory of the former Soviet Union and giving the distributions of nearly 300 *Carabus* species. Furthermore we refer to the European checklist and atlas of Turin *et al.* (1993), the basis for the present monograph. **Iconography** – Recently a relatively large number of works with qualitatively quite diverse photographs and drawings of *Carabus* species have appeared. For all species, we refer to the pages or plate numbers of the most relevant works, e.g. Battoni *et al.* (1995), Casale *et al.* (1982), Darnaud *et al.* (1977-1984b), Forel & Leplat (1995, 1998), Ghiretti (1996, 1997), Imura & Mizisawa (1996), Ratti *et al.* (1990) and Rautenstrauch (1994). Numbers in square brackets have been given if, in the respective treatment, a species number has also been used, e.g. Deuve (1994) and Imura & Mizusawa (1996). Also a reference has been given to the marvelous lithographs of Jakobson (1905).

◀ ***C. lefebvrei bayardi*** Solier. Italy, Latium (Rome). Photo by A. Vigna Taglianti (P. Maltzeff).

Taxonomy: If necessary, small general taxonomical and nomenclatorial notes have been made, mainly if species that are included in the present work, have been frequently treated as subspecies in the main checklists or keyworks, such as Březina (1994, 1999) and/or Deuve (1994). However, relevant notes concerning taxonomic characters and identification, have only been mentioned in the text of keys to adults and larvae. Eventually, cross-references have been given to the *Key to the adults* (Chapter 3). If new work has been carried out recently (e.g. concerning morphometry, finding of hybrid zones etc.), this has also been cited in the section '**Taxonomy**'.

Geographical distribution, chorotypes and range characteristics: Two types of geographical classification of species have been used. First, each species is classified to a certain 'chorotype' (sensu Vigna Taglianti *et al.*, 1993; Vigna Taglianti *et al.*, 1999, with some modifications), which characterise the main area of distribution of a species and assumes that area as a distribution centre (De Lattin, 1967) of the particular species. Second, a descripive and more detailed 'range characteristics' has been assigned to each species, too. For instance, **SEU-CADI: Balk(NW)** means *South European (Carso-Istrian-Dinaric) chorotype* of a species, distibuted in the northwestern part of the Balkan peninsula. The methodology of geographical classifications of the species ranges is described in Chapter 8, and is also briefly listed in the legend to the Appendix 8.1.

The following abbreviations are used for the purposes of arealogical classification of the species:

Abbreviations in brackets:

C – central, **N** – northern, **S** – southern, **W** – western, **E** – eastern, **P** – pan (=whole), respectively **SE** – southeastern, **NW** – northwestern and so on.

Chorotypes:

ASE = Asiatic-European, **SIB** = Siberian, **SIE** = Sibero-European, **EUR** = European, possibly extended (*i.e. C. coriaceus*) to part of Asia Minor, **CEU** = C-European, **SEU** = S-European (see sub-divisions below), **WEU** = W-European (see sub-divisions below), **EEU** = E-European (see subdivisions below), **NAF** = N-African, **WME** = W-Mediterranean, **EME** = E-Mediterranean.

CAUC = Caucasian (eventually extended to the mountains of S-Crimea or to the southernmost steppe region of European Russia), **CAUC-CRIM** – Caucasian-Crimean species, eventually extending to the southernmost steppe part of SE European Russia, **ANAT** = Anatolian (extended to the Balkan peninsula), **POCA** = Ponto-Caucasian (extended to some parts of SE-Europe).

EEU-CARP = E-European-Carpathian (extended sometimes to the neighbouring hilly regions of western Ukraine), **EEU-PANN** = E-European-Pannonian (Pannonian Plain, western Romania and northern regions of the Balkan peninsula), **EEU-SEEU** = E-European-SE-European (distributed from southern steppes of European Russia to the Pannonian Plain in the east and Balkans in the south), **EEU-SWRU** = E-European-SW-Russian (southwestern region of the Russian Plain, i.e. Central-Chernozem region, Ukraine, Moldova, sometimes in the adjacent regions of Romania and Poland), **EEU-CRUS** = E-European-Central Russian (middle region of European Russia, that is forest-steppe and steppe zone between Dnieper and Volga rivers), **EEU-URAL** = E-European-Uralian (endemic to the Ural mountain range).

WEU-PYRE = W-European (Pyrenees), **WEU-IBER** = W-European (Iberian peninsula, extended eventually to Rif), **WEU-IBEN** = W-European (northern part of Iberian Peninsula), **WEU-IBEC** = W-European (central part of Iberian peninsula), **WEU-IBES** = W-European (southern part of Iberian peninsula).

SEU-ALAP = S-European (Alpino-Apennine), **SEU-ALPW** = S-European (endemic to W-Alps, eventually extended to the Ligurian Apennines), **SEU-ALPC** = S-European (endemic to Central Alps), **SEU-ALPE** = S-European (endemic to E-Alps, eventually extended to Dinaric Alps), **SEU-ALPI** = S-European (Alpinian element, more or less extended to the Padanian Plain and/or Dinaric Alps), **SEU-ALCA** = S-European (Alpino-Carpathian), **SEU-APPE** = S-European (Apennine), **SEU-APDI** = S-European (Apennine-Dinaric, i.e. trans-adriatic/trans-ionian element), **SEU-CADI** = S-European (Carso-Istrian-Dinaric, eventually extended to C- and E-Prealps), **SEU-DIBA** = S-European (Dinaric-Balkanian, eventually extended to E-Alps), **SEU-CABA** = S-European (Carpatho-Balkanian), **SEU-TYRR** = S-European (Tyrrhenian), **SEU-SACO** = S-European (Sardo-Corsican endemic), **SEU-SICI** = S-European (Sicilian endemic), **SEU-CRET** (endemic to Crete, eventually extended to some Aegean Islands), **SEU-GRNC** = S-European (endemic to North and Central Greece), **SEU-THES** = S-European (endemic to Thessalia), **SEU-PELO** = S-European (endemic to Peloponnesos), **SEU-FRAS** = S-European (endemic to S-France).

Range characteristics:

Eur – European, **EEur** – E-European, **CEur** – C-European (and so on); **Balk** – Balkanian, **Alpi** – Alpinian (distributed in the Alps), **Carp** – Carpathian, **Apen** – Apennine, **Iber** – Iberian, **NAfr** – N-African, **Anat** – Anatolian, **Pont** – Pontic (territories around the Black Sea), **Cauc** – Caucasian **Sib** – Siberian, **WSib** – W-Siberian (and so on), **Asi** – Asian, **EAsi** – E-Asian (the Palearctic part of East Asia!).

Combinations of range characteristics:

Each range characteristics can consist of one chorological category, e.e. **EEur** or two or three categories, for instance **CEur-SEEur** (distributed in Central and Southeastern Europe), or **EEur(E)-Sib-EAsi** (distributed in the easternmost parts of Eastern Europe, Siberia and East Asia, i.e. from Japan to Korea and Northern China).

Distribution in Europe: In the present work, the concept 'Europe' has been restricted to the continent, Iceland, the British Isles and the Mediterranean isles, excluding Cyprus, the Canary Islands and the Caucasus. As a first entry to detailed information on distribution in Europe (apart from the listed subspecies, if any), the occurrences of species have been discussed either per political or geographical (national or supra-national) unit, such as 'Belgium', 'Fennoscandia' or 'Iberian peninsula'. Sometimes they have been subdivided according to the country or province level. These units as treated in the present work, serve in most cases as a geographical basis for the various existing checklists, Red Lists, catalogues and atlases. References to these sources have not been repeated in the species' texts. The arrangement is as follows (* = works with maps):

General works: Breuning (1932-1937*); Casale *et al.,* (1982*); Darnaud (1977*-1984b*); Turin (1981); Turin *et al.* (1993*). **Iceland** – Larsson & Gigja (1960); Lindroth (1939). **Fennoscandia** – Lindroth (1945*, 1949, 1985); Silfverberg (1992). **Denmark** – Bangsholt (1983*); Jørum (1996); Silfverberg (1992). **British Isles** – Hyman (1992); Lindroth (1974); Luff (1998*); Speight *et al.* (1982); Anderson *et al.* (2000*). **The Netherlands** – Turin (1990, 2000*); Turin *et al.* (1991). **Belgium & Luxembourg** – Desender (1986*); Desender *et al.* (1995*). **Germany** – Arndt (1989*); Horion (1941); Mossakowski (1991*); Trautner & Müller-Motzfeld (1995); Trautner *et al.* (1997). **Poland** – Burakowski (1973); Szyszko (1983). **Baltic** – Haberman (1968*); Rathlef (1905); Silfverberg (1992). **Byelorussia** – Alexandrovitch *et al.* (1996); **Russian Plain**[1] – Jakobson (1905); Breuning (1932-1937); Kryzhanovskij *et al.* (1995); Silfverberg (1992). Most information is based on both original, unpublished data and literature sources, sampled and compiled by L. Penev in various museum collections and libraries. This allows us to treat the faunistic information for this area in more detail than for the other regions, resulting in separate, detailed maps. Abbreviations used are: IERZ = Institute of Plant and Animal Ecology, Uralian Branch of the Russian Academy of Sciences, Ekaterinburg; IZ = Institute of Zoology of the Ukrainian Academy of Sciences, Kiev (collection of the Zoological Museum); MPGU = Moscow State Pedagogical University; ZIN = Zoological Institute of the Russian Academy of Sciences, St. Petersburg; ZM = Zoological Museum of the Moscow State University. **Moldova** – Neculiseanu & Matalin (2000). **Czechia & Slovakia** – Hůrka (1973; 1996); Pulpan & Hůrka (1993). **Hungary & Romania** – Csiki (1946); Panin (1952*); Szél (*in litt.*). **Bulgaria** – Guéorguiev & Guéorguiev (1995); Hieke & Wrase (1988). **Balkan Peninsula** – Apfelbeck (1904) – Including Albania, and Aegean Islands; Casale *et al.* (1982*); Drovenik (1995) – Slovenia, Croatia, Bosnia, Serbia, Montenegro, Macedonia; Pavicevic & Mesaros (1999*): cd-rom. **Austria** – Mandl (1956-1958*, 1972); Franz (1943, 1984). **Switzerland** – Du Chatenet (1986*); Marggi (1992*). **Italy** – Sturani (1962); Casale *et al.* (1982*); Magistretti (1965); Vigna Taglianti (1993). **France** – Bonadona (1971); Coulon *et al.* (2000*); Forel & Leplat (1995*); Jeannel (1941). **Iberian Peninsula** – Forel & Leplat (1998*); Herrera (1990*); Zaballos & Jeanne (1994). **Adjacent areas** – Morocco – Antoine (1955); N. Africa – Casale *et al.* (1982); Anatolia – Casale & Vigna Taglianti (1999); Darge (1991); Caucasus – Kryzhanovskij *et al.* (1995); Cavazzuti (1989); Siberia – Kryzhanovskij *et al.* (1995); Shilenkov (1996), Western Asia – Kryzhanovskij *et al.* (1995); Canary Islands – Machado (1992*).

Maps: **European map**: The results of information from the previous section, have been brought together in Eurapean distribution maps. These supersede those published earlier in Turin *et al.* (1993). The following symbols have been used on the maps: **e** - extinct, **i** - introduced, **?** - doubtful occurrence. See also some words on the compilation of distribution maps in the *Introduction* (Chapter 1). **Map of the distribution on the Russian Plain**[1]. Because of well-known (political and linguistic) reasons, it was for a long time hardly possible to obtain reliable data from E. Europe, as was clearly illustrated by the Provisional Checklist of European Ground-beetles (Turin, 1981). However, during the last decades, L. Penev was able to collect an enormous amount of distribution data from various sources within the former Soviet Union. The quality and quantity of this material, enabled us to add detailed, dotted maps for all species that occur in this area.

Subspecies: The faunistic information given in this section provides a second entry to a detailed description of the distribution in Europe and in many ways it completes the information that has been presented in the previous section and on the maps. This section lists subspecies included in the *Checklist* (Chapter 2) and *Key to the adults* (Chapter 3), without mentioning their morphological features. Except for additional literature, the sources that have been used for compiling the texts of 'Distribution in Europe' have not been repeatedly referred to in this section.

Ecology and Biology: Under this headings the results from the literature survey, and original data from the present authors, have been summarised. There are only a few important compilations and comprehensive studies on the ecology and biology of *Carabus*. Most important for Central and mainly South European species are the works of Arndt (1989), Burmeister (1939), Hůrka (1973) and Sturani (1962, 1965), the latter also being summarised and completed in Casale *et al.* (1982) and Forel & Leplat (1995). In the section **Ecology**, mainly the habitat preferences have been discussed with respect to conditions of soil type, moisture, temperature, vegetation cover of herbs and trees, altitudinal distribution and, eventually, climatic parameters, i.e. continentality. Under the heading **Transects**, for about 100 species, references are

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[1] European part of the former USSR, including Ukraine, Byelorussia, Baltic states and Karelia.

given to the figures (T01-T100) of Chapter 8, where the distribution of species over an altitudinal or lowland gradient has been shown for 100 localities across Europe. The transects show the occurrences of *Carabus*-species in the field in a very illustrative way, and give in this way a lot of additional information on geographical variation in habitat preferences. Moreover, the transects have been used for biogeographical analysis (see Chapter 8). In the section **Biology**, information is given on activity patterns (diurnal/nocturnal), life history characteristics, such as reproductive period, oviposition, development of eggs, larvae, pupation, occurrence of teneral animals, eventual dormancy, activity of young adults before winter, stage of hibernation and aggregation. Special attention was given to **Food** of adults and biology of **Larvae**, including a reference to their original description (mainly taken from Casale *et al.,* 1982 and Kryzhanovskij *et al.,* 1995), and also their **Food** in laboratory and field (Arndt, *in litt.*; Burmeister, 1993; Larochelle, 1990). Under the heading **Dispersal power**, as most *Carabus* species are brachypterous and generally have a relatively good locomotory power, notes are given for only a few species on their capacity of flight, speed of movement in the field and/or climbing capabilities if available from reliable observations.

Conservation: In this section, aspects of biological conservation, such as threats (endangered or not) as well as proposals according to habitat management, have been discussed. If possible the information has been separated for different climatic zones, mainly N. and N.W. (atlantic) Europe, N.E. Europe, C. Europe and the mediterranean region and S.W. Europe. Some information has been taken from various regional or national Red Lists (see above). However, it appears that in many cases Red Lists have been compiled on the basis of incorrect assumptions, using questionable criteria and by people with poor or no knowledge or field experience concerning the listed species. Therefore, it must be stressed that information taken from Red Lists should be accepted with some reserve. In many cases this has been indicated in the text by using terms such as 'possibly endangered' etc. For instance, as a rule, most species that inhabit montane forests and alpine habitats, have healthy populations and can be regarded as not endangered. On the other hand, the coastal and lowland populations may be exposed to environmental pressure and be seriously endangered, due to agriculture, pollution and especially urbanisation. If possible, and in cases of sufficient data, these differences have been briefly discussed. For a thorough discussion of various topics concerning conservation biology, see Chapter 9.

5.3 SPECIES ACCOUNTS

01. LIMNOCARABUS GÉHIN, 1876

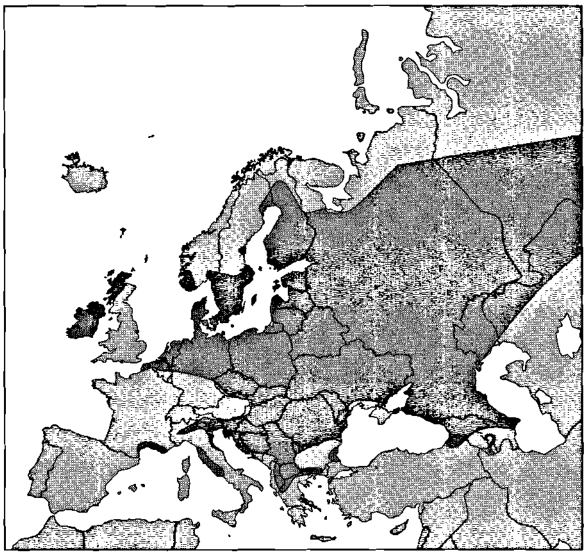
01.001. C. (Limnocarabus) clatratus

Linnaeus, 1761 (= *clathratus* Illiger, 1798)

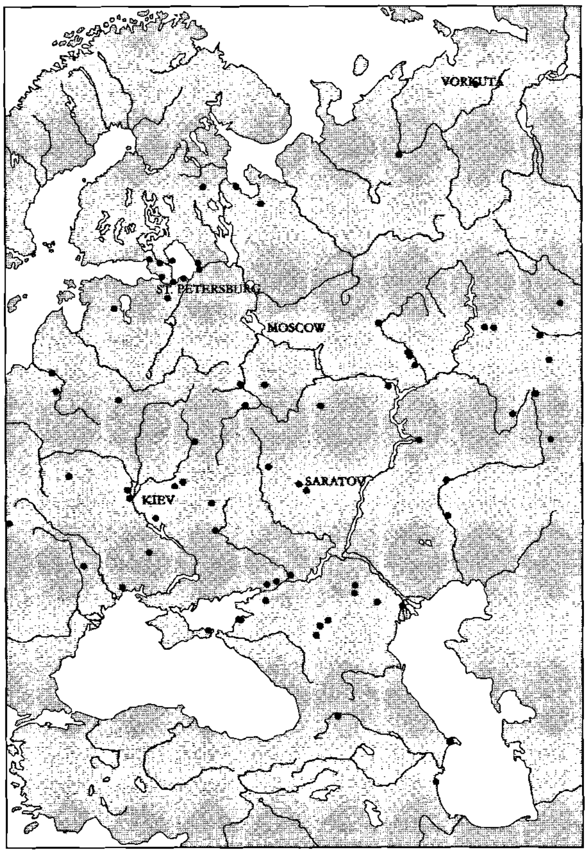
General literature: Checklists and catalogues – Breuning (1933): 545. Březina (1994): 12, (1999): 15. Deuve (1994): 79 [75]. Kleinfeld & Schütze (1999): 17. Kryzhanovskij *et al.* (1995): 42 [76]. Lorenz (1998): 79. Turin *et al.* (1993): 18. **Iconography** – Casale *et al.* (1982): fig 101. Forel & Leplat (1995): Pl. 1. Ghiretti (1996): 21-22. Imura & Mizusawa (1996): Pl. 22 [184]. Jakobson (1905): Pl. 5. Pavicevic & Mesaros (1997): cd-rom. Rautenstrauch (1994): Pl. 26.

Taxonomy: The subgenus includes one species in Europe. Many authors regard subspecies *maaki* Morawitz, 1862, living in the Far E. of Russia, N. China, Korea and N. Japan as a distinct species; others regard *C. clatratus* and *C. maaki* as subspecies of one transpalaearctic species.

Geographical range: Asiatic-European species. From N.W. Europe (British Isles; Alantic coast of Netherlands and Belgium) throughout most of Europe and Siberia to Korea and Japan (see under *Taxonomy*). Not in the larger part of France and also not in the Iberian peninsula, S. Italy, the S. part of the Balkan peninsula and the Mediterranean islands such as Corsica, Sardinia and Sicily. **Chorotype:** ASE. **Range characteristics:** Eur-Sib-EAsi. **Distribution in Europe: Fennoscandia** – Norway, very local in the S.; Sweden, local but sometimes common (Arndt, *in litt.*), scattered in two main areas in the S.W. and N.W. up to 68°N; Finland, to about 66°N. **Denmark** – Rare and local, decreasing. **British Isles** – In the past widely distributed in the W. and N., now restricted to Ireland (especially in the N.W.: valley of the River Erne, Fermanagh and area S. of this; probably extinct in the N.E.: Anderson *et al.,* 2000), and N.W. Scotland. Very old and unverified records exist from England (Suffolk and Norfolk); Luff (1998) states that the area on the S. coast of England indicated in the map by Turin *et al.* (1993), is in fact an error, based on unreliable transcriptions of old reports. **Netherlands** – Until about 1940, rather abundant in the C.W. part and some localities in the E. peat-moors. Now restricted to some of the Frisian Islands in the N., and a wet heathland area in the S. where it can be common in some years. **Belgium** – Restricted to the N. heathland area. Rare and vulnerable. **Germany** – In the beginning of the 20th century common, especially in N. and E. Germany, now rare and more or less restricted to the N. regions (Lower Saxony, Mecklenburg-Vorpommern, Brandenburg), especially along the coast of the E. Sea; without exception occurring on the Red Lists as seriously endangered or probably extinct (Berlin, Sachsen). Scattered occurrences also in the C. of E. Germany. (Sachsen-Anhalt, Thüringen). Not in the S.W and S. (Hessen, Rheinhessen, Baden-Würtemberg and Bayern). **Poland** – Mainly in the W. and N.; absent from the S.E. **Baltic** – Reported from all countries. **Byelorussia** – Recorded from all provinces. **Russian Plain & Caucasus** – Sporadically throughout all of European Russia and Caucasus; to 65°N from C. Karelia to Ust'Tsil'ma at Pechora River (ZIN). To the S. it extends along rivers to the semi-desert and desert zone and is known from Rostov province and Kalmyk republic (several localities according to



01 001 clatratus (Limnocarabus)



01 001 clatratus

Fomichev, 1983), S. Azerbaijan (Lenkoran'), Astrakhan (ZIN) and Uralsk province (Uralsk and Mergenevo after Arnol'di, 1952). A typical polizonal species which distribution depends on intrazonal habitats like swamps, bogs, saline and salinised soils along water basins. **Moldova** – Recorded from Budzhak, Kodry and the lower Dnestr regions. **Czechia & Slovakia** – Mentioned from all regions, but local and rare to very rare across the area. **Hungary** – Sporadic in the plains and hilly areas; only more abundant in the environments of larger waters, such as the lake Fertő, the Kis-Balaton; furthermore in the Duna-Tisza Mid-Region and in the north-eastern part of the Great Hungarian Plain. **Romania** – Distributed in the wet areas, but rare. **Bulgaria** – Very rare; only reported from the Danube Plain (near Russe) and the Black-Sea coast (near Burgas). **Balkan Peninsula** – N. Dalmatia, E. Croatia, N. and N.E. Serbia, S. Herzegovina; the N.-most part of Greece. **Austria** – Only in the E. of Niederösterreich, and Burgenland; seriously endangered. **Switzerland** – Only one old locality near Geneva, all other records incorrect; not found after 1890. **Italy** – In the N. Italian (Padanian) lowlands and along the W. coast (Tuscany) and N.E. coast (Ravenna). **France** – Only found in the S. coastal area between the rivers l'Hérault and the Rhône delta. It was previously also reported from the coastal area of the river Var near Nice and from lac du Bourget (Savoie) (Coulon *et al.*, 2000). Nowadays endangered and locally in a process of extinction.

Subspecies: a) subsp. clatratus – Europe except its N. and S. parts: Belgium, Netherlands, Germany, N. Switzerland, Czechia (probably extinct), Poland, Lithuania, Byelorussia, Moldova, Ukraine, W. Russia: provinces of Smolensk, Bryansk, Kaluga, Moscow, Ryasan, N. and E. Russia to C. Siberia and Kazakhstan. **b) subsp. jansoni** Kraatz, 1890 – British Isles (see Kryzhanovskij *et al.*, 1995, p. 42, note 29). **c) subsp. auraniensis** J. Muller, 1902 – S. Austria, Hungary, Czechia, only S. Moravia, S. Slovakia, Balkan states (in Greece only in N. parts). In the E. of area this subspecies forms the transition to subsp. *stygius*. **d) subsp. antonellii** Luigioni, 1921 – Endemic of N. and C. Italy from Piedmont to Lazio. The specimens from the Adriatic coast (province Venezia, Ravenna) are transitional to *auraniensis*, and morphologically more similar to the latter. **e) subsp. arelatensis** Vacher de Lapouge, 1903 – S. France (regions de Narbonne, Montpellier and Camargue). (Probably not European: **subsp. stygius** Ganglbauer, 1890 – Russia: Rostov province, Kalmykia; the N. and E. Caucasus; E. Anatolia. Mostly in slightly saline soils).

Ecology: Stenotopic, strongly hygrophilous, inhabiting muddy shores of rivers and lakes (E. Europe), but mainly marshes, bogs, swampy reedlands and wet grasslands (Sturani, 1962; Lindroth, 1985; Fedorenko, 1988). Tyrphophilous, but not restricted to peat soil (Anderson *et al.*, 2000; Turin, 2000; see below). It shows no clear preference for fresh or salt water, and is also found in coastal habitats, such as salt marshes and wet dune valleys (Frisian Islands: Netherlands and Germany) as well as on wet heathland, peat-moors (Netherlands, S. Europe and Kazakhstan) and in rice fields (Casale *et al.*, 1982; Du Chatenet, 1986; Koch, 1989). In N.W. Germany, it is mainly found in oligotrophic peat digging areas (Grossecappenberg *et al.*, 1978; Assmann, 1981). Sometimes in wet habitats at high altitude (up to 2000 m in E. Anatolia and Caucasus); in S. Europe (N. Italy, S. France) mainly a species of the lowlands (Casale *et al.*, 1982; Jeannel, 1941). Although seemingly with a preference for open habitats, mostly with luxurious vegetation, also found in moist forests, e.g. those occurring on floodplains (Hůrka, 1996; Stiprajs, 1961). All habitats have in common soil structure characteristics and hydrology, allowing the adults and larvae to move into and out of shallow water where they hunt (see also under *Conservation*). Within its area of distribution in the Netherlands, it has been found even in vehicle tracks on a sandy path in a forest, which were partly filled with water. The habitat preferences are rather constant throughout the distribution range; also Shilenkov & Averenskii (1990) report it for Yakutia from localities near swamps, lakes, water meadows along rivers (floodlands) and irrigated lands. In the Balkans, it is reported as hygrophilic, silvicol-praticol, occurring mainly in deciduous forests in hills and mountains (Pavicevic & Mesaros, 1997). According to Hůrka (1973), it is obviously thermophilic in the N.W. part of its area of distribution, which must be regarded a doubtful statement. It can stay under water for more than 15 minutes; Sturani (1962) observed that, when replenishing the air, only the fore body is lifted above the water surface, the air being stored under the apical side of the elytra. However, in N.W. Germany, several individuals were observed to replenish the air in the subelytral space by lifting the apex of the abdomen to the water surface, like many dytiscid beetles (Peus, 1928; Assmann, *pers. observ.*). It shows a stricter preference for wet peaty soil during the day than during the night, when it also was found running on dryer soil types. Moreover, after copulation, females particularly show a much greater preference for wet soils than before, and accordingly, the lowest mortality of young individuals was found on wet (eventually sandy) peat moor (Huk & Kühne, 1999). In contrast to the egg-laying females, males and larvae showed very little preference for soiltype (Huk & Kühne, 1999).

Transects: Chapter 1: I-2; Chapter 8: T-05-06, 14-15, 19, 21, 24, 38-40, 44, 46, 49, 51-52, 54-55, 58, 68, 72, 76, 78-79 and 83.

Biology: Activity – Predominantly nocturnal, but sometimes still active at dawn according to Casale *et al.* (1982). In N. & C. Europe, however, also diurnal and observed running in full sunshine between 11.00 and 13.00 h in wet grassland (Arndt, *pers observ.*). **Periodicity** – Spring breeding species, reproduction from April to August, summer active larvae (Stiprajs, 1961; Hůrka, 1973; Sharova & Dushenkov, 1979; Arndt, 1989). Main activity during May-June. Oviposition lasts for 6-8 weeks. Huk (1999) showed that the rather stronger preference of females for a wet (peaty) substrate, strongly improves the probability of survival of the larval stages (see under *Ecology*). According to Sturani (1962), the eggs (size 5 x 1.8 mm) are laid on bare soil. In the laboratory, a mean number of 9 eggs were obtained per female (Huk & Kühne, 2000). Development of eggs takes 6-9 days; that of the larvae, without having a diapause, is very short (duration from egg to adult: 30-60 days). In a breeding experiment in former Czechoslovakia, total development lasted 34-42 days (Hůrka, 1973), and according to Sturani (1962) for S. Europe 30-45 days, including prepupal stage of ca 5 days; the pupal stage taking another 7 days. Larvae have been recorded from May onwards with maximum numbers in June and have no diapause; pupation occurs at the end of July and during the first half of August. The young beetles emerge after ca 6-7 days at the end of the summer and can (occasionally) show a short period of activity before hibernation (Arndt, 1989), but Hůrka (*l.c.*) reports that they mostly do not leave the pupal chamber before the following spring. Hibernation of adults occurs from September onwards in the soil or, sometimes in numbers, behind the bark of old tree trunks (Du Chatenet, 1986; Sturani, *l.c.*). Surprisingly, the rearing of *C. clatratus* proved to be more successful than of *C. granulatus* for which high mortality rates were found in the larval stages (Huk & Kühne, 2000). **Food** (Larochelle, 1990) – In the field caterpillars of Noctuidae (Lepidoptera); snails, ticks (*Dermacentor* and *Boophilus* species), also carrion (Burmeister, 1939; Casale *et al.*, 1982). It regularly hunts in water, climbing along submerged plants, searching for crustaceans, leeches, larvae of aquatic insects (Ephemeroptera and Trichoptera; Assmann, *pers. observ.*), larvae of amphibians, small fishes and various aquatic molluscs (*Limnaea*, *Physa* and *Ancylus* species: Lindroth, 1985; Larochelle, 1990). Sturani (1962) reported that females sometimes eat their own eggs. In captivity, minced meat, earthworms, and raw meat, ginger bread and bread soaked in sugared milk, fish and apples are all accepted. In the field it has been baited with dead frogs; in the Netherlands with Limburg cheese (Teunissen *pers. comm.*). **Larva**: Described by Schiödte (1867: L2-L3), Vacher de Lapouge (1905: L3), Bentsson (1927: 1-3), Hůrka (1971b) and key: Arndt (1985, 1991b). Food – earthworms in the laboratory (Arndt, *pers. observ.*); chopped mealworms and in the field the same food as adults, and also fresh water shrimps (*Hirudo* and *Gammarus* species). Partly, also hunting in the water. **Dispersal power**: It is one of the very few *Carabus* species that is capable of flight, at least under certain critical conditions. Flight was observed in Bulgaria near the Danube by J. Ganev (*pers. observ.*), and others. Lindroth (1985) reported flying specimens from the Bothnian Bay. It moves very well in water (see above). It was one of the first immigrants to reach a newly created island in a 2.5 km wide lake in the Netherlands, appearing within one year (isle 'Dode Hond': 7 specimens caught in pitfall traps in 1968; distance to the nearest mainland ca. 1.5 km), likely due to flight. It is questionable whether population remnants in C. Europe still include macropterous individuals. Desender (1989) found, in a sample of about 80 specimens, no macropterous beetles. The same result was obtained from examining 119 individuals, caught in a peat bog in Lower Saxony (Assmann, 1981; *pers. observ.*). Therefore it is possible that populations, originally dimorphic, are now exclusively brachypterous (cf. Den Boer *et al.*, 1980).

Conservation: In former days, and certainly until the end of the Middle Ages, it must have been one of the most common *Carabus* species, as appeared from the numerous individuals found in cadavers from peat bogs. Nowadays, it is extremely endangered in many parts of its distribution because of the disappearance of its typical microhabitat, caused by drainage, lowering ground water levels and cultivation (Gries *et al.*, 1973; Desender & Turin, 1989; Hyman, 1992; Mahler *et al.*, 1996; Pavicevic & Mesaros, 1997). Forel & Leplat (1995) mention cultivation and urbanisation as the most serious threats for the species' habitat in the French Mediterranean area. The same applies to its occurrence in Italy (Casale *et al.*, 1982): highly endangered in the Padanian Plain, extinct near Venezia and near Roma (the latter, type locality of subsp. *antonellii*). As a possible cause, also 'over-collection' has been reported from Tuscany and from S. France. This species needs rather open vegetation with many small patches of stagnant, shallow water (10-30 cm), as well as dryer (moist) places between them. The habitat of this species is in need of serious protection throughout Europe. It is essential for this probably migratory species that a number of suitable habitats exist at not too long distance from each other, especially biotopes with micro-accidentation where the subsoil water reaches the average surface level.

02$^{\text{I}}$. **MORPHOCARABUS** GÉHIN, 1885
02$^{\text{II}}$. **TRACHYCARABUS** GÉHIN, 1885

Note: In agreement with the checklists of Březina (1994, 1999), Kleinfeld & Schütze (1999) and Kryzhanovskij *et al.* (1995), the genus ***Trachycarabus*** Géhin, has been re-accepted as a valid subgenus. In the checklist of Turin *et al.* (1993), following Deuve (1991), all species were placed in ***Morphocarabus*** Géhin. The numbering of genera and species has been maintained in the present work for reasons of consistency. In the *Key to the adults* (Chapter 3) all species of this group, have been treated for practical reasons in one key, together with ***Eucarabus*** Géhin.

02.001. C. (Morphocarabus) aeruginosus
Fischer von Waldheim, 1822.

General literature: **Checklists and catalogues** – Breuning (1932): 286. Březina (1994): 19, (1999): 15. Deuve (1994): 106 [149]. Kleinfeld & Schütze (1999): 10. Kryzhanovskij *et al.* (1995): 38 [18]. Lorenz (1998): 72. Turin *et al.* (1993): 18.

Iconography – Battoni *et al.* (1995): Pl. 9 = E. Siberian subsp. *incertus* Motschulsky). Ghiretti (1996): 70. Imura & Mizusawa (1996): Pl. 9 [62]. Ratti *et al.* (1990): Pl. 13.

Geographical range: Ural, Siberia. **Chorotype**: SIB. **Range characteristics**: EEur(E)-Sib. **Distribution in Europe**: **Russian Plain** – N.E. part of European Russia & Urals (Tartar, Bashkiria, Komi, provinces of Perm' and Ekaterinburg). W. to Volga River (49°E, two isolated localities near Kazan' and Stolbishchi – ZM), N. to the Polar Circle (Pechora Basin: 40 km S. of Pechora), Ust' Tsil'ma, Turun El', Bol'shaya Sinya River – Poppius, 1910, ZIN, MPGU; Salekhard – ZIN, ZM; S. to 53°N (Bashkir Reserve – Koz'minykh & Esjunin (*in litt.*); Malyi Yamantau Mt., Yuzhno-Ural Reserve – Kashevarov, 1986). Known from less than 20 localities, most of them in the Cisuralia and Urals (Sabla Mt., Krasnokamsk, Perm', Kachkanar, Berezniki, Mesyagutovo at Ai River, nature reserves Pechoro-Ilych, Basegi, Preduralye, (ZIN, Koz'minykh *et al.*, 1991b; Voronin, 1979; Zinovyev, 1991). From the forest-tundra to the S. taiga subzone.

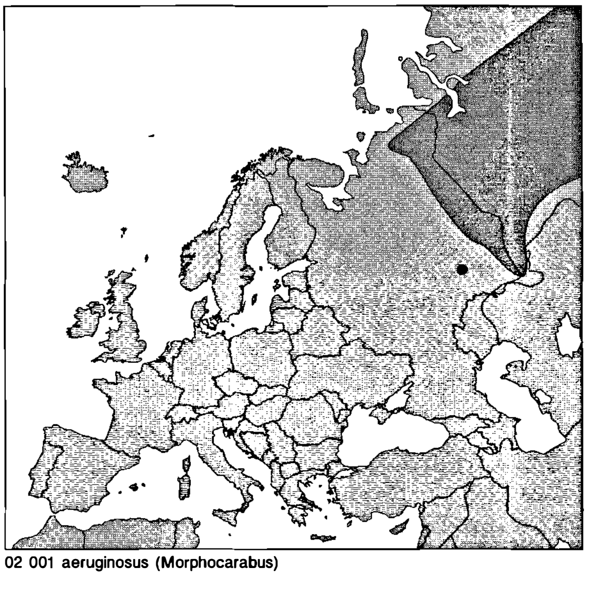
Subspecies: Except nominate, no subspecies in Europe.

Ecology: Andreeva & Eremin (1991) report that in the S. of the Yamal Peninsula, it is mainly a mesophilous forest species, inhabiting spruce and larch forests on interfluvial plains. Also found in larch forests in Yakutia (Shilenkov & Averenskii, 1991). Common in forests in Krasnoturanskiy Bor (C. Siberia), where it avoids open places (Anyushin, 1982). In the Basegi reserve (Middle Ural) it is relatively rare, inhabiting shrubby (montane) tundra and floodland forest, sporadically in meadows and mixed thinned forests (Esjunin *et al.,* 1995).

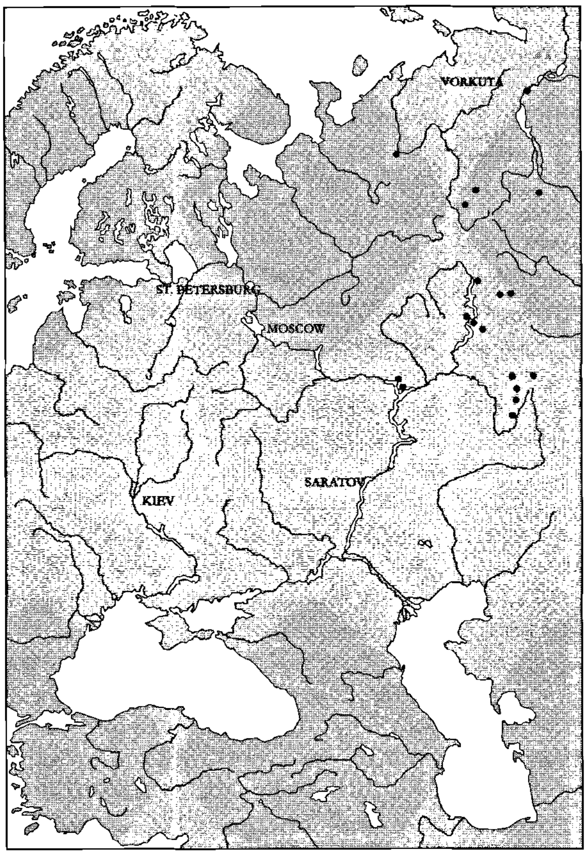
Transects: Chapter 1: I-2; Chapter 8: T-44-45, 47 and 50.

Biology: **Activity** – No data. **Periodicity** – The species breeds in autumn and the larvae hibernate. Berlov & Berlov (1997a) observed copulations in the period from the end of August until the end of September. The larval development takes about 30 days plus overwintering as third instar. **Food** – No data. **Larva**: unknown.

Conservation: Very common in Siberian taiga and not endangered.



02 001 aeruginosus (Morphocarabus)



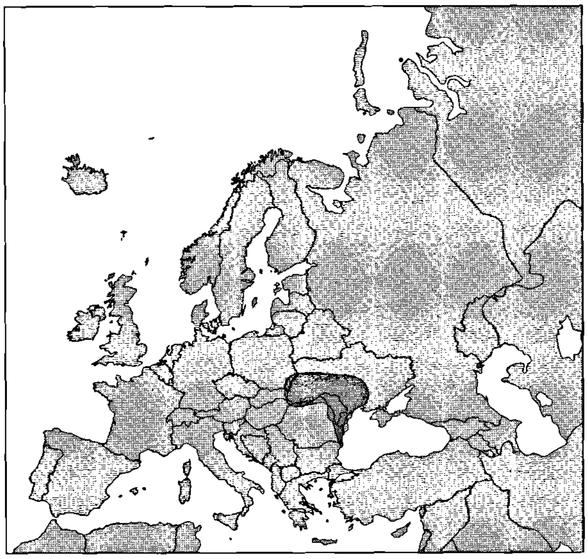
02 001 aeruginosus

02.002. C. (Trachycarabus) besseri

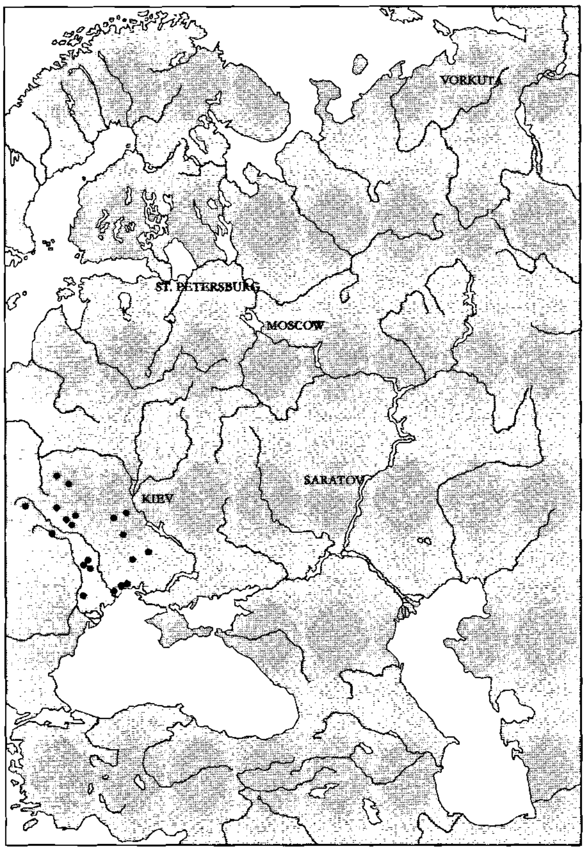
Fischer von Waldheim, 1822.

General literature: **Checklists and catalogues** – Breuning (1932): 491. Březina (1994): 22; (1999): 21. Deuve (1994): 111 [168]. Kleinfeld & Schütze (1999): 12. Kryzhanovskij *et al.* (1995): 40 [39]. Lorenz (1998): 75. Turin *et al.* (1993): 18. **Iconography** – Battoni *et al.* (1995): Pl. 11. Ghiretti (1996): 78. Imura & Mizusawa (1996): Pl. 12 [84]. Jakobson (1905): Pl. 2. Rautenstrauch (1994): Pl. 23.

Geographical range: Ukraine W. of Dnieper, Moldova, N.E. Romania, S.E. Poland. **Chorotype**: EEU-SWRU. **Range characteristics**: EEur(SW). **Distribution in Europe**: **Poland** – Although mentioned for Wyzina Lubelska and Roztocze in the S.E., no verified records exist from this territory. **Russian Plain** – Moldova and W. & C. Ukraine; in the E. it does not extend beyond the Dnieper River. Known from several localities in Moldova in the N. and C. parts (Beltz, Kodry Hills), Kagul – Karpova (1984); Roshu, Kishinev (MPGU); Kiprianovka (ZIN); Orgeev – Adashkevich *et al.* (1973); Rechula – Medvedev & Shapiro (1957) and Ukraine (Tschernovtsy and Ternopol (Breuning), Pod-



02 002 besseri (Trachycarabus)



02 002 besseri

olye, Khmel'nitskii, Kamenets-Podolsk (Begovitsa), Vinnitsa province (Maevskaya, Mestkovskaya, Ustanskaya) Rovno province (Krasnoe Dubno), Gusyatin, Cherkassy province (Luka, Murzintsy, Sinyava), Kherson province (Labrovka), Nikolaev province (Voznesensk, Elanets), Odessa – ZIN, IZ; Kirovgrad – Yatsentkovsky (1906); Dnestrovskii Liman – MPGU, Khadzibeiiskii Liman – V.G. Dolin (*in litt.*). From the mixed forests to the steppe zone. **Moldova** – In the N. and C. parts (Neculiseanu & Matalin (2000). **Romania** – Mentioned for N.E. Romania (Březina, 1999), not treated by Csiki (1946).

Subspecies: Except nominate, no subspecies in Europe.

Ecology: Mostly in forests-steppe landscapes, rather rare.

Transect: Chapter 8: T-61.

Biology: Neculiseanu & Matalin (2000) reported records (Moldova) from June and July.

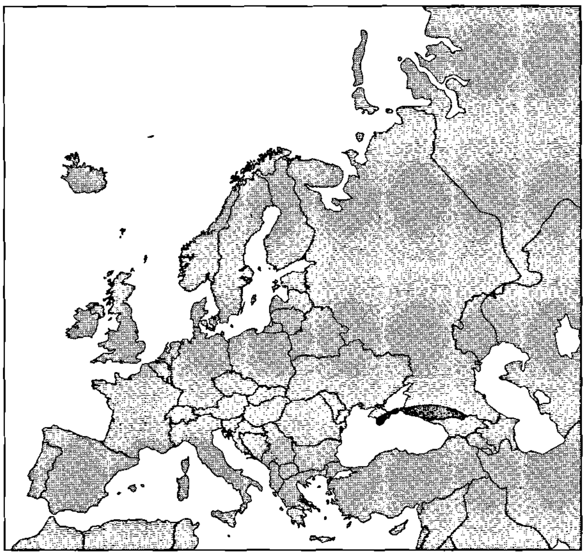
Conservation: No data.

02.003. C. (Trachycarabus) bosphoranus
Fischer von Waldheim, 1823.

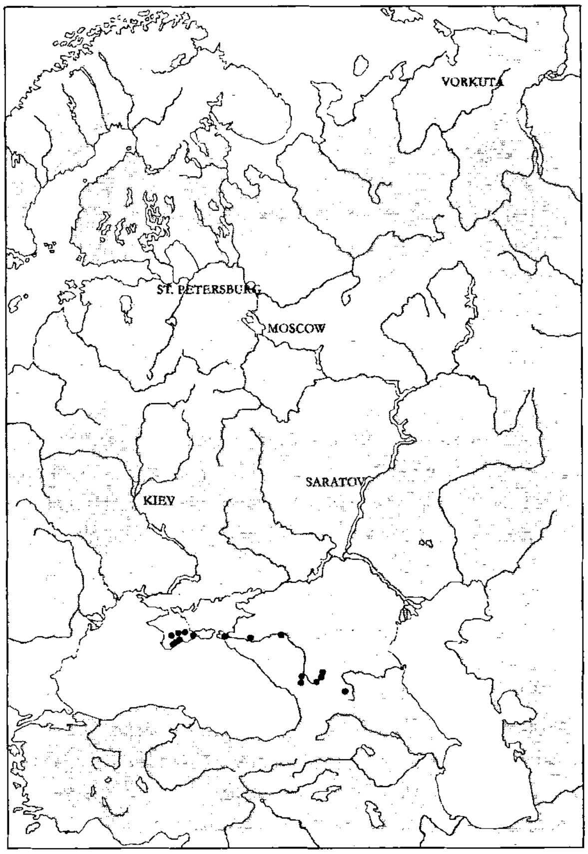
General literature: Checklists and catalogues – Breuning (1932): 484. Březina (1994): 22; (1999): 22. Deuve (1994): 110 [165]. Kleinfeld & Schütze (1999): 12. Kryzhanovskij *et al.* (1995): 40 [42]. Lorenz (1998): 75. Turin *et al.* (1993): 18. **Iconography** – Battoni *et al.* (1995): Pl. 10. Ghiretti (1996): 77. Imura & Mizusawa (1996): Pl. 12 [83].

Taxonomy: In Březina (1994, 1999) and Deuve (1994) listed as subspecies of *C. sibiricus* Fischer von Waldheim, 1822.

Geographical range: Crimea and the N. Caucasus. **Chorotype:** CAUC-CRIM. **Range characteristics:** Crim-Cauc. **Distribution in Europe: Russian Plain and the Caucasus** – Crimea (Jaila), Ciscaucasia and N. Caucasus; E. to N. Ossetia. Rather common on the S. coast of Crimea (Simpheropol, Karadag Reserve, Agarmysh, Ai-Petri, Babugan Yaila, Chatyrdag, Nikitskaya Yaila, Yalta, Roman-Kosh, Staryi Krym, Laspi, Zuya, Feodossiya – ZIN, ZM, IZ, MPGU). The range of this species forms a narrow stretch from the Crimea along the Don River (Taman Peninsula, Krasnodar, Kropotkin) to W. (Mrzikau, Lagonaki, Uchkulan, Ertchik, Taman', Khasayurt-Kharbaz) and C. Caucasus (Teberda, Kluhor-Pass, Kislovodsk, Elbrus – ZIN, ZM, IZ, MPGU).



02 003 bosphoranus (Trachycarabus)



02 003 bosphoranus

Subspecies: Except nominate, no subspecies in Europe.

Ecology: Montane steppes of Crimea, montane steppe and subalpine grasslands of N. Caucasus. Usually at altitudes higher than 1500 m. In N. Ossetian montane steppes it occurs from 1500 to 2500 m and can be considered as an ecological montane vicariant of *C. perrini* (Alekseev, *in litt.*).

Transect: Chapter 8: T-60.

Biology: No data.

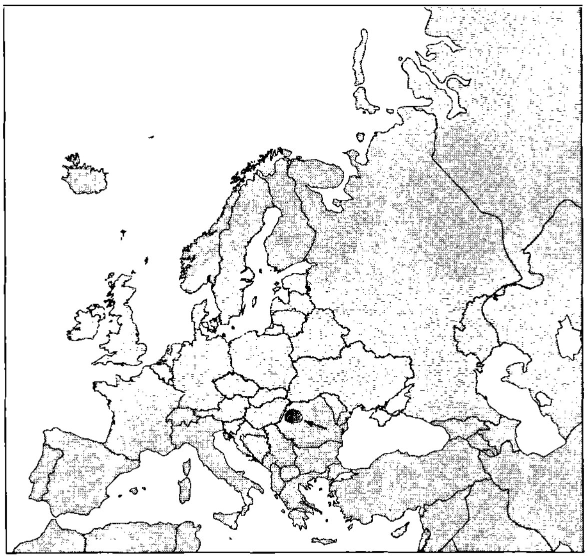
Conservation: No data.

02.004. C. (Morphocarabus) comptus

Dejean, 1831.

General literature: **Checklists and catalogues** – Breuning (1932): 353. Březina (1994): 20; (1999): 18. Deuve (1994): 104 [144]. Kleinfeld & Schütze (1999): 11. Lorenz (1998): 74. Turin *et al.* (1993): 18. **Iconography** – Battoni *et al.* (1995): Pl. 7. Ghiretti (1996): 67. Imura & Mizusawa (1996): not listed. Rautenstrauch (1994): Pl. 11-12.

Taxonomy: *C. comptus* is probably one of the most problematical of all *Morphocarabus* species. In Březina (1994, 1999), Deuve (1994) and Lorenz (1998) mentioned as a subspecies of *C. rothi* Dejean. However, it is very close and similar to *C. hampei* (*C. rothi* is much larger, therefore less similar to *comptus* than *hampei*). *C. hampei* has some smaller subspecies (f.e. *C. h. zilahiensis*) which are morphologically almost unseparable from *comptus* (Csiki, 1906).



02 004 comptus (Morphocarabus)

Geographical range: Endemic of the Romanian Carpathians. **Chorotype:** EEU-CARP. **Range characteristics:** Carp. **Distribution in Europe**: **Romania** – S. Carpathians within the limits of Romania; data for N. Serbia (Vojvodina) are doubtful. Distribution in Transylvania: Transylvanian Mts. (Bihor Mts., Magaslak, Cluj-Napoca, Gilau Mts., Somesu Cald, Rimetea), Pojana Rusca Mts. (Nadrag) and Caras-Severin Mts. (Retezat, Semenic).

Subspecies: No subspecies.

Ecology: Mostly at middle and upper mountain zones. Lie (1989) recorded *C. comptus* from *Fagus silvatica-Quercus petraea* forest near Nadrag (Pojana Rusca Mts. in Banat) at 300-400 m altitude, as well as at 1900-2000 m in the S. Carpathians (Tarcul Mts.) in alpine meadows, under stones.

Biology: No data.

Conservation: No data.

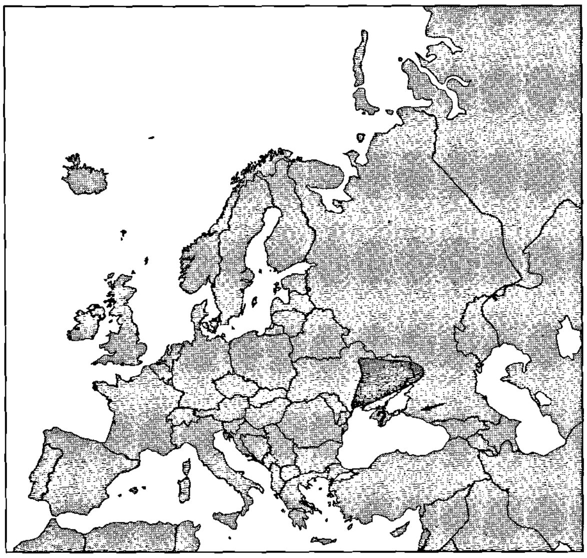
02.005. C. (Trachycarabus) errans

Fischer von Waldheim, 1823.

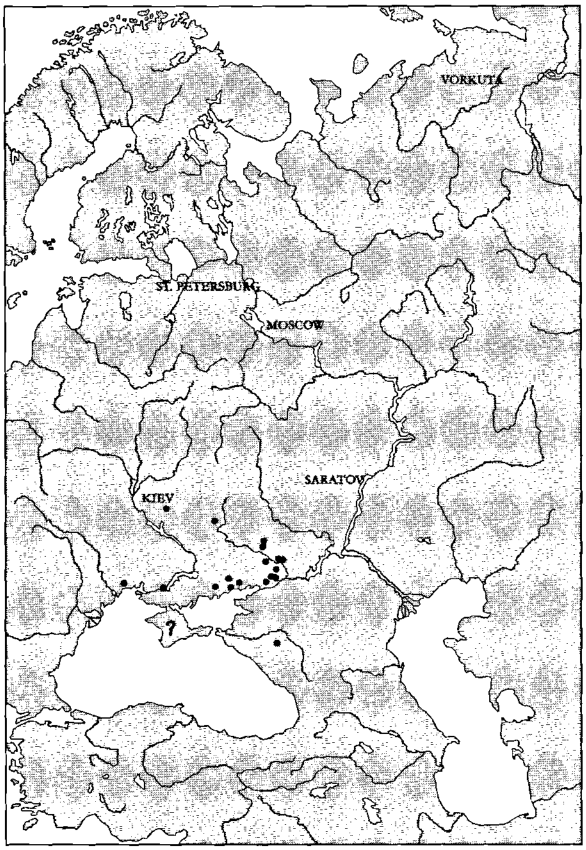
General literature: **Checklists and catalogues** – Breuning (1932): 384. Březina (1994): 22; (1999): 33. Deuve (1994): 110 [165]. Kleinfeld & Schütze (1999): 12. Kryzhanovskij *et al.* (1995): 40 [41]. Lorenz (1998): 75. Turin *et al.* (1993): 18. **Iconography** – Battoni *et al.* (1995): Pl. 10. Ghiretti (1996): 77. Imura & Mizusawa (1996): Pl. 12 [83].

Taxonomy: By Březina (1994; 1999) and Deuve (1994) listed as subspecies of *C. sibiricus* Fischer von Waldheim.

Geographical range: E. and S. Russia, Ukraine. **Chorotype:** EEU-SWRU. **Range characteristics:** Eeur(SW). **Distribution in Europe**: **Russian Plain** – S. steppes between the rivers Dniester and Don (30°E-42°E), in the N.



02 005 errans (Trachycarabus)



02 005 errans

to 50°N and in the S. to 46°N. According to Averin (1938), the N.-most localities seem to be Lokhvitsa in Poltawa province and Kharkov, the W.-most record is 'Bessarabia' (old specimen in collection of ZIN, without exact locality). Known from several localities in S. Ukraine (provinces of Kherson, Zaporozhye, Donetsk and Lugansk, Krasnodar (Maikop – MPGU) and Rostov province. The species has been recorded from Crimea by Lindeman (1871) and there is a single old specimen labelled with 'Tauria' in the ZIN collection, however its presence there has been questioned by Eidelberg *et al.* (1988). Seems not to occur to the S. of Rostov, though there is an old specimen in the collection of ZIN labelled from 'Bashakhta' in the Stavropol region; another distant locality is that at Maikop (see above). In general rather rare.

Subspecies: No subspecies.

Ecology: A species of dry steppes (Arnol'di, 1956).

Transects: Chapter 1: I-2; Chapter 8: T-57.

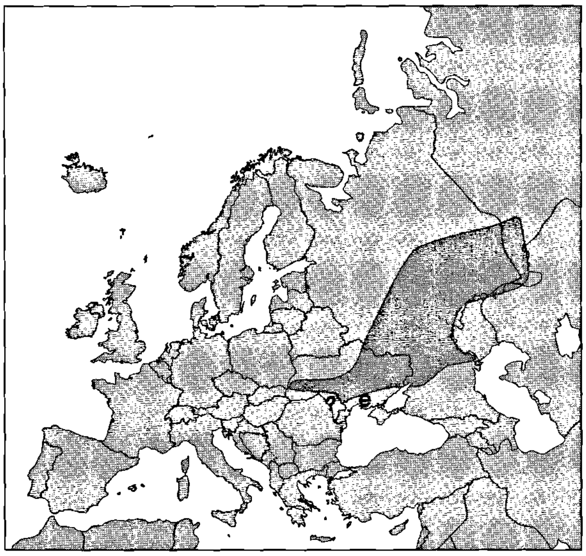
Biology: No data.

Conservation: No data.

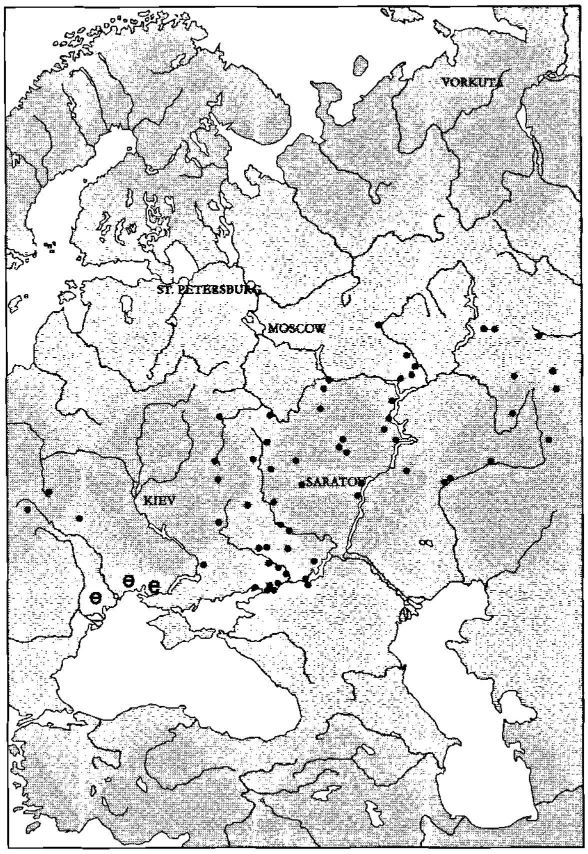
02.006. C. (Trachycarabus) estreicheri
Fischer von Waldheim, 1822.

General literature: **Checklists and catalogues** – Breuning (1935): 1343. Březina (1994): 22; (1999): 21. Deuve (1994): 109 [163]. Kleinfeld & Schütze (1999): 12. Kryzhanovskij *et al.* (1995): 40 [46]. Lorenz (1998): 75. Turin *et al.* (1993): 18. **Iconography** – Battoni *et al.* (1995): Pl. 10. Ghiretti (1996): 76. Imura & Mizusawa (1996): Pl. 12 [87]. Jakobson (1905): Pl. 7. Rautenstrauch (1994): Pl. 24.

Geographical range: From W. Ukraine and Moldova to W. Siberia and N.W. Kazakhstan, in the N. to Kaluga, Riazan, S. parts of Vyatka (=Kirov) and Perm provinces. **Chorotype: EEU. Range characteristics:** EEur(CS)-WSib. **Distribution in Europe**: **Russian Plain** – Widely distributed on the Russian Plain, more common E. of the Dnieper river, with a typical zonal range occupying the zones of the mixed forests, forest-steppe and steppe. The N.-most records in the W. parts of European Russia are known from N. Ukraine (Podolia, Proskurov (=Khmelnitskii) – Breuning) and coincides approximately with 49-50°N; in C. European Russia the N. range limit is shifted to the N. to about 55°N.



02 006 estreicheri (Trachycarabus)



02 006 estreicheri

(Kaluga province – Lutshnik, 1912 and Ryazan' – ZIN); E. of Moscow *C. estreicheri* riches about 56°N (Nizhnyi Novgorod – ZIN, further to the E. the range is shifted to 57-58°N (Kotelnich in Vyatka province – Yuferev, 1980; nature reserves Spasskaya gora and Preduralye in the Perm' province – Koz'minykh *et al.*, 1991b). Formerly, *C. estreicheri* has been reported from 'Bessarabien', the provinces of Odessa, Kherson and Astrakhan – (Breuning, Jakobson), however there are no new findings from those regions and the species can probably now be regarded as being extinct. The S. range limit goes through S. Ukraine – Rostov province – Uralsk (ZIN) – Bolotovsk (Lapshin, 1969, 1972) and seems not to occur S. of the rivers Don and Ural. The E. localities are known from the Urals (60-61°E) (Ekaterinburg – ZIN, Kozyrev, 1990; Chelyabinsk – Lagunov, *in litt.*; Troitsk reserve – Esjunin & Koz'minykh, *in litt*). **Moldova** – Only old records from S. Moldova, probably extinct.

Subspecies: Except nominate, no subspecies in Europe.

Ecology: Eurytopic (Feoktistov, 1979). Forest-steppe and N. steppe zones; absent from dry steppes. Locally common and abundant (Arnol'di, 1956). In the Ukraine, in mixed forests in the forest-steppe zone, and in 'bairak'[1] oak woods of the N. steppe subzone (Petrusenko, 1971).

Transects: Chapter 1: I-2; Chapter 8: T-44, 46-49, 51, 53 and 57.

Biology: **Activity** – No data. **Periodicity** – Neculiseanu & Matalin (2000) reported a record (Moldova) from July. **Food** (Larochelle, 1990) – In the field, larvae of *Loxostege sticticalis* L. (Lepidoptera, Pyralidae). **Larva:** Described by Sharova (1958: L3). Food – No data.

Conservation: No data.

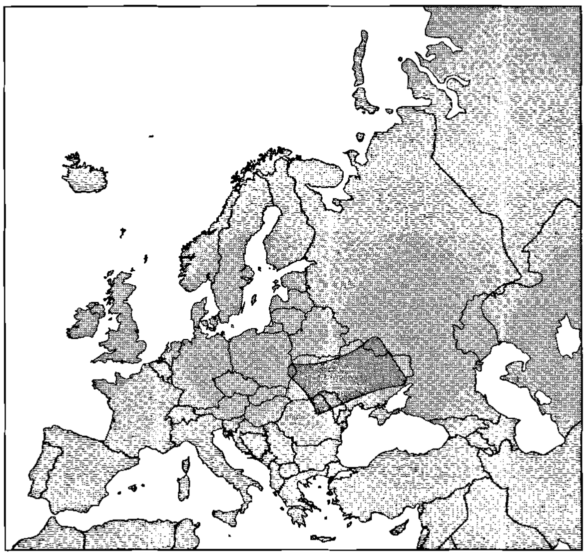
02.007. C. (Morphocarabus) excellens

Fabricius, 1798.

General literature: **Checklists and catalogues** – Breuning (1932): 322. Březina (1994): 19; (1999): 16. Deuve (1994): 104 [143]. Kleinfeld & Schütze (1999): 11. Kryzhanovskij *et al.* (1995): 39 [33]. Lorenz (1998): 73. Turin *et al.* (1993): 18. **Iconography** – Battoni *et al.* (1995): Pl. 8-9. Ghiretti (1996): 67. Imura & Mizusawa (1996): Pl. 11 [79]. Jakobson (1905): Pl. 5. Rautenstrauch (1994): Pl. 12.

Taxonomy: In Deuve (1994) treated as a subspecies of *C. monilis* Fabricius.

Geographical range: Rather local E. European species, N. of the Black Sea: S.E. Poland, N.E. Romania, Moldova, Ukraine (except the dry steppe and Crimea), S.W. Russia (Kursk, Belgorod provinces). **Chorotype:** EEU-SWRU. **Range characteristics:** EEur(SW). **Distribution in Europe:** **Poland** – Very restricted to the S.E.-most part of the country. **Byelorussia** – An old record from the S.E. only (Polessko-Pridneprovskij region). **Russian Plain** – A restricted distribution, known only from the S.W. regions (Moldova, Ukraine and Kursk Province), where, however, several localities have been reported. The N. range limit (52°N) coincides approximately with the political border of Ukraine (Volyn province – Chernigov – Sumy), E. (36°E) to the Kursk province (Ryl'sk district – ZIN; C.-Chernozem reserve nr. Kursk – MPGU, ZM). The S. limit follows the S. border of the forest-steppe zone (Bendery – Kodyma – Chernyi Les near Znamenka – Dnepropetrovsk –



02 007 excellens (Morphocarabus)

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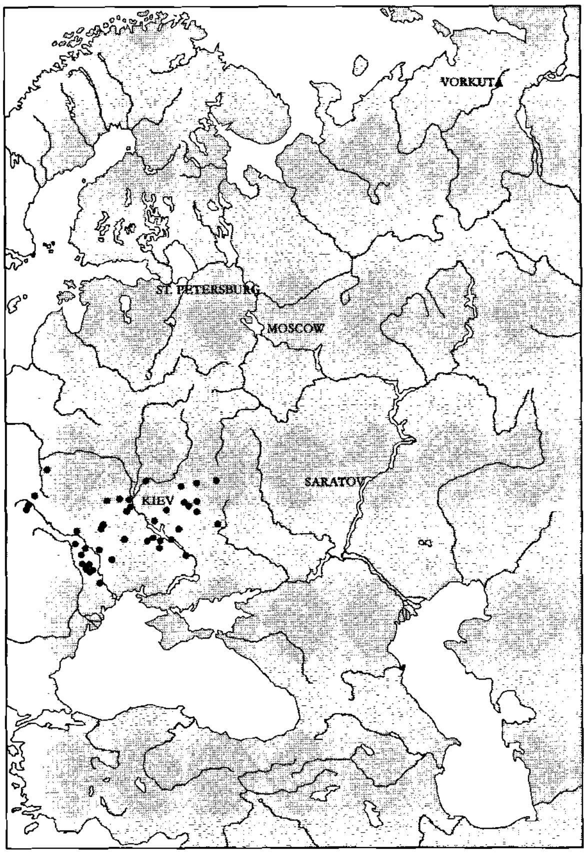
[1] 'Bairak' – insular forest patches in ravines in the steppe zone.



02 007 excellens

Kharkov). A species with a typical zonal distribution, rather common in the forests of the forest-steppe zone, known also from the S. subzone of the mixed forests, practically absent from the steppe zone. **Moldova** – Most of the territory W. of Dnestr river. **Hungary** – In the collection of the Hungarian National History Museum (Budapest) there are some – about 100 years old – specimens from Orlov and Tovarníky (Slovakia) and from Transylvania (Romania) of which, however, exact localities are missing.

Romania – N.E. Romania (Rarau Mts.; 'Jassy'=Iaşi).

Subspecies: Except nominate, no subspecies.

Ecology: Mostly in forests-steppe, absent from the mountains. In S. Russia (Dnieper region) not penetrating on the E. bank of the Dnieper river, but on the W. side penetrating into the lowland forest zone (Medvedev, 1928). In Ukraine in dry floodland woods at higher altitudes and oak woods of the forest-steppe zone (Petrusenko, 1971). In the Central-Chernozem Reserve, it seems to avoid non-mown steppe, being relatively common in oak groves, mown steppes and in open places in forests with tall grass (Grechanichenko, 2000).

Transects: Chapter 8: T-53, 58.

Biology: **Activity** – No data. **Periodicity** – According to Sharova & Dushenkov (1979), autumn breeder with a one year life cycle. The adults are active during summer and autumn, the larvae develop from autumn to spring. Neculiseanu & Matalin (2000) reported records (Moldova) from April-October.

Conservation: No data.

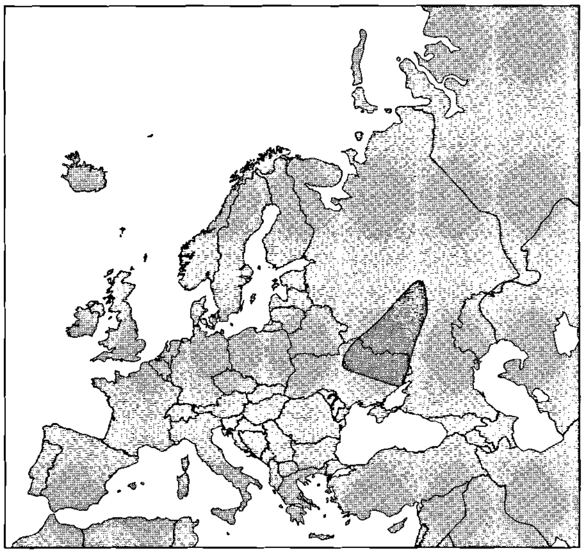
02.008. C. (Trachycarabus) haeres

Fischer von Waldheim,1823.

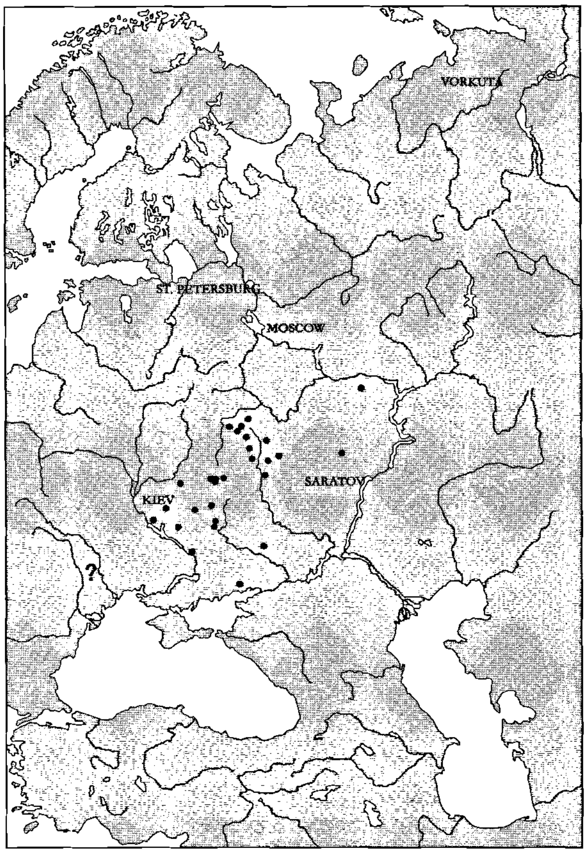
General literature: **Checklists and catalogues** – Breuning (1932): 483. Březina (1994): 22; (1999): 22. Deuve (1994): 110 [165]. Kleinfeld & Schütze (1999): 12. Kryzhanovskij *et al.* (1995): 40 [44]. Lorenz (1998): 75. Turin *et al.* (1993): 19. **Iconography** – Battoni *et al.* (1995): Pl. 10. Ghiretti (1996): 77. Imura & Mizusawa (1996): Pl. 12 [83].

Taxonomy: By Deuve (1994) and Březina (1999) treated as a subspecies of *C. sibiricus* Fischer von Waldheim.

Geographical range: Endemic species of the C. Russian plain. **Chorotype:** EEU-CRUS. **Range characteristics:** EEur(C). **Distribution in Europe**: **Russian Plain** – Forest-steppe and the N. part of steppe zone of C. European Russia and Ukraine between Dnieper and Volga (provinces of Cherkassy, Poltava, Sumy, Chernigov, Kharkov, Dnepropetrovsk, Donetsk, Belgorod, Kursk, Orel, Lipets, Tula, Tambov, Voronezh, Penza). The N. range limit coincides with the line Zolotonosha in Cherkassy province (Kiseritsky, 1912) – Baturin in Chernigov province (ZIN) – Tul'skie Zaseki Forestry in Tula province (ZM) – Ryazan (large series: 1994-1996 – MPGU). The E.-most locality (45°E) seems to be Penza (MPGU, ZIN), the record of Esterberg (1935) from Pil'na in Nizhni Novgorod province needs confirmation because of possible confusion with *C. sibiricus*. To the W., the species range is restricted by the Dnieper. The S. range limit seems to coincide with the border of the forest-steppe, the S.-most locality is Khomutovskaya Step' reserve in the Donets steppes (IZ). A species with a typical zonal range restricted to the forest-steppe zone. Few localities are known from the neighbouring zones of deciduous forests and steppes. **Moldova** – Only found in the Kodry Hills; the locality is rather distinct and needs to be verified.



02 008 haeres (Trachycarabus)



02 008 haeres

Subspecies: **a) subsp. haeres** – The N.E. part of area: regions of Tula, Ryasan, Lipetzk, Voronezh, Saratov, E. part of Kursk province. **b) subsp. fossulatus** Dejean, 1826 – W. districts of Kursk province, provinces of Sumy, Kharkov, Chernigov, Poltava, Kiev, Cherkasy.

Ecology: Species of the forest-steppe zone (Medvedev, 1950). According to Grechanichenko (2000), in the Central-Chernozem Reserve a typical inhabitant of the interfluvial forb-feather-grass steppe, absent from the oak forests and rare on arable land.

Transects: Chapter 8: T-48, 53, 56.

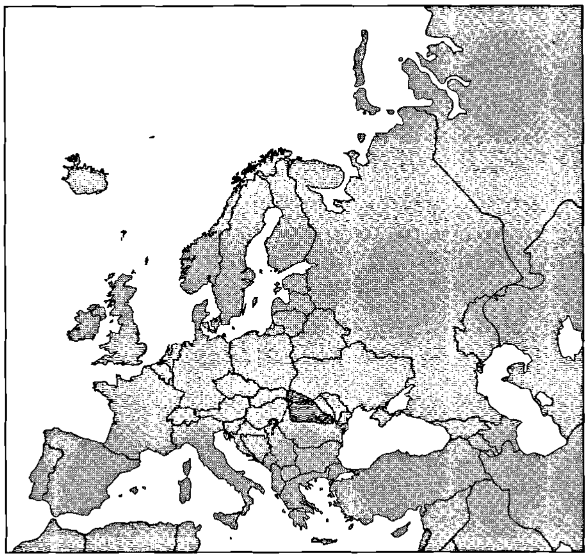
Biology: **Activity** – No data. **Periodicity** – A record from July was mentioned by Neculiseanu & Matalin (2000) from Moldova. **Food** (Larochelle, 1990) – In the field, caterpillars and larvae of various Coleoptera.

Conservation: No data.

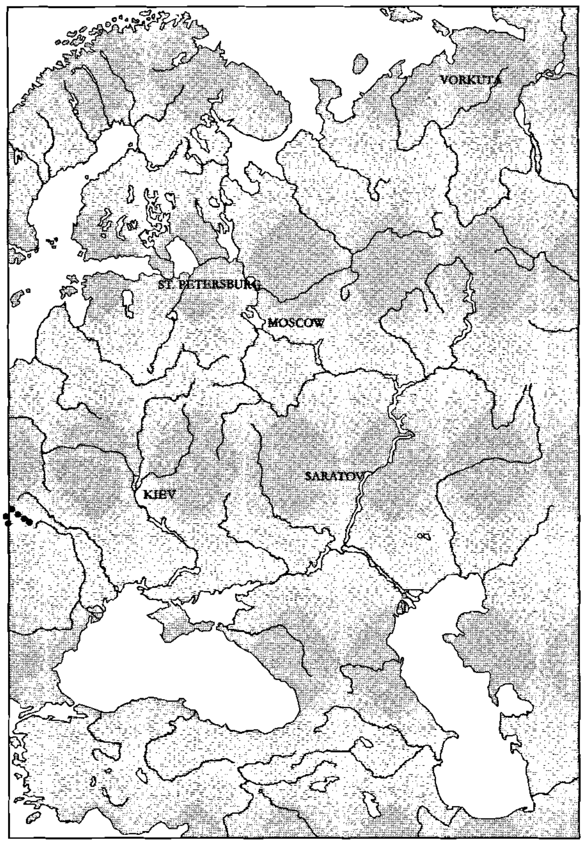
02.009. C. (Morphocarabus) hampei

Küster, 1846.

General literature: **Checklists and catalogues** – Breuning (1932): 350. Březina (1994): 20; (1999): 19. Csiki (1946): 146. Deuve (1994): 105 [144]. Kleinfeld & Schütze (1999): 11. Kryzhanovskij *et al.* (1995): 39 [34]. Lorenz (1998): 74. Turin *et al.* (1993): 19. **Iconography** – Battoni *et al.* (1995): Pl. 7-8. Ghiretti (1996): 68. Imura & Mizusawa (1996): Pl. 11 [78]. Rautenstrauch (1994): Pl. 10-11.



02 009 hampei (Morphocarabus)



02 009 hampei

Taxonomy: In Deuve (1994), Březina (1994; 1999) and Lorenz (1998) listed as a subspecies of *C. rothi* Dejean. Subspecies *incompsus* Kraatz, 1880 is perhaps a distinct species (see Ishikawa, 1973).

Geographical range: S.E. part of Transcarpathian Ukraine, N.E. Hungary, Romania except the E. provinces, ?N. Serbia (Vojvodina). **Chorotype:** EEU-CARP. **Range characteristics:** Carp. **Distribution in Europe: Russian**

Plain – S.E. part of Transcarpathian Ukraine: Zakarpatye and Ivano-Frankovo provinces, known from Goverla Mt., Yasinya and the districts of Beregovo, Velikii Bereznyi, Vinogradov, Mezhgosrk and Volovtsy (ZIN; ZM; Ponomartchuk, 1956; Koval', 1989; Rizun, 1990). **Hungary** – Only in the N.E.-most part, in the lowland near Tisza. **Romania** – Romania, mostly in the C.N. and C. parts (Gutin Mts.; Tibles Mts.; Transylvanian Mts.; Salaj; Transylvanian Basin: Targu Mures; NE., E. and S. Carpathians: Maramures Mts., Rodnei Mts., Sinaia).

Subspecies: a) subsp. hampei (=*mendax* Csiki, 1906) – S.E. part of Transcarpatian Ukraine, Romania (except its E. part: Rodney Mts.). Mostly in lowlands and valleys. – Specimens from Beregovo were described as *ormayi* Reitter, 1896; they are hardly different. **b) subsp. incompsus** Kraatz, 1880 – C. Romania: Persan Mts. (Crizbav, Maierus), Baraolt Mts. (Valcele), environs of Brasov (Cristianul-Mare Mts., Timis, Azuga, Sinaia), from foothills to alpine zone.

Ecology: Mesophilous species from open and half-open country, such as roadsides, scrub, light shelter belts etc. (Koval', 1989). From lowlands to the alpine zone.

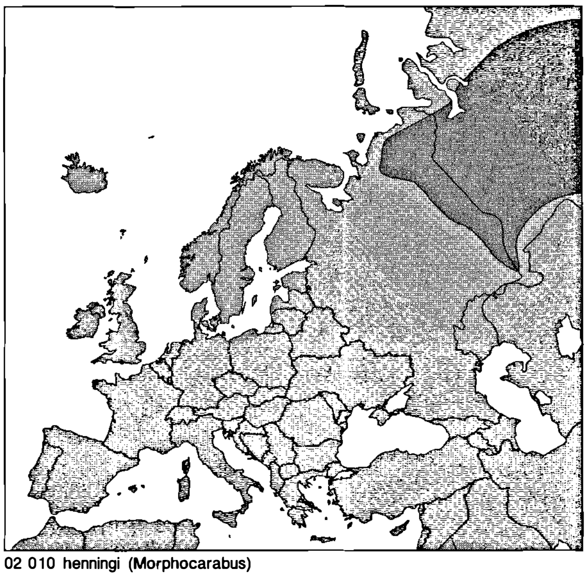
Transect: Chapter 8: T-76.

Biology: **Activity** – No data. **Periodicity** – Obviously a species that reproduces in autumn, hibernating mainly as L3 (Koval', 1989). Also adults that emerged in the spring before, hibernate after reproduction and probably reproduce for a second time in the following year. **Larva**: Described by Koval' (1989).

Conservation: No data.

02.010. C. (Morphocarabus) henningi
Fischer von Waldheim, 1817.

General literature: **Checklists and catalogues** – Breuning (1932): 275. Březina (1994): 19; (1999): 16. Deuve (1994): 107 [154]. Kleinfeld & Schütze (1999): 10. Kryzhanovskij *et al.* (1995): 39 [24]. Lorenz (1998): 73. Turin *et al.* (1993): 19. **Iconography** – Ghiretti (1996): 71. Imura & Mizusawa (1996): Pl. 10 [71]. Jakobson (1905): Pl. 4. Ratti *et al.* (1990): Pl. 12.



02 010 henningi (Morphocarabus)

02 010 henningi

Geographical range: E. Russia, W. and C. Siberia to Baikal and river Lena. **Chorotype:** SIB. **Range characteristics:** EEur(E)-CSib. **Distribution in Europe**: **Russian Plain** – Boreo-montane species according to Korobeinikov (1987). N.E. European Russia and the Urals, to the W. to the Pechora river basin, the W.-most locality (52°E) seems to be Ust'Tsil'ma at Pechora (ZIN) and 40 km S. of Pechora (MPGU). Known also from Vorkuta (MPGU), where it seems to be common in the tundras Bol'shezemel'skaya, Bolvanskaya and Yushinskaya (ZIN), and Polar Ural (Neroika Mt. (MPGU); Nenetz area, confluence of rivers Kolva and Kharyaga; district of Salekhard – ZIN; Korobeinikov, 1990). Along the Ural Mountains, this species penetrates to Bashkiria (Yuzhno-Ural Reserve – Kashevarov, 1986; Mesyagutovo at Ai-River – Zinovjev, 1991) and is recorded also from the province of Perm' (Nizhnyaya Kura, Preduralye – Koz'minykh *et al.*, 1991b); Lis'vensk district – Voronova, 1987) and Ekaterinburg province (Koz'minykh, *in litt.*). Distributed in the tundra and taiga zones, and the Ural mountains.

Subspecies: Three subspecies exist in Europe: **a) subsp. henningi** – Taiga zone of Komi and Middle Ural. **b)**

subsp. oviformis Behein & Breuning, 1943 – Polar Ural, Vorkuta. **c) subsp. peczoricus** Obydov, 2000 – Republic Komi (Pechora River basin).

Ecology: Mostly in forests on the European side. In the S. Yamal peninsula, where the species has a wide, but scattered distribution, it is generally rare, inhabiting grass-herb meadows and sometimes larch forests. Most common in scrub and forest edges (Korobeinikov, 1984; Andreeva & Eremin, 1991). In the Baikal region, it was found at 2500-2700 m (Berlov & Berlov, 1984).

Transects: Chapter 1: I-2; Chapter 8: T-43-44, 47.

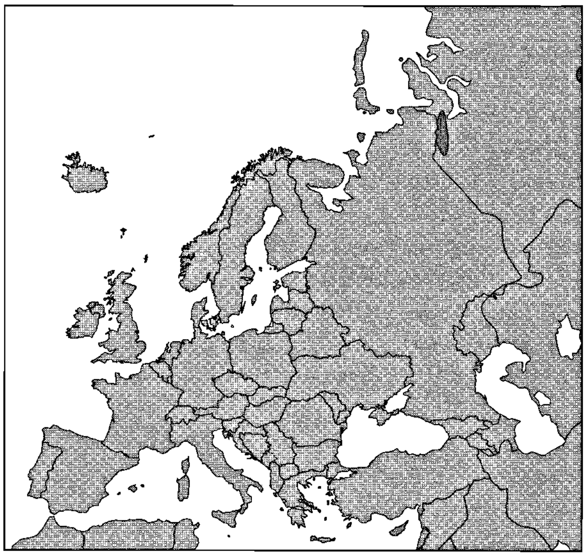
Biology: **Activity** – No data. **Periodicity** – In S. Yamal, the adults show two peaks of activity, the first during reproduction immediately after hibernation, from the second half of April onwards during spring, and the second in autumn when the fresh adults occur (Korobeinikov, 1984, 1990). Development was observed by Berlov & Berlov (1997a) in the laboratory (Baikal region), showing that copulation took place in May-June and oviposition in July-August (egg size 4.6 x 2.1 mm). Pupae were found in September and the adults hibernate (Berlov & Berlov, 1984). **Larva**: Size given by Berlov & Berlov (1984: L1-L3).

Conservation: No data.

02.011. C. (Morphocarabus) hummeli

Fischer von Waldheim, 1823.

General literature: **Checklists and catalogues** – Breuning (1932): 269. Březina (1994): 19; (1999): 16. Deuve (1994): 107 [154]. Kleinfeld & Schütze (1999): 10. Kryzhanovskij *et al.* (1995): 38 [23]. Lorenz (1998): 73. Turin *et al.* (1993): 19. **Iconography** – (Battoni *et al.* (1995): Pl. 9 = Mongolian subsp. *stolidus* Vacher de Lapouge). Ghiretti (1996): 72-73. Imura & Mizusawa (1996): Pl. 9 [61]. Jakobson (1905): Pl. 4. Ratti *et al.* (1990): Pl. 11.



02 011 hummeli (Morphocarabus)

02 011 hummeli

Geographical range: Polar Ural; widely distributed through Siberia to the Pacific ocean and N. Sakhalin, Primorye, Priamurye, Kolyma upper stream, N. Mongolia, N. China, and N. Korea. Not in Alaska as mentioned by Poppius (1910), see Bousquet & Larochelle (1994). **Chorotype:** SIB. **Range characteristics:** EEur(NE)-Asi. **Distribution in Europe (and adjacent areas)**: **Russian Plain** – Very rare: known from few localities in the N. Polar Ural (Salekhard, basins of the rivers Voikar, Malaya Khanema and Bol'shaya Khanema – ZIN). Recorded also from the Pechora river basin, but without exact data on the locality (Poppius, 1910). Tundra and forest-tundra zones.

Subspecies: Several subspecies, highly polychromous, mainly in E. Asia. European individuals belong to the nominate race. Recently described: **a) subsp. dshvangi** Mens'hikov & Gorbunov, 1997 from Polar Transuralia and Yamal peninsula. It is possible that all populations from the N.E. part of the Russian Plain belong to this subspecies.

Ecology: Forest species, in the mountains between 1200 and 1700 m (Baikal region: Berlov & Berlov, 1984). It is found in mossy tussocks in the S. Yamal peninsula (Andreeva & Eremin, 1991). In Yakutia, it was sampled from floodland (river) meadows and from steppe-like patches (Shilenkov & Averenskii, 1991).

Biology: **Activity** – No data. **Periodicity** – In the laboratory, copulations were observed in June and early July and oviposition from the end of June until the end of July (Berlov & Berlov, 1997a). Larval development takes place during the summer and autumn. Although pupae were found in October, it probably hibernates as third instar, but also as (older) adult (Berlov & Berlov, 1984). Fresh beetles were found in July and August. From these data, a two-year development can be supposed.

Conservation: No data.

02.012. C. (Morphocarabus) karpinskii

Kryzhanowskij & Matveev, 1993.

General literature: **Checklists and catalogues** – Březina (1994): 19; (1999): 16. Deuve (1994): 109 [159]. Kleinfeld & Schütze (1999): 10. Kryzhanovskij *et al.* (1995): 39 [27]. Lorenz (1998): 72. Turin *et al.* (1993): 19. **Iconography** – Ghiretti (1996): 74. Imura & Mizusawa (1996): Pl. 11 [75].

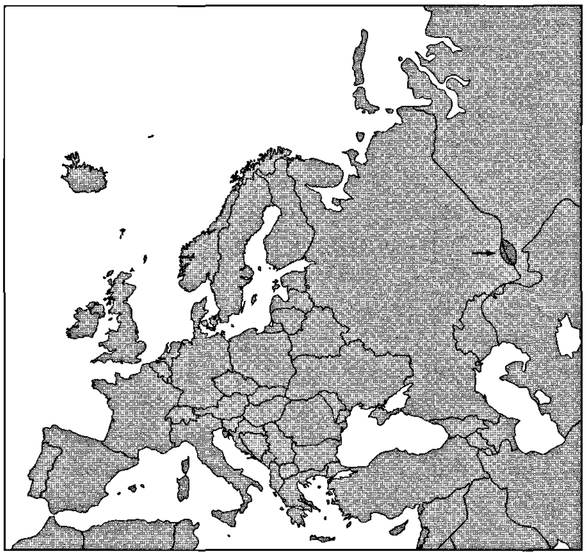
Geographical range: Endemic of S. Ural (loc. typ. Iremel Mt.). **Chorotype**: EEU-URAL. **Range characteristics**: Ural(S). **Distribution in Europe**: **Russian Plain** – A very local, endemic species, merely known from a few mountain peaks of the S. Urals – Malyi Iremel', Bol'shoi Iremel', Nurgush, Urenga (ZIN; Matveev, 1988; Logunov, *in litt.;* coll. L. Penev). Restricted to the montane tundras, where it occurs in stony fields.

Subspecies: no subspecies.

Ecology: It inhabits the alpine zone of peaks above 1200 m; stony montane tundra, rocky scree slopes and meadows (Lagunov *in litt.*; Penev, *pers. observ.*).

Biology: No data.

Conservation: No data.



02 012 karpinskii (Morphocarabus)

02 012 karpinskii

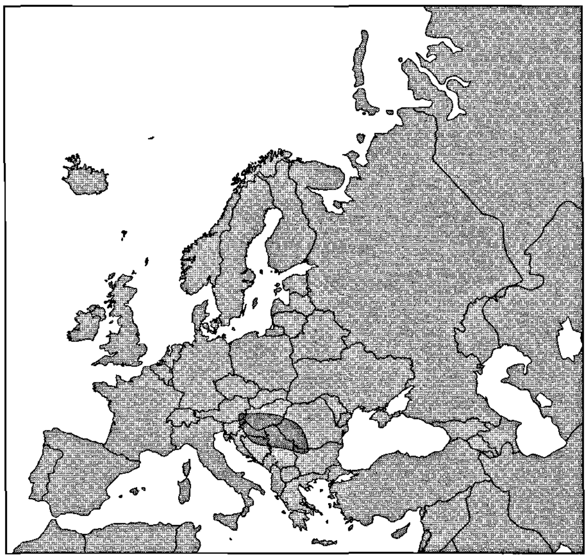
02.013. C. (Morphocarabus) kollari

Palliardi, 1825.

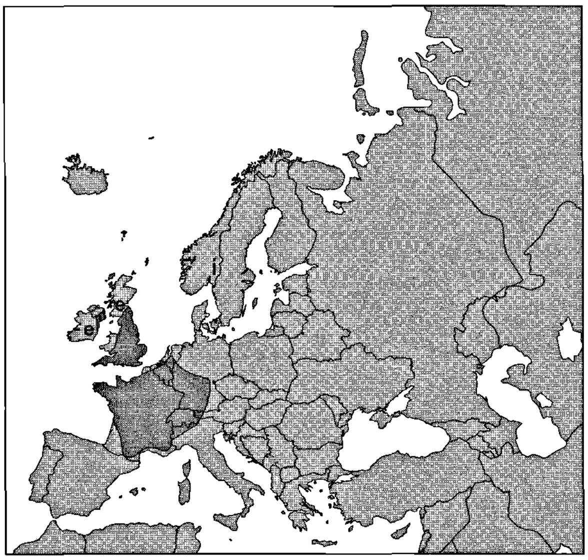
General literature: **Checklists and catalogues** – Breuning (1932): 317. Březina (1994): 21; (1999): 20. Csiki (1946): 145. Deuve (1994): 103 [143]. Kleinfeld & Schütze (1999): 11. Lorenz (1998): 73. Turin *et al.* (1993): 19. **Iconography** – Battoni *et al.* (1995): Pl. 5-6. Ghiretti (1996): 65. Imura & Mizusawa (1996): Pl. 11 [79]. Pavicevic & Mesaros (1997): cd-rom. Rautenstrauch (1994): Pl. 6-8 (part. as *praecellens*).

Taxonomy: By Březina (1994; 1999) and Deuve (1994) listed as a subspecies of *C. scheidleri* Panzer (*monilis* Fabricius). By Pavicevic & Mesaros (1997), the forms *curtulus* Ganglbauer, *illigeri* Dejean and *praecellens* Palliardi are listed as good species.

Geographical range: Endemic species of S.E. Europe, from S.E. Austria, W. Hungary, Slovenia, Croatia, W. and N. Serbia (including Vojvodina), Bosnia, Herzegovina, S.W. and C. Romania. **Chorotype**: EEU-CARP. **Range characteristics**: Pann-Carp. **Distribution in Europe**: **Romania** – S.W. Romania, Banat (near Bazias, Sasca Montana (= Szászkabánya in Hungarian), Resita, Banat Mts. (Mehadia). **Balkan Peninsula** – Mainly restricted to the inland of former Yugoslavia: Srem, W., C. and E. Croatia, Banat, Bosnia-Herzegowina (Bjelasnica), Serbia (Negotin, Vrsac, Cer Planina, Kopaonik, Tara planina-Mitrovac).



02 013 kollari (Morphocarabus)



02 014 monilis (Morphocarabus)

Subspecies: **a) subsp. kollari** – W. Romania: Banat, Mehadia, Baie Herculeane, Carasova, W. Walakhia. **b) subsp. semetricus** Kraatz, 1878 – S.W. Romania, N.E. Serbia (Negotin). **c) subsp. illigeri** Dejean, 1826 – Croatia, Bosnia. **d) subsp. curtulus** Ganglbauer, 1892 – Small montane form from Bosnia and Herzegovina, W. Serbia. **e) subsp. praecellens** Palliardi, 1825 – E. Serbia, Fruska Gora.

Ecology: Mostly in lowlands, but occurs up to the subalpine zone. Pavicevic & Mesaros (1997) describe it as a silvicol species, inhabiting deciduous forests in hills and mountains. Especially the form *curtulus* Ganglbauer, can also be found up to the alpine region where it inhabits pastures and eualpine habitats.

Transects: Chapter 8: T-62-63, 72-73.

Biology: No data.

Conservation: Pavicevic & Mesaros (1997) regard all forms as vulnerable or endangered.

02.014. C. (Morphocarabus) monilis

Fabricius, 1792.

General literature: **Checklists and catalogues** – Breuning (1932): 311; Březina (1995): 20; (1999): 17. Deuve (1994): 101 [143]. Kleinfeld & Schütze (1999): 11. Lorenz (1998): 74. Turin *et al.* (1993): 19. **Iconography** – Battoni *et al.* (1995): Pl. 1-3. Casale *et al.* (1982): fig. 95. Darnaud (1980a): Pl. 10. Forel & Leplat (1995): Pl. 3-7. Ghiretti (1996): 61-67. Imura & Mizusawa (1996): Pl. 11-12 [79]. Jakobson (1905): Pl. 5. Rautenstrauch (1994): Pl. 1-4.

Taxonomy: For taxa that are often treated as subspecies (see Březina, 1994; Deuve, 1994) of *C. monilis* (most of them attributed to *C. scheidleri*), see also *C. excellens* Fabricius, *C. kollari* Pall., *C. scheidleri* Panzer, *C. versicolor* Frivaldszky, and *C. zawadzkii* Kraatz (compare *Checklist* and *Key to the adults*).

SPECIAL PART

Geographical range: European species with a rather small, more or less Atlantic range. W. and partly C. Europe: British Isles, France (except the Mediterranean landscapes of the S.), Belgium, Netherlands, S., C. and W. Germany, Switzerland, Italy (only in W. Alps); other data refer to introduced individuals. **Chorotype:** EUR. **Range characteristics:** WEur-CEur. **Distribution in Europe**: **Fennoscandia** – Only in S.E. Norway; introduced near Frederikstad and now probably established. Not in Denmark. **British Isles** – A mainly S. and E. species (rare in the N.), which has declined everywhere since 1900 (Lindroth, 1974). Old records are known from Ireland (1902 and older – Anderson *et al.,* 2000) and Scotland but now probably extinct there. **Netherlands** – Mainly along the larger rivers in the S. and C. parts of the country (similar distribution to *C. auratus* and *C. coriaceus*); locally abundant, especially in the S. part of the province of Limburg in limestone grasslands. It seems to become rarer in the C. **Belgium** – Distributed throughout the C., but declining. Probably endangered in Flandria. **Germany** – Not in the N.E. (Schleswig-Holstein, Mecklenburg-Vorpommern, Berlin, Brandenburg, Sachsen). Scattered in the W. (N.W. to S.W.), from the W. part of the German Plain (including the lowlands of the rivers Weser and Aller in Lower Saxony, N. to Bremen; (Mossakowski, 1991), via the Lower Rhine basin to Voralberg; in most other areas noted as declining or heavily endangered (Sachsen-Anhalt, Thüringen); around 1900 common in Thüringen, now rare (Arndt, 1989). In E. Germany after 1960 only records from Magdeburg (doubtful record), Fahner Höhe, Frankenroda/Werra, near Erfurt, Arnstadt (where it was recorded recently as numerous on extensive meadows: Arndt, *pers. observ.*), Bad Salzungen and Breitenbach/Suhl. In W.-Falia, locally not uncommon, notably along the Rhine (Gries *et al.,* 1973). **Switzerland** – Greatest range and abundance on the N. side of the Alps, including the Jura and Wallis; nearly absent from Tessin and Graubünden. Declined in agricultural areas. **Italy** – Marginal element in the Italian fauna, penetrating into the N. territory via some alpine valleys in Piemonte, Aosta Valley and Ticino. Reported from the Cottian, Grajan and Lepontine Alps. **France** – Widely distributed across most of France, N. of the Garonne, and W. of the Rhône. Outside this territory there are isolated montane populations, e.g. in the C. Pyrenees, Cantal, Montagne Noire and the Alps of Dauphiné and the Provence. **Iberian Peninsula** – Restricted to a small area in the E. Pyrenees: Cerdaña fransesa.

Subspecies (see note in *Checklist*, p. 19): **a) subsp. monilis** – The majority of the area. **b) subsp. subpyrenaeus** Vacher de Lapouge, 1925 – N. slope of C. and E. Pyrenees. **c) subsp. alticola** Bellier, 1880 – Isolated form, living in the Prealps of the Provence. **d) subsp. saouensis** Mandl, 1967 – Drôme, Vercors. **e) subsp. consitus** Panzer, 1809 – Lowland of W. Switzerland and E. France. **f) subsp. schartowi** Heer, 1837 (= *taunicus* Heyden, 1871) – High mountains of E. France (Vosges, Jura, Alps of Dauphine), W. Switzerland, S.W. Germany (Taunus, Vogelsberg) (with *sabaudus* as synonym).

Ecology: Eurytopic, mesophilic. In N.W. and C. Europe often associated with cultivated habitats (Lindroth, 1985); in general a thermophilic species (Arndt, 1989; Turin *et al.,* 1991). According to Hoffmann (1907), in C. Europe mainly from lowlands up to 500 m, but in fact also higher in the mountains up to ca 2000 m. In the S. of its distribution it is even a strictly montane species that occurs mainly from 700-1000 m (Susa Valley; Central Massif) up to 2000-2200 m (e.g. Italy, Pyrenees), occasionally to 2500 m (Casale *et al.,* 1982). Typical species of open country, occurring in field habitats such as moderately damp grasslands, gardens and fallow land, often found in poor agricultural country, limestone grasslands, wasteland, and especially river meadows (Lindroth, 1974; Marggi, 1992). Sometimes in sparse forests, or scrubland, but usually rare (Du Chatenet, 1986; Turin *et al.,* 1991). Near the river Weser (Germany, Lower Saxony) also very abundant in oak woodlands that are inundated during the winter (Assmann, *pers. observ.*). It shows a preference for heavier soil types, such as clay, loam (loess) or limestone. According to Blumenthal (1981), there are two main 'ecotypes': 1) inhabiting grasslands in river meadows, and 2) populations occurring on montane grasslands, also living on limestone grasslands in N.W. and N.C. Europe, which is also the only ecotype present in the Italy (Alps).

Transects: Chapter 8: T-04, 17-18, 22, 30-32, 80, 89-91.

Biology: **Activity** – Mainly night active; sometimes hunting during daytime (Mandl, 1956). **Periodicity** – Reproduction in C.E. Europe in autumn; young beetles emerge during early summer and reproduce from end of July-September. From October onwards, a certain proportion of the adult population hibernates together with the larvae; these adults reproduce for a second time in the following year in May/June – June/July (Arndt, 1989; Hůrka, 1973). In W. Europe (Netherlands, France) reproduction takes place a little earlier, during the second half of spring and in the summer, larval development occurring during autumn and winter, and teneral animals appearing next spring. Forel & Leplat (1995) state: 'Because it is so far impossible to breed the species, the development is hardly known', but Hůrka (*l.c.*) presents data from various rearing experiments, resulting in the following picture: copulations were observed from the end of May to July, occasionally in August (Hölzel, 1942; Stiprajs, 1961). The females laid 50-100 eggs (size 3.5 x 1.5 mm); development of the eggs took 10-14 days. The larval development in C. Europe: L1: 7-14 days, L2: 11-16 days, L3: 7-8 months including hibernation diapause (Burmeister, 1939; Kern, 1921; Stiprajs, 1961). Larvae of all stages (L1: 1, L2: 4, L3: 13 individuals) were found in Germany by Lehman (1965) in July and August. L3 larvae were also found in August, October and November (Hůrka, *l.c.*). For S. Europe, duration of development was recorded by Sturani (1962): eggs ca 11-14 days and larvae, in total 30-40 days (including a prepupal stage of 7-10 days, and without hibernation). Adults were exclusively found in the period April-September and are active during this period without a summer aestivation; they hibernate deep in the soil, similar to *C. auratus* and like this species, are extremely difficult to find (not in the 'normal' winter shelters), even in places where the species is common. **Food** (Larochelle, 1990) – In the field, various larvae of insects, cockroaches, earthworms, living and dead snails; baited with crushed snails and honey (of *Cherleria sedoides*). In captivity, honey, beef hearts, earthworms, caterpillars, various insects, raw meat, fruits, bread soaked in sugared water. The adults show cannibalism. **Larva**: Described by Vacher de Lapouge (1905, 1929), Bengtsson (1927), Sturani (1962), Hůrka (1971b) and key: Arndt (1985, 1991b). Food – in the laboratory, earthworms, caterpillars of moths. In the field, baited with carrion of snails and sugar for trapping Lepidoptera.

Conservation: Blumenthal (1981) concluded it to be a suitable indicator species for the quality of W. European river water-meadows. The species is mentioned to be valuable as a major predator of noxious insects in extensively managed agricultural fields (Larochelle, 1990). In forests and mountains the species seems to be more or less stable. From a survey in different types of grasslands in the Netherlands, it seems to be less influenced by the use of fertilisers e.g. than *C. auratus* (Turin, 1983). However, in most regions, it is sensitive to intensive agricultural practices, especially the use of pesticides. This caused most probably a serious decline in vast agricultural (lowland) areas in larger parts of N.W. and C. Europe, sometimes even locally extinction, e.g. in the British Isles (Luff, 1998), the Netherlands (Turin, 2000), Flandria (Desender *et al.,* 1995), Germany (Arndt, 1989; Trautner & Müller-Motzfeld, 1995) and Switzerland (Marggi, 1992). On the other hand, results from pitfall trapping in the Rhineland near Cologne and Bonn, indicate very similar catching rates in 'conventionally' (= intensively) and 'alternatively' (= extensively, more natural) managed agricultural fields (Ingrisch *et al.*, 1989; Blumenthal, *pers. comm.*). Therefore, it can be supposed that the sensitivity to pesticides and other farming methods might not be the same in different populations of this species. This may be the result of different levels of pesticide resistance. In other areas, for instance in Switzerland, generally very common.

02.015. C. (Morphocarabus) odoratus
Motschulsky, 1844.

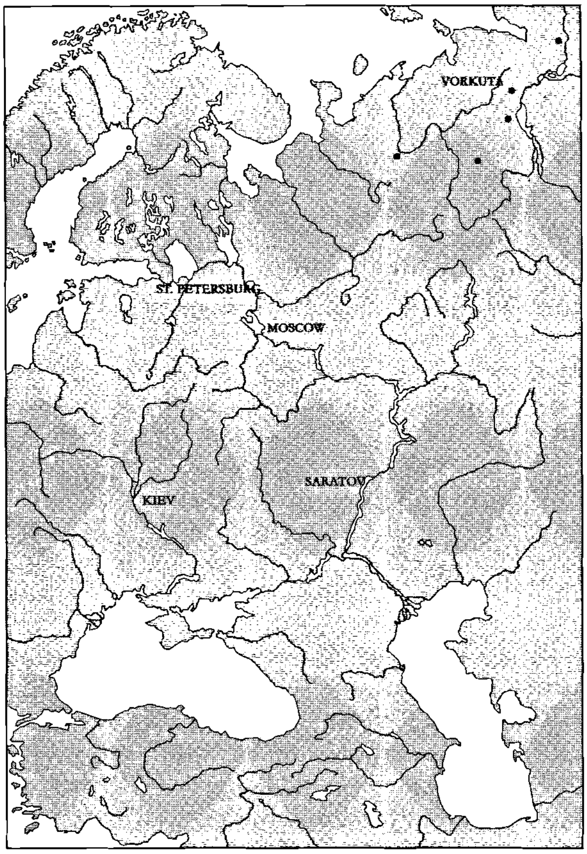
General literature: **Checklists and catalogues** – Breuning (1932): 296. Březina (1994): 20; (1999): 18. Deuve (1994): 109 [160]. Kleinfeld & Schütze (1999): 10. Kryzhanovskij *et al.* (1995): 39 [26]. Lorenz (1998): 73. Turin *et al.* (1993): 19. **Iconography** – Battoni *et al.* (1995): Pl. 10. Ghiretti (1996): 75-76. Imura & Mizusawa (1996): Pl. 10 [72]. Ratti *et al.* (1990): Pl. 13.

Geographical range: Polar Ural, N. Siberia and mountains of S. Siberia (Korobeinikov, 1984, 1987, 1990). **Chorotype**: SIB. **Range characteristics:** EEur(NE)-Sib. **Distribution in Europe (and adjacent areas)**: **Russian Plain** – Restricted to N.E. European Russia, N. and Polar Ural, the W.-most record from Ust'-Tsil'ma at Pechora river (ZIN), known also from the district of Salekhard (ZIN), Neroika Mt. (MPGU) and Shor-Sabia Mt. in the N. Urals (ZIN). Common in S. Yamal Peninsula (Andreeva & Eremin, 1991), from the forest-tundra to the N. taiga.

Subspecies: The only European subspecies is: **a) subsp. septentrionalis** Breuning, 1932. – Polar Ural.

Ecology: Boreo-montane species. In taiga and forest-tundra zones; in the S. inhabiting the alpine zone in the mountains. In S. Yamal, where it is common, it prefers scrubby-moss tundras and scrubby-moss thinned-out larch forests (Andreeva & Eremin, 1991). In Yakutia, it was found on arable land (Shilenkov & Averenskii, 1991). In the polar Ural in stony tundras, in ravines between hills (Korobeinikov, 1984; 1990).


02 015 odoratus (Morphocarabus)



02 015 odoratus

Transect: Chapter 8: T-43.

Biology: **Activity** – No data. **Periodicity** – The species has a 2 year (or longer) life cycle. In S. Yamal, reproduction in spring from June to the first half of July; first hibernation as larva (L3), and young adults appear from the end of July to the middle of August of the following year (Korobeinikov, 1987, 1990). For the Baikal region, a similar pattern can be seen in the data from breeding experiments (Berlov & Berlov, 1984). Copulations were observed in June and early July and oviposition also in June-July (egg size 4.2 x 1.9 mm). Fresh beetles were found in July. The new adults hibernate before they take part in reproduction in the summer of the third year (Berlov & Berlov, 1984; Korobeinikov, *l.c.*). **Food** – no data. **Larva**: Size given by Berlov & Berlov (1984: L1-L3). Food – No data.

Conservation: No data.

02.016. C. (Trachycarabus) perrini
Dejean, 1831 (?= *planus* Géhin, 1855; = *campestris* Fischer von Waldheim, 1822).

General literature: **Checklists and catalogues** – Breuning (1932): 479. Březina (1994): 22; (1999): 21. Deuve (1994): 110 [164]. Kleinfeld & Schütze (1999): 12. Kryzhanovskij *et al.* (1995): 40 [44] (*campestris*). Lorenz (1998): 75.

Turin *et al.* (1993): 19. **Iconography** – Battoni *et al.* (1995): Pl. 10. Ghiretti (1996): 76. Imura & Mizusawa (1996): Pl. 12 [80]. Jakobson (1905): Pl. 4.

Taxonomy: In Březina (1999) *campestris* Fisch., 1822 is treated as a junior homonym of *campestris* Fisch., 1817, and *planus* Géhin, 1885 is treated as valid name. As a result, *planus* is ranked by Březina as a subspecies of *perrini* Dej., 1831.

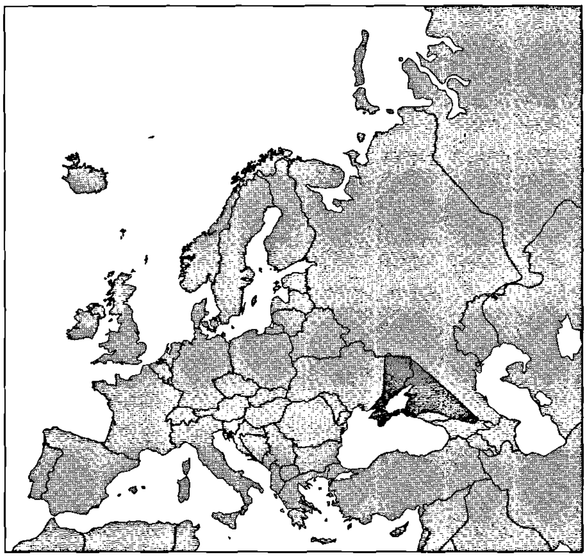
Geographical range: S. Ukraine (including the Crimea), Rostov province and the N. Caucasus. **Chorotype:** CAUC-CRIM. **Range characteristics:** EEur(S). **Distribution in Europe (and adjacent areas)**: **Russian Plain & Caucasus** – Widely distributed in the S. of the Russian Plain between the rivers Dnieper and Don, Crimea, Ciscaucasia and the Caucasus. The N.-most locality 'Kharkov' (Averin, 1938) and the W.-most 'Gerbovets nr. Bendery' (Topchiev, 1970) need confirmation. According to old data from collections, it seems that it was common in the S.-most regions where steppe habitats existed (provinces of Nikolaev, Kherson, Crimea, Zaporozhye, Rostov, Krasnodar, Stavropol – ZIN; IZ; ZM), recently mostly found in the steppe reserves (Strel'tsovskaya Step', Kamennye Mogili, Andreeva Balka, Sukhaya Balka – IZ, coll. V.G. Dolin). Confined to the S. stretch of the steppe zone. In N. Ossetia rare on the Naklono-Ossetinskaya Plain; it does not reach Alaghir (Alekseev, *in litt.*).

Subspecies: Rather variable in appearance and elytral sculpture but not forming distinct geographical races (see note on the questionable subsp. *planus* under *Taxonomy*).

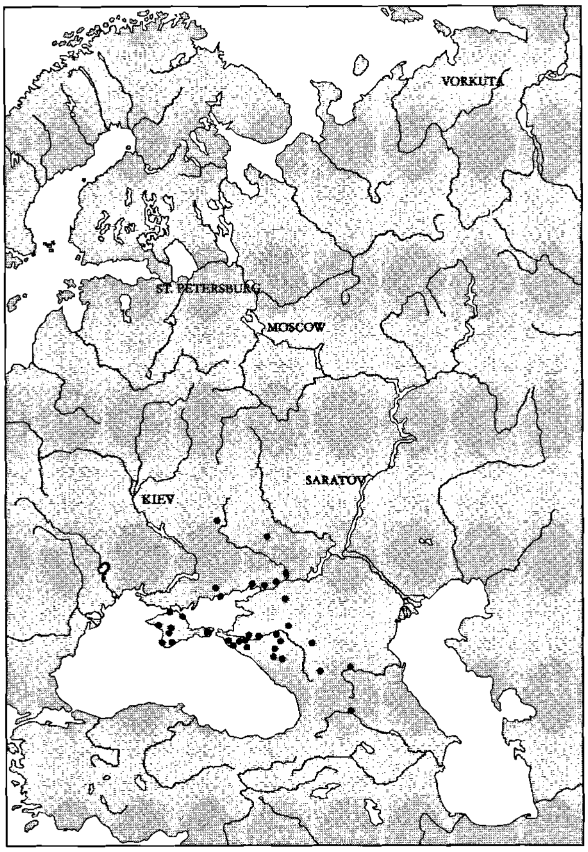
Ecology: Dry steppes; in mountains to 1500 m. In N. Ossetia, very rare in dry steppes and semi-deserts; common in foothills of the Terskii and Sunzhenskii Mts. (Alekseev, *in litt.*).

Transects: Chapter 8: T-57, 60.

Biology: **Activity** – No data. **Periodicity** – No data. **Food** – No data. **Larva**: Described by Sharova (1958: L2-L3). Food – No data.



02 016 perrini (Trachycarabus)



02 016 perrini

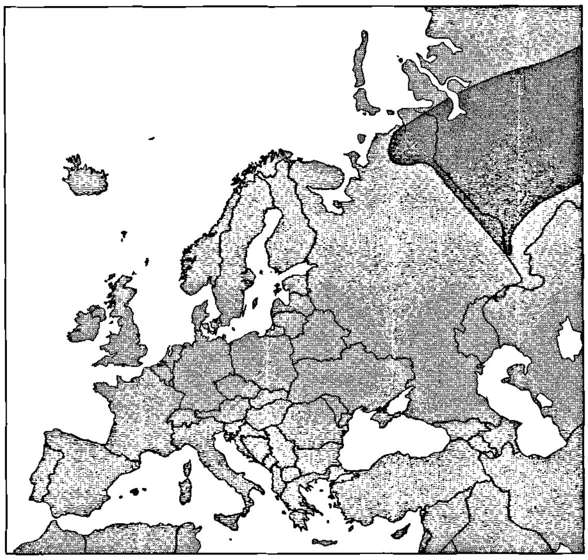
Conservation: The species seems to be confined to natural steppes and is negatively influenced by ploughing.

02.017. C. (Morphocarabus) regalis

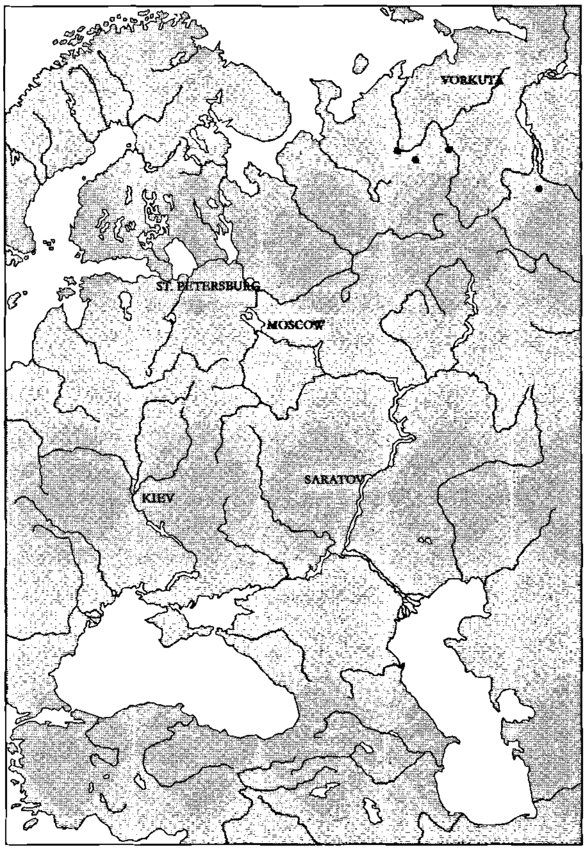
Fischer von Waldheim, 1822.

General literature: Checklists and catalogues – Breuning (1932): 279. Březina (1994): 20; (1999): 18. Deuve (1994): 105 [145]. Kleinfeld & Schütze (1999): 10. Kryzhanovskij *et al.* (1995): 39 [32]. Lorenz (1998): 73. Turin *et al.* (1993): 19. **Iconography** – Ghiretti (1996): 69. Imura & Mizusawa (1996): Pl. 10 [70]. Jakobson (1905): Pl. 4. Ratti *et al.* (1990): Pl. 12.

Geographical range: E. part or European Russia, Siberia in the E. to the river Lena and Lake Baikal; N. Mongolia. **Chorotype:** SIB. **Range characteristics:** EEur(E)-CSib. **Distribution in Europe (and adjacent areas)**: **Russian Plain** – Only in N.E. European Russia, N. and Middle Ural, to the S. to Ekaterinburg province (Kozyrev, 1989) and Bashkiria (Matveev, 1990). It seems to be distributed in the basin of Pechora river (ZIN; Poppius, 1910; 40 km S. of Pechora – MPGU) (the W.-most record from Ust'-Tsil'ma, known also from the Bol'shezemel'skaya Tundra (ZIN) and Shor-Soblya Mt. in the N. Urals (ZIN)), absent however to the N. of the Polar Circle, not in the Polar Ural and S. Yamal Peninsula (Andreeva & Eremin, 1991; Korobeinikov, 1990). From the N. taiga to the mixed-forest zone.



02 017 regalis (Morphocarabus)



02 017 regalis

Subspecies: Except nominative, no subspecies in Europe.

Ecology: Mostly in the taiga zone, inhabiting light forests, meadows and cultivated lands. In Yakutia, it lives in grass-herb forests and meadows with a dense vegetation; sometimes at the edges of arable land (Shilenkov & Averenskii, 1991). In Krasnoturansky Bor (C. Siberia), inhabiting pine forests on N. slopes and interfluvial plains (Anyushin, 1982).

Transects: Chapter 1: I-2.

Biology: **Activity** – No data. **Periodicity** – In the laboratory (Berlov & Berlov, 1997a), copulation was observed from June until early August and oviposition from June until the end of August (egg size 5.3 x 2.2 mm). Juveniles were found in June, which may suggest a two-year development. According to Kozyrev (1989), in the middle Ural hibernating as larvae, but Berlov & Berlov (1984) reported from Baikal region in Siberia, that the species overwinters mainly as adult and probably also as larva. **Food** – No data. **Larva**: Unknown.

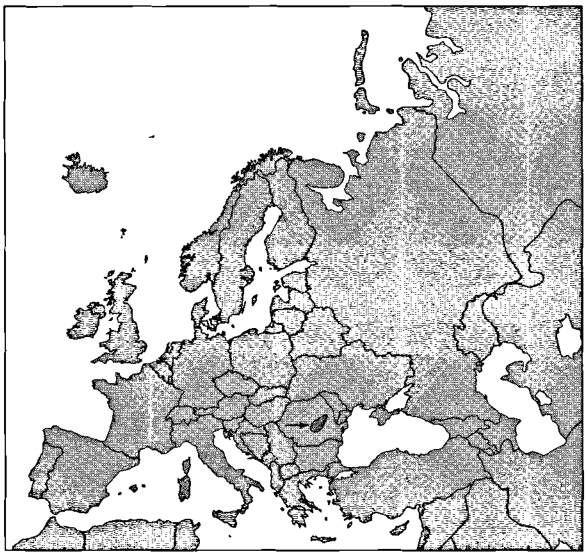
Conservation: Very common in Siberian taiga, not endangered.

02.018. C. (Morphocarabus) rothi
Dejean, 1829

General literature: **Checklists and catalogues** – Breuning (1932): 352. Březina (1994): 20; (1999): 18. Deuve (1994): 104 [144]. Kleinfeld & Schütze (1999): 11. Lorenz (1998): 74. Turin *et al.* (1993): 19. **Iconography** – Battoni *et al.* (1995): Pl. 6-7. Ghiretti (1996): 67-69. Imura & Mizusawa (1996): Pl. 11 [78]. Rautenstrauch (1994): Pl. 9.

Taxonomy: Here taken in the narrow sense. *C. alutensis* is considered a separate species by some workers (Lie, 1999, 2001; Szél, *in litt.*), because the two taxa differ from each other by the 4th primary intervals forming chains and strongly elevated in the case of *alutensis* (*cancellatus*-like character). Moreover, *rothi* occurs in the environments of Olt S.-wards until Turnu roshu (South Carpathians, formerly in Hungary, today in Romania), while *alutensis* is found only S. of the Carpathians (i.e.: near Calimanesti and Ramnicu-Vâlcea in Romania), also along the river Olt.

Geographical range: Endemic species of Romania. **Chorotype**: EEU-CARP. **Range characteristics**: Carp. **Distribution in Europe**: **Romania** (Csiki, 1946; Panin, 1952) – C. Romania: the S. part of the Transylvanian Basin



02 018 rothi (Morphocarabus)

(Targu Mures), Southern Carpathians (Sibiu Mts., Fagaras Mts.), upper and C. course of Olt river valley.

Subspecies: a) subsp. rothi Dejean & Boisduval, 1829 – Sculpture rough, irregular. Rodnei Mts., N. slopes. **b) subsp. alutensis** Savulescu, 1972 – Sculpture regular, primary intervals catenulate, *cancellatus*-like. – Rodnei Mts., S. slopes.

Ecology: It prefers the open (but not completely treeless) wet meadows with more or less dense vegetation. Collected also in gardens and agricultural lands.

Biology: **Activity** – No data. **Periodicity** – No data. **Food** – no data. **Larva**: See Chapter 4. Food – no data.

Conservation: No data.

02.019. C. (Trachycarabus) rybinskii

Reitter, 1896.

General literature: **Checklists and catalogues** – Breuning (1932): 484. Březina (1994): 22; (1999): 22. Deuve (1994): 110 [165]. Kleinfeld & Schütze (1999): 11. Kryzhanovskij *et al.* (1995): 40 [40]. Lorenz (1998): 75. Turin *et al.* (1993): 19. **Iconography** – Battoni *et al.* (1995): Pl. 10. Ghiretti (1996): 77. Imura & Mizusawa (1996): not listed.

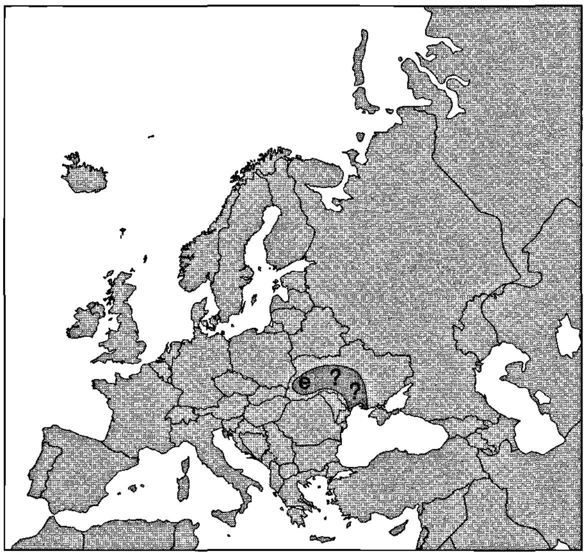
Taxonomy: In Březina (1994) listed as synonym of *C. sibiricus*, subspecies *errans* Fischer von Waldheim; in Březina (1999) and Deuve (1994) as a separate subspecies of *C. sibiricus* Fischer von Waldheim.

Geographical range: Endemic of E. Europe. **Chorotype**: EEU-CARP. **Range characteristics**: EEur(W). **Distribution in Europe**: **Russian Plain** – W. Ukraine: Lvov and Ternopol regions. Very rare and insufficiently known. Recent records missing. Probably extinct.

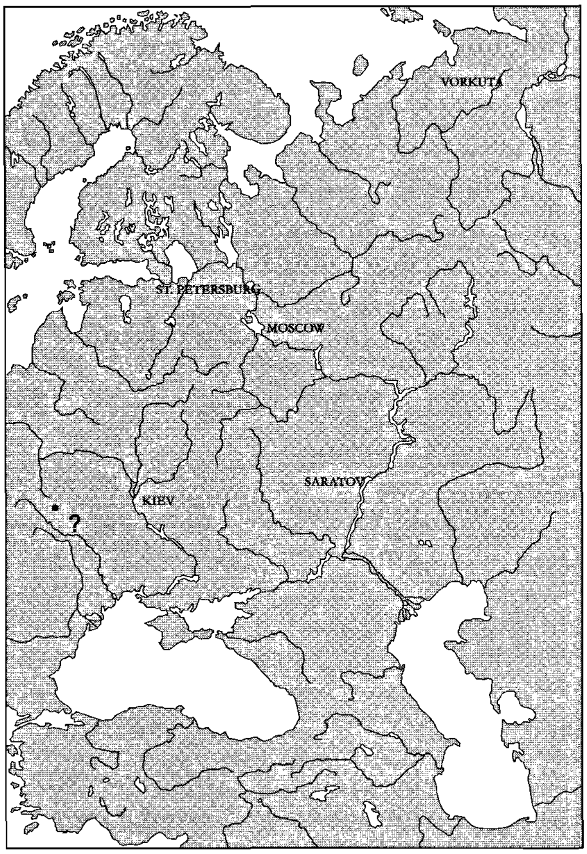
Ecology: No data.

Biology: **Activity** – No data. **Periodicity** – No data. **Food** – No data. **Larva**: Food – No data.

Conservation: No data.



02 019 rybinskii (Trachycarabus)



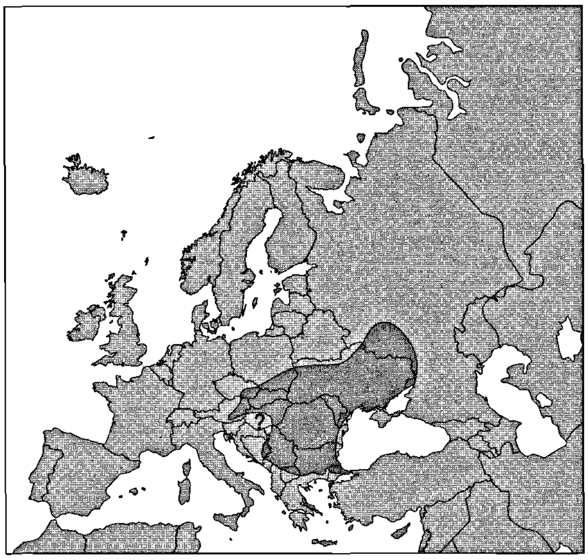
02 019 rybinskii

02.020. C. (Trachycarabus) scabriusculus

Olivier, 1795.

General literature: **Checklists and catalogues** – Breuning (1932): 494. Březina (1994): 22; (1999): 21. Csiki (1946): 149. Deuve (1994): 111 [169]. Kleinfeld & Schütze (1999): 12. Kryzhanovskij *et al.* (1995): 40 [45]. Lorenz (1998): 75. Turin *et al.* (1993): 19. **Iconography** – Battoni *et al.* (1995): Pl. 11. Ghiretti (1996): 78-79. Imura & Mizusawa (1996): Pl. 12 [85]. Jakobson (1905): Pl. 7. Pavicevic & Mesaros (1997): cd-rom. Rautenstrauch (1994): Pl. 23-24.

Geographical range: C. and S.E. European species, reaching from E. Austria, S.E. Czechia, Slovakia, S. Poland to Bosnia, Bulgaria, Ukraine and river Don. **Chorotype**: EEU-SEEU. **Range characteristics**: EEur(W)-CEur-SEEur. **Distribution in Europe**: **Poland** – Recorded from Wyzyna Lubelska, Roztocze, Nizina Sandomierska and Beskid Wschodni in the S.E. **Russian Plain** – S.W. of the Russian Plain, in E. to Don river and Rostov, N. to the line Lutsk – Bryansk (ZIN). The E.-most localities are Dolgorukovo, 50 km S. of Elets (ZIN), and Zernograd, ca 60 km S.E. of Rostov (MPGU). Widely distributed in Ukraine and Moldova, more common in the forest-steppe and steppe zones, in the S. to the coasts of Black and Azov Seas. There is an old specimen in the collection of ZIN labelled with 'Tauria', but the species does not occur in the Crimea (Eidelberg *et al.*, 1988). From the S. of the deciduous forests to the steppe zone. **Moldova** – reported from the



02 020 scabriusculus (Trachycarabus)

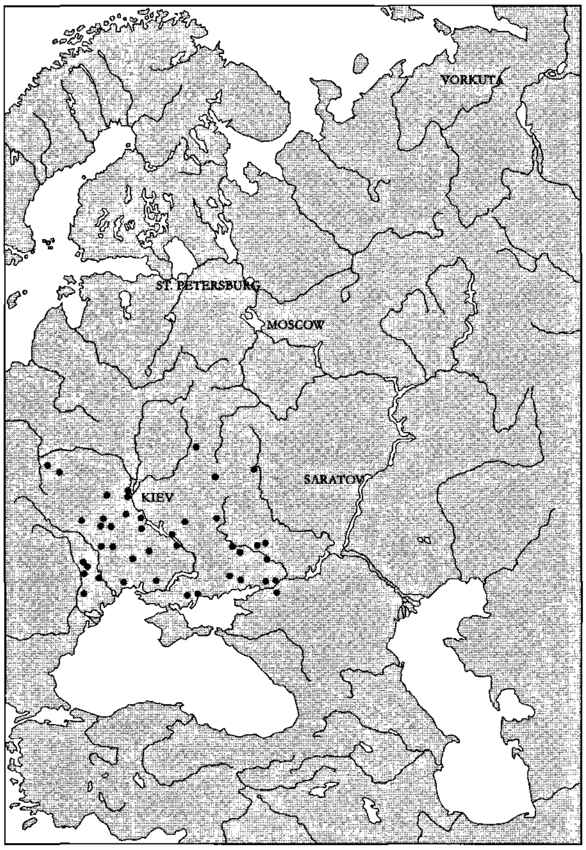
N. as well as from the C. (Kodry Hills) and S. regions (Budzak, S. Moldova, S. Dnestr region). **Czechia & Slovakia** – S. Moravia and S. parts of Slovakia. **Hungary** – Widely distributed throughout the country, most abundant in the hills and mountains, but also in the lowlands. **Romania** – All over the territory, not rare. **Bulgaria** – Widespread throughout the entire territory. **Balkan Peninsula** – Widespread from C. Bosnia, to the Black Sea: Bosnia-Herzegowina, N. (isolated: Srem), C. & S. Serbia, N. and E. Montenegro, N. Macedonia; apparently not in Greece. **Austria** – E. part of the country; restricted to E. Niederösterreich, Steiermark, Burgenland and E. Kärnten; here a seriously endangered species.

Subspecies: **a) subsp. scabriusculus** – Specimens with red femora (*erythropus* Fischer von Waldheim, 1822) are not rare in the Ukraine W. of Dnieper. – Inhabits the main part of the area: C. Europe, including Austria, Czechia, Slovakia, most of Hungary, N. Romania, Moldova, Ukraine, except its E.-most provinces, Lipetzk and Voronezh provinces of Russia. Mostly in forest-steppe or meadow-steppe. **b) subsp. inapertus** Motschulsky, 1850 – E. Ukraine: Kharkov, Lugansk, Donetzk provinces; Russia – Rostov province. Data for the Crimea and Stavropol provinces are incorrect. **c) subsp. lippii** Dejean, 1926 – Present in Hungary but rare, in some places of the E. part of the Great Hungarian Plain (Debrecen, Mezőkovácsháza), Moldova. Throughout the most of Romania especially its W. and C. provinces. **d) subsp. bulgarus** Vacher de Lapouge, 1908 – Balkan peninsula, except its W. part: S. Romania, Serbia, Bosnia, N. Macedonia, Bulgaria, European Turkey, mostly in foothills.

Ecology: A thermophilous, xerophilous and rather eurytopic species of open habitats, steppes, pastures, vineyards and montane grasslands (Hůrka, 1996). Mostly in the lowlands and hills of the forest-steppe zone. In Austria reported from dry and warm areas, in alpine prairies at 2000-3000 m (Mandl, 1956). In Hungary known as a forest-steppe species of hills and mountains, less in the lowlands. Mostly on dolomitic slopes, but also in dry grasslands and in agricultural fields. For the W. area of former Yugoslavia, characterised as praticol-silvicol, occurring in meadows, pastures and deciduous forests of lowlands, hills and mountains (Pavicevic & Mesaros, 1997). In Bulgaria from sea level to 1800 m (Guéorguiev & Guéorguiev, 1995). Often found under stones, heaps of grasses or debris (Du Chatenet, 1986).

Transects: Chapter 8: T-58, 62, 69-70, 72, 75, 78.

Biology: **Activity** – No data. **Periodicity** (Hůrka, 1973) – Reproduction in spring, May-June. Larvae develop rapidly, without diapause, according to data from Hůrka (*l.c.*) who reports that, during breeding experiments, development from L1 to L3 took from mid-end June at a mean temperature of 21.5°C. Fresh animals were observed from the beginning of July onwards (Slovakia). Burmeister (1939) reported that teneral animals appeared in autumn. The development of eggs take about 7 days, L1: 8-11 days and L2: 5-6 days. The young adults are active before they hibernate in soil (Niedl, 1958). Neculiseanu & Matalin (2000) mentioned records (Moldova) from March-April and June-July. **Food** – It is reported to climb plants where it hunts on Scarabaeidae (Coleoptera), e.g. *Amphimallon solstitialis* L. (Burmeister, 1939). In captivity, it accepted minced meat, earthworms, fish and apples. **Larva**: Described by Hůrka (1970: L1-L3). Food – in captivity, chopped mealworms and earthworms.



02 020 scabriusculus

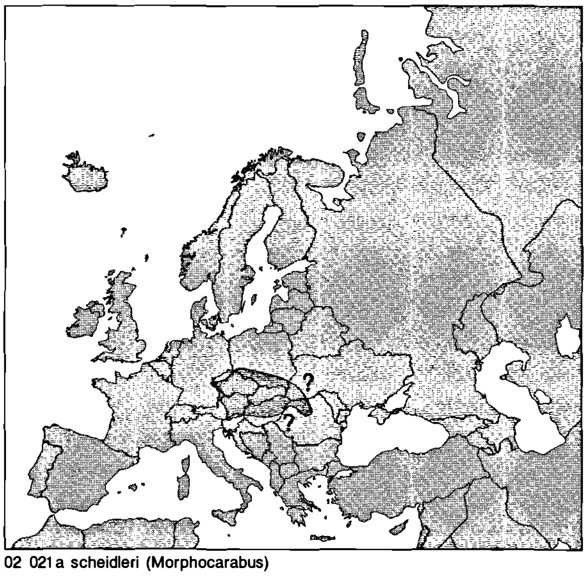
Conservation: Mentioned as endangered in parts of its range, such as for Austria, according to Franz (1983), although not supported by reliable data. Pavicevic & Mesaros (1997) also mention the species as endangered for the Balkan Peninsula.

02.021a. C. (Morphocarabus) scheidleri
Panzer, 1799.

General literature: **Checklists and catalogues** – Breuning (1932): 316. Březina (1994): 21; (1999): 19. Deuve (1994): 103 [143]. Kleinfeld & Schütze (1999): 11. Kryzhanovskij *et al.* (1995): 39 [35]. Lorenz (1998): 74. Turin *et al.* (1993): 19. **Iconography** – Battoni *et al.* (1995): Pl. 3-5. Ghiretti (1996): 63. Imura & Mizusawa (1996): Pl. 11 [79]. Jakobson (1905): Pl. 5. Rautenstrauch (1994): Pl. 4-5.

Taxonomy: In Březina (1994) and Deuve (1994), this taxon has been listed as a subspecies of *C. monilis* Fabricius. Also *C. kollari* Palliardi, *C. versicolor* Frivaldszky and *C. zawadzkii* Kraatz (also listed as subspecies of *C. scheidleri* in Deuve, *l.c.*), are treated as proper species in the present work.

Geographical range: European species. S. Germany (E. Bavaria), E. Austria. Czechia, W. Slovakia, S.W. Poland, W. Hungary. **Chorotype**: EEU-PANN. **Range characteristics**: CEur. **Distribution in Europe**: **Germany** – Only mentioned for Bayern; endangered. **Poland** – Restricted to the S.W. and C.S. territory. **Russian Plain** – Ukranian Carpathians (Kryzhanovskij *et al.* 1995), however, this occurrence might be based on the presence of some of its 'subspecies' *kollari* or *zawadzkii*, regarded as valid species in the present work. **Czechia & Slovakia** – All over the territory, locally common. **Hungary** – Widely distributed and in some places not rare; mainly in the higher parts. **Romania** – Occurring in the W. and the N. (Maramures). **Austria** – Not mentioned for Vorarlberg and Tirol, but widely distributed in the C. and E. (Salzburg, Oberösterreich, Niederösterreich, Steiermark, Burgenland, Kärnten, Osttirol); possibly an endangered species.


02 021a scheidleri (Morphocarabus)

Subspecies: **a) subsp. scheidleri** – E. Bavaria; reaching S. and E. Bohemia, S. Moravia and S.W. Slovakia; S. Poland, S. and E. Austria (except true mountane regions), W. Hungary. Mostly in open landscapes. In the forests of E. Austria one can find large (30-35 mm) individuals (m. *floriani* Penecke, 1905). *Note*: Mařan (1947) characterises the form *C. scheidleri tucinensis* Mařan, as a pleistocene race, dating from the Riss-Würm interglacial. **b) subsp. preysleri** Duftschmid, 1812 – N.E. Austria. The form from Slovakia and N. Hungary was described as *pseudopreyssleri* Breuning, 1932. **c) subsp. helleri** Ganglbauer, 1892 – N.E. Bohemia, N. half of Moravia and Slovak Republik: Bratislava, Nitra, Trenczen (Hůrka, 1996), N. Hungary, ?W. Ukraine. **d) subsp. styriacus** Kraatz, 1887 (= *pannonicus* Csiki, 1906) – S.E. Austria: Styria; N. Slovenia, W. Hungary. A typical Hungarian form is *C. scheidleri jucundus* Csiki, 1906, living in forests near Budapest (Buda and Pilis Mts.). *C. scheidleri distinguendus* Csiki, 1906 lives in open, wet meadows of lowland near Budapest.

Ecology: Predominantly a forest species, but in the lowlands also in field habitats, meadows, vineyards and pastures. From lowland to montane forests, although Hoffmann (1907) mentioned it only from lowlands up to 300 m. It often occurs along rivers and smaller streams (Hůrka, 1996; Mandl, 1956). In Hungary it inhabits mainly forests (beech) in the hills and mountains but also, less, in hardwood river forests; probably a vicariant of *C. zawadzkii*.

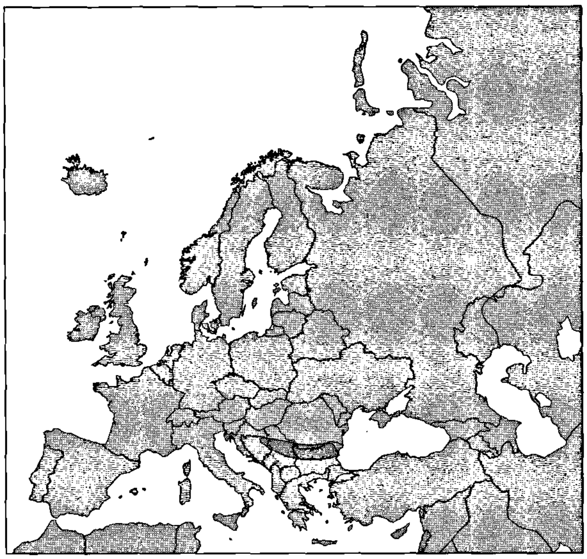
Transects: Chapter 8: T-34, 75, 77.

Biology: **Activity** – Adults and larvae are active at night (Arndt; Assmann, *pers. observ.*). **Periodicity** – Seasonal activity and reproduction similar to that of *C. monilis*. In the E. part of Burgenland (Austria), females in oogenesis were found in September (chorionised oozytes detected by ovary section – Assmann, *pers. observ.*). **Food** – In the field, earthworms and snails, caterpillars of *Agrotis* (Lepidoptera, Noctuidae). In captivity, also caterpillars without hairs, larvae of *Leptinotarsa decemlineata* (Say) (Coleoptera, Chrysomelidae), chopped snails, various insect larvae, minced meat, fish and apples (Larochelle, 1990). **Larva**: Described by Vacher de Lapouge (1907: L2-L3; 1929: L1-L3), Arndt (1982, 1985) and key: Arndt (1985, 1991b). Food – earthworms in the laboratory (Arndt, *pers. observ.*).

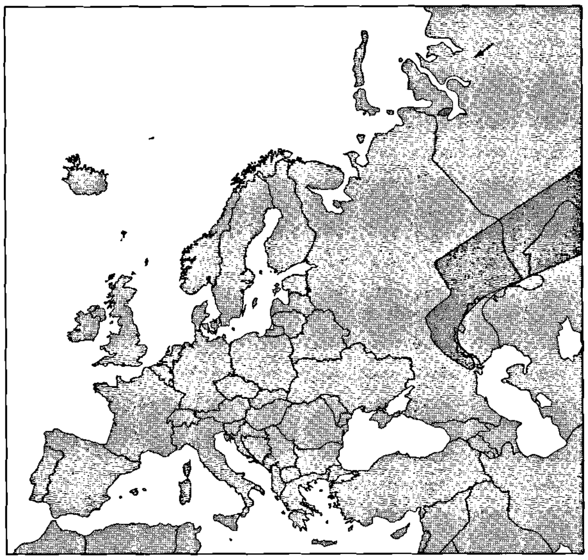
Conservation: Endangered in part of its range; listed in the Red List of Austria as a potentially endangered species (Franz, 1983). This is however, not supported by reliable data.

02.021b. C. (Morphocarabus) versicolor
E. Frivaldszky, 1835.

General literature: **Checklists and catalogues** – Breuning (1932): 316. Březina (1994): 21; (1999): 20. Deuve (1994): 102 [143]. Kleinfeld & Schütze (1999): 11. Lorenz (1998): 75.



02 021b versicolor (Morphocarabus)



02 022 sibiricus (Trachycarabus)

Turin *et al.* (1993): 19 (listed as a subspecies of *C. scheidleri*). **Iconography** – Battoni *et al.* (1995): Pl. 6. Ghiretti (1996): 64. Imura & Mizusawa (1996): not listed. Pavicevic & Mesaros (1997): cd-rom. Rautenstrauch (1994): Pl. 8-9.

Taxonomy: By Březina (1994, 1999) and Deuve (1994) listed as a subspecies of *C. scheidleri* Panzer, 1799 (*monilis* Fabricius). By Kleinfeld & Schütze (1999) listed as a synonym of *C. simulator* Kraatz, 1876.

Geographical range: Endemic species of the Balkan Peninsula: E. Serbia, N.E. Bosnia, Bulgaria (except in the S.). **Chorotype:** SEU-DIBA. **Range characteristics:** Balk. **Distribution in Europe**: **Bulgaria** – Reported from the Danube Plain and a few localities in the Stara Planina (Peak Kom, Sliven, Peak Chumerna). **Balkan Peninsula** – N.E. Bosnia (Bjelasnica), E. Serbia (Tekia, Mt. Krs).

Subspecies: See remarks in the *Key to the adults* (p. 84). **a) subsp. versicolor** – Bulgaria (Stara Planina). **b) subsp. simulator** Kraatz, 1876 – N.E. Serbia (Maidanpek, Kucaina, Milanovac).

Ecology: Mostly in foothills. For E. Serbia characterised as a silvicol species, inhabiting deciduous forests in hilly regions (Pavicevic & Mesaros, 1997). In Bulgaria from 50 to 1800 m (Gueorguiev & Gueorguiev, 1995).

Transect: Chapter 8: T-69.

Biology: **Activity** – No data. **Periodicity** – No data. **Food** – No data. **Larva**: Food – No data.

Conservation: According to Pavicevic & Mesaros (1997), all forms that occur in E. Serbia are critically endangered, however no evidence has been given.

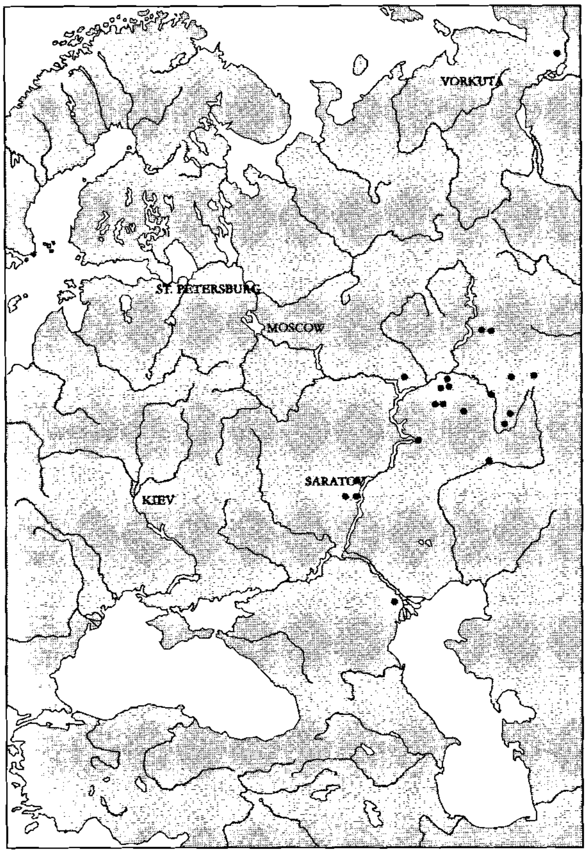
02.022. C. (Trachycarabus) sibiricus
Fischer von Waldheim, 1822.

General literature: **Checklists and catalogues** – Breuning (1932): 482. Březina (1994): 22; (1999): 22. Deuve (1994): 110 [165]. Kleinfeld & Schütze (1999): 12. Kryzhanovskij *et al.* (1995): 40 [50]. Lorenz (1998): 75. Turin *et al.* (1993): 19. **Iconography** – Battoni *et al.* (1995): Pl. 10-11. Ghiretti (1996): 77-78. Imura & Mizusawa (1996): Pl. 12 [83]. Rautenstrauch (1994): Pl. 22.

Taxonomy: A few taxa have been listed as subspecies of *C. sibiricus* in most literature, but treated as proper species in the present work: *C. bosphoranus*, *C. errans* and *C. haeres*. Recently a new species has been described from the S. Ural: *Carabus (Trachycarabus) kolosovi* Zinovjev, 1997. The type specimens were described from Bashkiria, Duvan District (Mesyagutovo village, bank of Ai River). After having examined the type specimens, we expect it to be synonymised with *C. sibiricus karelini* (Makarov, *pers. comm.*)

Geographical range: From E. Russia, through Siberia to Jakutia and Irkutsk province, N.E. Kazakhstan, W. Mongolia. **Chorotype:** SIB. **Range characteristics:** EEur(E)-CSib. **Distribution in Europe (and adjacent areas)**: **Russian Plain** – E. European Russia and Ural, in the W. bordered by the Volga river; further to the W., it is replaced by the related species *C. haeres*. Reported from the Tartar republic (Pavlovka nr. Bugul'ma – ZIN; Muslyumovo – ZM) and also known from the environs of Samara (Utrobina, 1964) and Saratov (IZ). With a scattered distribution in Bashkiria (Ufa, Sulli – ZIN; Ai-River nr. Mesyagutovo – Zinovjev, 1991; Bashkir and Shulgan-Tash reserves – Koz'minykh, *in litt.*), as well as in the provinces of Perm' (Preduralye and Spasskaya Gora reserves – Koz'minykh, *in litt.*) and Chelyabinsk (Kusinski Zavod – ZIN). An isolated locality in the N., beyond the Polar Circle (S. Yamal Peninsula), was recently recorded by Andreeva & Eremin (1990). A species of the forest-steppe and steppe zones.

Subspecies: For Europe we mention only: **a) subsp. karelini** Fischer von Waldheim, 1830 – Transvolga region – Bugul'ma, provinces of Kazan, Samara and Saratov (ZIN; Utrobina, 1964).



02 022 sibiricus

Ecology: Forest-steppe and grassland steppe. In the S. Yamal peninsula, where it is an uncommon species, usually on grassy herb patches within fields with boulder (Andreeva & Eremin, 1991); in Yakutia it inhabits floodland (river) meadows and steppe-like patches (Shilenkov & Averenskii, 1991).

Transects: Chapter 1: I-2; Chapter 8: T-43, 46-47.

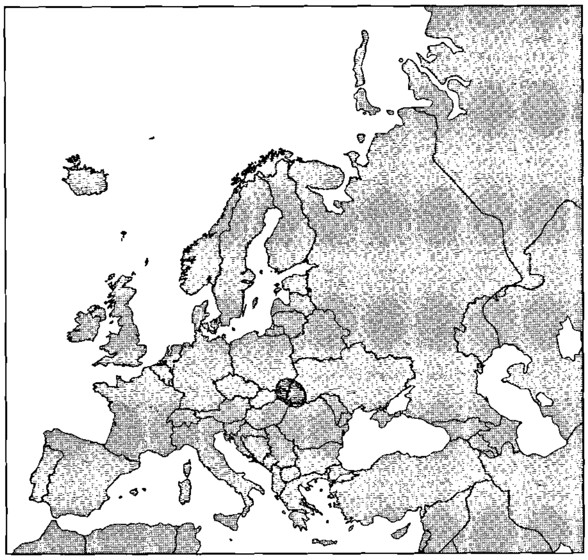
Biology: **Activity** – No data. **Periodicity** – No data. **Food** – No data. **Larva**: Food – No data.

Conservation: No data.

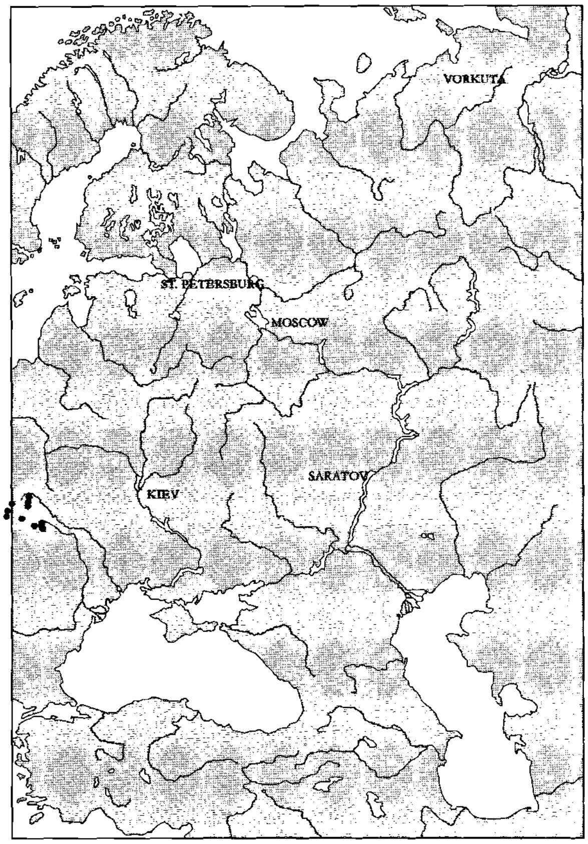
02.023a. C. (Morphocarabus) zawadzkii
Kraatz, 1854.

General literature: **Checklists and catalogues** – Breuning (1932): 322. Březina (1994): 21; (1999): 20. Csiki (1946): 142. Deuve (1994): 104 [143]. Kleinfeld & Schütze (1999): 11. Kryzhanovskij *et al.* (1995): 39 [36]. Lorenz (1998): 75. Turin *et al.* (1993): 19. **Iconography** – Battoni *et al.* (1995): Pl. 5. Ghiretti (1996): 67. Imura & Mizusawa (1996): Pl. 11 [79]. Rautenstrauch (1994): Pl. 5-6.

Taxonomy: By several authors (e.g. Březina, 1994; Deuve, 1994; Pulpán & Hůrka, 1993), treated as a subspecies of *C. scheidleri* Panzer, or *C. monilis* Fabricius). Examination of the internal sac of *C. z. seriatissimus* Reitter, 1896 proves that it is possibly a good species, and not a subspecies. Localities of *Carabus z. seriatissimus* are the S. part of Maramures Mts. and Rodnei Mts. (Szél, *in litt.*).



02 023 zawadzkii (Morphocarabus)



02 023 zawadzkii

Geographical range: A localised species, distribution stretching along the N. Carpathians. **Chorotype:** EEU-CARP. **Range characteristics:** Carp(N). **Distribution in Europe**: **Poland** (Burakowski, 1973): Most probably absent from this territory. **Russian Plain** – W. Ukraine (districts of Lvov, Ivano-Frankovsk, Uzhgorod, Tshernovtsy): Ukrainian Carpathians and the adjacent regions (E. Beskids anf Ung County (= Komitat Ung), known from several localities in the provinces of Zakarpatye, L'vov (IZ; ZM; MPGU; Ponomarchuk, 1956; Rizun, 1991). **Slovakia** – E.-most part of Slovak Republik. **Hungary** – Very limited distribution in the montane forests of N.E. Hungary: Zemplén Mts., Cserhát Mts. and the water-meadow forests and wet meadows of the rivers Hernád and Bodrog. **Romania** – N.-most part of Romania, Maramures; Komitat Ung.

Subspecies: Individuals from a restricted area (E. Slovakia; vicinity of Uzhgorod), with more pronounced intervals, were described as subsp. *ronayi* Csiki, 1906. In Hungary the form *C. zawadzkii zawadzkii* lives in Zemplén Mts. and along the Bodrog River, while *C. zawadzkii ronayi* Csiki, 1906 inhabits the Cserehát Mts. and borders of the Hernád River. See note on questionable subsp. *seriatissimus* under *Taxonomy*.

Ecology: Predominantly a forest species of lowlands hills, foothills and middle montane altitudes (Hûrka, 1996).

Transects: Chapter 8: T-76.

Biology: **Activity** – No data. **Periodicity** – No data. **Food** – No data. **Larva**: Some morphological remarks have been given by Stiprajs (1961: L3). Food – No data.

Conservation: No data.

02.023b. C. (Morphocarabus) zherichini

Shilenkov, 1990.

General literature: **Checklists and catalogues** – Březina (1999): 21. Kleinfeld & Schütze (1999): 11. Kryzhanovskij *et al.* (1995): 39 [30]. Lorenz (1998): 73.

Geographical range: *C. zherichini* Shilenkov 1990, inhabiting vast areas of N. Siberia, is recently recorded also from the Polar Urals and with a distribution pattern that is quite similar to *C. odoratus, C. truncaticollis, C. ermaki* etc., it can probably be treated as a representative of European fauna. Maybe only a subspecies of *C. mestscherjakowi* Lutshnik, 1924. **Chorotype:** SIB. **Range characteristics:** EEur(E)-Sib.

No further data.

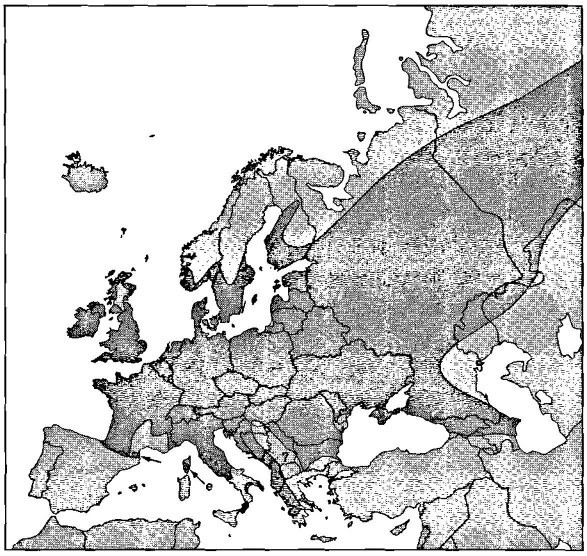
03. CARABUS S.STR.

03.001. C. (Carabus) granulatus

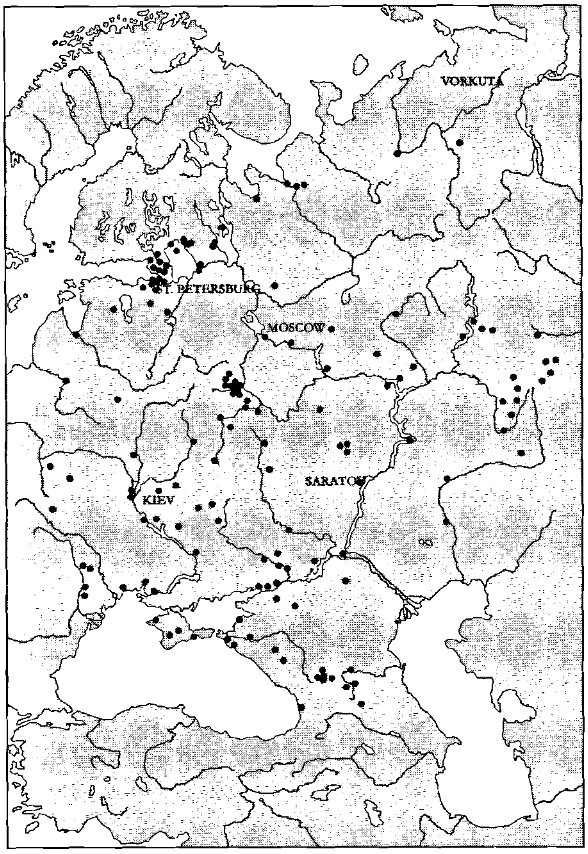
Linnaeus, 1758.

General literature: **Checklists and catalogues** – Breuning (1933): 525. Březina (1994): 15; (1999): 8. Deuve (1994): 89 [116]. Kleinfeld & Schütze (1999): 7. Kryzhanovskij *et al.* (1995): 37 [12]. Lorenz (1998): 69. Turin *et al.* (1993): 20. **Iconography** – Casale *et al.* (1982): fig. 101. Forel & Leplat (1995): Pl. 1; (1998): fig. 1. Ghiretti (1996): 40-41. Imura & Mizusawa (1996): Pl. 2 [21]. Jakobson (1905): Pl. 5. Pavicevic & Mesaros (1997): cd-rom. Rautenstrauch (1994): Pl. 25.

Geographical range: Asiatic-European species. Distributed throughout Europe and N. Asia, from Ireland and N. Spain to E. Siberia, Corean Peninsula, Sakhalin, Mongolia, N. and E. China (environments of Beijing) and Japan (Hokkaido, Honshu); in the N. to N. limits of forest zone, in the S. to N. Spain, S. Italy, Greece, Anatolia, the N. Caucasus, S.E. Kazakhstan. Introduced and established in N. America. **Chorotype:** ASE. **Range characteristics:** Eur-Sib-EAsi. **Distribution in Europe (and adjacent areas): Fennoscandia** – Norway, along the S. coast, up to Bergen; Sweden, not rare in the S. districts, up to about 63°N; Finland, relatively abundant and widely distributed in the S., scattered to Oulu area in the N. **Denmark** – All over the country, common. **British Isles** – Widespread and abundant, especially in Ireland (commonest species); only few (older) records from the E, highlands of Scotland. **Netherlands** – One of the commonest and most widespread species. **Belgium** – Same as for the Netherlands. **Germany** – Widespread and common; in all Germany the most abundant species in moist, open biotopes. **Poland** – Common throughout the territory. **Baltic** – Reported for all countries. **Byelorussia** – Recorded in all provinces, but nevertheless it seems to be uncommon. **Russian Plain** – All of European Russia, the N. range limit reaches 65°N and goes through S. Karelia (Petrozavodsk), Onega, Archangelsk, Pechora and Ust' Tsil'ma river basins (ZIN: Poppius, 1905). To the S., *C. granulatus* penetrates along rivers into the steppe zone (S. Moldova, Odessa, Kherson, Crimea, Provinces of Rostov, Volgograd, Uralsk and Orenbrug – ZIN, ZM), and is also known from Ciscaucasia and Caucasus. A polyzonal species. **Moldova** – In the S., the floodplain forests E. of the Prut river, and in the Kodry Hills. **Czechia & Slovakia** – All over the territory and common. **Hungary & Romania** – Distributed across the territory, ranging from frequent to common. **Bulgaria** – Mainly in the W. and C. part of the country, including the Thracian lowland and lowlands in the S.W. (Boboshevsko-Simitly valley, Sandanski-Petric valley; also along the Black-Sea coast



03 001 granulatus (Carabus s.str.)



03 001 granulatus

(Kranevo, Kamchiya, Vasiliko, Arkutino). **Balkan Peninsula** – Especially in the lowlands and hills, covering vast areas in Slovenia, W. and E. Croatia, Dalmatia, C. Bosnia, Serbia as well as few occurrences in S.E. Macedonia and in S. Herzegovina; but absent from a major part of the C. montane territory; Greece including the Peloponnisos. **Austria** – Widespread throughout the territory. **Switzerland** – On the N. side of the Alps, including the hills and montane zone of the Jura; also in the S. valleys of Graubünden and Tessin. Absent fron the C. Alps and valleys in this area. **Italy** – Distributed in N. Italy and a large part of the C.W. peninsula; very rare in S. Italy: Calabria. **France** – Most of France; in the mainland only absent from the Mediterranean 'olive' area in the S. In Rhône-Alpes not widespread, obviously restricted to the river areas. Also present in the E. humid regions of Corsica; absent from C. and W. Corsica. **Iberian Peninsula** – Only in the N.E. of Cataluña: High plateau of the river Fluviá, not in the lowland Mediterranean part.

Subspecies: **a) subsp. granulatus** – Femora black, sometimes red. Inhabits the most of the species area in Europe from Scotland, Norway, N. Russia (Murmansk, Arkhangelsk provinces) to N. Spain (Cataluña), S. France (except lowlands of Provence), Switzerland, Croatia, N. Bosnia, Bulgaria, S. Ukraine. In W. England transitional populations to subsp. *hibernicus*, in S. Alps to subsp. *interstitialis*. **b) subsp. hibernicus** Lindroth, 1956 – Ireland. **c) subsp. interstitialis** Duftschmid, 1812 – Italy, Corsica, S.E. Alps in Austria, W. part of Balkan peninsula from Dalmatia to Albania. – Large individuals from Albania have been described as *miridita* Apfelbeck, 1901, they form no geographical race. Similar specimens can be found on Corsica too (*corsicus* Born). **d) aetolicus** Schaum 1857 – N. Greece. A form with the characters of this subspecies has recently been discovered in W. Turkey, and in S.E. Italy (Puglia and Basilicata). **e) subsp. crimeensis** Breuning, 1933 – Foothills and mountains of the Crimea. **f) subsp. parallelus** Faldermann, 1835 – Russia: Lower Volga, N. Caucasus, in lowlands and foothills. **g) subsp. duarius** Fischer von Waldheim, 1844 – E. part of the European Russia (Samara, Orenburg provinces, S. Ural); W. and C. Siberia (in forest-steppe and taiga zones), Kazakhstan, environments of the foothills of Tian-Shan in Central Asia, N.W. Mongolia. **h) subsp. calabricus** Spettoli & Vigna Taglianti, 2001 – S. Italy, Calabria, montane forests in Serre Calabre region.

Ecology: In general, a very eurytopic species of moist to wet habitats (Sharova, 1984; Matveev, 1988). Rather hygrophilous, living mostly in lowlands or foothills sometimes up to the montane region, e.g. in the Swiss Jura (Hûrka, 1996; Marggi, 1992) but not in alpine habitats (Koch, 1989). According to Hoffmann (1907), in C. Europe mainly from lowlands up to 800 m. In Italy as a rule from 0 to 1500 m, sometimes (very rare) up to 2000 m (Casale *et al.,* 1982). In Ireland on a broad variety of wet soils, widespread and common (Anderson *et al.,* 2000). Generally inhabiting moist to wet, not too dense forests and meadows, also along shores of lakes and rivers and it is often abundant on cultivated land, especially in wet grasslands (Basedow *et al.*, 1976; Lindroth, 1985; Thiele, 1977). In Germany and the Netherlands a dominant species in flood plain and water meadows along lowland rivers such as the Rhine (Jarmer, 1973; Thiele, 1977; Turin, 2000). Tolerant of inundation (Blumenthal, 1981); in a meadow in N.W. Germany, the beetles were able to survive an inundation of six months during hibernation (Fuellhaes, 1997). In the Rhône-Alpes (Coulon *et al.*, 2000) where it reaches the S.E. of the distribution in France, restricted to the humid and cool lowland-river areas in the N. of this region. Besides this, also present in isolated populations in some valleys, sometimes up to 1000 m. In Hungary everywhere in soft-wood river forests, wet meadows and reedland. Mostly absent from Mediterranean landscapes. In former Yugoslavia also quite eurytopic, inhabiting swampy areas, meadows, deciduous forests, generally confined to lowlands and hills. In Bulgaria from 0 to 1000 m (Guéorguiev & Guéorguiev, 1995). The habitat preferences are similar in Yakutia where it also inhabits wet meadows, scrub along rivers and irrigated arable land (Shilenkov & Averenskii (1991). In Moscow province in humid deciduous or mixed forests, wet fields, swampy places and agricultural habitats (Fedorenko, 1988). In the Ukraine in floodland forests (Petrusenko, 1971). Weber (1965b) carried out an experiment, which indicated that the animals could detect a moisture gradient with availability of 5 antennal segments, but not when the antennae were reduced to 4 segments. In the Netherlands, it has no special preference for coastal habitats (Turin, 1991, 2000). *Note*: Like several other carabid species (e.g. *Pterostichus (Melanius) madidus* f. *concinus*), *C. granulatus* has a form with red legs (f. *rufofemoratus*). It occurs in the Netherlands especially on the island of Texel and in the W. part of Denmark (Bangsholt, 1983); in Germany, it is also widely distributed (Barner, 1937; Mletzko, 1970). The distribution of the proportion of red-legged individuals in a population is probably linked to climatic factors, possibly to a cooler and more maritime climate; compare e.g. with the study of the distribution of leg-colour morphs (form *concinnus* Sturm) of *Steropus (Steropidius) madidus* (Fabricius, 1775) (Terrell-Nield, 1990), and with the form *rufifemoratus* Stephens of *Platysma (Melanius) nigrita* (Paykull, 1790) (Anderson, 1993).

Transects: Chapter 1: I-1, 2; Chapter 8: T-04-07, 09, 12-14, 16-18, 20-33, 35-36, 38-41, 44, 46-48, 50, 54-58, 60-61, 63-64, 68-69, 71-73, 75-81, 83-85 and 88-90.

Biology: **Activity** – It is reported to be active both during the night and the day (Thiele & Weber, 1968; Hůrka, 1973) but in the N. probably predominantly nocturnal (Thiele, 1970; Lindroth, 1985; see also under *Dispersal power*). Also Drees & Huk (2000) reported a mainly nocturnal, especially active during the first hours of darkness, but also substantial diurnal activity with significantly higher activity of females in the afternoon. For both sexes there was an almost linear correlation with temperature, with an equal threshold of about 8°C. **Periodicity** – In general, it can be characterised as a spring breeder without larval, but with an obligatory adult diapause. Adults are most active in May-June; the hibernated adults become active and copulate from the end of March onwards. Oviposition (appr. 25-40 eggs – Huk & Kühne, 2000; Scherney, 1959), size 4 x 1 mm in separate cells in the soil, from May to August, but mainly during May-June (Arndt, 1989; Forel & Leplat, 1995; Hůrka, 1973). Berlov & Berlov (1984) found for the Baikal region egg sizes of 4.2 x 1.8 mm. The eggs hatch after one week. Larvae occur from May onwards and remain active during the summer. L1 occurs from May to August, with maximum numbers in July, L2/L3 from May to September, with maximum numbers in August-September (Hůrka, *l.c.*). Development to adult, without larval diapause, takes 7 to 9 weeks (40-55 days, including prepupal stage of 6-10 days after Sturani, 1962). Development of eggs: 6-12 days, L1: 7-10 days, L2: 7-12 days, L3: 16-21 days and the pupation lasts 7-12 days. Similar figures were found during laboratory experiments in the Baikal region (Berlov & Berlov, 1997b; 1984). Teneral animals can be found from July to the end of September. According to Hůrka (*l.c.*), some young adults hibernate in their pupal chambers, but most are active for a period (especially in the forests) before they hibernate from October onwards under bark or at the foot of trees often near water, often aggregated in very large groups (Arndt, 1989; Casale *et al.*, 1982; Lindroth, 1974; 1985; Scherney, 1961; Turin, 2000). Many old adults hibernate and reproduce for a second time. Population-genetic studies in Westphalia (Germany) revealed a large variation in local abundance and reproduction during the year as well as recurring fragmentation of a population (separation of local groups) and subsequent reassembly during hibernation (Horstmann & Reimann, *in litt.*). **Food** (Larochelle, 1990; Casale *et al.*, 1982) – Snails, worms and insect larvae, such as of *Leptinotarsa decemlineata* (Coleoptera, Chrysomelidae), pupae of ants. Also adults belonging to Coleoptera (e.g. Carabidae and Staphylinidae), carrion of snails and frogs. In captivity, they also accept caterpillars, raw meat, live snails, chopped mealworms (Coleoptera, *Tenebrio*), gingerbread, bread soaked in sugared milk or water, and even plain bread. In Poland it was observed to predate most frequently earthworms and, if available, leatherjackets (Diptera, Tipulidae), but to avoid wireworms (Coleoptera, Elateridae) (Lukasiewicz, 1996). Feeding has also been investigated by serobiological methods (Gryuntal & Sergeeva, 1987), revealing that no preferences could be shown for the 10 tested groups of soil inhabiting fauna. **Larva** – Described by Schiödte (1876: L3), Vacher de Lapouge (1905: L2), Verhoeff (1917: L1-L3) and key: Arndt (1985, 1991b). Food – Earthworms in the laboratory and in the field, in general the same as the adult (Arndt, *pers. observ.*). The larva moves very well and is able to cross water easily during rainfall (Forel & Leplat, *l.c.*). **Dispersal power**: Wing dimorphic; like most *Carabus* species regularly unwinged in most parts of its distribution, but long winged individuals occur in C. European populations in low numbers, and according to Lindroth (1985), flight observations are available from C. Europe (Henseler, 1938). Neculiseanu & Matalin (2000) reported flight records to light from Moldova, Vigna Taglianti & Rossetto (in: Casale *et al.*, 1982) from Italy and Larochelle (1975) from Quebec. In Germany, winged specimens have mainly been found in the lowlands (Horion, 1941). However, most specimens examined in N.W. and N.C. Europe, showed no functional wings and no developed flight muscles (Bangsholt, 1983; Desender, 1989; Tietze, 1963). The species is able to swim short distances (Casale *et al.*, 1982). It has a good locomotory power. In the laboratory, Mossakowski & Stier (1983) recorded a maximum speed of 20 cm/sec, and Scherney (1960c) measured an effective movement in the field of 120 m in 10 days. The results from experiments in fenced enclosures showed that locomotory activity for both sexes started at ca 8°C (at ground level) and increased with temperature to a maximum at ca 20°C (Drees & Huk, 2000). Moreover, the males showed significantly higher activity and more directed walk than the females, whereas the latter appeared to be more active during day time, especially the afternoon. The directed walk of the (almost exclusively nocturnal) males can be explained by active search for females leading to a regular change of location. The females with the partly diurnal activity, lay eggs during the resting period of the males, without interruption by individuals that want to copulate (Drees & Huk, *l.c.*). The species moves and climbs well in dense vegetation (Heydemann, 1957); in moist woodland also on trees and many observations on *Alnus* trunks (Assmann, *pers. observ.*). It was the first *Carabus* species that successfully invaded the newly reclaimed polders in the C. Netherlands (Haeck, 1971), where it first colonised the (older) dikes that already surrounded the polder.

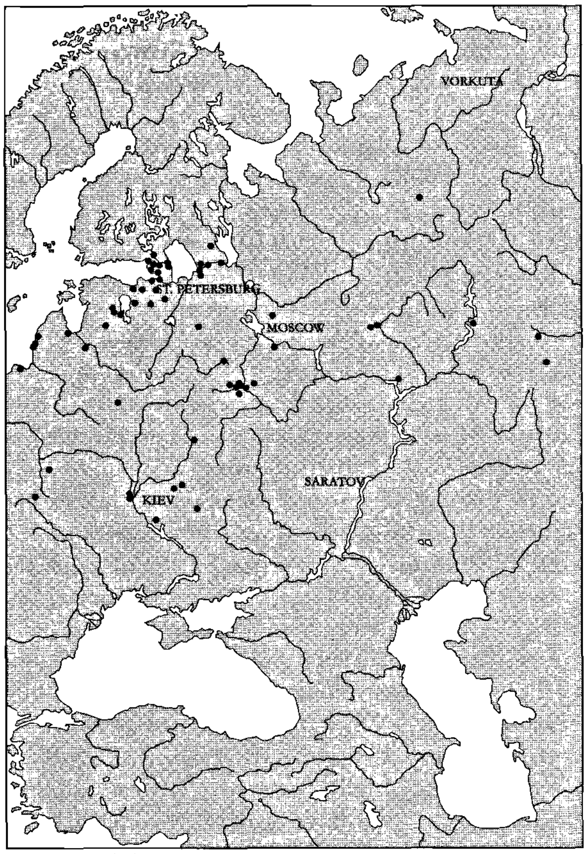
Conservation: The species is, within its area of distribution, one of the commonest of all *Carabus* and generally not endangered. In many N.W. European regions, the numbers of records increased recently and it is probably expanding (Desender & Turin, 1989). It seems to be tolerant of agricultural fertilisation and pollution; in Byelorussia (Mogilev district) it was one of the few survivors on a heavily chemically polluted field (Chumakov, 1986). This applies also to the situation in Italy. However, it is declining in some over-cultivated habitats and furthermore it is very localised in S.-most of its distribution (S.E. Italy, Puglia and N. Greece). In general, the removal of old trees and trunks, in which the species hibernates, will probably affect it adversely. Pavicevic & Mesaros consider the form *paludicola* Müller from S. Dalmatia and S. Herzegovina, as vulnerable.

03.002. C. (Carabus) menetriesi
Hummel, 1827.

General literature: **Checklists and catalogues** – Breuning (1933): 544. Březina (1994): 15; (1999): 9. Deuve (1994): 90 [117]. Kleinfeld & Schütze (1999): 7. Kryzhanovskij *et al.* (1995): 38 [15]. Lorenz (1998): 69. Turin *et al.* (1993): 20. **Iconography** – Ghiretti (1996): 42. Imura & Mizusawa (1996): Pl. 2 [19]. Rautenstrauch (1994): Pl. 25.

Taxonomy: A single female was recorded from S.W. Bulgaria (Belasitsa Mt.) possibly belonging to an undescribed subspecies according to Guéorguiev & Guéorguiev (1995). The locality, however, seems very doubtful from a faunistic point of view.

03 002 menetriesi (Carabus s.str.)



03 002 menetriesi

Geographical range: European species. In C. Europe a relict of the last glacial period. N.E. Europe and the W.-most part of Siberia, and isolated populations in the mountains of C. Europe and doubtfully in W. Bulgaria. **Chorotype:** EEU. **Range characteristics:** CEur-EEur(NC)-WSib. **Distribution in Europe (and adjacent areas)**: **Fennoscandia**: Extreme S.E. Finland, Karelia (Du Chatenet, 1986). **Germany** – Mentioned as an extremely endangered species for Mecklenburg-Vorpommern, Sachsen and Bayern. Several populations are currently known from SE Bavaria (Bayerischer Wald) and S Bavaria (pre-alpine morainic area), another population from Mecklenburg-Vorpommern (Peenetal); the situation in Saxony (Hermannsdorfer Wiesen, see Nüssler, 1969; Arndt, 1989) is not cleared yet, because the last record dated from 1980 (Trautner and Tolke, *pers. comm.*). **Poland** – Scattered throughout the E. part of the country, not in the S. montane area. **Baltic** (Stiprajs, 1961; Spuris, 1983) – Scattered occurrences in all three countries. **Byelorussia** – In most of the W. territory. **Russian Plain** – N. to Vyborg district, near Finnish border; Karelia, near river Svir. The middle stretch of European Russia, from S. Karelia and Komi (62-63°N) to C. Ukraine (50°N) and Middle Urals. More common in the N.W. regions of the Russian Plain (including Estonia, Lithuania and Latvia).

Known also from Byelorussia (Berezina reserve – Khot'ko *et al.,* 1989), N.W. Ukraine (old records, not found in the last 50 years – Rizun, *in litt.*) and C. Ukraine, in the S. to the provinces of Poltava (Zolotonosha, Domontovo – Kieseritsky, 1915; ZIN) and Sumy (Trostyanets Forestry – Smetanin, 1981). The S. range margin coincides with the line Poltava – Kazan' (IZ) – Ekaterinburg. Distributed from the middle taiga subzone to the N. forest-steppe. **Czechia & Slovakia** – Bohemian and Saxonian mountains (Sumava and Krusne Hory Mts.); two confirmed records from Slovakia. **Bulgaria** – One doubtful record from Belasitsa Mt. (ssp. *pacholei*; needs confirmation, see under *Taxonomy*). **Austria** – Mentioned from N. Oberösterreich – N. Niederösterreich and Tirol, indicated as a glacial relict. The population in Tirol is probably extinct.

Subspecies: The following subspecies have a restricted distribution within Europe: **a) subsp. menetriesi** – Main area of distribution: N. and C. parts of European Russia (to the S. part of the taiga zone), W. Siberia (Tyumen province), N.E. Ukraine, Baltic States, Poland, N.W.-Slovakia. In general fairly rare. **b) subsp. pacholei** Sokolar, 1911 – C. Europe: S. and N.E. Czechia, Saxony, Mecklenburg-Vorpommern, E. and S.E. Bavaria, E. and N. Austria, scattered, rare and most probably endangered; one doubtful record from Bulgaria, Belasitsa.

Biogeography: Relict of the last glacial period, with several isolated populations in C. European mountains in Bavarian and Bohemian forests, as well as in N.E. Austria (Du Chatenet, 1986; Hůrka, 1996; Mandl, 1956-1958).

Ecology: The species lives in wooded *Sphagnum* bogs and forest swamps on alluvial and dilluvial grounds, often in more or less isolated populations. *C. menetriesi pacholei* is, according to our current knowledge, restricted to transition mires and quaking bogs and – only few records until now – raised bogs (Trautner, *pers. comm.*) In part also in montane forest and grassland bogs and swamps (mostly with *Sphagnum*). It is a pronouncedly hygrophilous species with a behaviour that is reported to resemble that of *C. clatratus* (Lindroth, 1985), but according to recent records, restricted to transition mires and quaking bogs (Trautner, *pers. comm.*).

Transects: Chapter 1: I-2; Chapter 8: T-40 and 44.

Biology: In general, the biology is very similar to that of *C. granulatus* (Arndt, 1989). **Activity** – At least partly diurnal (Nüsler, 1969). **Periodicity** (Hůrka, 1973) – Reproduction takes place in spring or summer depending on altitude. Oviposition from April onwards to the end of July; highest activity of the adults in Latvia in May (Stiprajs, 1961). The duration of oviposition can be up to a month per female during which period 10-25 eggs can be laid (Nüssler, 1969; Stiprajs, 1961). No observations on larvae are available from the field. From various breeding experiments, Hůrka (*l.c.*) concludes that the development takes place without larval diapause and he mentions the following data: eggs: 4-8 days, L1: 6-7 days, L2 and L3: both 8-9 days and the pupae: 10-11 days; all together 45-50 days. Teneral animals occur in autumn and most of them are active before they hibernate in tree trunks or under mosses. According to Nüssler (1969), the adults do not live much longer than 10 weeks after the winter period. **Food** – Diptera, Plecoptera and Trichoptera and small slugs (Larochelle, 1990; Nüssler, 1969). **Larva** – Described by Hůrka (1970, 1971a: L1-L3). Food – Earthworms (Nüssler, *l.c.*).

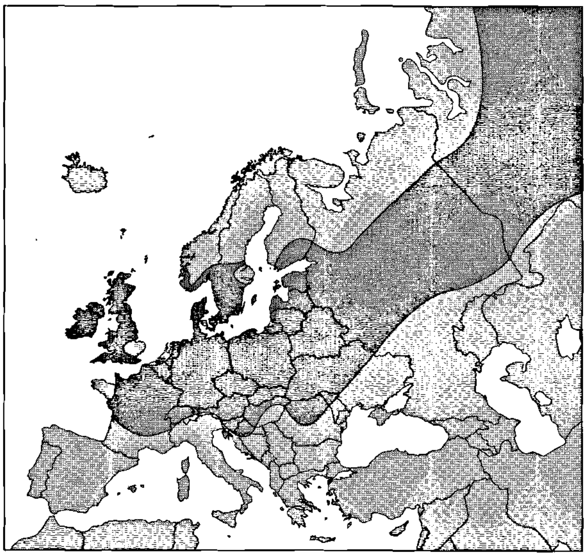
Conservation: According to the impression of several collectors, it is declining in many areas, probably, partly, due to the same reasons as for *C. clatratus*, which also inhabits wetlands. Especially the subsp. *pacholei* Sokolar, seems to be seriously endangered in its C. European area. In contrast to *C. clatratus*, it might be especially endangered because it often inhabits very restricted and local habitat patches (Arndt, *pers. observ.*).

04. EUCARABUS GÉHIN, 1885

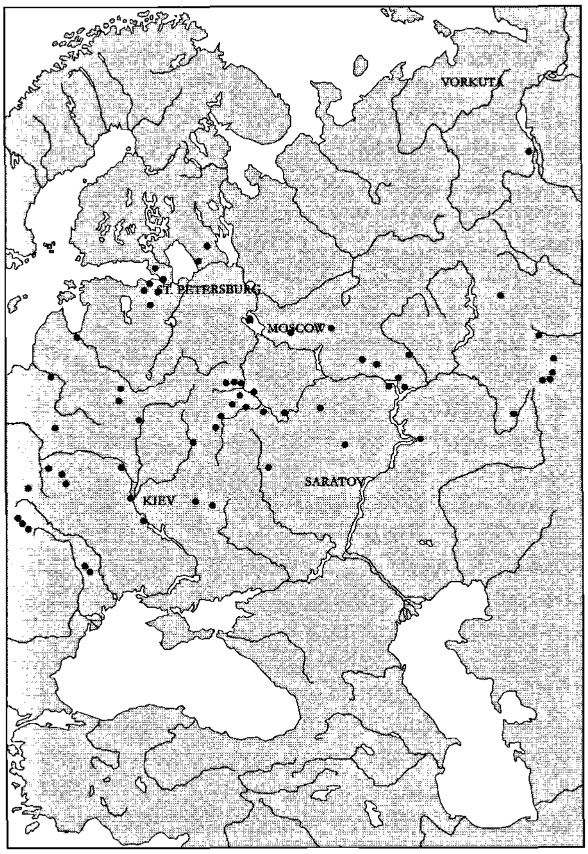
04.001. C. (Eucarabus) arvensis

Herbst, 1784 (= *arcencis* auct.).

Note: It is already for a long time unsure what is the right name for this species. In the original description the name *arcensis* has been published. However soon after, Paykull (1790) mentioned it as *arvensis* and this was widely accepted, e.g. in the important works of Sturm (1815), Heer (1837, 1841), Redtenbacher (1858), Ganglbauer (1892), Heyden *et al.* (1906), Reitter (1908), Breuning (1923), Vacher de Lapouge (1929-1932), Jeannel (1941) and Casale *et al.* (1982). In his Coleopterorum Catalogus, Csiki (1927) was perhaps one of the first to mention it *arcensis* again. However the note of Lindroth (1974) in his key to the British carabids: '*arcensis* no doubt printer's error', seemed to established the situation and also in the world list of Deuve (1994) the name *arvensis* was accepted.



04 001 arvensis (Eucarabus)



04 001 arvensis

However, the recent lists of Březina (1999) and Lorenz (1998) use *arcensis* again. Because it is clear that *arcensis* is not correct in Latin and should be regarded as *nomen lapsus*, we consider the most widely used *arvensis* as the valid name for this species, and are in this supported by the Code of Zoological Nomenclature, edition 1999, art. 32.5.1, valid since 1st of January, 2001.

General literature: **Checklists and catalogues** – Breuning (1932): 382. Březina (1994): 16; (1999): 7. Deuve (1994): 92 [123]. Kleinfeld & Schütze (1999): 7. Kryzhanovskij *et al.* (1995): 35 [3]. Lorenz (1998): 70. Turin *et al.* (1993): 20. **Iconography** – Casale *et al.* (1982): fig. 94. Forel & Leplat (1995): Pl. 1-2. Ghiretti (1996): 43-46. Imura & Mizusawa (1996): Pl. 2 [16]. Jakobson (1905): Pl. 5. Pavicevic & Mesaros (1997): cd-rom. Rautenstrauch (1994): Pl. 17-18.

Geographical range: Palaearctic species. Distributed throughout N. and C. Europe and Siberia to Sakhalin, N. China, Korea, Kurils and N. Japan. **Chorotype:** SIE (polyzonal – Sharova *et al.,* 1984). **Range characteristics:** Eur-Sib-EAsi. **Distribution in Europe (and adjacent areas): Fennoscandia** – Norway: only in the S.; Sweden: to about 61°N but rare; Finland: rare in the S. **Denmark** – Mainly E. Jutland and Zealand, local and rare. **British Isles** – Ireland, widespread in the upland, but local, most common in the N. (Anderson *et al.,* 2000). Most of Britain: England, N. to Cumberland, Wales, Scotland, especially occurring in the upland and wetter parts, locally not uncommon. **Netherlands** – Mainly in the C. and E. part of the country, locally common. **Belgium** – Seriously declined in N. and C.; now almost restricted to the E. **Germany** – A scattered distribution is reported, covering all of the territory; in general uncommon and for many regions, vulnerable or endangered. **Poland** – Distributed throughout the territory. **Baltic** – Occurring in all three countries. **Byelorussia** – All over the territory. **Russian Plain** – Distributed from the Ukrainian Carpathians, through the middle stretch of European Russia to the C. Urals, N.E. European Russia and Polar Ural. N. to the Svir province, to about 61°N in the W. (Vyborg and Petrozawodsk provinces), and 65-67°N in the E. (two old records from Pechora Basin (Lindroth, 1945, after Sahlberg, 1898) and Polar Ural – ZIN), S. to the line Kishinev – Kanev – Les-na-Vorskle Reserve – Voronezh Reserve – Penza – Samara – Bashkir Reserve, which coincides with the S. margin of the forest-steppe zone. Known from S Karelia (Uzenbaev *et al.,* 1986, ZIN), Latvia (Gartsiems – Stiprajs, 1961; ZM), Lithuania (Yurbarkas – ZIN), Estonia (Riga – Haberman, 1968; ZIN), Byelorussia (Berezina, Belovezha, Pripyat and Nalibokskaya pushcha reserves, Mogilev, Ushachi – Khot'ko *et al.,* 1989; Chumakov, 1987, 1990; ZIN; MPGU), N. and C. Ukraine (Transcarpathia and Carpathians – Ponomarchuk, 1956; Rizun, 1991; Markovichi – ZIN; Rostochye Reserve – Zagaikevich *et al.,* 1989; Kanev Reserve – MPGU), N. and C. Moldova (Kipriyani – Adashkevich *et al.,* 1973, Kishinev – MPGU), several localities from the provinces of St. Petersburg, Vologda (Darwin Reserve – Matveeva *et al.,* 1984), Kostroma, Vyatka, Moscow, Kaluga, Ryazan', Bryansk, Belgorod, Voronezh, Penza, republics of Komi (Koz'minykh, *in litt.*), Mordovia (Mordov Reserve – Feoktistov, 1979), Mari (Svetlyi nr. Yoshkar-Ola – MPGU), and Tartar (Kazan' – IZ, ZM; Raifa Reserve – Zherebtsov, 1979). In Cisuarlia and Urals known from Bashkiria (Bashkir Reserve – Koz'minykh, *in litt.*), Perm' (Basegi Reserve – Koz'minykh *et al.,* 1991b; Spas-Barda – Shilenkov & Voronov, 1973), Ekaterinburg (ZIN), Chelyabinsk (Bol'shoi Kuyash Lake – Field report of the Institute of Evolutinary Morphology & Ecology, Moscow, 1981; Chelyabinsk – IERZ; Il'men Reserve – Lagunov, 1982; Misyash – Voronin, 1987). There is a doubtful record from the Caucasus (Teberda, Uriup River – ZIN). From the S. taiga subzone to the S. limits of the mixed forests, isolated also in the forest-steppe. **Czechia & Slovakia** – All of territory, locally common. **Hungary** – Sporadically found in the mountains. **Romania** – C. and C.E. Romania (generally distributed in the E. and S. Carpathians and in Transylvanian Mts.). **Balkan Peninsula** – Restricted to the N.; Slovenia (Julian Alps, Prekmurje, Pohorje) and an isolated occurrence in E. Croatia (Slavonia). **Austria** – Reported from nearly all parts of the country. **Switzerland** – In the Jura from Geneva (where it has declined heavily; formerly common but no records for 80 years) to Soloturn (montane); near Basel (hills) and in the Kalkalpen from Schrattenfluf to the Walensee (sualpine to alpine). **Italy** – Restricted to the N./N.E. mountains; Venetia and Venetia Tridentina (a record from the frontier Piedmont-France (Monginevro) has to be confirmed). **France** – Reported from the larger part of the territory, but mostly uncommon. It is absent from Bretagne and the area S. of the line La Rochelle (Atlantic coast) – Nice.

Subspecies: a) subsp. arvensis – Germany (except its S.W. parts), Austria (except the Alps), N. Czechia, Poland, Fennoscandia, Baltic States, N. and C. Russia. In the E. of Volga, some populations have very short lobes at the hind angles of the pronotum (*baschkiricus* Breuning, 1932); they form the transition to the Siberian subsp. *conciliator* Fischer von Walheim, 1822. W. Hungary (Sopron Mts., Kőszeg Mts., Őrség and Bakony Mts.). **b) subsp. noricus** Sokolar, 1910 – Jura, N. and E. Alps to S.E. Austria and N.E. Italy, mountains of Czechia; mostly alpine meadows above 1800 m. **c) subsp. carpathus** Born, 1902 – S. Alps, Carpathian Mts. of N. Moravia, entire Slovakia, S. Poland, Romania, Ukraine; also in the lowlands of Ukraine to Kharkov province. N. Hungary (Mátra Mts. and Zemplén Mts.) **d) subsp. venetianus** Bernau, 1914 – fully isolated geographically: S.E. Alps in N.E. Italy ('Alpi e Prealpi Venete, Venezia Tridentina') and S.W. Slovenia. **e) subsp. sylvaticus** Dejean, 1826 – British Isles, N. and C.E. France (also in Rhône-Alpes), Belgium, Netherlands, S.W. Germany, W. Switzerland. In the mountains of S.E. France, several isolated populations have been described as distinct subspecies (*jarrigei* Colas, 1971; *thebaudi* Colas, 1971). Quite distinct specimens from the Cévennes, have been described as *costalis* Vacher de Lapouge, 1908.

Ecology: Characterised as a xero-thermophilic species that occurs on sandy or peaty soil by many authors, in the N. part of its area of distribution a very typical, often dominant species of heath vegetations (Koch, 1992; Mossakowski, 1970b; Thiele, 1977). According to Hoffmann (1907), in C. Europe mainly from 300 to 2000 m. In N.W. Europe (British Isles, Netherlands, Denmark, Scandinavia) usually in rather dry and open habitats such as *Calluna* heaths, sandy grasslands, often with scattered (pine) trees, but also in thin forests and especially forest clearings (Lindroth, 1974, 1985; Turin *et al.,* 1991). In N. Germany, it prefers wet heathlands and peat bogs, overgrown with *Sphagnum* (Mossakowski 1970b; Assmann, 1983). In N. Ireland, primarily montane, but also on the Atlantic heaths of Donegal (Anderson *et al.,* 2000). In E. and S. Europe predominantly in forest habitats, including forest edges, clearings and scrub communities (Stiprajs, 1961; Petrusenko, 1971; Zherebtsov, 1979; Du Chatenet, 1986), less frequently in open habitats and heath vegetation; at high altitudes in the C. and E. and in the S. Alps of Italy in alpine pastures (2000 m: Casale *et al,* 1982) also in alpine pastures and steppes in Slovakia (Hůrka, 1973, 1996; Arndt, 1989). For Switzerland, it was reported from quite different habitats: a) in the Jura up to 1600 m from poor meadows, b) near Basel especially from forested hills, and in the C. Alps (Kalkalpen) from alpine habitats, up to 2100 m and higher (Marggi, 1992). In Hungary first of all a species of montane coniferous forests (Bazziano-Abietum prealpinum, Piceetum abietis, Genisto nervatae-Pinetum), but also in Carici brizoidis-Alnetum as well as in open meadows. In the Moscow province, mostly in coniferous forests (spruce and pine), rarely in oak forests (Fedorenko, 1988). Shilenkov & Averenskii (1991) report the species (ssp. *conciliator*) for Yakutia as inhabiting places near water basins and wet herb meadows, which differ considerably from the habitat preferences in W. Europe. Some of the various habitat preferences are clearly related to particular subspecies.

Transects: Chapter 1: I-1, 2; Chapter 8: T-04-09, 11, 13-17, 21, 23-28, 30-31, 33-35, 38-40, 45, 55, 58, 73, 75-76, 79 and 89-90.

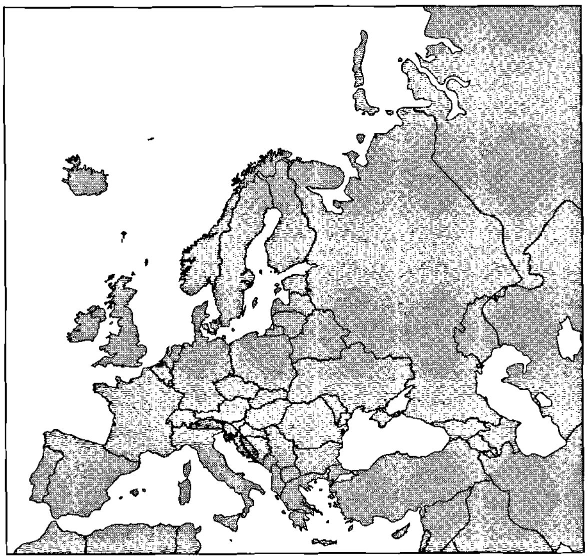
Biology: Activity – It is reported to be active during the night and day (diurnal activity about 70%: Lauterbach, 1970; Van der Ent, *pers. comm.*; about 22%: Grüm, 1966). Mainly day active (> 70%, Van der Ent, *pers. comm.*). **Periodicity** – An early species, reproduction in spring, larval development in summer and hibernation as imago; this pattern holds for most parts of Europe (Sturani, 1962; Hůrka, 1973; Arndt, 1989; Kozyrev, 1989; Turin, 2000). The females lay ca 25 eggs (size: 4 x 1 mm) in a period of ca. 10 days after copulation in spring and early summer: April-May (at lower altitudes) to June-July (in the mountains). Stiprajs (1961) observed that, in captivity, females can have fertile eggs in their ovaries from April onwards. Development of larvae takes only a few weeks, they occur, depending on altitude, from May to August. The larvae remain, without diapause, active at the soil surface, especially during sunshine (Den Boer, 1977). Pupae occur in July-August, occasionally by June. Most of the young adults emerge in early autumn (August-September) and are active until hibernation takes place (Arndt, 1989; Casale, 1982). In two N.W. German populations, the beetles caught in late summer/autumn (after period of oogenesis) were, except for very few specimens, young adults (mostly newly hatched). In the following spring, before oogenesis starts, however, the proportion of old adults (showing *corpus luteum*) was about 30-40 %. Therefore, a dormancy of many months (from the end of the oogenesis period in June/July to April of the next year) has to be assumed for the old adults (results from ovary sections: Storre *et al.,* 1996). Larvae developing in late summer, hibernate probably as L3 and pupate next spring (Hůrka, 1973). The development lasts about 2-2.5 months (Denmark: Larsson, 1939), whereas Stiprajs (*l.c.*), refering to his rearing experiments, states the following periods: development of eggs 9-12 days, L1 7-8 days, L2 7-8 days, L3 8 days and the pupa 8-11 days, in total 41-43 days. For S. Europe, Sturani (1962) mentions 30 days for development of larvae. Hibernation in N. Germany, mainly under mosses in the soil, in S. Germany often aggregated under bark (Blumenthal, 1981). **Food** – In the field, larvae of *Agrotis* (Lepidoptera, Noctuidae) and snails (e.g. *Helix arbustorum*). In captivity, it accepted earthworms, caterpillars, raw meat, minced meat, crushed snails, fruits (apples), ginger bread and bread soaked in sugared milk (Larochelle, 1990). It disliked myriapods, larvae of elaterids (Coleoptera, Elateridae) and Araneae; but could eat 25-75% of its own weight of earthworms (Pankevitch, 1978). Feeding has also been investigated by serobiological methods (Gryuntal & Sergeeva, 1987), revealing that no dear preferences could be shown to 10 tested main groups of soil invertebrates. **Larva**: Described by Vacher de Lapouge (1907: L1-L3), Hůrka (1971b) and key: Arndt (1985, 1991b). Food – in captivity the same as the adults; also chopped mealworms (Larochelle, *l.c.*). **Dispersal power** – Van der Ent (1990) investigated a Dutch heathland, and showed a mean adult dispersal of 6.5 m per day, effectively resulting in an average (theoretical) displacement (relocation) of 140 m during the yearly period of activity.

Conservation: In N.W. Europe (Belgium, Netherlands and Denmark), a declining species (Desender & Turin, 1989), most probably due to nutrient deposition (by rain) on poor soils in heathland and subsequent domination of grasses (*Deschampsia*). Management by means of periodic removal (perhaps also accidentally by fire) of the upper layer of heathland, overgrown by grasses, can be of help for survival of populations, if performed in a step by step program. The beetle declined after sod cutting in a Dutch heathland and was seemingly absent for a period of 4 years but increased subsequently (Den Boer & Van Dijk, 1994). A dramatic increase in catching rate was found by the authors after burning (from 0 to 478 and 299 individuals, respectively, in the two following years). By Van der Ent (1990) it was calculated that the minimum area for longterm survival of populations should be at least 60 ha. More research has to be done for an effective conservation program. In S. areas (Alps) very localised, but not endangered (high altitude), populations can be found.

04.002. C. (Eucarabus) catenulatus
Scopoli, 1763 (= *catenatus* Panzer, 1805).

General literature: **Checklists and catalogues** – Breuning (1932): 367; Březina (1995): 17; (1999): 9. Deuve (1994): 96 [135]. Kleinfeld & Schütze (1999): 8. Lorenz (1998): 70. Turin *et al.* (1993): 20. **Iconography** – Casale *et al.* (1982): fig. 95. Ghiretti (1996): 52-53. Imura & Mizusawa (1996): Pl. 3 [24]. Jakobson (1905): Pl. 5. Pavicevic & Mesaro (1997): cd-rom. Rautenstrauch (1994): Pl. 14.

Geographical range: S.E. European species; N.E. Italy, S.E. Austria, N.W. part of Balkan Peninsula. **Chorotype:** SEU-CADI. **Range characteristics:** Alpi-Dina. **Distribution in Europe**: **Balkan Peninsula** – Istria, Slovenia, W. Croatia (Kapela and Velebit Mts., Dalmatian coast), W. and S. Bosnia to Herzegowina. **Switzerland** – Few recent records exist from the S.-most point of Tessin, near Chiasso. **Italy** – Restricted to the C.N. and N.E. Alps and Prealps (Lombardia, Venetia, Venetia Tridentina, Venetia Giulia).



04 002 catenulatus (Eucarabus)

Subspecies: Pavicevic & Mesaros (1997) recognise 4 subspecies. Two subspecies have been treated here: **a) subsp. catenulatus** – N.C. to N.E. Italy (to the W. to the Como lake), S. Switzerland (Tessin), Slovenia, N.W. Croatia (except its Adriatic part), Bosnia, Herzegovina. **b) subsp. fontanellae** Reitter, 1897 – Croatia: Velebit Mts., Dalmatian shore and adjacent islands.

Ecology: In forests from lowland to subalpine zone (1500 m – Burmeister, 1939), especially habitats situated on calcareous or sandy soil (Casale *et al.*, 1982; Marggi, 1992). According to Hoffmann (1907), in C. Europe mainly between 500 and 1200 m. According to Du Chatenet (1986) and Magistretti (1965), up to 2500 m. At lower altitudes sometimes in forest clearings. Pavicevic & Mesaros (1997) described it as prati-silvicol in the Balkan Peninsula, where it occurs in meadows and forests in the coastal area, and in forests and alpine pastures in the montane areas.

Transects: Chapter 8: T-74 and 81.

Biology: **Activity** – Mostly nocturnal, but sometimes diurnal (Du Chatenet, 1986; Assmann, *pers. observ.*). **Periodicity** (Hůrka, 1973) – Probably a spring occurring species at lower altitudes and summer breeder at high altitudes. Adults were mostly reported from the end of April to November; most abundant in June-July; Sturani (1962) reported adult activity from February until October. A larva was recorded in March (Burmeister, 1939). Hibernating adults can be found in soil and mosses, less often in old tree trunks (Casale, *pers. observ.* in many localities; Du Chatenet, 1986). Sturani (1962) reports the following data from rearing: development of eggs (size 3.5 x 1.5 mm) lasting 9-

12 days, larva (all stages) 30 days, without larval diapause. **Food** – In the field, snails. In captivity also earthworms, caterpillars, crushed snails, raw meat, fruits, bread soaked in sugared water. **Larva**: Described by Sturani (1962), Hůrka (1971b) and Raynaud (1976). Food – In captivity same as adults.

Conservation: Common, sometimes very abundant, not endangered.

04.003a. C. (Eucarabus) cristoforii

Spence, 1821.

General literature: **Checklists and catalogues** – Breuning (1932): 380. Březina (1994): 31; (1999): 41. Deuve (1994): 129 [224]. Kleinfeld & Schütze (1999): 19. Lorenz (1998): 84. Turin *et al.* (1993): 21. **Iconography** – Forel & Leplat (1995): Pl. 11; (1998): fig. 21-23. Ghiretti (1996): 109. Imura & Mizusawa (1996): Pl. 29 [37]. Rautenstrauch (1994): Pl. 16.

Taxonomy: Included in the subgenus *Autocarabus* (= *Tachypus*) auct. by Deuve (1991), Lorenz (1998) and Březina (1999), and in *Eucarabus* by some others.

Geographical range: Endemic species of the C. Pyrenees. **Chorotype**: WEU-PYRE. **Range characteristics**: Iber(NE). **Distribution in Europe**: **France** – Distributed exclusively in the C. Pyrenees from Lac de Laurenti (Aude) to Soum de Nère (Hautes Pyrenees, Pyrenees Atlantiques). **Iberian Peninsula** – C. Pyrenees from Vignemale to Carlitte.

Subspecies: No subspecies.

Ecology: Mainly in subalpine and alpine steppes between 1800 and 2500 m, in general above 2000 m. Under rocks, near the edges of snow fields (Du Chatenet, 1986). Although it is possible to catch *C. cristoforii* and *C. pyrenaeus* in the same pitfall trap, both species have a different habitat preference. *C. cristoforii* mainly inhabits grassland and avoids stony and rocky, poorly vegetated slopes (Assmann, *pers. observ.*).

Transects: Chapter 8: T-93-94.

Biology: **Activity** – Night active, during daytime hidden in the soil or under stones (Forel & Leplat, 1995). **Periodicity** – The adults appear between the end of June and the end of July. The eggs are deposited superficially in the soil and the larval development takes about 1 month (Forel & Leplat, 1998). **Food** – Small snails, insects, larvae and myriapods. **Larva**: Described by Raynaud (1975).

Conservation: Like many other montane species, no decline has been reported.

04.003b. C. (Eucarabus) deyrollei

Gory, 1839.

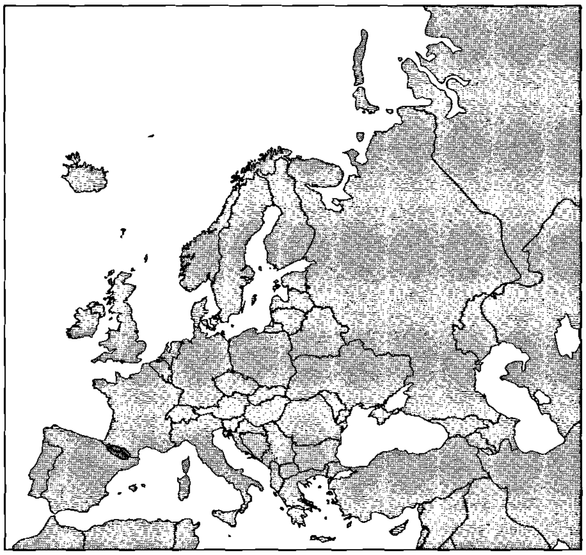
General literature: **Checklists and catalogues** – Breuning (1932): 378. Březina (1994): 17; (1999): 8. Deuve (1994): 93 [124]. Kleinfeld & Schütze (1999): 8. Lorenz (1998): 70. Turin *et al.* (1993): 20. **Iconography** – Forel & Leplat (1998): fig. 2-10. Ghiretti (1996): 46. Imura & Mizusawa (1996): Pl. 2 [18]. Rautenstrauch (1994): Pl. 15-16.

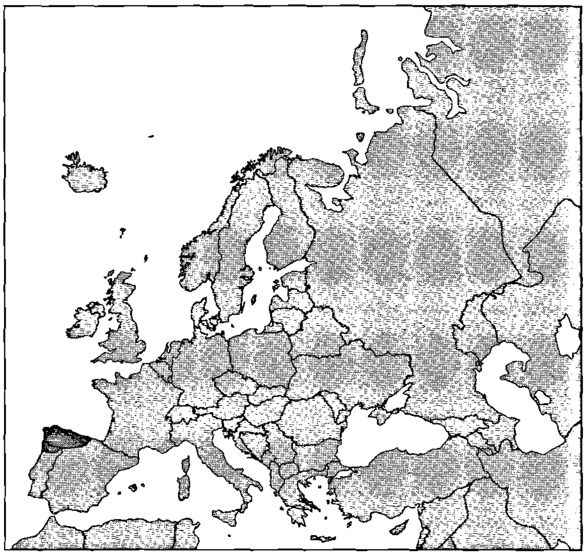
Geographical range: Endemic species of the Iberian Peninsula. **Chorotype**: WEU-IBEN. **Range characteristics**: Iber(NW). **Distribution in Europe**: **Iberian Peninsula** – N. Portugal, N.W. Spain: Galician and Cantabrian mountains from Serra do Gerez (Portugal) through the mountains of León to Burgos.

Subspecies: No subspecies.

Ecology: Montane species, living between 500 and 1500 m. It inhabits mainly beech and oak forests as well as open grassland, preferably close to standing or slowly running water; under stones and mosses (Du Chatenet, 1986; Forel & Leplat, 1998). In the basal and lower montane regions Sierra del Gaurel also in chestnut forests (*Castanea sativa*) (Novoa, 1979).

Transects: Chapter 8: T-95-96 and 98.


04 003a cristoforii (Eucarabus)


04 003b deyrollei (Eucarabus)

Biology: **Activity** – Active beetles seen in afternoon and collected during the night in pitfall traps (Assmann, *pers. observ.*). **Periodicity** – Adults can be found during the whole year. The adults become active from the beginning of the summer, and the data of Novoa (1989) indicate a peak of catches during September. Additional data on the period of oogenesis and occurrence of teneral adults are lacking. **Food** – Unknown. **Larva** – unknown.

Conservation: Abundant, not endangered.

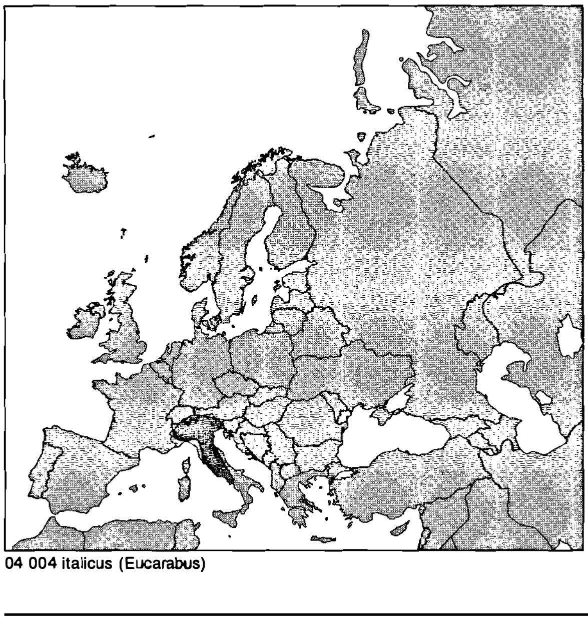
04.004. C. (Eucarabus) italicus
Dejean, 1826.

General literature: **Checklists and catalogues** – Breuning (1932): 430. Březina (1994): 17; (1999): 9. Deuve (1994): 97 [136]. Kleinfeld & Schütze (1999): 8. Lorenz (1998): 71. Turin *et al.* (1993): 20. **Iconography** – Casale *et al.* (1982): fig. 97. Ghiretti (1996): 53. Imura & Mizusawa (1996): Pl. 3 [26]. Rautenstrauch (1994): Pl. 22.

Geographical range: Endemic species of Italy and the S.E. of Switzerland, and Slovenia. **Chorotype:** SEU-ALAP. **Range characteristics:** Alpi-Apen. **Distribution in Europe**: **Slovenia** – Sempas near Nova Gorica. **Switzerland** – Restricted to the S.E. (S. Tessin); a few (recent) records near Locarno and Chiasso. **Italy** – Widespread in N. and C. Italy; distributed from the S. Alps to Campania and Abruzzi, absent from the Adriatic shore of the Italian peninsula. Greatly declined in the N.

Subspecies: a) subsp. italicus – N. Italy. **b) subsp. rostagnoi** Luigioni, 1904 – C. and partly S. Italy from the S. Tuscany to Campania.

Ecology: Mainly in wet meadows or along shores of canals and ditches, sometimes in marshes, damp scrubland and wet forests. Especially in the lowlands, rarer at higher altitudes. Sometimes in foothills and even mountains, up to 1000-1500 m. (Casale *et al.,* 1982). Marggi (1992) reported Swiss catches (Tessin) from a pasture and from fields of maize.


04 004 italicus (Eucarabus)

Transects: Chapter 1: I-3; Chapter 8: T-81, 85 and 88.

Biology: **Activity** – No data. **Periodicity** – Egg size 3 x 1.4 mm. Adults start being active very early in the year, from February until July (Sturani, 1962). Copulation and oviposition in April and May. Development of the eggs lasts 9-10 days. Larval development, including prepupal stage, 30-40 days (average temperature of +20°C). The adults enter a short aestivation during July-August. A second peak of activity of fresh and old adults takes place during September-October. Hibernation of adults from October to February, on hill slopes, in trunks or cavities in (dead) wood of *Populus*, *Alnus* or *Salix* (Casale *et al.,* 1982). **Food** (Larochelle, 1990) – In the field, insects, snails and various molluscs, earthworms. In captivity, snails, small slugs, earthworms, caterpillars with hairs, minced meat, fish, gingerbread, and apples. **Larva:** Described by Binaghi (1937: L2), Sturani (1962) and Raynaud (1976). Food – in the field, various insects (Burmeister, 1939). In the laboratory, chopped mealworms, earthworms, fruits (if no other food available), crushed snails, liver. **Dispersal power:** Wing dimorphic. The winged form (*ronchettii* Born) was never observed flying.

Conservation: The species was very common in Italy until some decades ago, but the numbers and occurrences decreased rapidly, especially in the Padanian Plain, due to intensification of agriculture and urbanisation. Now localised. Hygrophilous populations (occurring in marshes) of C. Italy (subspecies *rostagnoi*) are endangered due to urbanisation and habitat changes, particularly in the classic localities near Rome.

04.005. C. (Eucarabus) obsoletus
Sturm, 1815.

General literature: **Checklists and catalogues** – Breuning (1932): 360. Březina (1994): 17; (1999): 10. Deuve (1994): 97 [137]. Kleinfeld & Schütze (1999): 8. Kryzhanovskij *et al.* (1995): 36 [9]. Lorenz (1998): 71. Turin *et al.* (1993): 20. **Iconography** – Ghiretti (1996): 53-54. Imura & Mizusawa (1996): Pl. 3 [25]. Rautenstrauch (1994): Pl. 13.

Taxonomy: In Lorenz (1998) listed as a synonym of *C. euchromus sacheri* Letzner 1850.

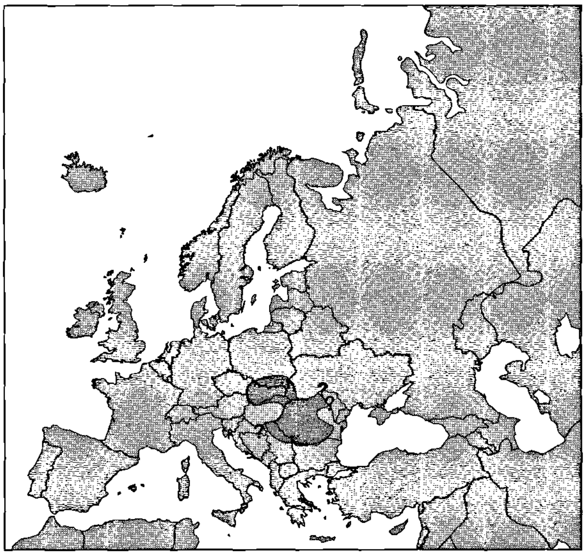
Geographical range: Endemic species of the Carpathians and adjacent mountain chains from Moravia and Tatra to N. Serbia. **Chorotype:** EEU-CARP. **Range characteristics:** Pann-Carp. **Distribution in Europe**: **Poland** – Only in the S.E. mountain area (Beskydy, Tatry Mts.). **Russian Plain** – Only in the Ukrainian Carpathians, where it is known from several localities in the provinces of Zakarpatye, Lvov and Ivano-Frankovo (Rizun, 1990). **Moldova** – Recorded from N. and C. (Kodry) by Neculiseanu & Matalin (2000); the occurence needs confirmation. **Czechia & Slovakia** – Beskid Mts. (Moravia); in Slovakia distributed in montane areas, rather common. **Hungary** – Local and rare, only known from the Aggtelek Karstland and the Zemplén Mts. **Romania** – Carpathians, C., W. and S.W. Romania ('Transylvanian Alps'; Bihor Mts.), S. to Banat (Hůrka, 1996). **Balkan Peninsula** – Questionable presence: N. Serbia, E. Croatia.

Subspecies: a) subsp. obsoletus – Mountains of Moravia, Tatras, Beskides, N. Carpathians from Slovakia to Bukovina, N. Moldova and Hungary. **b) subsp. uhligi** Vacher de Lapouge, 1908 (= *mallasȥianus* Breuning, 1932) – E. Carpathians: Ceahleu, Caliman, Rareul, subalpine and alpine zone. **c) subsp. prunneri** Mallasz, 1901 – Romania: N.E. Transylvania and N. Moldova. **d) subsp. fossulifer** Fleischer, 1893 – Romania: W. Transylvania: Cluj, Aiud, Hunedoara, Mts. Bihar. **e) subsp. carpathicus** Palliardi, 1825 – Romania: S. Transylvania; Serbia: Vojvodina (Banat). This form has been described referring to larger individuals from the lower mountainous zone; small specimens (17-20 mm) from the subalpine zone of Vojvodina are named *euchromus* Palliardi, 1825.

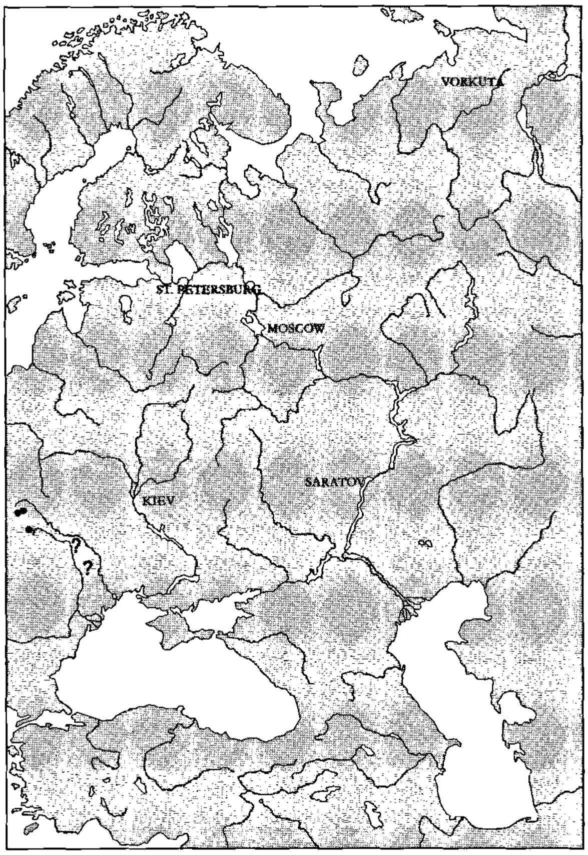
Ecology: Predominantly a forest species. From light, thin forests in foothills and valleys to the alpine zone, occasionally above the timber line in alpine steppes (Hůrka, 1996). In Hungary in montane forests (Aegopodio-Alnetum, Alnetum glutinosae-incanae, Melittidi-Fagetum, Phyllitidi-Aceretum, Piceetum abietis cultum and Waldsteinio-Querco-Carpinetum); rare. In the Ukraine inhabiting dark, coniferous forests of the W. forest-steppe, bordering the Carpathians, but rare (Petrusenko, 1971).

Transects: Chapter 8: T-35, 62-63 and 75.

Biology: **Activity** – No data. **Periodicity** (Hůrka, 1973) – In the Low Tatras (Czechia), copulation was observed during end of May and beginning of June. In captivity, Stiprajs (1961) observed copulations in February and May, with animals that were caught at the end of July, with oviposition in August. The same females laid, after hibernation, again next year between February 25th and April 11th. Larvae belonging to all 3 stages were observed in July by Hůrka (*l.c.*). Adults are active from April onwards and have their maximum in the period May-July. Freshly hatched animals have only a short period of activity before hibernation. The development of this mainly spring reproducing species takes place without larval diapause (eggs: 8 days, L1: 8 days, L2: 6 days, L3: 19 days and pupa about 16 days; all together 45-60 days). The adults hibernate. **Food** (Larochelle, 1990) – In captivity, earthworms, minced meat, fish and apples. **Larva** – Some notes by Stiprajs (1964: L1) and description by Hůrka (1970: L1-L3).



04 005 obsoletus (Eucarabus)



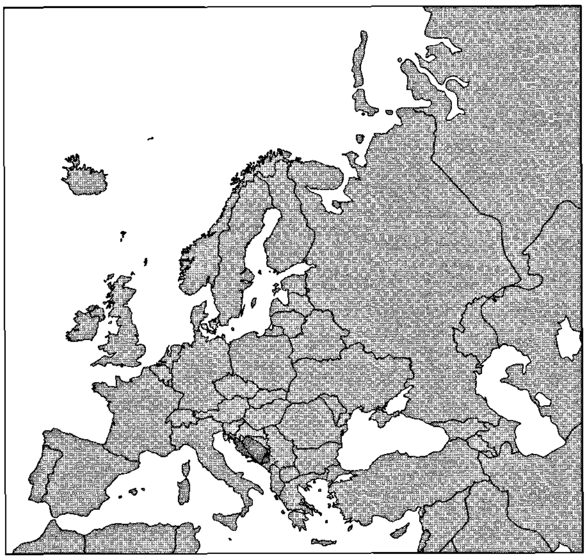
04 005 obsoletus

Conservation: No data, but generally common and widespread, not endangered.

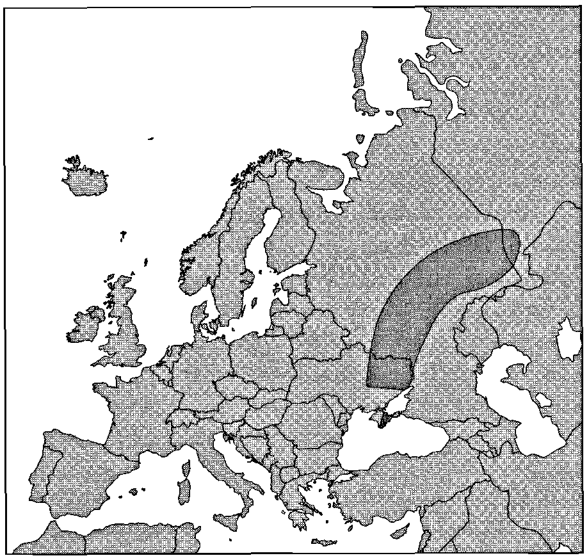
04.006. C. (Eucarabus) parreyssii
Palliardi, 1825.

General literature: **Checklists and catalogues** – Breuning (1932): 372. Březina (1994): 17; (1999): 10. Deuve (1994): 97 [138]. Kleinfeld & Schütze (1999): 8. Lorenz (1998): 71 (*paraysi*). Turin *et al.* (1993): 21. **Iconography** – Ghiretti (1996): 54-55. Imura & Mizusawa (1996): Pl. 3 [23]. Pavicevic & Mesaros (1997): cd-rom. Rautenstrauch (1994): Pl. 14-15.

Geographical range: Endemic species of the N.W. part of Balkan peninsula. **Chorotype:** SEU-CADI. **Range characteristics:** Balk(NW). **Distribution in Europe**: **Balkan Peninsula** – Croatia (Dalmatia, Dinarian Alps), N.W., W.



04 006 parreyssii (Eucarabus)



04 007 stscheglowi (Eucarabus)

and C. Bosnia, N., E. and S. Herzegovina (Plasa Planina, Prenj Planina), N. Montenegro (Durmitor, Tudorov).

Subspecies: **a) subsp. parreyssii** (= *gattereri* Géhin, 1882) – Croatia, Bosnia, N. Herzegovina, E-Serbia ((ssp.) *tippmannianus*) (see *Checklist* and *Key to the adults*). **b) subsp. plassensis** Born. 1907 – Bosnia: Bihac, Drenovac, Prenj Planina; Herzegovina: Plasa, vicinity of Mostar.

Ecology: The habitat preference resembles the adelphotaxon *C. catenulatus*, of which it is the geographical and ecological vicariant. Generally in very large, undisturbed forests (Casale, *pers. observ.*), however according to Pavicevic & Mesaros (1977), regarded as a praticol species of subalpine habitats, living in open habitats in hills and mountains as well.

Transect: Chapter 8: T-70.

Biology: Same as *C. catenulatus* (see ecology).

Conservation: According to Pavicevic & Mesaros (1997), all forms are endangerd, however we observed it as a very common species (Casale, *pers. observ.*).

04.007. C. (Eucarabus) stscheglowi
Mannerheim, 1827.

General literature: **Checklists and catalogues** – Breuning (1932): 376. Březina (1994): 17; (1999): 9. Deuve (1994): 98 [140]. Kleinfeld & Schütze (1999): 9. Kryzhanovskij *et al.* (1995): 36 [5]. Lorenz (1998): 71. Turin *et al.* (1993): 21. **Iconography** – Ghiretti (1996): 55. Imura & Mizusawa (1996): Pl. 2 [17].

Geographical range: N.E. Ukraine, the foothills of Crimea, E. Russia, S.W. Siberia. The S. part of the forest zone and the forest-steppe. **Chorotype:** EEU. **Range characteristics:** EEur(C)-Wsib. **Distribution in Europe (and adjacent areas)**: **Russian Plain** – Distributed throughout the middle stretch of the Russian Plain, to the W. to the Dnieper river and Crimea. The N. border rubs through the provinces of Kursk (C.-Chernozem reserve – MPGU), Tula (Chern' district – ZIN), Vladimir (environs of Vladimir and Davydov – ZIN, ZM), Mari republic (environments of Ioshkar-Ola – MPGU), Vyatka (Kotel'nich – Yuferev, 1980) and Perm' (Spasskaya Gora reserve – Koz'minykh *et al.* (1991b); Bol'shoe Savino – Koz'minykh, *in litt.*). The S.-most locality seems to be Rostov (Fomichev, 1983); the S. margin coincides approximately with the border between the forest-steppe and N. steppes and extends from the provinces of Dnepropetrovsk (W.-most locality: Andreevka – IZ), Lugansk (Belovodsk, Derkul', Dolgoe, Kiseleva Balka – Arnol'di,

04 007 stscheglowi

1956), Voronezh (Voronezh reserve – L. Penev), Tellerman Forestry nr. Borisoglebsk – ZM, MPGU), Saratov (Balashov – ZIN), Samara (environs of Samara – ZIN), Bashkiria (Bashkir reserve – Koz'minykh *in litt.*; Ai-River nr. Mesyagutovo – Zinovjev, 1990) and Orenburg (Verkhnyaya Karaganka river – ZIN; Krasnokholmsk Forestry – MPGU). Known also from the Tartar republics (Kazan' – ZM), where the species now seems to be extinct (Shafigullina, 1990). Widely distributed also in the S. and C. Urals (Chelyabinsk , Il'men reserve, Bol'shoi Terenkul Lake – Lagunov, *in litt.*; Troitsk reserve – Esjunin & Koz'minykh, *in litt*; Soimon – ZIN; Ekaterinburg – Kozyrev, 1989). An isolated population occurs in Crimea (Kurortnoe – ZIN; Feodosiya – ZM; Chatyrdag – Koval', 1990). A species with a typical zonal range, overlapping almost completely with the forest-steppe zone, with only few localities in the neighbouring zones of mixed forests and steppes.

Subspecies: Except nominate, no subspecies in Europe.

Ecology: Eurytopic in the N. of the forest zone and Cisuralia (Grechanichenko, 2000). Mesophilous species of deciduous and mixed forests (Arnol'di, 1956). In Ukraine, especially in oak woods of the forest-steppe zone (Petrusenko, 1971).

Transects: Chapter 1: I-2; Chapter 8: T-44, 46, 48-49, 53-54, 60.

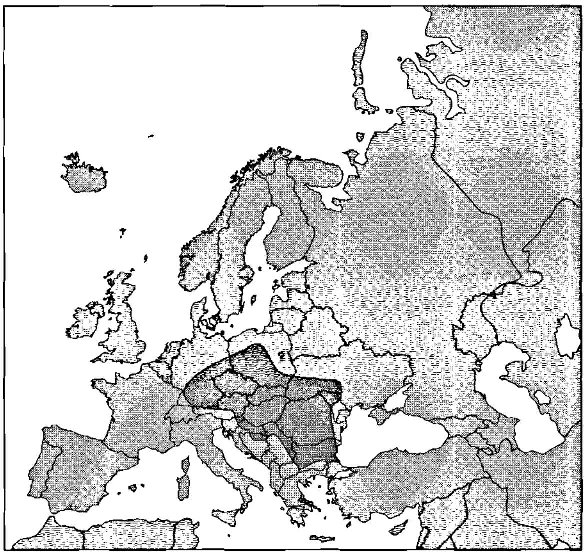
Biology: **Activity** – No data. **Periodicity** – In the middle Urals reproduction takes place in spring and larval development during summer. Teneral animals appear in autumn and hibernate subsequently (Kozyrev, 1989). **Food** – No data. **Larva**: See Chapter 4. Food – No data.

Conservation: No data.

04.008. C. (Eucarabus) ulrichii

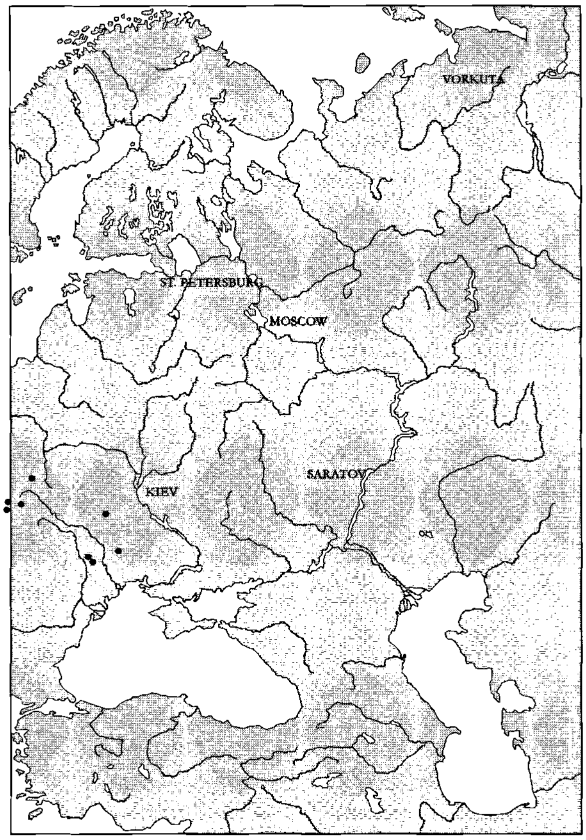
Germar, 1824 (= *ullrichi* auct).

General literature: **Checklists and catalogues** – Breuning (1932): 416. Březina (1994): 17; (1999): 10. Deuve (1994): 95 [134]. Kleinfeld & Schütze (1999): 8. Kryzhanovskij *et al.* (1995): 36 [8]. Lorenz (1998): 71. Turin *et al.* (1993): 21. **Iconography** – Ghiretti (1996): 49-52. Imura & Mizusawa (1996): Pl. 3 [28]. Jakobson (1905): Pl. 2 and 5. Pavicevic & Mesaros (1997): cd-rom. Rautenstrauch (1994): Pl. 20-21.



04 008 ulrichii (Eucarabus)

Geographical range: C. and S.E. Europe from S.W. Germany and E. Austria to S. Poland, W. Ukraine, Serbia, Bulgaria. **Chorotype:** CEU. **Range characteristics:** CEur-SEEur. **Distribution in Europe**: **Germany** – Scattered distribution in the S. and E. (Hessen, Rheinhessen, Baden-Würtenberg, Bayern, Sachsen and Thüringen); absent from the C. and N. In general rare and in many places declining and endangered. **Poland** – Reported from the C. and S. part of the country; not in the N., N.E. and C.E. **Russian Plain** – Only in the Ukrainian Carpathians, W. Ukraine and Moldova, E. to 30°E. Known from the provinces of Zakarpatye (Uzhgorod (MPGU), Plishka, Maloe Bereznoye – Ponomarchuk, 1956) and Lvov (Sambor; Turye in Starosambor district – Rizun, 1990; Rostochye reserve – Rizun, 1991), as well as from Vinnitsa (Averin, 1938), Mikhailovka nr. Ananyev (ZM). Only in the zones of deciduous forests and forest-steppe. **Moldova** – Kishinev, Kapriyama (MPGU; Kipriyani – Adashkevich *et al.,* 1973), Budzhak, Kodry Hills and Prut flood plains. **Czechia & Slovakia** – Reported from all regions, in the N.E. parts (ssp. *ulrichii*) rare but locally common. **Hungary** – Widely



04 008 ulrichii

distributed but not common, mainly in the hills and mountains. **Romania** – Across all of the Carpathians. **Bulgaria** – Mainly in C., W. and S.W. regions of the country. **Balkan Peninsula** – In the N. part of the peninsula. Slovenia, N. and E. Croatia, Banat (Vojvodina), N.W., N.E., E. and S.E. Serbia (Negotin, Vrsaki breg), C. and E. Bosnia. **Austria** – Most of the country, except Vorarlberg and Osttirol; likely an endangered species. **Switzerland** – Not belonging to the indigeneous fauna, only very few records exist of introduced animals.

Subspecies: (see remarks in the *Key to the adults* (p. 82). **a) subsp. ulrichii** – N.E. and W. part of species area: S.W. Germany, S.E. Germany (Niederbayern, Sachsen), W., E. Austria, and S. Austria, N.E. Croatia, Czechia, N.E. parts of Bohemia, Moravia and Slovak Republik, S. Poland, Hungary, Romania (except in the S.), Moldova, W. Ukraine. **b) subsp. fastuosus** Palliardi, 1825 – Central subspecies (not alpine): N. Serbia, S.W. Romania. Transitional specimens to subsp. *arrogans* from S.W. Romania and Vojvodina have been described as *superbus* Kraatz, 1878. **c) subsp. rhilensis** Kraatz, 1876 (*stussineri* Géhin, 1885) – S.E. Austria (Carinthia – transitional populations to subsp. *ulrichii* (*s.str.*)), Slovenia, Croatia, Bosnia, S. Serbia, Bulgaria. **d) subsp. arrogans** Schaum, 1858 – E. Serbia: Negotin, Majdanpek, Milanovac.

Ecology: Rather eurytopic, from grasslands, gardens, vineyards and other open habitats to scrub, hedge rows, forest edges and open forests; although in general avoiding dense forests, in the S. of E. Germany regularly found in deciduous forests, preferably on heavy soil types such as loam and limestone, frequently under thermophilic conditions (Arndt, 1989). In Czechia and Slovakia, a species from lowlands and foothills, inhabiting meadows, fields, scrub and open forests (Hůrka, 1996). According to Hoffmann (1907), in C. Europe mainly from lowlands up to 500 m. In Hungary mainly in several montane forest associations (beech), but also in the plains in water-meadow forests and in the hills. For the N. of former Yugoslavia, characterised as praticol, inhabiting lowland meadows and cultivated areas; in the C. and E. territories, it is predominantly a forest dweller from hills and mountains (Pavicevic & Mesaros, 1997). In the S. and E. also montane; in Bulgaria from lowlands up to 600 m (Guéorguiev & Guéorguiev, 1995). Mandl (1972) characterised some subspecies as silvicol, others steppicol. In Ukraine, in beech forest of the Carpathians and near-Carpathian regions ('Prikarpatye').

Transects: Chapter 8: T-32, 35, 62-65, 69, 72-73, 75-78.

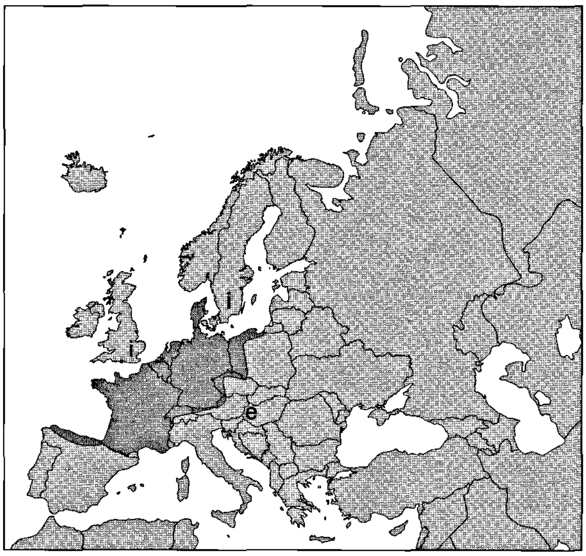
Biology: **Activity** – Day and night active. **Periodicity** (Hůrka, 1973) – Reproduction in spring from April onwards, without larval diapause. Adults hibernate. Copulations were observed in spring (May), but by young adults caught in W. Ukraine in autumn (end of August – beginning of September – Stiprajs, 1961). Oviposition from the second half of April to June (Burmeister, 1939; Raynaud, 1943). The females lay about 25-50 eggs (Burmeister, 1939; Scherney, 1957b, 1959; Verhoeff, 1921). Larvae were reported from April to August (Hůrka, *l.c.*). Adult beetles occur from March to September; the fresh imagines appear during the second half of August (occasionally from the end of July onwards), and they are active for some time, before hibernation. Development takes about two months (60-66 days); Stiprajs (1961) published the following schedule, egg: 11 days, L1: 7 days, L2: 7 days, L3: 17 days and pupa: 11 days. Hůrka (*l.c.*) found these mean values from 6 individuals: eggs 7-10 days, L1: 10 days, and 28 days to reach the L3 stage. Adult hibernate from the end of September onwards. **Food** (Larochelle, 1991) – In the field, earthworms and various insect larvae. In captivity, earthworms, minced meat, fish and apples. **Larva**: Described by Vacher de Lapouge (1906: L2-L3), Verhoeff (1917: L1-L3), Hůrka (1971b) and key: Arndt (1985, 1991b). Food – Chopped mealworms (larvae of *Tenebrio molitor* (Coleoptera Tenebrionidae)) and earthworms.

Conservation: In N. Europe generally noted on Red Lists as declining or endangered. The species is probably not endangered in S. Europe.

05. TACHYPUS WEBER, 1801

05.001. C. (Tachypus) auratus
Linnaeus, 1761.

General literature: **Checklists and catalogues** – Breuning (1933): 638. Březina (1994): 30; (1999): 37. Deuve (1994): 133 [226]. Kleinfeld & Schütze (1999): 19. Kryzhanovskij *et al.* (1995): 36 [10]. Lorenz (1998): 82. Turin *et al.* (1993): 21. **Iconography** – Darnaud (1983b): Pl. 15. Forel & Leplat (1995): Pl. 13-20; (1998): fig. 28-29. Ghiretti (1996):



05 001 auratus (Tachypus)

116-119. Imura & Mizusawa (1996): Pl. 29 [236]. Jakobson (1905): Pl. 3. Rautenstrauch (1994): Pl. 31-32.

Geographical range: W. European (semi-atlantic) species. W. and C. Europe from W. France and N.E. Spain to N. Germany and W. Poland; in the S. to S.E. France, N. Switzerland, W. Austria, Czechia; in E. Germany and Poland it spreads E.-ward; Lindroth (1974, 1985) also reports a generally rapid W.-ward expansion on the continent. Originally absent from the British Isles, Fennoscandia (see below) and also from the Alps and Carpathians. Introduced in the U.S.A. (New England). **Chorotype:** CEU. **Range characteristics:** WEur. **Distribution in Europe**: **Fennoscandia** – Not in the E. part of the area; all others are recent introductions. **Denmark** – Only accidental introductions were known, until repeated records from the Island of Aerö (S. of Funen) indicated that the occurrence of an established population was very probable (Jørum & Jørum, 1996). **British Isles** – Introduced in the S.W., but not established (Luff, 1998). **Netherlands** – Mainly along the big rivers and in the W.; rare on, or absent from the sandy-soil region in the E. and C.S. **Belgium** – Widespread but declining. **Germany** – Formerly restricted to W. Germany (cf. Von Lengerkerken, 1921); in E. Germany first record of 1840, and later distributed in the lower plains and expanding E.-ward, in 1940 to the Oder (Horion, 1941). Now reported from the whole area; endangered in Schleswig-Holstein and Berlin, rare in Bayern. **Poland** – Restricted to the W. part of Poland, reaching to Wyzina Malopolska in the C.E. **Czechia & Slovakia** – Restricted to N.W. Bohemia, very rare; probably an endangered species in this area. **Hungary** – Only old records are known from Szeged and Sopron in W-Hungary (last record collected in 1946); probably extinct now. Pisó (1885) collected a small seria of *C. auratus* in Maramures Mts. (former Hungarian localities, at present part of Ukraine (Bustina and Velikij Bicskov). **Austria** – Only occurring in the W.-most part (rare: Vorarlberg, Tirol); reported as introduced in Oberösterreich. **Switzerland** – Widely distributed on the N. side of the Alps, including the Jura, but declining recently; also in Unterwallis, and parts of Graubünden; not in C. Wallis and Tessin. **France** – This semi-atlantic species is widely distributed and one of the most frequent and common ones in the French territory. It is only absent from the S.E. (area of the Alpes Maritimes) and from the larger part of the Pyrenées Orientales. However still widespread in Rhône-Alpes (Coulon *et al.*, 2000). **Iberian Peninsula** (Herrera & Arricibita, 1990; Zaballos & Jeanne, 1994) – Restricted to and scattered in the N.W. part of the peninsula: Mts. de Mieres, Canales Cantabrian and Basque Mts.

Subspecies: a) subsp. auratus – Inhabits the major part of the species range except S. France (see remarks in the *Key to the adults* concerning forms in the Pyrenees, p. 89). **b) subsp. lasserrei** Doué, 1855 – S.W. and C. France: Cevennes and adjacent departments in the N. to Loire. **c) subsp. lotharingus** Dejean, 1826 – C. part of S. France in the 'Zone d'olivier' from Roussillon to Provence (was described erroneously from Metz). **d) subsp. honnoratii** Dejean, 1826 – S.E. France (dept. Basses Alpes, Vaucluse, Haute Provence). The population from Mt. Ventoux (*nicolasi* Chobaut, 1897) is black with bluish lustre and yellow legs.

Ecology: Praticol (inhabiting grassland), thermophilic, heliophilic in N.W. Europe rather eurytopic (Koch, 1989; Mandl, 1972; Thiele, 1977). It inhabits mainly (warm) open landscapes, such as loamy soil on cultivated fields, forest edges, limestone grasslands, dry pastures. Although frequently on cultivated land, it seems to avoid heavily fertilised habitats (Turin, 1983). Sometimes even found in forest clearings (Lauterbach, 1964). In general, a species from the lowlands and hills of W. Europe, preferably living on clayish or loamy soil. According to Hoffmann (1907), mainly from lowlands up to 500 m. Several authors mention that the species avoids sandy soil types (e.g. Lindroth, 1985; Arndt, 1989), which is in contradiction with some records from the C. Netherlands, where it frequently was found in gardens on pure sandy soil, however, not far from river Rhine and its extensive river meadows with clay soil (Turin, 2000). In S.E. France (Rhône-Alpes) very eurytopic, only absent from high altitude habitats (Coulon *et al.*, 2000); in the C. (Loire, Ardèche) found on silicate and volcanic soil types (Cleu, 1952), but in S. France also present on sandy soil (Perpignan). In the N. of the Iberian Peninsula in open, waste sites, cultivated and natural grasslands (Herrera & Arricibita, 1990). Rare at high altitudes, however, in France it can be found from sea level to about 1200 m (even on top of Mt. Ventoux: 1900 m), mostly in open habitats, especially grasslands, but also along forest edges and along the border zone of swamps (Forel & Leplat, 1995). In the E. of its distribution (Berlin, Poland, Bohemia) more stenotopic and rather xerophilic (Barndt, 1991; Hůrka, 1996). Thiele (1977) mentions that the species orientates in the field mainly on temperature.

Transects: Chapter 8: T-17-18, 20, 22, 29-33, 80, 89-91.

Biology: **Activity** – Active during the day time and at dawn (Lindroth, 1985; Hůrka, 1996), at least in N.W. Europe; frequent observations also in the Netherlands. Is is extremely tolerant to light intensity (Thiele & Weber, 1968); diurnal activity > 45% (Thiele & Weber, 1968). However, Forel & Leplat (1995) call it a nocturnal species that hides during daytime. That the thermophily of the species is limited was illustrated by an investigation on the S. exposed limestone hills in the Netherlands. During high summer, the animals nearly completely 'disappear' from the open grassland and migrate to adjacent scrub, forests and forest edges, where they occur in high numbers, for a short period. From August onwards, they re-appeared in the grasslands (Turin, 1983). **Periodicity** – A lot can be learned from the extensive survey of Hůrka (1973). Reproduction takes place in spring, in N.W. Europe from the beginning of April onwards. Oviposition in April-May. The females dig themselves with the entire body into the soil (Lengerken, 1921) and lay on average

50-60 eggs in small subterranean cells (Scherney, 1957b, 1959); size of eggs ca 5 x 2 mm (Sturani, 1962). Development, without larval diapause, takes in total 75-90 days, after Burmeister (1939) and Scherney (1957b). Development of eggs takes 5-10 days, L1: 10-14 days, L2: 15-21 days, L3: 28-36 days (including a 6 days prepupal stage) and the pupation lasts 8-14 days (Hůrka, *l.c.*). Sturani (*l.c.*) estimated the larval development at 30-40 days. After pupation in late summer, the teneral animals stay in their pupal chambers in the soil and do not surface and become active before the winter starts (e.g. Scherney, 1961). They are very hard to find during the winter and an obligatory long (adult) hibernation period must be assumed. In S. France, the beetles also hibernate in rotten wood (e.g. of *Castanea*; Assmann, *pers. observ.*). In captivity, an age of 5 years was observed by Nickerl (1889: in Kern, 1912). **Food** – It is an agressive hunter that preys especially upon earthworms and larvae of insects; it was even found attacking young snakes (*Natrix*, *Vipera* – Arndt, 1989) and young birds fallen from the nest. During the hunt, it searches a 3 cm wide path, theoretically resulting in an effective exploitation of 0.2 m²/min in open field (Heydemann, 1957), which will be undoubtedly lower in reality. Larochelle (1990) compiled an enormous number of observations concerning the food in the field and laboratory, varying from insects and insect larvae, caterpillars, earthworms, snails, eaten alive or dead and chopped or crushed, to more artificial items such as raw meat, bread soaked in sugar, cooked carrots and all kinds of fruits. Canibalism was also observed in the adults. **Larva**: Described by Snellen (1860: L3), Vacher de Lapouge (1905: L2-L3), Lengerken (1920: L1-L3), Hůrka (1971a) and key: Arndt (1985, 1991b). Food – earthworms, pupae of large Diptera, Coleoptera (Arndt, *pers. observ.*). **Dispersal power** – A maximum walking distance of 120 m in 10 days was recorded (Scherney, 1960c). According to Heydemann (1957), the species reaches only low speed in dense grassland vegetation of less than 0.5 m/min, compared to open country where it can reach a speed of 6-8 m/min (by 8°C). It readily climbs plants and trees to hunt. The rapid expansion into the E. parts of the distribution range (see under *Geographical range*), indicates a strong power of dispersal.

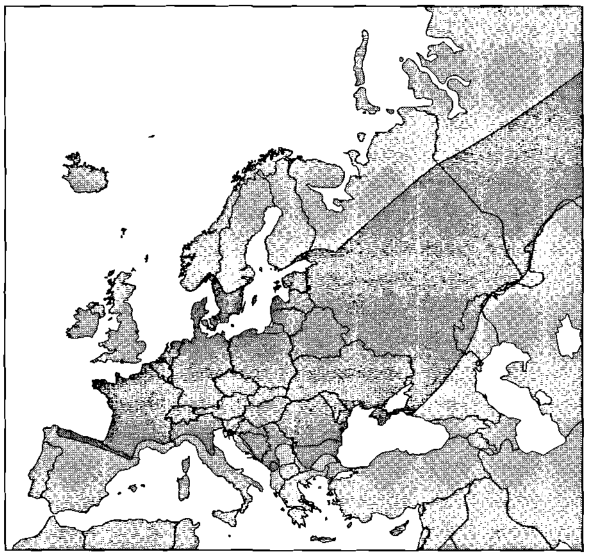
Conservation: Blumenthal (1981) states that is is a good indicator for un- or poorly fertilised grasslands on heavy soil. Normally very abundant (less in forests). In Schleswig-Holstein, Basedow (1987) demonstrated in a long-term study, that this *Carabus* species is very sensitive to insecticides. It disappeared completely as a result of intensive farming management, but remained abundant in extensively cultivated fields. Coulon *et al.* (2000) mention also the obvious negative influence of phytosanitary treatments on population densities, and suggest that this probably also applies to other species with similar biology. Until 40-50 years ago, it was present in the parks and gardens of Paris (Breuning, *pers. comm.*). In the period of 1965-1970, some populations in the S.W. of France (subspecies *lotharingus*) became rare because of intensive use of insecticides against flies (Mourgues, *pers. comm.*). In a survey on limestone grasslands in the S. part of the Netherlands, it seemed to be less tolerant to fertilisation than *C. monilis* (Turin, 1983).

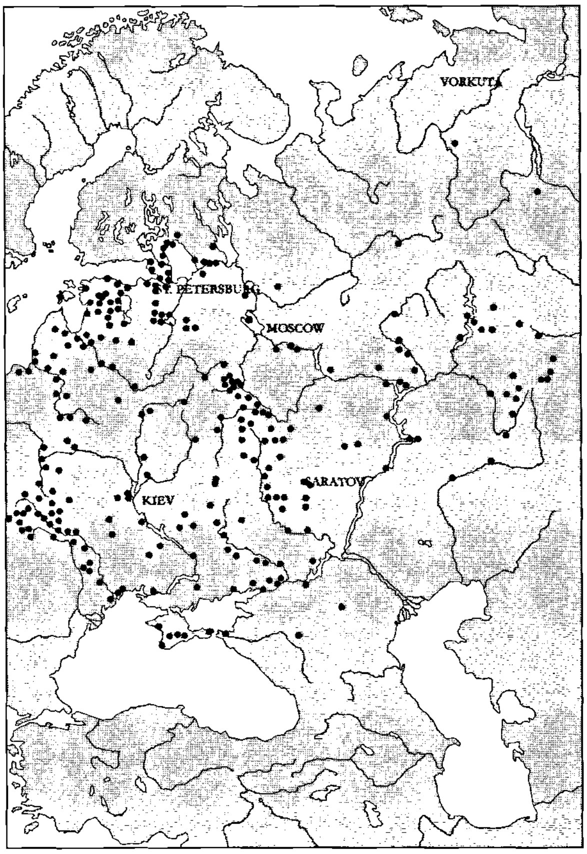
05.002. C. (Tachypus) cancellatus
Illiger, 1798.

General literature: **Checklists and catalogues** – Breuning (1933): 556, 1571. Březina (1994): 31; (1999): 38. Deuve (1994): 130 [225]. Kleinfeld & Schütze (1999): 20. Kryzhanovskij *et al.* (1995): 37 [11]. Lorenz (1998): 83. Turin *et al.* (1993): 21. **Iconography** – Casale *et al.* (1982): fig. 106. Forel & Leplat (1995): Pl. 12-13; (1998): fig. 24-27. Ghiretti (1996): 109-116. Imura & Mizusawa (1996): Pl. 28 [235]. Jakobson (1905): Pl. 5. Pavicevic (1997): cd-rom. Rautenstrauch (1994): Pl. 27-31.

Taxonomy: *C. cancellatus* was most exensively trearted by Breuning (1932-1937) in his monograph on *Carabus*; later Eidam (1941b) reviewed that section, adding a lot of comments.

Geographical range: From W. France and N.W. Spain throughout C. and N. Europe to E. Siberia (Lena river, Lake Baikal, Yakutsk area). Absent from the British Isles, most of the Iberian Peninsula, C. and S. Italy, Greece, as well as from the S. Balkan peninsula, Crimea, and from the Caucasus. Its N. limit reaches to about 62°N. There are large gaps between local populations, especially in N.W. Europe. **Chorotype:** SIE. **Range characteristics:** Eur-CSib. **Distribution in Europe**: **Fennoscandia** – Norway, mainly restricted to the S.E.; Sweden, rare in the S., also Öland; Finland, in the C. and S.E., rather common in the E. **Denmark** – Scattered, rare and declining rapidly. **British Isles** (Lindroth, 1974) – Occasionally introduced in Britain (also in Ireland) but never established. **Netherlands** – Rather widespread before 1950. However, it declined strongly and is now restricted to a few


05 002 cancellatus (Tachypus)



05 002 cancellatus

small localities in the E. and S. **Belgium** – Rather widespread, except in the W.-most parts. However, characterised as vulnerable because of a strong decline in all parts of Flandria. **Germany** – Reported across the whole area; especially in E. Germany widespread and in some places not rare. However in the latest reports, populations are described as being vulnerable or endangered. **Poland** – Widespread across the whole area. **Baltic** – Reported from all countries. **Byelorussia** – All the territory. **Russian Plain** – Widely distributed throughout most of European Russia, known from many localities. To 62°N (the line Petrozavodsk – Syktivkar – Shukht-Gort), although there is a record from the basin of the Pechora River, which needs confirmation. The S. margin of the range coincides approximately with 45°N, from the S. coast of Crimea to Kuban valley and Stavropol. Further, the range limit goes to the N. through Kalmyk republic (Fomichev, 1982), Volgograd province (Komarov, 1990), Uralsk (Arnol'di, 1952) and S. Urals (Yuzhno-Ural Reserve – Kashevarov, 1986). A polizonal species distributed from the middle taiga subzone to the steppe and semidesert zones, which it penetrates along rivers. **Czechia & Slovakia** – Widespread all over the territory. **Hungary** – Widely distributed and rather common. **Romania** – In the lowlands as well as in the hills and mountains, across the territory. **Bulgaria** – Mainly in the W. and C. mountains (Stara Planina); also in the Danube Plain, along the Black-Sea coast and in Sakar-Tundzha region. Seemingly absent from many parts in the S.

Balkan Peninsula – Present in most of the former Yugoslavian territory, except S.W. Serbia and Macedonia. Although it is also seemingly absent from some areas, such as most of C. Serbia (Pavicevic & Mesaros, 1997), it is widely distributed in Slovenia, Croatia, Bosnia-Herzegowina (e.g. Sanskimost, Dervent, Zepce, Mostar, Gacko, Avtovac), Montenegro, Serbia (Negotin). In the S. to N. Albania. **Austria** – Widespread in all parts of the country; listed as a possibly endangered species. **Switzerland** – Widely distributed on the N. side of the Alps, also in the hills and montane zone of the Jura, up to 1000 m. It has also been found in the S. valleys of Graubünden and Tessin, where it can be found up to 1600 m. **Italy** – Distributed in the N., Alps and Prealps and part of the Padanian Plain, as well as an isolated, probably post-glacial relict area in the N. Apennines. **France** – Present all over the French territory, except the S.E.-most area (Alpes Maritimes). **Iberian Peninsula** – Restricted to the N.: Galician Mts., Cantabrian Mts., Basque Mts., Pyrenees and Navarra; E. to Cerdaña Francesa and Olot.

Subspecies: **a) subsp. cancellatus** Illiger – All E. and N. parts of species area: Germany (except the W. part), Fennoscandia, Baltic states, Poland, Byelorussia, most of Ukraine, Russia in the E. to C. Siberia. We have included the races *tuberculatus* Dejean, 1826 (rufofemoral, loc. typ. Warszawa) and *sulinensis* Born, 1902 (nigrofemoral, loc. typ. Sulin in N.E. Romania) into this nominate subspecies. Many authors, especially Kolbe (1913) and Breuning (1932-1937), attached great importance to the colour of femora, but this character is extremely variable across this large area, although nigrofemoral populations dominate in S. and W. parts and rufofemoral ones in the N. and E. parts; the populations that are mixed with respect to this character, inhabit the C. part of European Russia and N.E. Ukraine. Exclusively rufofemoral populations occur in the Urals and Siberia. Green, blue or black individuals predominate in C. and S. Byelorussia (*conspersus* Vacher de Lapouge, 1902). **b) subsp. emarginatus** Duftschmid, 1812 – Alpine: France, Haute Savoie, N. Italy, Piemonte, Venetia Giulia, Toscan Apennines (in the S. to Florence), S.E. Switzerland (Tessin), Slovenia, Croatia. **c) subsp. corpulentus** Kraatz, 1880 – Croatia: Dalmatian coastal region; Italy: Golfo del Canaro (Magistretti, 1965). **d) subsp. alessiensis** Apfelbeck, 1901 – N. Albania; one of the most distinct subspecies. **e) subsp. intermedius** Dejean, 1826 – S. Europe from S.E. Austria (Carinthia: Klagenfurt; Styria) to Slovenia, Bosnia and Bulgaria (except the S.-most districts). Very large form (26-32 mm) living in C. Bosnia and S. Croatia, the elytra have a smooth or feebly granulate background, and was described as *maximus* Haury, 1880. Such specimens have also been found in Herzegovina, and with *aurosplendens*, they could form a distinct subspecies. **f) subsp. graniger** Palliardi, 1825 – Serbia (including Vojvodina), W. and C. Romania. **g) subsp. carinatus** Charpentier, 1825 – main part of France, N.W. Spain (Spanish Pyrenees, Cantabrian Mts., to Galicia), Belgium, S. Netherlands, W. Germany, N.W. Switzerland. Several local forms are known; the name *progressivus* Kolbe, 1912, is applied to populations intermediate between *carinatus* and *cancellatus* (*s.str.*) living in the N.E. part of subspecies range. **h) subsp. tibiscinus** Csiki, 1905 – E. (low) Austria, Burgenland, Hungary, S. Slovakia, N.W. Romania, Transcarpathian Ukraine. This subspecies is the intermediate form between W. (*intermedius*, *graniger*) and N.E. races (*cancellatus s.str.* and related forms).

Ecology: Mesophilic, praticol-silvicol (Mandl, 1972). For C. and E. Europe known as an extremely eurytopic species that avoids dense forests (Arndt, 1989). It inhabits open as well as shaded habitats of the lowlands, hills and the middle mountain belt (Hůrka, 1973; 1996). According to Hoffmann (1907), in C. Europe mainly from lowlands up to 1000 m. In C.E. and E. Europe also often present in cultivated land and even an abundant or dominant species (Franz, 1983; Stiprajs, 1961; Thiele, 1977). In Hungary in a wide range of biotopes; forests and forest edges in the mountains and hills as well as in open, moist to wet meadows in the lowlands. In Moscow province a common species of meadows and light forests (Fedorenko, 1988); in Ukraine in 'bairak' oak woods of the N. steppe zone, in oak woods of the forest-steppe zone, and in floodland woods on uplands (Petrusenko, 1971), also in scrub communities. In general, it prefers open landscapes, fields and meadows and also clearings in deciduous forests (Broen, 1965; Lauterbach, 1964; Arndt, 1989; Herrera & Arricibita, 1990). On the Balkans it inhabits wet, open biotopes especially in the W. lowland parts and in the N. Danube zone, and mainly forested places in the C. parts (Pavicevic & Mesdaros, 1997). In W. Europe (e.g. Netherlands), and C.N. the species is rather uncommon and confined to highly specific habitats, often on loamy soil, notably on 'loess' that occurs on hills along rivers in the C. and S. (Turin, 2000). In 'Drenthe' (E. Netherlands), even found in *Sphagnum* bogs and on inland sand dunes and heath; less frequently on arable land (Den Boer, 1977). In Scandinavia and Denmark it also inhabits open land, preferably on clayish soil, but also sandy grass areas, forest clearings and Corynephoretum (Lindroth, 1985; Schjötz-Christenssen, 1965). For France, it is reported to live in habitats that in general do not exceed 1000 m (Forel & Leplat, 1995); in Italy from the plain and hills (50-500 m near Torino) up to 2000 m (Casale *et al.,* 1982). Although seemingly rather eurytopic, the preference for open or shaded habitats is often related to subspecies; Mandl (1972) characterises the different subspecies from silvicol to praticol.

Transects: Chapter 1: I-1, 2; Chapter 8: T-15-18, 21-24, 28-32, 35-37, 39, 44, 46-48, 54-58, 60-62, 64, 69-74, 76-81, 88 and 93-94.

Biology: **Activity** – At least partly, day active (Weber, 1966a; Weber & Thiele, 1968; Casale, 1982; Turin, *pers. observ.*). More than 45% day active (Thiele, 1977). It regularly hunts during the day, and it readily climbs plants when hunting. **Periodicity** – Similar to that of *C. vagans*, with a one year life cycle. Reproduction takes place in spring (Hůrka, 1973); larvae develop during the summer without a diapause and the adults are active mainly in spring and autumn, without summer aestivation (Casale *pers. observ.*, Lindroth, 1949; 1985; Sharova & Dushenkov, 1979). Copulations of young adults were observed in late autumn before hibernation (Den Boer, 1977), but this mostly occurs immediately after. Oviposition during the period April/May – August (Arndt, 1989). Skuhravy (1959b) found fertile eggs in the ovaries, mostly from the second half of June onwards; oviposition (in total 45-100 eggs: Scherney, 1959; Stiprajs, 1961) takes place in a small underground tunnel, where each egg (size 5 x 1.5 mm – Sturani, 1962) is laid in a separate chamber. The development, without larval diapause, in total, takes about 60-70 days (Forel & Leplat 1995; 1998). Hůrka (1973) presents the data from various breeding experiments (Kern, 1924; Kirchner, 1927; Stiprajs, 1961), where the period of development varies from 35 to 83 days. Sturani (1962) presents the data for development in S. Europe: eggs 8-9 days, larva (including prepupal stage of 4-5 days) 40-50 days: L1: 7 days; L2 ca 14 days; L3: 25-30 days, and pupa: 14-20 days. Teneral animals appear in late summer and autumn, and are active until they hibernate. Hibernation usually occurs behind tree bark at the edges of forests adjacent to open habitats (Turin, 2000), especially in forested areas, but can also regularly occur in the soil in open habitats (Arndt, 1989; Casale, *pers. observ.*, Scherney, 1957b). Hůrka (1973) reports a facultative hibernation diapause for the adults. Activity of adults that have hibernated previously decreases rapidly after August. A second hibernation is rare. **Food** (Larochelle, 1990): The species is generally considered to be a natural enemy of pests in crops and forests in the Ural. In Russia it was observed eating caterpillars of Noctuidae (*Agrotis*) and larvae of Coleoptera (*Amphimallon*, *Harpalus*, *Leptinotarsa*, *Staphylinus*) as well as larvae of Diptera. An enormous variety of recources was reported: pupae of ants, snails, larvae and earthworms; in the laboratory it accepted hairless caterpillars, fruits, larvae of various Coleoptera species, chopped mealworms (*Tenebrio*), live and dead slugs, even bread and beer. **Larva**: Described by Vacher de Lapouge (1905: L1-L3), Hůrka (1971b) and key: Arndt (1985, 1991b). Food – earthworms in the laboratory (Arndt, *pers. observ.*). Burmeister (1939) reports that *C. cancellatus* primarily feeds on carrion and is a less active hunter. **Dispersal power**: Although unwinged like most other *Carabus* species, it moves very well. Scherney (1960b) measured an effective relocation of 15 m/day and 120 m in 10 days.

Conservation: In N.W. Europe a strongly declining species (Desender & Turin, 1989). This is also the case in many other parts of Europe. Also declining in lowland in N. Italy, due to the loss of suitable habitats, such as riparian bushes and due to over-cultivation; no decline has been reported for the populations of foothills and mountains. Pavicevic & Mesaros (1997) report the status of endangered or vulnerable for all Balkan forms. Shilenkov & Averenskii (1991) report that in Yakutia it was widely distributed, but it has now probably dissapeared from that area. Blumenthal (1981) considers it a less suitable indicator, because its distribution on local scale is insufficiently known. The causes of decline in lowland areas are not clear. Obviously, it is able to resist a severe pollution, at least in E. Europe where it is rather eurytopic; it was one of three surviving species on a field close to a chemically polluted area in Byelorussia (Chumakov, 1986).

Note: *Carabus* (*Eucarabus*) *cristoforri* Spence, 1823 was previously placed in *Tachypus*. Evidence discussed in Chapter 7. *Phylogeny* justify replacement in *Eucarabus*.

05.004. C. (Tachypus) vagans
Oliver, 1795.

General literature: **Checklists and catalogues** – Breuning (1933): 554. Březina (1994): 33; (1999): 41. Deuve (1994): 129 [223]. Kleinfeld & Schütze (1999): 20. Lorenz (1998): 84. Turin *et al.* (1993): 21. **Iconography** – Casale *et al.* (1982): fig. 106. Forel & Leplat (1995): Pl. 11. Ghiretti (1996): 109. Imura & Mizusawa (1996): Pl. 28 [234]. Rautenstrauch (1994): Pl. 27.

Geographical range: Endemic species of S.E. France and N.W. Italy. **Chorotype**: SEU-ALPW. **Range characteristics**: Alpi(W). **Distribution in Europe**: **Italy** – Marginal faunal element, restricted to N.W., W. Liguria (the distribution in this region has to be confirmed); Bordighera, Albenga, Sassello, Bussana Vecchia. Its distribution in the region has to be verified. **France** – Species of the S.E.: Dept. Basses Alpes, Vaucluse and Alpes Maritimes. The distribution is scattered in more or less isolated populations.

Subspecies: A status of subspecies has often been attributed to different subpopulations (see Forel & Leplat, 1995), however we do not follow that concept here, in agreement with the opinion of Březina (1999).

Ecology: Predominantly a species of lowlands (also near the sea on sandy soil) and foothills (sub-montane), inhabiting light cork-oak forest, along the edges of fields and gardens (Du Chatenet, 1986). Classic locality of Fréjus, France. Also in cultivated land; frequently in gardens, meadows and arable land (Casale *et al.*, 1982). Under stones and low plants; often found under lumps of soil or in alluvial detritus. Forel & Leplat (1995) also report that the habitat can vary from dry places along rivers, to gardens and alluvial deposits.

Biology: **Activity** – No data. **Periodicity** – The species has two periods of activity, one (reproduction period) in spring, from April to July and the other in autumn, from September to October (Forel & Leplat, 1995). During summer diapause (July-August) hidden in the soil (Du Chatenet, 1986; Sturani, 1962). The adults hibernate from November onwards. Duration of development is probably similar to that of *C. cancellatus*. **Larva**: Described by Raynaud (1966), see also Casale *et al.* (1982).

Conservation: Especially in coastal localities, decreasing due to urbanisation and loss of habitat.

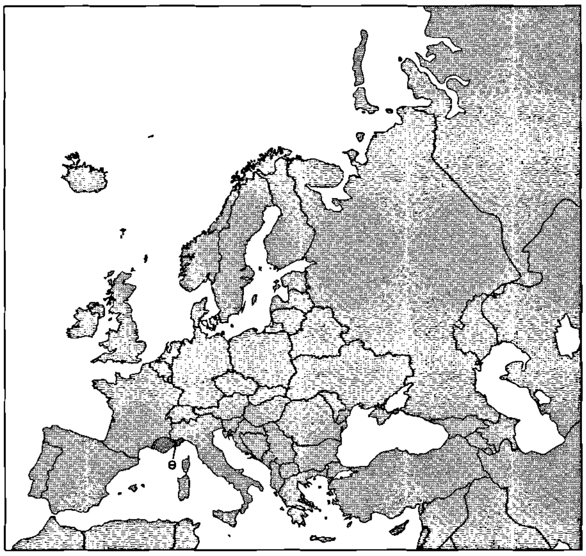
06. ARCHICARABUS SEIDLITZ, 1887

06.001. C. (Archicarabus) alysidotus
Illiger, 1798.

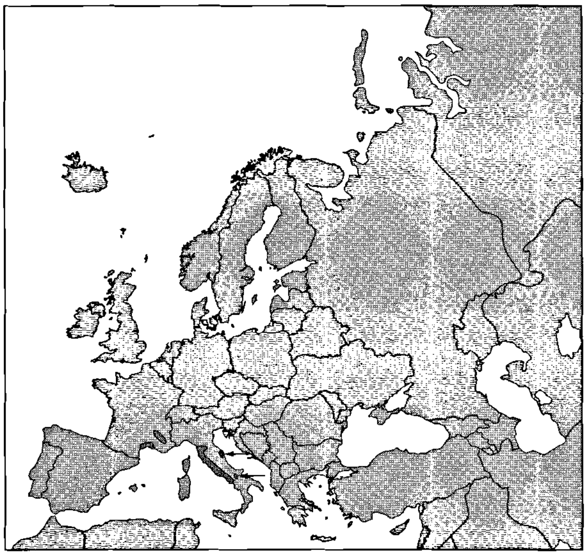
General literature: **Checklists and catalogues** – Breuning (1933): 655. Březina (1994): 25; (1999): 37. Deuve (1994): 121 [208]. Kleinfeld & Schütze (1999): 13. Lorenz (1998): 76. Turin *et al.* (1993): 21. **Iconography** – Casale *et al.* (1982): fig. 67. Forel & Leplat (1995): Pl. 7. Ghiretti (1996): 93. Imura & Mizusawa (1996): Pl. 28 [233]. Rautenstrauch (1994): Pl. 33.

Taxonomy: Placed in the monotypical subgenus *Rhipocarabus* Reitter, 1896 by Březina (1994; 1999).

Geographical range: S. France, N.W. and C. Italy. **Chorotype**: SEU-TYRR. **Range characteristics**: Alpi(W). **Distribution in Europe**: **Italy** – It has a scattered distribu-



05 004 vagans (Tachypus)



06 001 alysidotus (Archicarabus)

tion from the coastal 'Alpes Maritimes', along the W. coastal area of the mainland with populations in Tuscany (Livorno, Pisa) and Lazio (Campagna Romana, Paludi Pontine). Also small, isolated areas exist near Ancona (Adriatic coast), in the Tuscany Apennines and in the Abruzze Mts. (Vinchiatura, Valle di Luppa). **France** – Distribution in two relatively small areas near Montpellier (Camargue area, Var) and in the Alps of Provence between Nice and Montélimar, up to 1200 m.

Subspecies: a) subsp. alysidotus – Italy: Coastal regions of Tyrrhenian sea between 44 and 41°N from Alpes Maritimes to Tuscany (absent in Liguria), Lazio and Campania, Isle of Giglio, also Abruzzo and localities along the Adriatic coast. **b) subsp. stagnalisaequalis** Vacher de Lapouge, 1916 – S. France from Alpes Martimes to Hérault, more common in Camargue.

Ecology: Strongly hygrophilous, littoral, along the coast near salty water under stones or vegetation. Adults have been observed to stay submerged for 15 minutes (Casale *et al.,* 1982). In swamps and damp meadows, sometimes in forests up to the altitude of 1000-1200 m (Casale *et al.,* 1982). Less frequently along ditches (Forel & Leplat, 1995).

Transects: Chapter 1: I-3; Chapter 8: T-83, 85.

Biology: **Activity** – Night active; the species is also subaquatic. **Periodicity** – Active from spring to autumn, mainly April-August (Sturani, 1962) with an aestivation diapause in more open habitats. In C. Italy, near Rome, the species is mostly active in winter, between December and March (Bruschi & Vigna Taglianti, *pers. observ.,* cited in: Casale *et al.,* 1982). Reproduction in spring, eggs laid separately in soil (egg size 5 x 2 mm), hatch within 10 days; development of larvae 30-40 days; hibernation takes place from September/ October until March (Casale *et al.,* 1982; Sturani, *l.c.*). **Food** – (Larochelle, 1990): In the field, earthworms and small slugs. In captivity, meat, fruit, slugs and snails, earthworms, caterpillars, raw meat, cooked carrots and sugared water. **Larva**: Described by Sturani (1962) and Raynaud (1966, 1976). Food – In general the same as the adults (Larochelle, *l.c.*).

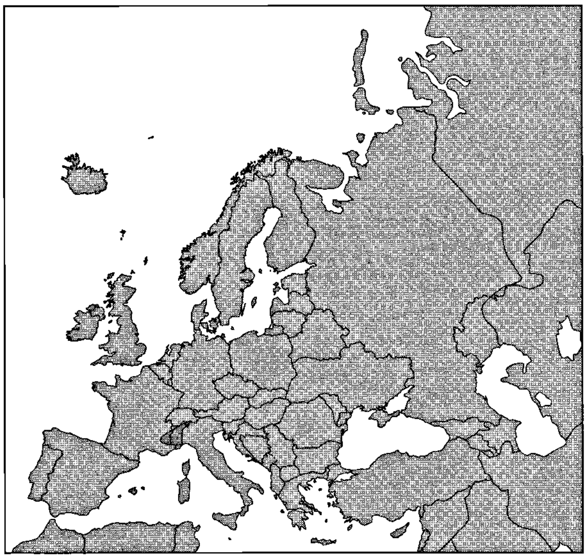
Conservation: The species has lost much of its habitat by draining of marshland and urbanisation of coastal regions and areas close to Rome (Casale *et al.,* 1982).

06.002. C. (Archicarabus) monticola

Dejean, 1826.

General literature: **Checklists and catalogues** – Breuning (1933): 661. Březina (1994): 25; (1999): 24. Deuve (1994): 123 [213]. Kleinfeld & Schütze (1999): 13. Lorenz (1998): 76. Turin *et al.* (1993): 21. **Iconography** – Casale *et al.* (1982): fig. 70. Forel & Leplat (1995): Pl. 10. Ghiretti (1996): 96-97. Imura & Mizusawa (1996): Pl. 16 [125]. Rautenstrauch (1994): Pl. 34.

Geographical range: Endemic species of the W. Alps and Ligurian Apennines; S.E. France and N.W. Italy. **Chorotype:** SEU-ALPW. **Range characteristics:** Alpi(W). **Distribution in Europe**: **Switzerland** – Only old records from the S.-most part of Tessin. **Italy** – From the Ligurian and Maritime Alps, via Cottian, Grajan, Pennine Alps, through Prealpi Bellesi and Varesine to Ticino; also in W. Ligurian Apennines and the hills near Torino. **France** – Restricted to the S.E.: Alpes de Haute Provence; Alpes Maritimes, Basses Alpes, Dauphinian Prealps. Coulon *et al.* (2000) report that the citation from the Préalpes (Vercors) by Jeannel (1941) and old record from Savoie, are at least enigmatic, because this southern species hardly reaches the S. of the Hautes Alpes. **Iberian Peninsula**: Herrera & Arricibita (1990) reported it as new to the Iberian fauna, which must be regarded as erroneous: ref. *C. pseudomonticola.*



06 002 monticola (Archicarabus)

Subspecies: Several subspecies were described, but both Jeannel (1941) and Casale *et al.* (1982) regarded the species as monotypic. Rather characteristic forms are the most S. populations from the French Maritime Alps (*maritimensis* Born, 1923) and from the Italian Ligurian Alps at high altitude, up to 1200-1500 m (*liguricus* Born, 1898).

Ecology: Forest species, living in dry to moderately humid montane forests at the foot of mountains or in low parts of montane valleys, at altitudes betweeen 200 and 2000 m; above the timberline in alpine steppes and meadows, but rare (Casale *et al.,* 1982). Sometimes very abundant in forest. In Switzerland (Tessin) at 600-1200 m (Marggi, 1992).

Transects: Chapter 8: T-81 and 88.

Biology: **Activity** – Night active (Casale, *pers. observ.*). **Periodicity** – Very early species, adults at lower altitudes active from early spring (February/March), with an aestivation diapause during June/July-August (Casale *et al.,* 1982); at higher altitudes active in late spring, mainly during VI-VII. Like the other *Archicarabus*, the female makes small tunnels in the soil, where she lays about 30 eggs in total (size 4.5 x 2 mm), 6-8 per tunnel, each in a separate cell; they hatch after 10-17 days (see Sturani, 1962: 86, fig. 3). Total larval development takes about 2 months (47-67 days including a prepupal stage of 6 days, after Sturani, 1962). Hibernation as adult, from October onwards. **Food** (Larochelle, 1990): In captivity, an enormous variation of food is accepted: dead and live insects, raw and cooked meat and liver, cooked potatoes, ant pupae, fruits (including lemon), earthworms and also bread soaked in sugared milk. It might be assumed that it is also a rather polyphagous species in the field (compare *C. nemoralis*). **Larva**: Described by Sturani (1962), Raynaud (1976) and Casale *et al.* (1982). Food – earthworms in the laboratory (Arndt, *pers. observ.*).

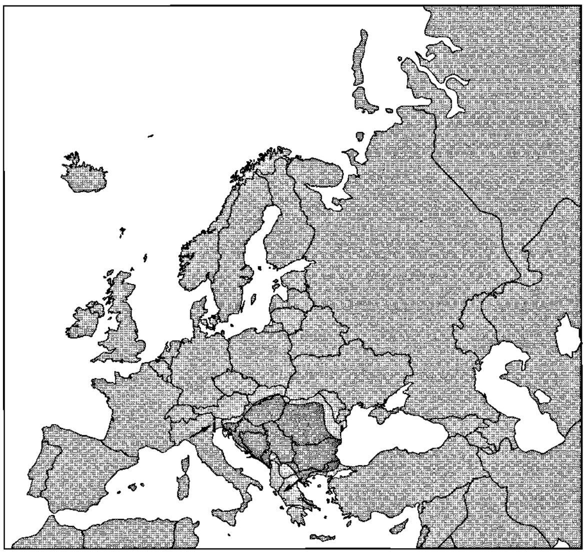
Conservation: As a forest and montane species, no conservation problems at present.

06.003. C. (Archicarabus) montivagus

Palliardi, 1825.

General literature: **Checklists and catalogues** – Breuning (1933): 671. Březina (1994): 25; (1999): 25. Deuve (1994): 123 [214]. Kleinfeld & Schütze (1999): 13. Lorenz (1998): 77. Turin *et al.* (1993): 21. **Iconography** – Casale *et al.* (1982): fig. 67. Ghiretti (1996): 97-98. Imura & Mizusawa (1996): Pl. 16 [124]. Pavicevic & Mesaros (1997): cd-rom. Rautenstrauch (1994): Pl. 37.

Geographical range: S.E. European species: from the Adriatic, widespread in the Balkan Peninsula, N. to S.E. Slovakia, E. to Bulgaria, the Black Sea, and S. to Greece (Epirus, Macedonia). **Chorotype:** SEU-CABA. **Range characteristics:** SEEur. **Distribution in Europe**: **Slovakia** – Reaching S. and S.E. Slovakia. **Hungary** – Sporadic (Szél *in litt.*). **Romania** – In montane habitats of the C. and W. parts; Banat Mts. **Bulgaria** – Widespread, across most of the territory. **Turkey** (Darge, 1990) – European part (not in Anatolia). **Balkan Peninsula** – Istria, Slovenia, W. Croatia (Dalmatia, Adriatic coast), to C. Bosnia-Herzegowina, N., W. and S.W. Montenegro, Serbia, E. Macedonia, N. Albania; in the S. to N. Greece. **Italy** – recently introduced in the Italian C. Alps (Monte Bondone near Trento (Vigna Taglianti *et al.,* 2000). The specimens are very similar to the nominate subspecies.



06 003 montivagus (Archicarabus)

Subspecies: **a) subsp. montivagus** – E. part of area: S. Slovakia, Hungary, W. and S. Romania, Serbia, E. Macedonia, Bulgaria, N.E. Greece. Introduced in the Italian Alps, near Trento, in montane forests (Vigna Taglianti *et al.*, 2000). **b) subsp. vellepiticus** Hampe, 1850 – N.W. Slovenia, forest of Tarnova on Mt. Maggiore, Croatia, Bosnia and Herzegovina, Montenegro, N. Albania, N. Greece (Epirus). *Note*: From Slovakia, Hungary and Romania (excl. Banat), the form *C. m. blandus* Frivaldszky, much smaller than the nominate, was described.

Ecology: An inhabitant of mostly open forests (*Carpinus*), forest steppes of lowlands and foothills, most abundant on flat, preferably limestone, soil between 800 and 2000 m (subsp. *vellepiticus* Hampe); a typical element of the 'Caricetum-Seslesictorum' at 900-1000 m in montane Istria (Brandmayr, 1972). In the S. (Balkan peninsula), also high in the mountains to 1800-2000 m (Bulgaria 0-1600 m, Guéorguiev & Guéorguiev, 1995), present also in forests and more open places. In Bulgaria rather common in forests in lowland and foothills (Penev, *pers. observ.*). In S.E. Slovakia in light deciduous forests (Hůrka, 1996). In Hungary, it inhabits siliceous rock swards, shrubby forest, oak-hornbeam forest in the hills and mountains, as well as the Aceri tatarico-Quercetum in the lowland. In former Yugoslavia, silvicol-praticol, living in deciduous forests in hills and mountains, in the W. (*vellepiticus* Hampe, and form *sutumorensis* Reitter) more in open meadows and alpine habitats (Pavicevic & Mesaros, 1997). Specimens belonging to the small isolated population in N.E. Italy (Trentino), which is most probably an introduction by man, were recorded from alpine grassland (Seslerio-Caricetum sempervirens) at 1700 m (Vigna Taglianti *et al.,* 2000).

Transects: Chapter 8: T-62, 64-68, 70-71, 74-75.

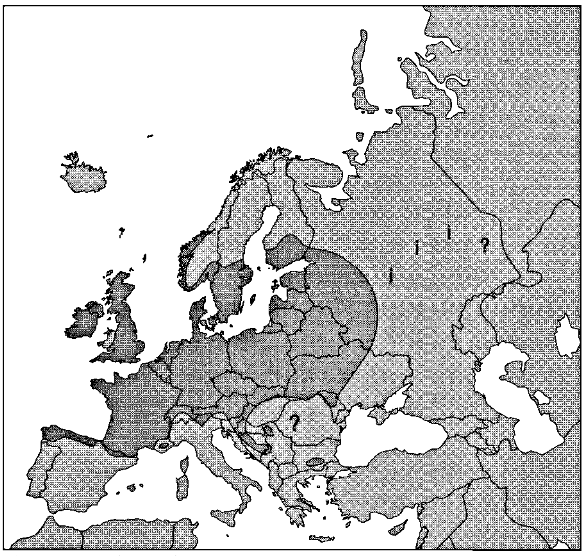
Biology: **Activity** – Night active. **Periodicity** – Data on development are almost completely absent from literature (Hůrka, 1973); larvae of L1- and L2-stages were found in S. Slovakia in May, and of L3s, in June. Adults are reported from Bulgaria in the period April-June (Guéorguiev & Guéorguiev, 1995) and in Italy in the period June-August (Sturani, 1962). Teneral animals were reported to occur from June with a short period of activity immediately after emerging. 'Hibernating' individuals can be found in tree trunks (Sturani, 1962) very early, from late summer onwards (September-May). The larva develops rapidly without diapause (Hůrka, *l.c.*). **Food** (Larochelle, 1990) – In captivity, minced meat, earthworms, fish and apples. **Larva** – Described by Vacher de Lapouge (1906, 1929) and Hůrka (1971b). Food – No data.

Conservation: Not endangered in most of the territory. Pavicevic & Mesaros (1997) call it endangered in the W. of former Yugoslavia, this is however not supported by reliable data. Moreover, it is doubtful; the remarkable ecological flexibility of this species has been illustrated by the fact that it obviously succeeded in founding a new population in the N. Italian Alps, far outside its main area of distribution, most probably introduced by military activities of Austro-Hungarian troops during the First World War (Vigna Taglianti *et al.* 2000).

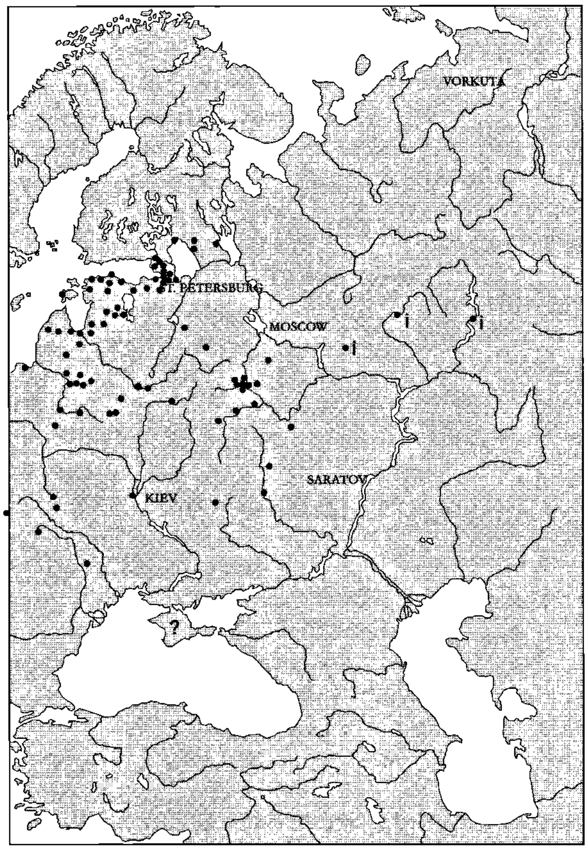
06.004. C. (Archicarabus) nemoralis
O. F. Müller, 1764.

General literature: Checklists and catalogues – Breuning (1933): 665. Březina (1994): 25; (1999): 25. Deuve (1994): 122 [212]. Kleinfeld & Schütze (1999): 13. Kryzhanovskij *et al.* (1995): 42 [73]. Lorenz (1998): 77. Turin *et al.* (1993): 22. **Iconography** – Casale *et al.* (1982): fig. 70. Forel & Leplat (1995): Pl. 8-10; (1998): fig. 18-20. Ghiretti (1996): 94-96. Imura & Mizusawa (1996): Pl. 17 [128]. Jakobson (1905): Pl. 3. Pavicevic & Mesaros (1997): cd-rom. Rautenstrauch (1994): Pl. 35-36.

Geographical range: Europe, except the high N. latitudes, the steppe zone and Mediterranean landscapes; settled E.-ward to Urals and S.E. Kazakhstan (Kryzhanovskij *et al.,* 1995). Occasionally introduced in N. America, where it is now widely distributed (Spence, 1990). **Chorotype:** EUR. **Range characteristics:** WEur-CEur. **Distribution in Europe**: **Fennoscandia** – Norway, along the coast to 64°N; Sweden, distributed and common in the S., to about 61 °N; Finland, common in the S. half of the territory. **Denmark** – Common all over the country. **British Isles** – Widespread in Ireland and Britain, especially in England and Scotland (less records from Wales), usually common and abundant at low altitudes. In many parts probably becoming more abundant, except in Sussex and the London district where it is declining (Clapp, *pers. comm.*; Lindroth, 1974). **Netherlands** – Widespread and common except in the S.W. delta area; one of the most abundant *Carabus* species. **Belgium** – Distributed throughout the country, very common, however reported as declining in the E. **Germany** – Widespread all over the territory and usually common and one of the most abundant *Carabus* species, especially in the C. and S. **Poland** – Distributed throughout most of the country, except in the highest parts in the S.W. and S.E. (Sudeti Wschodnie, Beskid Wschodni, Bieszcady). **Baltic** – Known from all countries. **Byelorussia** – Mainly in the N.W. provinces. **Russian Plain** – W. and C. European Russia, from S. Karelia in the N. to C. Moldova, to the river Svir. In the S., the range limit coincides with the S. border of the forest-steppe, most of the records are from big cities and their environs. The natural E. margin of range seems to go through the provinces of Moscow and Voronezh, to the E. of Moscow recorded mostly from urbanized areas (Vyatka – Yuferev, 1980; Perm', – Koz'minykh *et al.,* 1991b; Ekaterinburg – Koz'minykh, *in litt.*); the records probably concern occasional introductions. The species expands to the E. and is reported also from the city of Novosibirsk (Kozlov, 1991). There is an old specimen in the collection of ZIN labelled from 'Laspi' (Crimea), however its presence in this area has not been confirmed by new observations. It inhabits the area from the S. taiga to the forest-steppe. **Moldova** – Reported from the Kodry Hills. **Czechia & Slovakia** – Reported from the whole territory, often very common. **Hungary** – Distributed and abun-



06 004 nemoralis (Archicarabus)



06 004 nemoralis

dant, but obvioulsy absent from the Great Hungarian Plain. **Romania** – Seemingly not in the territory. **Bulgaria** – Recorded from Sredna Gora Mts., Thracian lowlands and W. Rhodope Mts. **Balkan Peninsula** – Slovenia (Prekmurje), E. Croatia, N.W. Bosnia (Vucja Luka; Sarajevo), W. Serbia (also Fruska Gora (Srem)) and N. Montenegro. **Austria** – Widespread in all parts. **Switzerland** – Widely distributed and common in the N.W. from Geneva to the Bodensee; usually rare above 600 m. In the W. also in the Jura and Unterwallis. Not in the Alps and Alp-valleys. **Italy** – A marginal species, restricted to the N., Valle d'Aosta and Trentino – Alto Adige; old citation from other areas (Piemonte, Veneto, and Emilia) are incorrect. **France** – The species is widely distributed in most of the territory, except for Provence, where however small, isolated populations exist. In the S. reaching to Cevennes and Pyrenees. **Iberian Peninsula** – In this area a strictly N. species, where its distribution ranges from Galicia (province of Coruña), via Cantabrian Mts. and Basque Mts., W. Pyrenees, Sierras de la Demanda and d'Urbion to Valle d'Aran in the C. Pyrenees.

Subspecies: Numerous forms have been described, mainly from France and Spain, but we believe that only two of them merit the status of subspecies (compare also Deuve, 1994): **a) subsp. nemoralis** – In most of the area, except the extreme S.W. **b) subsp. prasinotinctus** Heyden, 1880 (=*pascuorum* Vacher de Lapouge, 1908) – S.W. France (Massive Central, Pyrenees and their foothills, valley of Garonne); N. Spain (not found below 1800 m – Forel & Leplat, 1998).

Biogeography: An extensive biogeographical study has been carried out by Krumbiegel (1932), which showed geographic (N./S. and E./W.) variation correlated to day/night activity; this is also related with the size of the eyes. In E. Europe, the adults showed to be predominantly night active, but in W. and S. Europe, they also showed day activity. The experimental results of Krumbiegel have been discussed by Thiele (1977).

Ecology: Eurytopic, mesophilous, forest species predominantly on humus rich soil, clearly favoured by human activities (Knopf, 1962; Gries *et al.,* 1973; Lindroth, 1985; Turin & Heijerman, 1988; Arndt, 1989; Turin *et al.,* 1991; Anderson *et al.,* 2000). Hoffmann (1907) mentions it for C. Europe mainly from 300 m up to 1000 m. It has no special preference for any soil type, but, at least in the N.C. European lowlands, seemingly avoids peaty soils (Turin, 2000). Predominantly in shaded habitats; eurythermic and with a preference for shadow (Thiele, 1977). It occurs frequently in parks, scrub, gardens, hedgerows, forest edges and all kinds of forest (Stiprajs, 1961; Thiele, 1977); in C. Europe, from open, dry as well as dark, humid lowland forests (Lauterbach, 1964; Den Boer, 1977; Barndt *et al.,* 1991) to (open) mountain forests (Lindroth, 1985; Hůrka, 1996). Sometimes also in grasslands with tall herbs; not in alpine prairies (Thiele, *l.c.*; Koch, 1989), but in some subalpine zones of the E. Alps (e.g. 2100 m, Koralpe, Carinthia – Assmann, *pers. observ.*). In Hungary a typical forest dweller, abundantly occurring in all kinds of shadow-rich forests in the hills and mountains. In situations with sparse vegetation, e.g. on limestone grasslands, preferably on N. slopes. In former Yugoslavia, silvicol, inhabiting deciduous and coniferous forests in hilly and montane regions (Pavicevic & Mesaros, 1997). In Moscow province, it seems to avoid natural, non-disturbed forests, and especially prefers recreational forests, gardens and parks (Fedorenko, 1988). In Ukraine, it inhabits hornbeam and oak-hornbeam forests of the forest-steppe zone, and 'bairak' oak woods of the N. steppe zone (Petrusenko, 1971). In C. Europe (Switzerland) most abundant in the hills and mountains up to 600 m, rare in higher places, although records to 1200 and sometimes 1500 m exist in the Jura (Marggi, 1992). In the S. localities (Italy) it is a montane species which can be found at 1000 m, mostly in subalpine grasslands and forest clearings at 1100-1500 m, locally to over 2000 m (Casale *et al.,* 1982). Not in Mediterranean landscapes and habitats.

Transects: Chapter 1: I-1; Chapter 8: T-01, 03-06, 08-09, 11-21, 23-33, 36-39, 44, 55, 70, 73, 75-77, 80, 89-92, 94-95, 98.

Biology: **Activity** – Most authors report it to be almost exclusively night active; less than 15% day activity (Thiele & Weber, 1968). However, geographic variation has been observed by Krumbiegel (1932), see under *Biogeography*. **Periodicity** – In N.E and C. Europe, the beetles become active in early spring, sometimes from the beginning of March and start to reproduce soon after (Stiprajs, 1961; Den Boer, 1977). Copulations have been observed from March onwards. Copulation of young adults can occasionally take place in late autumn; ripe (= fully developed) eggs were also found in hibernating females (Hůrka, 1973). Xambeau (1898) observed oviposition in autumn. Normally, oviposition occurs in spring from March until May. About 30-60 eggs are laid in series of 6-10 (size 5 x 1.5 mm) each placed in separate cells in a small corridor made by the female. The adults remain active until about July when they enter an aestivation diapause during August-September (Sturani, 1962). Larvae occur during the period April/May – August/September: L1: April-June, L2: May-July and L3: May-August (Larsson, 1939; Stiprajs, 1961). Development of the eggs 10-17 days and the larva 40-60 days: L1: 5-16 days, L2: 10-22 days and L3: 17-25 days (including 8 day prepupal stage); pupae develop in ca 12-15 days, depending on temperature and altitude, all together 55-90 days in France and Italy (Sturani, 1962; Raynaud, 1969) and ca 3.5 months in Denmark (Larsson, 1939). There is no larval diapause (Hůrka, *l.c.*). Teneral adults emerge in W. Europe from the end of June until the end of August, in E. Europe a little later in autumn (July-September), and become active before winter starts (Arndt, 1989; Sturani, 1962). 'Old' adults that already have hibernated, become later active in the autumn, than the young (freshly emerged) adults (Fennemann & Kurz, 1999). Hibernation, under mosses or litter in the soil (mainly in N. areas, but also in the Pyrenees (Casale *pers. observ.*)), in rotten trunks and decaying wood (mainly in the S.), lasts from October to March in the lowlands, but much longer at high altitude, until May (Sturani, *l.c.*). A one-year life cycle, with spring breeding and summer activity of larvae, was reported for Russia (Sharova & Dushenkov, 1979; Dushenkov, 1989). Biennial development in the N. of Scandinavia (Lindroth, 1985). **Food** – An enormous amount of observations exists (Larochelle, 1990). In the field it eats caterpillars of many species (moths and butterflies), earthworms, molluscs (snails and slugs), various insects and insect larvae. Also an attack on young snakes was observed. In captivity, it accepts ham, bacon, raw and minced meat, chopped mealworms (*Tenebrio* sp.), sugar syrup, bread soaked in sugared water or milk and gingerbread, Gruyere cheese and many kinds of fruits, such as bananas, apples, mandarine oranges, dry raisin etc. Many of these things work well as bait in pitfall traps, especially fruits and chopped slugs. **Larva** – Described by Heer (1836: L3), Schiödte (1867: L1), Vacher de Lapouge (1905: L2-L3), Hůrka (1971b) and key: Arndt (1985, 1991b). During a study in Moscow province (near Sosnovka), larvae were only found in interfluvial habitats and not in the flood plains. Food – earthworms, small snails and a wide range of insect larvae and pupae (Arndt, *pers. observ.*).

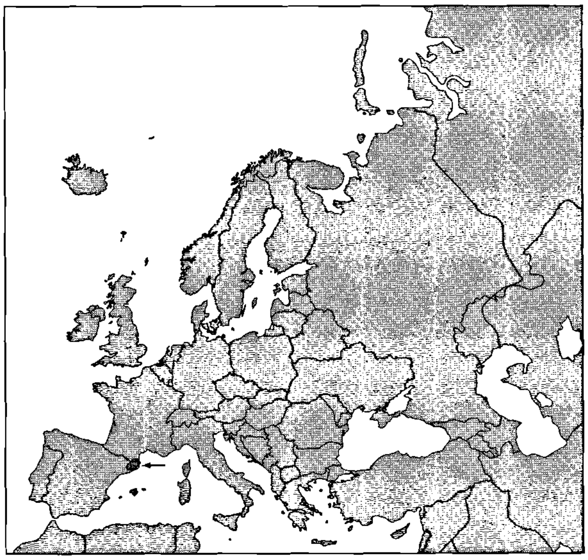
Conservation: In N.W. and N.C. Europe (especially, Denmark, Netherlands and Belgium, Germany) it seems to be favoured by human activities and can be regarded as an increasing species (Desender & Turin, 1989), and it even occurs in parks, gardens, hedges and so on, up to the city centres. In the British Isles, less synanthropic than on the continent, and less common than *C. violaceus* which seems to hold the synantrophic niche (Lindroth, 1974; Luff, 1998). According to Blumenthal (1981), at least in N.W. Europe, it is too eurytopic to be an indicator species. For the Balkan Paninsula, it has been denoted as endangered (Pavicevic & Mesaros, 1997).

06.005. C. (Archicarabus) pseudomonticola
Vacher de Lapouge, 1908.

General literature: **Checklists and catalogues** – Breuning (1933): 661. Březina (1994): 26; (1999): 25. Deuve (1994): 122 [211]. Kleinfeld & Schütze (1999): 13. Lorenz (1998): 77. Turin *et al.* (1993): 22. **Iconography** – Forel & Leplat (1995): Pl. 7; (1998): fig. 15-17. Ghiretti (1996): 93-94. Imura & Mizusawa (1996): Pl. 17 [127]. Rautenstrauch (1994): Pl. 35-36.

Taxonomy: Previously considered rare and poorly known; some authors believed that *pseudomonticola* was only a subspecies of *C. nemoralis* (e.g. Jeannel, 1941). However, nowadays a well-known species which is not considered rare. In the E. Pyrenees, both taxa are sympatric, but no hybrids are known; therefore both forms seem to be true species.

Geographical range: Endemic species of the E. Pyrenees. **Chorotype: WEU-PYRE. Range characteristics:** Iber(NE). **Distribution in Europe**: **France** – Restricted to a small area in the S.: Pyrenees Orientales, from the massif of the Puigmal d'Err to the Canogou and the Alberes. **Iberian Peninsula** – N.E. Spain: mountains of Cataluñia (Montserrat, Montseny); E. Pyrenees, W. to upper streams of Segre and Llobregat.


06 005 pseudomonticola (Archicarabus)

Subspecies: No significant subspecies.

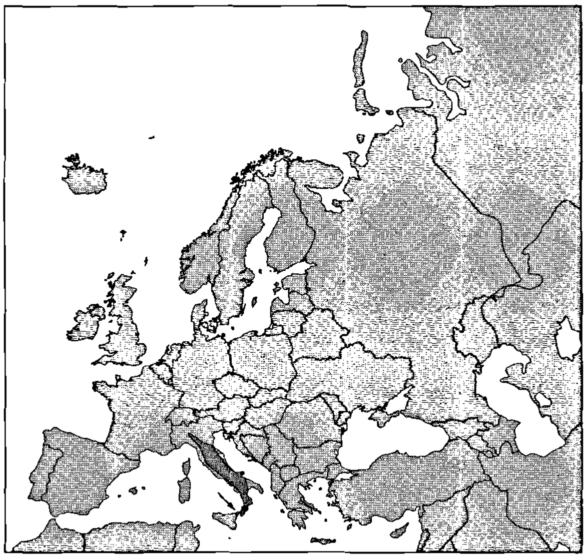
Ecology: Habitat preference most similar to that of *C. nemoralis.* Montane and subalpine, rather eurytopic, shaded places, such as montane forests, forest edges, grasslands with dense vegetation and sometimes in ruderal places (Forel & Leplat, 1998).

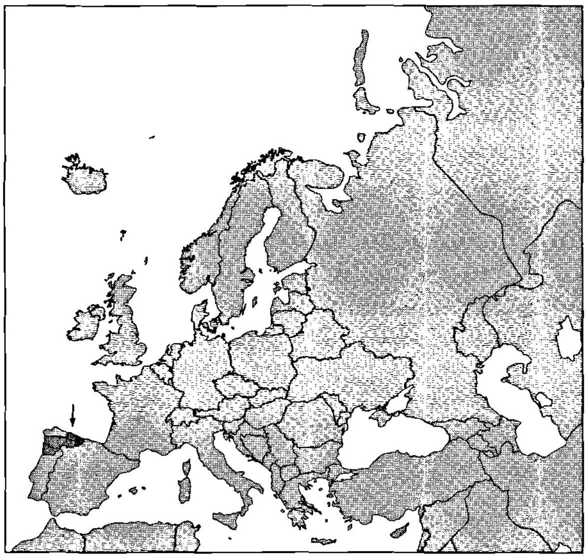
Biology: **Activity** – Both day and night active (Casale, *pers. observ.*). **Periodicity** – Reproduction regularly in spring or summer: at lower altitudes it becomes active at the beginning of spring, at higher altitudes it appears in early summer (beginning of July). Copulation starts immediately after the young adults have emerged; oviposition in small underground, horizontal corridors where the female lays eggs (4 x 2 mm) in separate cells. The eggs hatch after 8-10 days; larval development takes 30-40 days; hibernation near the surface under mosses or at the foot of trees (Forel & Leplat, 1995; 1998) and in rotten wood (Assmann, *pers. observ.*). At the beginning of November, in Alberes, the species was found hibernating, and also a couple that were active during daytime and copulating (Casale, *pers. observ.*). **Food** – Insects, larvae, and other soil arthropods. Also observed eating plant material. **Larva**: unknown.

Conservation: As a eurytopic forest species, no conservation problems at present.

06.006. C. (Archicarabus) rossii
Dejean, 1826.

General literature: **Checklists and catalogues** – Breuning (1933): 656; Březina (1995): 26; (1999): 26. Deuve (1994): 121 [209]. Kleinfeld & Schütze (1999): 13. Lorenz (1998): 76. Turin *et al.* (1993): 22. **Iconography** – Casale *et*


06 006 rossii (Archicarabus)


06 007 steuartii (Archicarabus)

al. (1982): fig. 68. Ghiretti (1996): 93. Imura & Mizusawa (1996): Pl. 16 [119]. Rautenstrauch (1994): Pl. 33.

Geographical range: Endemic of Italy. **Chorotype:** SEU-APPE. **Range characteristics:** Apen. **Distribution in Europe**: **Italy** – Endemic and montane species, distributed from Piedmont (Turin – Langhe to Savona) and all the peninsula, along all Apennines to Calabria and N. Sicily; absent from the N.E.

Subspecies: Highly variable, but Casale *et al.* (1982) regarded it as a monotypic species.

Ecology: Euryzonal and eurytopic species, from lowlands at sea level through montane regions up to 2000 m (Casale *et al.,* 1982). Scattered and very localised in bushes on foothills in the N.W. part of its range (Piedmont).

Transects: Chapter 1: I-3; Chapter 8: T-83-85.

Biology: **Activity** – Diurnal. **Periodicity** – Adults occur from the end of February/March to October/November with a diapause from May/June to September. A proportion of the adult population is active during November-December, before hibernation during January-February (Sturani, 1962). Breeding in spring. Development of eggs (size 5 x 2.5 mm) takes 9-10 days; larvae: ca 55 days including prepupal stage of 12 days and pupae ca 12 days (Sturani, *l.c.*). **Food** – (Larochelle, 1990; Casale *et al.*, 1982): In the field, plant material, fruits, caterpillars, Orthoptera and small Coleoptera. Often under cadavers of birds, reptiles and mammals. In captivity, fruits and raw meat, small slugs and crushed snails. It also accepts earthworms, omelettes, gingerbread and bread soaked in sugared milk. **Larva**: Described by Schiødte (1867), Vacher de Lapouge (1905) and Sturani (1962). Food – in captivity, same as adults.

Conservation: Abundant, and in general no problems or threats apparent. Only in some N.W. populations, such as in Piedmont (hill near Torino), the species seems to have become rare and localised, probably due to urbanisation and loss of habitat.

06.007. C. (Archicarabus) steuartii
Deyrolle, 1852.

General literature: **Checklists and catalogues** – Breuning (1933): 659. Březina (1994): 26; (1999): 26. Deuve (1994): 122 [210]. Kleinfeld & Schütze (1999): 13. Lorenz (1998): 77. Turin *et al.* (1993): 22. **Iconography** – Forel & Leplat (1998): fig. 11-14. Ghiretti (1996): 93. Imura & Mizusawa (1996): Pl. 16 [126]. Rautenstrauch (1994): Pl. 34.

Geographical range: Endemic species of the Iberian Peninsula. **Chorotype:** WEU-IBEN. **Range characteristics:** Iber(NW). **Distribution in Europe**: **Iberian Peninsula** – N. Portugal, N.W. Spain. From Puerto de Pajares in Cabtabrian Mts. via Galician Mts. to Sierra da Estrella.

Subspecies: No subspecies.

Ecology: A generally rare species (Du Chatenet, 1986), mostly found in forests, but also in wasteland at middle altitudes. Alonso *et al.* (1988) found the species in montane grasslands with *Nardus* and *Festuca.* According to Forel & Leplat (1998), it inhabits forests in the zones below 1000 m, but also subalpine prairies in the N. of Portugal and Spain, with a preference for N. facing slopes.

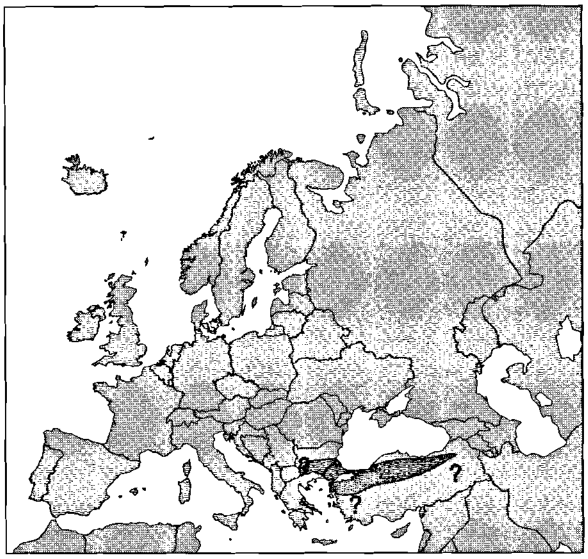
Transects: Chapter 8: T-96-97.

Biology: **Activity** – No data. **Periodicity** – Probably reproducing in autumn. The adults are active from the middle of July until the beginning of October (Forel & Leplat, 1998). **Food** – No data. **Larva** – Unknown.

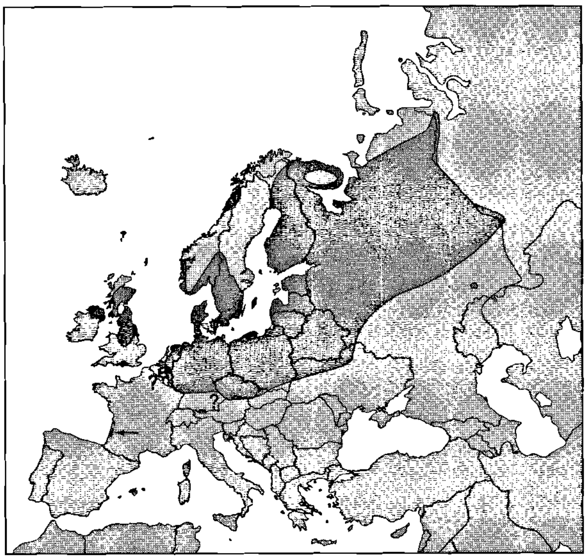
Conservation: Probably not endangered.

06.008. C. (Archicarabus) wiedemanni
Ménétriés, 1836.

General literature: **Checklists and catalogues** – Breuning (1933): 677. Březina (1994): 26; (1999): 26. Deuve (1994): 124 [215]. Kleinfeld & Schütze (1999): 14. Lorenz



06 008 wiedemanni (Archicarabus)



07 001 nitens (Hemicarabus)

(1998): 77. Turin *et al.* (1993): 22. **Iconography** – Ghiretti (1996): 98-100. Imura & Mizusawa (1996): Pl. 16 [123]. Rautenstrauch (1994): Pl. 38.

Geographical range: E. Bulgaria, Greece, European Turkey and Asia Minor. **Chorotype:** ANAT. **Range characteristics:** Balk(SE)-Anat. **Distribution in Europe (and adjacent areas)**: **Bulgaria** – Recorded from S.W. and S.E., not in Danube Plain and Thracian lowlands; localities in S.W. Bulgaria need confirmation! **Turkey** (Casale & Vigna Taglianti, 1999; Darge, 1990) – European part (Guéorguiev & Guéorguiev, 1995); N., C. and W. Anatolia. **Balkan Peninsula** – Besides Bulgaria, only the extreme N.E. of Greece (Alexandropolis).

Subspecies: Several subspecies, but only the nominate one in Europe ('morpha' *burgassiensis* Apfelbeck, 1904, is certainly not a good subspecies). Guéorguiev & Guéorguiev (1995) mention *vaitoiani* Strasser, 1900.

Ecology: Mostly in dry forests and scrubland. In Bulgaria from 0 to 1400 m (Guéorguiev & Guéorguiev, 1995).

Biology: **Activity** – No data. **Periodicity** – No data. **Food** – In captivity, crushed snails, raw meat, fruits and bread soaked in sugared milk (Larochelle, 1990). **Larva:** Described by Raynaud (1975). Food – in captivity, same as adults.

Conservation: No data.

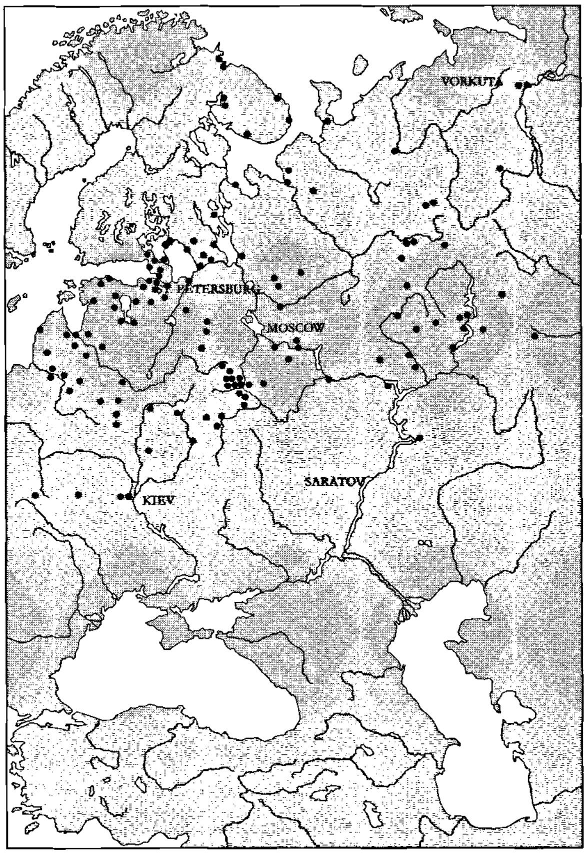
07. HEMICARABUS GÉHIN, 1876

07.001. C. (Hemicarabus) nitens

Linnaeus, 1758.

General literature: **Checklists and catalogues** – Breuning (1933): 850. Březina (1994): 28; (1999): 31. Deuve (1994): 140 [258]. Kleinfeld & Schütze (1999): 17. Kryzhanovskij *et al.* (1995): 43 [79]. Lorenz (1998): 80. Turin *et al.* (1993): 22. **Iconography** – Casale *et al.* (1982): fig. 159. Forel & Leplat (1995): Pl. 11. Ghiretti (1996): 129. Imura & Mizusawa (1996): Pl. 23 [186]. Jakobson (1905): Pl. 5. Rautenstrauch (1994): Pl. 62.

Geographical range: European species. N. and C. Europe, covering most of the area, N. of ca 50°N, from the Atlantic coast to W. Siberia and from Scotland and N. Fennoscandia to W. France, Austria, Carpathian Mts., N. Ukraine. **Chorotype:** SIE. **Range characteristics:** NCEur. **Distribution in Europe**: **Fennoscandia** – Norway, disjunct distribution with an isolated area along the N. coast; Sweden, widely distributed in the S. but not common; Finland, widely distributed but local. **Denmark** – Uncommon, local and decreasing recently. **British Isles** – Very localised in Ireland, not in the S. half of the island, possibly indicating late incursion, probably from Scotland; widespread but not common in N. Ireland (Anderson *et al.*, 2000). In Great Britain also localised and scattered, restricted to wet areas in S.W. and N. England, less widespread in Scotland than *C. arvensis* and probably absent from most of Wales (Lindroth, 1974). **Netherlands** – Formerly a relatively widespread species. However, during the second half of the 20th century, it has strongly decreased due to drainage; recently there was a remarkable revival in three main areas (S., C. and N.), probably caused by a combination of successful nature (heathland) management and favourable climatic changes during the last decade (see Den Boer & Van Dijk, 1995). In the province of Drenthe (N.E.), it appeared to be a dominant species in a large wet heath area (Van Essen, 1993). **Belgium** – Mainly distributed in the N. heathland area. Threatened, its area of distribution is nowadays reduced to 1/3 compared to before 1950. **Germany** – Formerly a widespread species but nowadays heavily endangered (Schleswig-Holstein, Lower Saxony, Mecklenburg-Vorpommern, Brandenburg, Bayern) or probably extinct (Sachsen-Anhalt, Sachsen, Thüringen, Baden-Würtemberg); not known from Hessen and Rheinhessen. **Poland** – A widespread species, known from most regions. **Baltic** – Re-



07 001 nitens

corded from all countries. **Byelorussia** – Mainly in the N. half of the territory. **Russian Plain** – Widely distributed throughout the N. and C. regions of European Russia, up to the coasts of Kola peninsula in the N. (70°N), the N. range margin in the E. coincides with the Polar Circle (S. of Kanin Peninsula – Poppius, 1909); Salekhard (several localities in the S. Yamal Pensinsula – Andreeva & Eremin, 1991), Nenetz area, bifurcation of the rivers Kolva and Kharyaga – MPGU). Perm – Basegi (Voronin, 1999). The S. margin goes along the border between the forest zone and the forest-steppe (right-bank of Dnieper: Medvedev, 1950), from the Ukrainian Carpathians (several localities indicated in museum collections, but not found the last 50 years! – Rizun, 1990) through the provinces of Kiev (ZIN), Gomel' (Molodova, 1990), Bryansk and Kaluga (ZIN), republic of Mari (Eremin, 1986), province of Kazan' (Zherebtsov, 1979), Bashkiria (Matveev, 1990; ZM) and Chelyabinsk province (Field report of the Institute of Evolutinary Morphology & Ecology, Moscow, 1981). From the tundra to the mixed forest zone. **Czechia & Slovakia** – Mentioned for Bohemia, Czechia and Slovakia, but rare. **Hungary** – Only one doubtful record (specimen lost) was published by Freh (1878) from the Kőszeg Mts. **Austria** – Few scattered occurrences in Tirol, Oberösterreich, Niederösterreich and Steiermark; endangered or possibly extinct. Franz (1970) gives localities of *C. nitens* in Austria, near the W. Hungarian border: Leibnitz, Steinfeld, Baden. **Italy**: old citations from Brenner only: no recent data. **France** – The species was reported from wet sandy habitats scattered along the Atlantic coast from Belgium to Landes. It probably disappeared from most of the former area of distribution and survives now in a very isolated population near the Bassin d'Arcachon, just S. of Bordeaux. It is possible that it still exists near the Baie de Somme in the N.W. but this has to be verified.

Subspecies: Very homogeneous; no subspecies.

Ecology: In N.W. Europe, this species shows a peculiar 'split' habitat preference. Predominantly it is a sun-loving species, occurring in humid meadows and marshes, moist heathland and peat bogs with *Erica*, but it is also frequently found on the dry sandy soil of inland dunes, *Calluna*-heath and in open pine forest (Rabeler, 1947; Stiprajs, 1961; Mossakowski, 1970a; Den Boer, 1977; Koch, 1992; Hůrka, 1996). In N. Ireland and Britain mainly inhabiting wet upland biotopes such as wet dwarf scrub heath and upland or lowland blanket bog or N. wet heath, wet dune slacks, and it obviously avoids dry biotopes completely (Anderson *et al.,* 2000; Luff, 1998). Lindroth (1985) reports it from the 'Alvar' steppes on Öland and Gotland. In N.C. Europe, often found in wet heathlands where also *C. clatratus* occurs. According to Andreeva & Eremin (1991), it inhabits mesotrophic alder groves in the S. Yamal peninsula. In C. Europe, not alpine (Koch, 1989); after Burmeister up to 1200 m, but after Horion (1941) not over 400 m; indeed almost absent from the C. montane areas. In the British Isles, in open country and dry places, usually where heather grows (Lindroth, 1974; Gardner, 1991). In Germany mostly in light heath-forests, on peat moors, wasteland and coastal dune valleys (Arndt, 1989). In the Lüneburger Heath, the area with the largest heathlands in Germany, the species prefers sites in the *Calluna* heath where the vegetation is sparse (mainly in the building phase) and not with a higher vegetation of ericaceous shrubs (mainly the mature and degenerate phases of *Calluna*) (Assmann & Janssen, 1999). In the S.-most area of the range confined to coastal dunes along standing water (Du Chatenet, 1986). In Ukraine, rare in mixed and pine forests of the forest-steppe zone (Petrusenko, 1971).

Transects: Chapter 1: I-2; Chapter 8: T-01, 04-06, 08-09, 11, 13-17, 19, 21, 23-24, 35, 43, 45 and 55.

Biology: **Activity** – Heliophilic: a mainly diurnal species (Weber, 1966a; Thiele & Weber, 1968). **Periodicity** (Hůrka, 1973) – Reproduction starts in early spring (perhaps by the second half of April) with a maximum between May and the end of June (N.W. Europe – Arndt, 1989). Sturani (1962) mentions adult activity for the period June-August and hibernation from September to May. In C. Europe, the adults occur from March to September, with a clear maximum during May and June and show in general very little activity in autumn (Lindroth, 1985). The young adults hibernate in the pupal chambers (Larsson, 1939). L1 is reported from May and June, and L3 from July (Luff, 1969). The duration of the development is rather short, about 35-40 days, including an 8-9 day pupal stage (Hůrka, *l.c.*). Pupation was recorded by Stiprajs (1961) at the end of July; fresh animals occur in summer, from August onwards. Larsson (1939) assumed that hibernation took place in pupal cells, however in Germany a proportion of the population is active before hibernation (Mossakowski, 1970b; Assmann & Janssen, 1999). In August and September, no old beetles seem to be active. In two successive spring seasons (according to the results from ovary dissections detecting *corpora lutea* before oogenesis), the Lüneburger Heath populations chiefly consisted of animals that had already reproduced (and therefore were older than one and a half years (Assmann & Janssen, 1999). **Food** (Larochelle, 1990) – In captivity, it seems to accept a variety of food, such as raw meat, minced meat, earthworms, fish and apples. In the field, it was observed hunting caterpillars of moths. **Larva**: Described by Bengtsson (1927: L1-L3), Hůrka (1971b) and key: Arndt (1985, 1991b). Food – No data, but probably the same as adults.

Conservation: A strong decline was reported from all parts of N.W. Europe (Arndt, 1989; Desender & Turin, 1988). Also in Moscow province rather common until the 1950's, but recently only single records are available (Fedorenko, 1988). In the Netherlands, where it has declined strongly during the last decades (Turin, 2000), it recovered in various places, when the (acid) upper soil-layer was partly removed from many wet heathland reserves. Especially in the first years after applying this type of management, it not only recovered or perhaps recolonised, but became a dominant species (Reinholt & Vermaat, 1989; Van Essen, 1993; Den Boer & Van Dijk, 1994). The species is a very suitable indicator of the quality of oligotrophic, open heathland and dune habitats and also peat-bogs with an intact water regime (Blumenthal, 1981). However, it seems to have a high resistance to chemical pollution and was observed to be one of few surviving species on polluted fields in the Netherlands (Turin, 2000) and in Byelorussia (Chumakov, 1986).

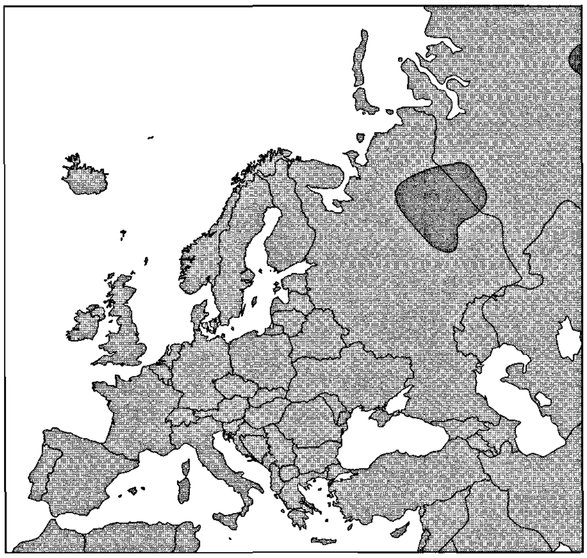
08. DIOCARABUS REITTER, 1896

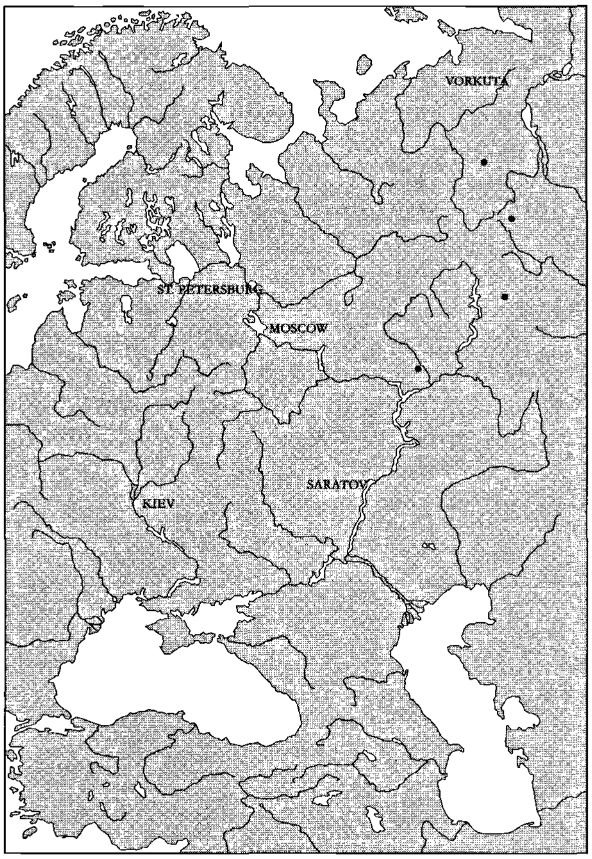
08.001. C. (Diocarabus) loschnikovii
Fischer von Waldheim, 1823.

General literature: Checklists and catalogues – Breuning (1932): 308. Březina (1994): 34; (1999): 32. Deuve (1994): 143 [272]. Kleinfeld & Schütze (1999): 18. Kryzhanovskij *et al.* (1995): 44 [94]. Lorenz (1998): 81. Turin *et al.* (1993): 22. **Iconography** – Ghiretti (1996): 133. Imura & Mizusawa (1996): Pl. 25 [200]. Jakobson (1905): Pl. 7. Ratti *et al.* (1990): Pl. 14.

Geographical range: N.E. European Russia (in S.W. to Kirov), Siberia to Baikal. **Chorotype: SIB. Range characteristics:** EEur(E)-CSib. **Distribution in Europe (and adjacent areas)**: **Russian Plain** – The population in N.E. Russia and the N. Urals is isolated from the main Siberian range (Shilenkov & Averenskii, 1991). E. regions of European Russia and the Urals to the W. to 50°E., known from Narodnaya Mt. – MPGU, and from few localities in Tyman Mt. Range (Belaya river – ZIN), the provinces of Vyatka (Malmyzh – ZIN), Perm' (Basegi reserve – Voronin & Esjunin, 1989), the Polar Ural (Neroika Mt. – MPGU); N. Ural (Man'ya river baisn – ZIN).

Subspecies: Except nominate, no subspecies in Europe.


08 001 loschnikovii (Diocarabus)



08 001 loschnikovii

Ecology: In the forests of mainly lower and middle mountain belts. In the Basegi reserve (Middle Ural), very common in the shrubby-lichen tundra and in thin birch forests (Esjunin *et al.,* 1995).

Transects: Chapter 1: I-2; Chapter 8: T-45.

Biology: Especially numerous during July and August (Esjunin *et al.,* 1995).

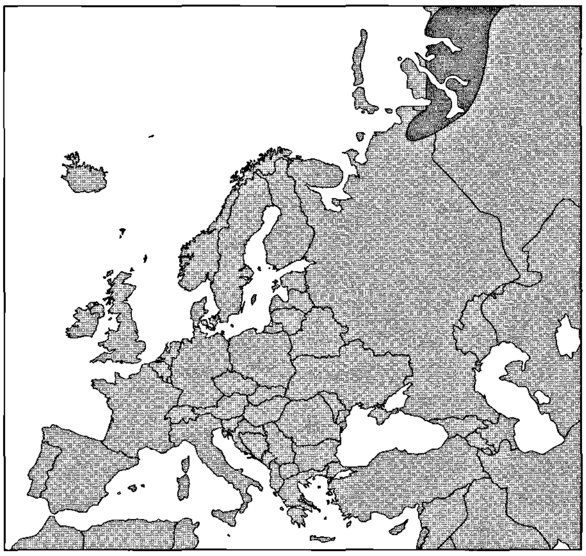
Conservation: No data.

08.002. C. (Diocarabus) truncaticollis
Eschscholtz, 1833.

General literature: **Checklists and catalogues** – Breuning (1933): 775. Březina (1994): 34; (1999): 50. Deuve (1994): 152 [307]. Kleinfeld & Schütze (1999): 18. Kryzhanovskij *et al.* (1995): 43 [90]. Lorenz (1998): 81. Turin *et al.* (1993): 23; see note under *Taxonomy*. **Iconography** – Ghiretti (1996): 150-151. Imura & Mizusawa (1996): Pl. 38 [318]. Jakobson (1905): Pl. 7.

Taxonomy: In the checklists of Turin *et al.* (1993), Deuve (1994) and Březina (1999)), this species was included in subgenus 09. *Aulonocarabus*.

Geographical range: N.E. European Russia, N. Siberia, Kamchatka, Aleut Islands (Poppius, 1910) and N.-most Alaska and Canada (N.W. territories). **Chorotype:** SIB (circumpolar). **Range characteristics:** EEur-Sib. **Distribution in Europe (and adjacent areas): Russian Plain** – N.E. part of the Russian Plain, N. of the Polar Circle and Polar Ural. Collected in the environs of Vorkuta (MPGU), the basin of Adzyva river (ZIN, Poppius, 1905), Salekhard (ZIN; Poppius, 1905), S. Yamal Peninsula (common – Andreeva & Eremin, 1991; Khadyta-Yakha field station – Korobeinikov, 1991), Nenets Area (the rivers Kolva and Karyaga; Yugor peninsula – MPGU). Inhabits the tundra and the N. border of the forest-tundra zone (Shilenkov & Averenskii (1991).



08 002 truncaticollis (Diocarabus)

08 002 truncaticollis

Subspecies: Except nominate, no subspecies in Europe.

Ecology: Forest-tundra and S. tundra zones. In the S. Yamal peninsula, where it is a very common species, it inhabits all types of tundra and open, scrubby larch forests with mosses; sometimes found in wet interfluvial alder groves. It is a mesophilous species that tolerates a wide range of habitats with respect to humidity (Andreeva & Eremin, 1991). Shilenkov & Averenskii (1991) report that the non-European subspecies *polaris* is found in Yakutia near water bassins.

Transects: Chapter 8: T-42 and 43.

Biology: **Activity** – No data. **Periodicity** – In S. Yamal, adults occur from the end of June to the beginning of August and females with eggs occur during July-August; teneral specimens were recorded from the beginning of August; hibernating L3 and adults of several generations (at least 3) were found in Russia (Korobeinikov, 1990). Other figures (data after Ryabitsev, 1995; 1998) indicate that 96% of the investigated populations consist of specimens of the same year and that 1.5% have hibernated a first and merely 0.5% a second time. Males would live not longer than 2 years and females up to 4 years (Ryabitsev, *l.c.*). **Food** – No data. **Larva**: Described by Vacher de Lapouge (1907: L3). Food – Lindroth (1961) reported predation of larvae of *Tipula* (Diptera, Tipulidae) in Canada.

Conservation: No data.

09. AULONOCARABUS REITTER, 1896

09.001. C. (Aulonocarabus) canaliculatus
Adams, 1812.

General literature: Checklists and catalogues – Breuning (1932): 249. Březina (1994): 29; (1999): 49. Deuve (1994): 155 [317]. Kleinfeld & Schütze (1999): 24. Kryzhanovskij *et al.* (1995): 43 [81]. Lorenz (1998): 88. Turin *et al.* (1993): 23. **Iconography** – Ghiretti (1996): 153-154. Imura & Mizusawa (1996): Pl. 37 [314]. Jakobson (1905): Pl. 7. Ratti *et al.* (1990): Pl. 7.

Taxonomy: In the checklist of Kleinfeld & Schütze (1999), included in *Leptocarabus* Géhin, 1885.

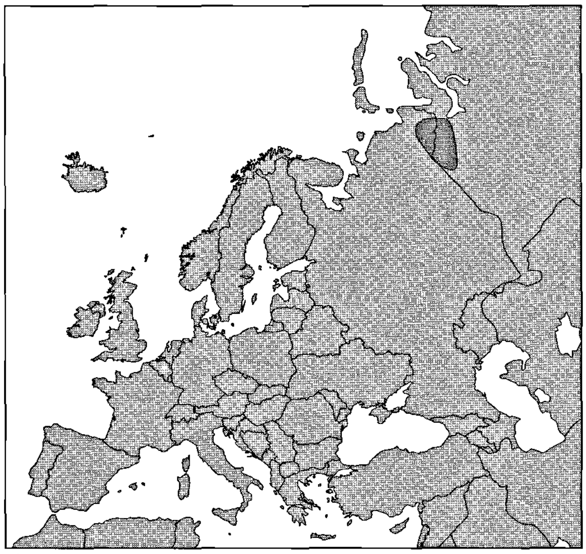
Geographical range: Russia: Ural, Siberia to the Far E.; Primorye, Priamurye (Budarin & Matis, 1981), Altai and Enisei, N. Mongolia, N.E. China, N. Korea. **Chorotype:** SIB. **Range characteristics:** EEur(NE)-Sib-EAsi. **Distribution in Europe**: Known from only three localities in Polar Ural (Sob' River Basin, district of Salekhard – ZIN) and N. Ural (Manya River Basin – ZIN). This species does not occur in the W. part of the Ural Mts. The presence on the Polar Ural is isolated from the main range of this E. Siberian species (Shilenkov & Averenskii, 1991).

Subspecies: Several subspecies exsist, but only the nominate one is present in Europe.

Ecology: It lives in taiga forests, e.g. in Yakutia where it is very common in pine forests, rarely in larch or willow stands or scrub; sometimes on arable land (Budarin & Matis, 1981; Shilenkov & Averenskii, 1991). In Krasnoturanskiy Bor (C. Siberia), in pine forests on steep slopes of mountains, in dunes and tussocky birch forest (Anyushin, 1982).

Transect: Chapter 1: I-2.

Biology: **Activity** – No data. **Periodicity** – Probably a summer (or early autumn) breeder; the adults occur from the first half of July to the end of August (Budarin & Matis, 1981). **Food** – No data. **Larva**: Described by Makarov (1992). Food – No data.



09 001 canaliculatus (Aulonocarabus)

09 001 canaliculatus

Conservation: Extremely abundant; not endangered.

10. MESOCARABUS C. G. THOMSON, 1875

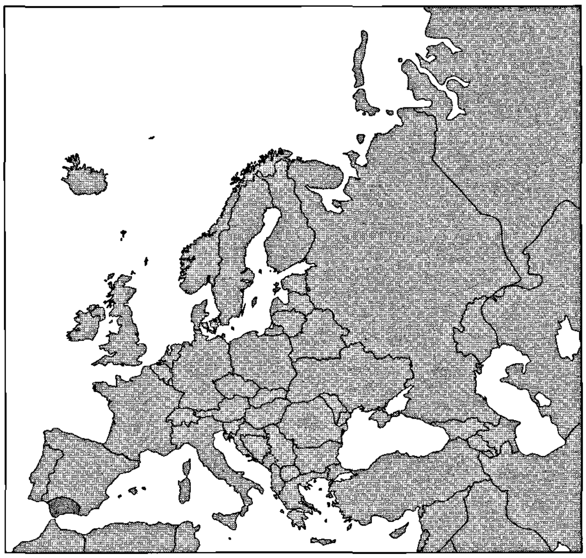
10.001. C. (Mesocarabus) dufourii
Dejean & Boisduval, 1829.

General literature: Checklists and catalogues – Breuning (1933): 827. Březina (1994): 43; (1999): 41. Deuve (1994): 174 [390]. Kleinfeld & Schütze (1999): 20. 84. Turin *et al.* (1993): 23. **Iconography** – Forel & Leplat (1998): fig. 90-93. Ghiretti (1996): 188. Imura & Mizusawa (1996): Pl. 29 [240]. Rautenstrauch (1994): Pl. 58.

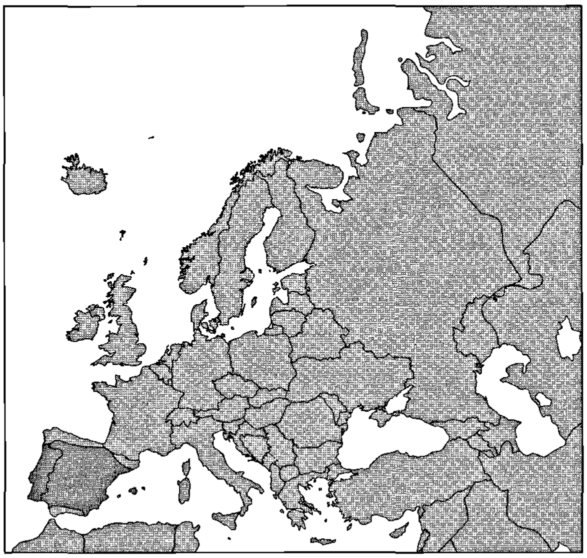
Geographical range: Endemic species of the Iberian Peninsula. **Chorotype:** WEU-IBEC. **Range characteristics:** Iber(SW). **Distribution in Europe**: Iberian Peninsula S. of Guadalquivir: most of Andalusia from Atlantic coast to Sierra Nevada and Sierra de Gador in the S. and to Sierra de Segura in the E.

Subspecies: No subspecies.

Ecology: From sea level in the W. to 2500 m in the E. (occasionally up to 3000 m). Preferably on humid sites, in open country as well as places shaded by woods, so it can be considered an eurytopic species (Du Chatenet, 1986; Forel & Leplat, 1998; Cárdenas & Hidalgo, 2000).



10 001 dufourii (Mesocarabus)



10 002 lusitanicus (Mesocarabus)

Transect: Chapter 8: T-100.

Biology: **Activity** – no data. **Periodicity** – Depending on altitude, adults have been reported from March/June to September (Du Chatenet, 1986; Forel & Leplat, 1998). The seasonal activity and the reproductive biology was described in detail by Cárdenas & Hidalgo (2000). The periodicity is similar to those of the N. African winter-breeders such as *C. morbillosus*. There is a high reproductive activity during October-December. The number of eggs laid per oviposition is on average 1-6 (with a maximum of 12). In the period of January to March, most animals are inactive. The fresh specimens appear during March-April and immature females are active until the end of June. During July and August, the animals seem to be completely inactive. Pre-reproductive females occur mainly in October and November. The development in the laboratory showed an average of 12 days for the incubation of the eggs (with a survival rate of nearly 70%), 12.5 days for the first instar (survival 80%), about 9 days for the second instar (survival 85%), 23 days for the third instar (survival 80%) and 10.5 days for the pupa (with a low survival of 31%). Under outside conditions, these figures were (no data on egg development): 19 days for the first instar (survival 81.7%), about 18.5 days for the second instar (survival 96%), 50.6 days for the third instar (survival 85%) and 16 days for the pupa (with a much higher survival than inside rearing, of 62%). **Food** – similar to other *Mesocarabus* species (Forel & Leplat, *l.c.*). **Larva**: unknown.

Conservation: Generally not endangered, but declining in some localities (for instance near Gibraltar), due to urbanisation.

10.002. C. (Mesocarabus) lusitanicus

Fabricius, 1801.

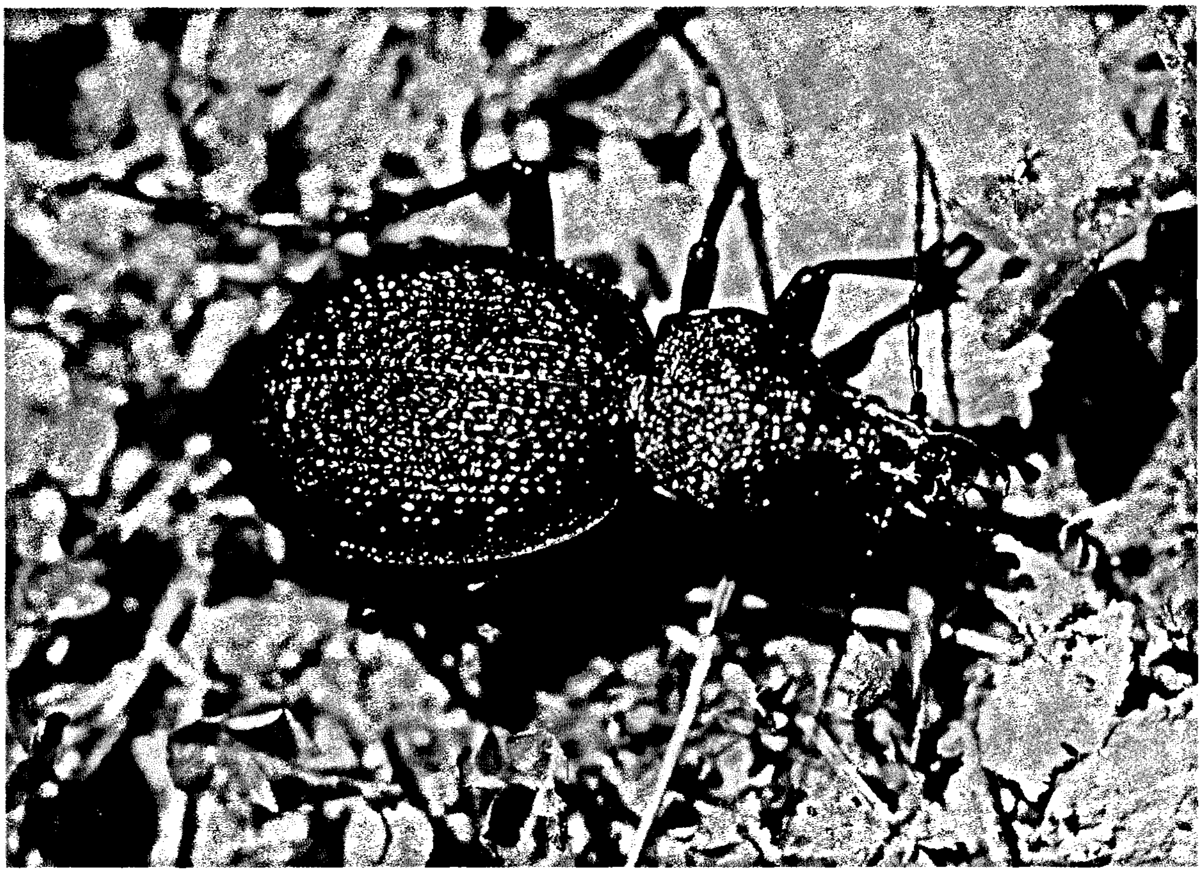
General literature: **Checklists and catalogues** – Breuning (1933): 830. Březina (1994): 43; (1999): 41. Deuve (1994): 173 [389]. Kleinfeld & Schütze (1999): 20. Lorenz (1998): 84. Turin *et al.* (1993): 23. **Iconography** – Forel & Leplat (1995): Pl. 26; (1998): fig. 48-89. Ghiretti (1996): 188-192. Imura & Mizusawa (1996): Pl. 29 [239]. Rautenstrauch (1994): Pl. 58-60.

Taxonomy: We maintain here two distinct species, which are, more correctly, two main semispecies, *C. lusitanicus* and *C. macrocephalus* Dejean, 1826; hybrid zones exist between them, and natural hybrids are also known in areas of parapatry.

Geographical range: Endemic species of the Iberian Peninsula and Pyrénées Atlantiques. **Chorotype:** WEU-IBER. **Range characteristics:** Iber(P). **Distribution in Europe**: **France** – Restricted to the Atlantic Pyrenees, close to the N. Spanish border. **Iberian Peninsula** – All of the Iberian Peninsula, except the N.W. part where it is bordered by the S. Galician mountains (Sil Valley), Montes de León and the provinces of Valencia and Burgos. In the N. of the peninsula up to the C. Pyrenees (Esera Valley) and E. Pyrenees in the area between the rivers Segre, Ebro and Ter.

Subspecies: (Breuning, 1926: map; Forell & Leplat, 1998: maps): one of the most differentiated species in Europe. **a) subsp. lusitanicus** – Coastal area of Extremadura, between Coimbra and Lisbon. **b) subsp. schaumi** Gaubil, 1849 – Spain, C. Montane System to C.W. Portugal. **c) subsp. bolivari** Breuning, 1926 – Spain, C. Montane System: Sierra de Béjar. The characters to distinguish *fuentei* Breuning, 1926, from the Sierra de Gata and Peña de Francia, seem variable. **d) subsp. brevis** Dejean, 1826 – Spain, C. Mountains System: Sierra da Avila and S. de Guadarrama regions. **e) subsp. complanatus** Dejean, 1826 – Spain, N. Meseta, Zaragoza, Soria and Burgos regions. **f) subsp. molossoides** Lassalle, 1984 – Spain, C. Montane System, W. and C. Sierra de Gredos, Tras la Sierra mountains. **g) subsp. helluo** Dejean, 1826 – Spain, N. Iberian and S. Ibe-

C. **rutilans** Dejean
East Pyrenees, Ceret,
France.
Photo by
A. Casale &
G. Delitala.



C. **gigas** Creutzer
Greece, Pindus.
Photo by
A. Vigna Taglianti.

C. *rossii* Dejean
Italy.
Latium (Rome).
Photo by
A. Vigna Taglianti.

C. cenisius fenestrelleanus
Beuthin
Italy. Cottian Alps
(C. Finestre).
Photo by
A. Vigna Taglianti.

rian chains, E. Baetic chain. **h) subsp. castilianus** Dejean, 1826 – Meseta region of Salamanca. **i) subsp. egesippei** Laferté-Sénectère, 1847 – Mountains of N. Portugal. **j) subsp. antiquus** Dejean, 1826 – S. Portugal and S.W. Spain, N.E. to Salor and Zapaton rivers. **k) subsp. albaracinus** Ganglbauer, 1886 – Spain, Sierra de Albarracin and Sierra de Cuenca. **l) subsp. latus** Dejean, 1826 (= (*antiquus*) *gougeleti* Reiche, 1863; see Silfverberg, 1977) – Spain, S. Meseta, to the Sierra Morena, to E. to the Toledo and Cordoba regions. **m) subsp. baguenai** Breuning, 1926 – Spain, N. Baetic chains, Almeria and Granada regions. **n) subsp. trabuccarius** Fairmaire, 1857 – Spain, Catalunian chain, E. and C. Pyrenees. Very small specimens at high altitude, from C. Pyrenees (Ordesa, Cinca and Esera valleys) have been described as *trypalsi* Breuning, 1975.

Ecology: From coastal areas (e.g. in Portugal) and foothills to high altitude pastures at 2000 m (locally up to 2500 m), mostly in open hilly country with dry bushes and open pine forests (Du Chatenet, 1986; Forel & Leplat, 1998).

Transects: Chapter 8: T-95-100.

Biology: **Activity** – No data. **Periodicity** – Active from May-October, in the S. until November and December. Little is known about the development, because it is very difficult to breed this species (Forel & Leplat, 1995). Reproduction takes place in autumn, and the larvae hibernate as second stage instars; larval development lasts until spring (Forel & Leplat, 1998). **Food** (Larochelle, 1990) – In the field, snails, small insects and apples. It is probably a specialised snail eater, able, like *C. coriaceus*, to chrush the shells with its short and strong mandibles (Boettger, 1921). **Larva**: Described by Raynaud (1974).

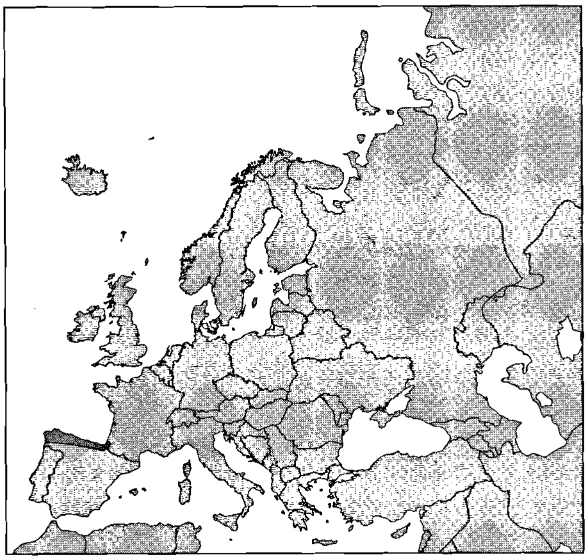
Conservation: Abundant in most localities, and not endangered.

10.003. C. (Mesocarabus) macrocephalus
Dejean, 1826.

General literature: **Checklists and catalogues** – Breuning (1933): 834. Březina (1994): 43; (1999): 43. Deuve (1994): 173 [389]. Kleinfeld & Schütze (1999): 21. Lorenz (1998): 84. Turin *et al.* (1993): 23. **Iconography** – Ghiretti (1996): 192. Imura & Mizusawa (1996): Pl. 29 [239].

Taxonomy: Treated as a subspecies of *C. lusitanicus* Fabricius by Březina (1994, 1999), Deuve (1994) and Kleinfeld & Schütze (1999).

Geographical range: N. Spain, from Galicia to the Basque Pyrenees, Sierra de Andia. France, W. Pyrenees. **Chorotype:** WEU-IBEN. **Range characteristics:** Iber(N). **Distribution in Europe**: **France** (Jeannel, 1941; Bonadona, 1971) – W. Pyrenees. **Iberian Peninsula** (Breuning, 1926; Zaballos & Jeanne, 1994) – N. part of the peninsula: Galicia including the mountains, Cantabrian Mts., E. to Basque mountains, Sierra de Andia and W. Pyrenees.


10 003 macrocephalus (Mesocarabus)

Subspecies (Breuning, 1926: map): **a) subsp. macrocephalus** – W., C. Cantabrian chain. There is a slight distinction between the E. (*barcelecoanus* Vacher de Lapouge, 1924; *amayensis* Lassalle, 1984) and the W. populations (Jeannel, 1941). **b) subsp. macrocephaloides** Jeanne, 1972 – N.E. Spain, Sierra de Andia. **c) subsp. cantabricus** Chevrolat, 1840 – Mountains of Galicia. **d) subsp. asturicus** Born, 1925 – W. Cantabrian Mountains. **e) subsp. joaquini** Breuning & Toulgoët, 1974 – W. Cantabrian Mountains, on the S. side. **f) subsp. moroderi** Breuning, 1926 – Spain, mountains of Léon. *Note*: This subspecies, and the following, seem to be transitional forms to *macrocephalus* (and this makes questionable the specific separation of the latter from *lusitanicus* by Zaballos & Jeanne (1994), and subspecies of a 'semi-species' *macrocephalus* (of *lusitanicus*) by Deuve (1994). **g) subsp. breuningi** Csiki, 1927 – Spain, S. Galicia. **h) subsp. barcelecoanus** Vacher de Lapouge, 1924 – According to Deuve (1994) and Březina (1999), *barcelecoanus* is markedly distinct from *macrocephalus* (*s.str.*). Characterised by narrow, elongate body and reduced sculpture – N.C. Spain (Santander to Pomplona), E. Cantabrian chain, W. Pyrenees on both sides.

Ecology: In open country on rocky soil, in clearings, especially in montane beech forest areas, but also at lower altitudes in *Quercus* and *Castanea* stands. In the subalpine and alpine zone, mostly restricted to the area between 1000 and 2000 m (Herrera & Arricibita, 1990).

Transect: Chapter 8: T-98.

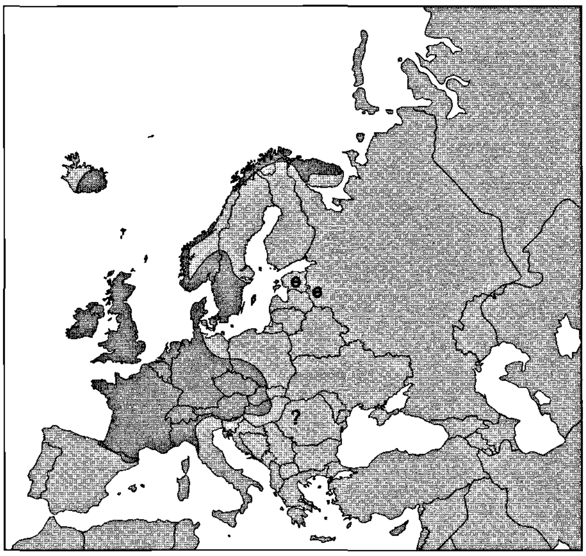
Biology: **Activity** – Predominantly nocturnal. **Periodicity** – Similar to *C. lusitanicus*. At higher altitudes (about 1500 m, Ibaneta, and 2000 m, Peña Ubiña) females are in oogenesis (observations from ovary dissections) during August and September. Tenerals were found during May and June. Probably an autumn breeder. In September, tenerals were also recorded from *Castanea* woodlands (Assmann, *pers. observ.*). **Food** (Larochelle, 1990) – Adults were baited in the field with gingerbread, raw meat, snails, earthworms and beer. **Larva**: Described by Raynaud (1975). Food – no data.

Conservation: Abundant, not endangered.

10.004. C. (Mesocarabus) problematicus

Herbst, 1786.

General literature: **Checklists and catalogues** – Breuning (1933): 806. Březina (1994): 44; (1999): 42. Deuve (1994): 171 [388]. Kleinfeld & Schütze (1999): 21. Kryzhanovskij *et al.* (1995): 45 [108]. Lorenz (1998): 84. Turin *et al.* (1993): 24. **Iconography** – Casale *et al.* (1982): fig. 52. Forel & Leplat (1995): Pl. 23-26; (1998): fig. 42-47. Ghiretti (1996): 184-188. Imura & Mizusawa (1996): Pl. 29 [241]. Rautenstrauch (1994): Pl. 56-57.



10 004 problematicus (Mesocarabus)

10 004 problematicus

Geographical range: C. and N. European species, from E. Spain in the W., to Poland and Hungary in the E. In the N., it reaches Iceland and Murmansk district; in the S. to the Alps and N.W. Italy. **Chorotype: EUR. Range characteristics:** NEur-CEur-WEur. **Distribution in Europe**: **Iceland**: (Larson & Gigja, 1959) – The only *Carabus* species from Iceland, represented by a distinct subspecies (see below). **Fennoscandia** – Present on the Faeroer Islands. Not in C. and E. Fennoscandia. Distributed from the S. along the Norwegian coast to the high N. and Kola peninsula, common in most places. **Denmark** – Restricted to Jutland, widespread and not uncommon. **British Isles** – One of the commonest species, widely distributed and abundant in the N.; less common in C. and E. England. **Netherlands** – Widely distributed and abundant in the sandy areas in the C. and E. part of the country; together with *C. granulatus* and *C. nemoralis* belonging to the commonest species of the territory. **Belgium** – Widespread in the sandy and forested areas, mainly in the C. and E. **Germany** – Widely distributed and especially abundant in the W., but seemingly absent from the N.E. (Berlin, Mecklenburg-Vorpommern). Widespread and frequently found in the mountains but rare and less common in the mountain foreland. Towards the E. it becomes rapidly scarcer and more scattered in progressively smaller populations, very local E. of the river Elbe (Blumenthal, 1981). **Poland** – Mainly in the S.W. and C.; not along the N. coast and in the N.E.; also not in the S.E. **Baltic** – No clear reports; doubtful single old records exist from Estonia or E. Latvia (see also: Lindroth, 1945). **Russian Plain** – A species with a rather unusual range, common along the coasts of the Kola Peninsula (several localities – ZIN, MPGU), in the S to Khibiny Mts. In the Kola Peninsula distributed from the tundra to the N. taiga. Isolated populations seem to have existed in N.W. European Russia (Remda in Pskov province – ZIN; Estonia – Haberman, 1968), its presence there needs to be confirmed. Interesting in this respect is a recent record from C. Siberia (!) – Krasnoyarsk Area, 3 km N. of Nazarovo (21.VII.1989, leg. Tsurikov, vide Makarov), however, this occurrence may be due to introduction by man, although the species must have established locally. **Czechia & Slovakia** – Recorded from all regions, but scattered and only locally common. **Hungary** – Local and rare in the montane region. **Romania** – Occurrence in Transylvania needs confirmation; reported as sporadic from the E. and S. Carpathians (Balan, Brasov Mts. and Retezat Mts.) **Austria** – Widespread in nearly all parts of the country; not reported from Osttirol. **Switzerland** – Mainly in the area from Geneva to the N.E. in foothills and mountains, rarely subalpine; in the Jura to the peaks, but in the C. Alps not reaching the same hight. The highest altitudes are reached in S.W. Wallis, up to 2000-2200 m. **Italy** – In the N.most parts: Alps and Prealps of Piedmont, Liguria, Lombardia, Venetia, Ticino; isolated in Ligurian and Toscan-Emilian Apennines. **France** – Widely distributed throughout the territory; absent from N.W. Brittany and near Calais – Dunkerque (Valemberg, 1997a). Alpine in the Pyrenees, up to over 2400 m. **Iberian Peninsula** – Restricted to the Pyrenees and the atlantic N. of the peninsula, from the W. (Valle d'Irati) to the N. side of the Catalan chain, S. of river Ter.

Subspecies: *C. problematicus* is morphologically rather homogeneous across its distribution. Its ability to adapt to different ecological conditions allows the species a nearly uninterrupted distribution across its entire range. Nevertheless, dozens of infraspecific forms (subspecies, 'nationes', 'morphae', etc. for small colour variations, small montane specimens, inconstant variability of elytron sculpture and shape of the pronotum) have been described. These examples of incorrect use of infraspecific names were already criticised by Jeannel (1941) and Casale *et al.* (1982). Also the usually well-considered keys of Breuning (1932-1936) are quite useless for *C. problematicus.* We believe, with Březina (1994, 1999 partim), that only a few main subspecies can be maintained at present: **a) subsp. problematicus** – Slovakia, Moravia, S. and E. Germany, Alps: Austria, Switzerland, N. Italy, S.E. France. **b) subsp. planiusculus** Géhin, 1885 – W. Europe, from N. Spain (Pyrenees, Navarra and Catalonian chain = five subspecies only described for this area!), to C. and W. France. **c) subsp. inflatus** Kraatz, 1878 – S.E. France (Provence), Maritime- and Ligurian Alps, N. Apennines, S. Piedmont (Langhe). **d) subsp. harcyniae** Sturm, 1815 (= *wockei* Born, 1898) – British Isles, N. and N.E. France, N. Switzerland, Belgium, Netherlands, Denmark, S. and C. Norway, Sweden, C. and N. Germany, N. Poland, Bohemia (often referred to as ssp. *gallicus* Géhin, 1885; see: Anderson *et al.,* 2000; Lindroth, 1985; Luff, 1998). **e) subsp. strandi** Born, 1926 – N. and E. Scandinavia, Kola Peninsula Region. **f) subsp. feroensis** Vacher de Lapouge, 1910 – Faeroes, Hebrides, Shetland and Orkney Isles. Known from a fossil in the Faeroes, referred to as from either the sub-boreal or subatlantic period, before the arrival of man. **g) subsp. islandicus** Lindroth, 1968 – Iceland: probably separated since the early Würm glaciation period (Lindroth, 1968, 1970). **h) subsp. relictus** Hellén, 1934 – Known from only one specimen, from the Hogland island in the bay of Finland (perhaps introduced).

Ecology: Rather eurytopic, mesophilic; silvicol and less in open, sun-exposed lowland sites, however, according to various experiments, thermophilic (Casale *et al.,* 1982; Thiele, 1977). In C. and W. Europe predominantly a forest species, but in the N. also in more open habitats, such as heathlands with scattered pine trees (Gries *et al.,* 1973; Lindroth, 1985; Arndt, 1989). In the N. and W. in moderately dry and open lowland forests at sea level (oak-birch), to montane forests (Fagetalia) (Thiele, *l.c.*); in Britain in open forests, heath and tall grass vegetations (Luff, 1998). In Ireland mostly in upland heath or forests, far less common below 200 m (Anderson *et al.,* 2000). At least in N. Fennoscandia, the species is able to live on permafrost (Lindroth, 1945). In C. Europe in hills and mountains, rarely in subalpine biotopes. In the S. of its range (e.g. Pyrenees) usually in rather dry alpine pastures to ca 2500 m. In the N.W. Swiss Jura up to the peaks at 1300-1600 m, but in the Alps usually not that high, except in S.W. Wallis where it has been recorded from 1300-2200 m (Marggi, 1992). In S. France and N. Spain (Pyrenees) up to 2700 m (Forel & Leplat, 1995, 1998), also in rather dry environments (e.g. in the true alpine zone of the Canigou – Assmann, *pers. observ.*; in Andorra and Maritime Alps at ca 2400 m – Turin, *pers. observ.*). In E. Europe (Czechia, Slovakia, Hungary) in forests of hills and mountains (Hůrka, 1996). In Hungary, the most localities have calcifuge plant associations. In Romania, it was found in the Harghita Mts. in subalpine pastures at 1500 m, while in the Retezat Mts. it was mainly found in spruce forests at 1700 m. In E. Germany most abundant at middle altitudes (Arndt, 1989). The species occurs in various types of forest (deciduous, mixed or coniferous); most abundant in C. Europe (Switzerland) in spruce monocultures (Marggi, 1992). In the Netherlands, it was regularly found far (2-3 km) from the nearest forest, on vast areas of open *Calluna*-heathland, where it most probably does not reproduce (Den Boer, 1977; Nelemans, 1979a; Rijnsdorp, 1980). In W. Germany, more abundant in hedgerows and forest edges than in the adjacent open habitats (Thiele, 1964b). At least in N. and W. Europe, it seems to have a clear preference for gravelly (Scandinavia: especially morene – Lindroth, 1985), sandy or peaty soil, generally avoiding heavier, clayish and loamy soil types (Netherlands – Den Boer, 1977; Turin *et al.,* 1991), in Thüringen also regularly on limestone (Arndt, *pers. observ.*). According to Herrera & Arricibita (1990), it behaves rather eurytopically in N. Spain and occurs in montane grasslands as well as in beech or chestnut forests. Neumann (1971) proved that the species was attracted by forests, if the angle (from the point of view of the beetle) with the upper line of the forest canopy was more than 15°. In experiments, it preferred significantly a structure of bold vertical lines above horizontal ones (Bathon, 1974), which can be explained as a preference for forest-like structures. Investigations in plots with different presence of other *Carabus* species (especially with or without *C. glabratus* and *C. hortensis*) in N. Germany, showed that this kind of 'competition' from other species does not influence body length or body mass, but that there are slight shifts in seasonal activity, possibly caused by food competition (Günther & Assmann, 2000).

Transects: Chapter 1: I-1; Chapter 8: T-02-13, 15-21, 23-31, 33, 79-81, 88-93.

Biology: **Activity** – A strictly nocturnal species (Van der Drift, 1951; Kirchner, 1964; Lauterbach, 1964; Weber, 1966b; Thiele & Weber, 1968). **Periodicity** (Hůrka, 1973) –

In C. Europe, reproduction and oviposition (egg size 5.5 x 2.5 mm) take place from early autumn onwards, with a maximum in August-September. There are also reports of copulations in May, immediately after hibernation (Hůrka, *l.c.*; Larsson, 1939). Sturani (1962) assumed a first period of adult activity from April to July and a short aestivation in August, a second peak during September-October and hibernation from the end of October onwards. Van der Drift (1958) found that specimens, in spring, become active when the temperature is above 7°C and inactive for hibernation when the temperature drops below 6°C. From various sources, the following life history pattern can be described: development of the larva to third instar lasts about 40-55 days (eggs (size 5.5 x 2.5): 10-14 days, L1: 12-14 days; L2: 7-23 days) and subsequently it hibernates (usually as L3) under mosses or in dead tree trunks. According to Den Boer (1977), the larvae remain (partly) active during winter, as long as the minimal temperature at soil remains above 2°C (Betz, 1992). After a prepupal stage of 12-15 days (Sturani, *l.c.*), pupation takes place in May-July, occasionally at the beginning of June. Fresh adults appear, depending of latitude and altitude, in spring or summer (even in autumn); in Norway in August and in Germany from May until September. Notably, in cases of summer aestivation diapause (with gonadal dormancy: Van der Drift, 1958), they appear in late summer and reproduce next autumn (Houston, 1981; Lindroth, 1945, 1985; Van der Drift, 1959). Duration of development in the field 9-10 months; under rearing conditions this can vary from about 80 days (Sturani, 1962) to 7 months (Hůrka, *l.c.*). A proportion of the adult population hibernates and the beetles reproduce for a second time in the next summer-autumn. Summarising, one can say that the adults are active in the period April-September/October, with a short aestivation diapause around the second half of July and the first half of August; hibernation of larvae and second year adults, takes place from October-April (Forel & Leplat, 1995). In the lowlands of C. Europe, active adults can be found in the period February-October; in N. Scandinavia and at high altitudes from June to September, often with biennial life cycle (Du Chatenet, 1986; Houston, 1981). In Wales (Snowdon) between 660 and 1055 m, the lower populations appeared to have an annual and the highest biennial cycle (Sparks *et al.,* 1995). The periodicity of *C. problematicus* in Italy runs always late, compared to other species of the community (Casale *et al.,* 1982). **Food** (Larochelle, 1990): In the field, small insects, small (crushed) snails and slugs, insect larvae, earthworms and caterpillars. In the laboratory, it accepted also minced and raw meat, fresh fish, chopped mealworms, gingerbread soaked in water (very appreciated), bread soaked in sugared milk and various ripe fruits (banana, apples, peaches, apricots), as well as Gruyere cheese. **Larva**: Described by Fauvel (1889: L3), Bengtsson (1927: L1-L3), Hůrka (1971b) and key: Arndt (1985, 1991b). Food – earthworms in the laboratory (Arndt, *pers. observ.*). **Dispersal power**: It has a good locomotory power and can cover an average distance of 70-75 m per night, which can result in an average effective relocation of about 7 m in 24 hours (Neumann, 1971). The fastest animal, in a study in N.W. Germany using harmonic radar in order to follow the specimens in the field, covered a distance of more than 132 m (as the crow flies)) during one night (Assmann, 1998), see Chapter 6 (p. 294) for a description of locomotory abilities. It also seems to have strong tendency to leave woodlands (its main reproduction habitat in C. Europe) (Den Boer, 1977; Rijnsdorp, 1980). Moreover, it can climb trees very well and in the Netherlands beetles were found during the night in tops of pine trees (Van der Ent, 1990). It was also often encountered on sirup, used as bait on tree trunks, to catch moths.

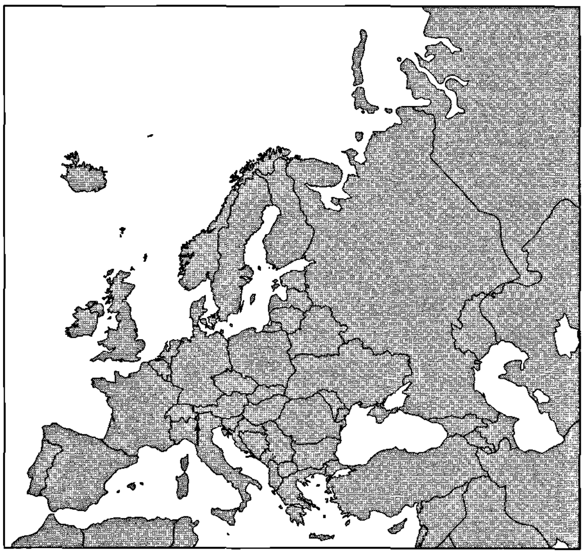
Conservation: The minimum area for survival of (sub)populations, was calculated to be more than 50 ha (Netherlands: Van der Ent, 1990). In N.W. and N.C. Europe and in the Alps, it is extremely abundant in many regions, and almost nowhere endangered.

11. ORINOCARABUS KRAATZ, 1878

11.001. C. (Orinocarabus) adamellicola
Ganglbauer, 1904.

General literature: **Checklists and catalogues** – Breuning (1933): 755. Březina (1994): 35; (1999): 44. Deuve (1994): 160 [338]. Kleinfeld & Schütze (1999): 22. Lorenz (1998): 86. Turin *et al.* (1993): 24. **Iconography** – Ghiretti (1996): 172; Imura & Mizusawa (1996): Pl. 31 [256]. Rautenstrauch (1994): Pl. 49.

Taxonomy: In the checklists of Březina (1995) and Deuve (1994), and also in Breuning (1933), this taxon is treated as a subspecies of *C. alpestris.*



11 001 adamellicola (Orinocarabus)

Geographical range: Endemic species of Italy; C.E. Alps. **Chorotype:** SEU-ALPC. **Range characteristics:** Alpi(C). **Distribution in Europe**: **Italy** – Endemic to the C.E. Italian Prealps, Adamello and Brenta massifs, from Brescia (Oglio Valley) to Adige Valley. In limestone massifs, from 1600 to 2500 m.

Subspecies: No subspecies.

Ecology: Eualpine and subalpine species, inhabiting calcareous as well as dolomitic habitats. Normally living over 1800 m, up to 2500 m (Casale *et al.,* 1982).

Biology: **Activity** – No data. **Periodicity** – Largely unknown; adults occur from May/June to September/October. The L1 and L2 hibernate together with second year adults, similar to *C. alpestris*. **Larva**: Unknown, see Casale *et al.* (1982).

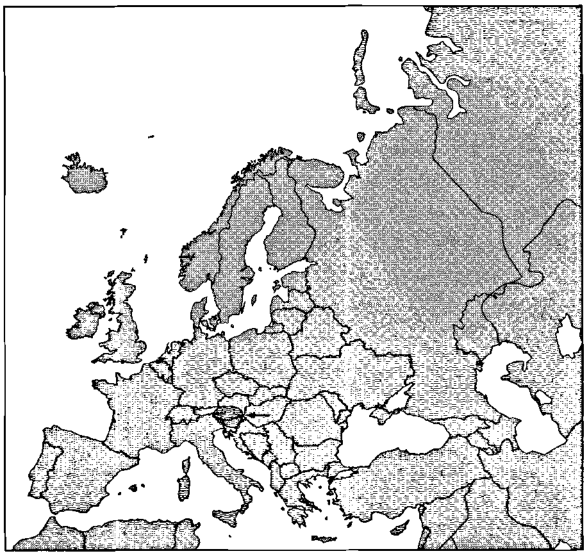
Conservation: Not endangered.

11.002. C. (Orinocarabus) alpestris

Sturm, 1815.

General literature: **Checklists and catalogues** – Breuning (1933): 755. Březina (1994): 35; (1999): 44. Deuve (1994): 160 [338]. Kleinfeld & Schütze (1999): 22. Lorenz (1998): 86. Turin *et al.* (1993): 24. **Iconography** – Ghiretti (1996): 172. Imura & Mizusawa (1996): Pl. 31 [256]. Rautenstrauch (1994): Pl. 48.

Geographical range: E. Alps on both sides. From Dolomiti and Tyrol in the W., to Slovenia in the E. (Breuning, 1927; Mandl, 1956-1958). In some localities sympatric with *C. (O.) bertolinii*, or with *C. (O.) carinthiacus*. **Chorotype:** SEU-ALPE. **Range characteristics:** Alpi(CE). **Distribution in Europe**: **Germany** (Trautner & Müller-Motzfeld, 1995) – Only known from Bayern, but annotated as rare. **Balkan Peninsula** – Slovenia (Julian Alps). **Austria** – Widely distributed in the high parts of Tirol, Salzburg, Oberösterreich, Niederösterreich (Schneeberg), Steiermark, Kärnten and Osttirol, locally abundant. **Italy** – Just reaching the N.E.-most territory; Dolomites, around Val Pusteria, S. Tirol Mts.



11 002 alpestris (Orinocarabus)

Subspecies: a) subsp. alpestris – S. and C. lower Austria to Styria. **b) subsp. dolomitanus** Mandl, 1956 – E. Alps, Dolomites, E. and C. parts of the Pusteria Valley, Carnian and Julian Alps, N. Slovenia, Karawanks and Savinische Alps. **c) subsp. hoppei** Germar, 1824 – Austria: from Tyrol to Klagenfurt. Italy: Pusteria Valley, Arnia Valley and Vizze Valley.

Ecology: In alpine and subalpine steppes, mostly from 1700 to 2700 m (Hoffmann, 1907; Mandl, 1956-58), exceptionally at 1100 m in Slovenia (Planica). Characterised by Mandl (*l.c.* and 1972) as petrophil, found on stony soil, including limestone, under large stones and mostly in rather humid places. Franz (1970) divides the species in 'calciphilous and 'acidophilous' races. This is not confirmed in the Eastern Alps (Dolomiti) (Brandmayr & Zetto-Brandmayr, 1988), where the species primarily lives in alpine pastures that are not induced by human activity.

Transects: Chapter 8: T-77 and 79.

Biology: **Activity** – Mainly night active, but during the reproduction period also showing diurnal activity (Thiele & Weber, 1968). **Periodicity** – Only little is known, but in general like other *Orinocarabus*, the adults can be encountered from June until the end of August (Du Chatenet, 1986; Hůrka, 1973; Sturani, 1962). A summer breeder with oviposition during the late summer and early autumn, and obligatory larval diapause during the winter. In the Eastern Alps, it is an autumn breeder (Brandmayr & Zetto-Brandmayr, 1988). The L1 and L2 hibernate together with second year adults, from the end of August onwards. Teneral adults occur in early summer (Hůrka, *l.c.*). **Food** (Larochelle, 1990): In captivity, snails, earthworms and caterpillars without hairs. **Larva**: Described by Hůrka (1970, 1971b: L1-L2) and Casale *et al.* (1982).

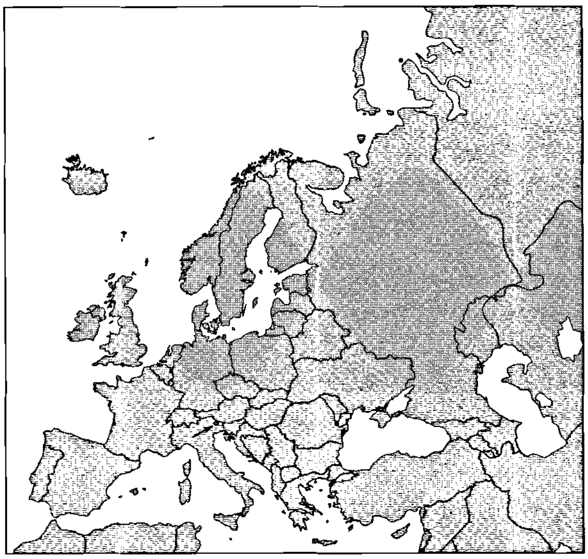
Conservation: Not endangered.

11.003. C. (Orinocarabus) bertolinii

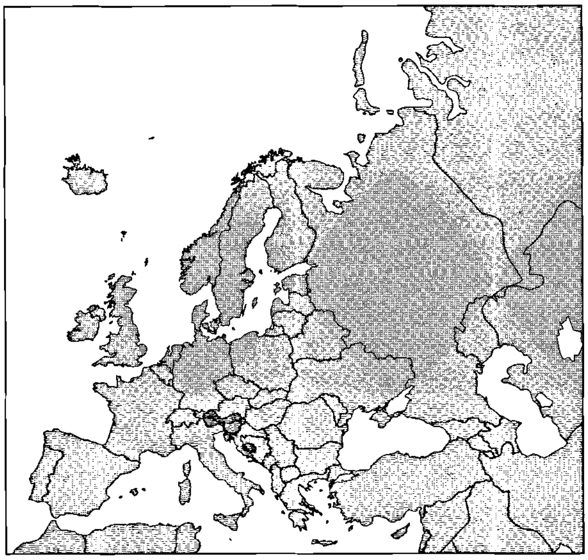
Kraatz, 1878.

General literature: **Checklists and catalogues** – Breuning (1933): 762; Březina (1995): 35; (1999): 44. Deuve (1994): 161 [339]. Kleinfeld & Schütze (1999): 22. Lorenz (1998): 86. Turin *et al.* (1993): 24. **Iconography** – Casale *et al.* (1982): fig. 86. Ghiretti (1996): 173. Imura & Mizusawa (1996): Pl. 32 [257]. Rautenstrauch (1994): Pl. 50.

Geographical range: Endemic species of the Italian E. Alps and Prealps. **Chorotype:** SEU-ALPE. **Range characteristics:** Alpi(C). **Distribution in Europe**: Italy: Trentino (Dolomiti), Veneto (Belluno), and Friuli Prealps, from high Valle dell'Adige to Valle dell Tagliamento. It can be seen as a vicariant of *C. alpestris*, but with a centre of distribution more to the S. and without a verified zone of sympatry.



11 003 bertolinii (Orinocarabus)



11 004 carinthiacus (Orinocarabus)

Subspecies: Specimens from Veneto and Friuli have been described as *cavallensis* Berneau, 1914.

Ecology: Living above the timber line; abundant in alpine and subalpine pastures along morene zones, from 1600 to 2900 m; rare in other zones (Casale *et al.,* 1982). Both on calcareous and silicious soils, in sunny, dry pastures with high density of grass (Firmeta seslerio-sempervirenteta) (Brandmayr & Zetto-Brandmayr, 1988). It can be found under stones or at the edge of permanent snow (Du Chatenet, 1986). The species is more localised than the other *Orinocarabus* species.

Transect: Chapter 8: T-82.

Biology: **Activity** – Generally nocturnal. **Periodicity** – In general following the same pattern as *C. alpestris* (Sturani, 1962). Summer-autumn breeding with winter larvae; adults occur from June to August/September (Brandmayr & Zetto-Brandmayr, 1988; Du Chatenet, 1986), hibernation from September to June. **Food** (Larochelle, 1990) – In captivity, raw meat, small snails, fruits, bread soaked in sugared water. **Larva**: Described by Casale *et al.* (1982). Food – in captivity, same as adults (Larochelle, 1990).

Conservation: Not endangered.

11.004. C. (Orinocarabus) carinthiacus

Sturm, 1815.

General literature: **Checklists and catalogues** – Breuning (1933): 774. Březina (1994): 35; (1999): 45. Deuve (1994): 162 [342]. Kleinfeld & Schütze (1999): 22. Lorenz (1998): 86. Turin *et al.* (1993): 24. **Iconography** – Casale *et al.* (1982): fig. 89. Ghiretti (1996): 175. Imura & Mizusawa (1996): Pl. 32 [260]. Pavicevic & Mesaros (1997): cd-rom. Rautenstrauch (1994): Pl. 52.

Taxonomy: By Březina (1999) placed in *Oreocarabus* Géhin.

Geographical range: Endemic species of W. Balkan and E. Alps; N.W. Italy, S. Austria, Carinthia; N.W. Slovenia. Some isolated populations exist in the mountains of Bosnia. **Chorotype**: SEU-ALPE. **Range characteristics**: Alpi(E)-Balk(W). **Distribution in Europe**: **Balkan Peninsula** – Slovenia (Julian Alps), disjunct occurrences in C. Bosnia-Herzegowina (Gola Jahorina, Zec-Planina, Vranica, Vares). **Austria** – Restricted distribution in the C. and S. part of the country (Tirol, Salzburg, Steiermark, S. Kärnten, Osttirol). **Italy** – From the Adige and Isarco Valley to Friuli.

Subspecies: Despite the isolated populations in Bosnia, no subspecies (Casale *et al.,* 1982).

Ecology: Montane to alpine species, living as a true forest species at lower altitudes unlike other *Orinocarabus* species (Mandl, 1956-1958). Mostly in montane *Fagus* and *Picea* forests, down to 1500 m, occasionally to 1000 m. Above the timber line it lives in the subalpine *Rhododendron*-zone (Brandmayr & Zetto-Brandmayr, 1988), and in the alpine steppes and meadows, up to 2000 m (Casale *et al.,* 1982), occasionally to 2400 m (Du Chatenet, 1986). For former Yugoslavia (Slovenia, Bosnia), it is called praticol-silvicol, and primarily mentioned to inhabit high altitudes (Pavicevic & Mesaros, 1997).

Transects: Chapter 8: T-79 and 82.

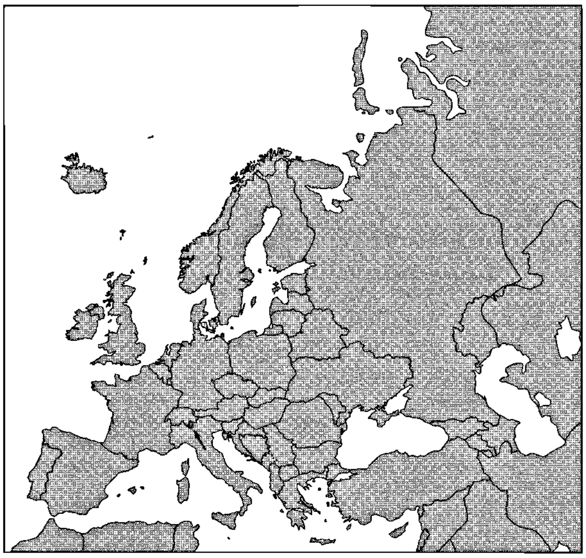
Biology: **Activity** – Night active. **Periodicity** – Adults occur from May-June to September (Du Chatenet, 1986; Sturani, 1962). Hibernating as adults in the soil from October to May. **Food** (Larochelle, 1990) – In the field, carrion. Casale *et al.* (1982) report arthropods and molluscs. **Larva**: Described by Hůrka (1971b), compare Casale *et al.* (1982). Food – No data.

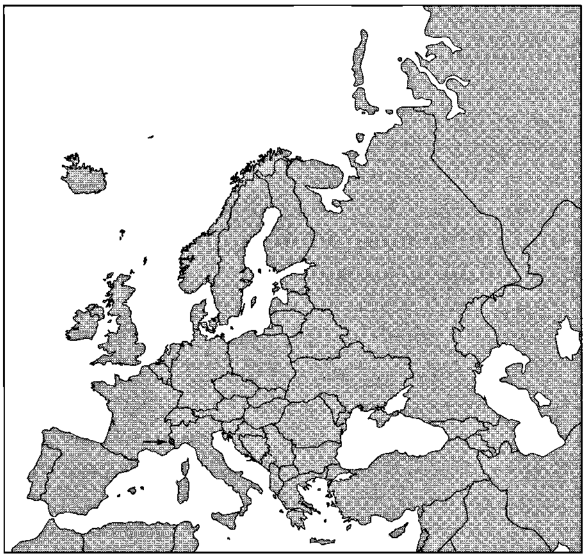
Conservation: There seem to be no problems in the N. population (Slovenia, Austria), but the Bosnian population possibly endangered (Pavicevic & Mesaros, 1997).

11.005 C. (Orinocarabus) castanopterus

A. & G.B. Villa, 1833.

General literature: **Checklists and catalogues** – Breuning (1933): 755. Březina (1994): 35; (1999): 44. Deuve


11 005 castanopterus (Orinocarabus)


11 006 cenisius (Orinocarabus)

(1994): 160 [338]. Kleinfeld & Schütze (1999): 22. Lorenz (1998): 86. Turin *et al.* (1993): 24. **Iconography** – Ghiretti (1996): 172. Imura & Mizusawa (1996): Pl. 31 [256]. Rautenstrauch (1994): Pl. 49.

Taxonomy: In Březina (1994) and Deuve (1994), listed as a subspecies of *C. alpestris* Sturm. Treated as a distinct species in Březina (1999). See also Deuve, 2002 (Addendum).

Geographical range: Endemic species of S.E. Switzerland and C.N. Italy; S. slope of C. Alps. **Chorotype:** SEU-ALPC. **Range characteristics:** Alpi(C). **Distribution in Europe**: **Italy/Switzerland** (Casale *et al.*, 1982; Marggi, 1992) – E. Lepontine Alps (Tessin Alps), Orobian (Bergamascan) Alps, Valtellina, E. to Valcamonica Valley. In Switzerland very restricted, along the E. border of Canton Tessin (E. of Valle Mesolcina), to S. Graubünden between St. Moritz and Poschiavo. Erroneously characterised as being endemic for Italy by Magistretti (1965).

Subspecies: No subspecies.

Ecology: Alpine and subalpine pastures above the timber line, 1600 to 2500 m; optimum about 1600-1700 m (Marggi, 1992). In montane heathland, under stones.

Transects: Chapter 8: T-81.

Biology: **Activity** – No data. **Periodicity** – No data, however, the pattern of periodicity will most probably follow that of other alpine *Orinocarabus*. **Larva**: Unknown, see Casale *et al.* (1982).

Conservation: Not endangered.

11.006. C. (Orinocarabus) cenisius

Kraatz, 1878.

General literature: **Checklists and catalogues** – Breuning (1933): 746. Březina (1994): 36; (1999): 44. Deuve (1994): 160 [336]. Kleinfeld & Schütze (1999): 22. Lorenz (1998): 86. Turin *et al.* (1993): 24. **Iconography** – Ghiretti (1996): 170. Imura & Mizusawa (1996): Pl. 31 [254]. Rautenstrauch (1994): Pl. 44-45.

Taxonomy: In Březina (1994) and Deuve (1994) listed as a subspecies of *C. fairmairei* Thompson.

Geographical range: Endemic species of the W. Alps, from N. Cottian Alps (Mt. Albergian) to Grajan Alps. **Chorotype:** SEU-ALPW. **Range characteristics:** Alpi(W). **Distribution in Europe**: **Italy** (see the recent detailed map in Bisio, 2000) – Eualpine: S. Grajan Alps, Val d'Aosta and N. Cottian Alps; Levanna Massif: in this area as S. vicariant of *C. heteromorphus*. **France** (Jeannel, 1941; Bonadona, 1971) – Haute-Maurienne, Haute Tarentoise and Vanoise.

Subspecies: a) subsp. cenisius (s.str) – W. (N. Cottian) and Grajan Alps, both on the French and Italian sides. In Italy from Stura di Viù Valley to Mocenisio and Dora Riaria (Susa) Valley. *Note*: Specimens from Savoie (Iseran Massive) have been described as *iseranus* Deuve & Simard, 1977; they could represent a transitional form (hybrid zone) to *heteromorphus*. **b) subsp. ceresiacus** Born, 1896 – Grajan Alps, from Stura di Lanzo to Levanna Massif. **c) subsp. fenestrellanus** Beuthin, 1899 – Cottian Alps, mountains from the right side of the Susa Valley to Chisone (Mt. Albergian) Valley.

Ecology: In alpine and subalpine pastures under stones, from 1600 to 2700 m (Casale *et al.*, 1982).

Biology: **Activity** – No data. **Periodicity** – Reproduction in late spring and summer. Adults occur from June to September and normally have a diapause in August (Du Chatenet, 1986; Sturani, 1962). The eggs (size 3.3 x 1.5 mm) develop in ca 13 days. A second peak of activity takes place in September. Hibernation from October until June. **Food** (Larochelle, 1990) – In captivity, raw meat, small snails, fruits and bread soaked in sugared water. **Larva**: Described by Sturani (1962: *C. cenisius fenestrellanus* Beuth.), see also Casale *et al.* (1982). Food – in captivity, same as adults.

Conservation: Not endangered.

11.007a. C. (Orinocarabus) concolor
Fabricius, 1792.

General literature: Breuning (1933): 740. Březina (1994): 35; (1999): 44. Deuve (1994): 160 [337]. Kleinfeld & Schütze (1999): 22. Lorenz (1998): 86. Turin *et al.* (1993): 25. **Iconography** – Casale *et al.* (1982): fig. 79. Ghiretti (1996): 171-172. Imura & Mizusawa (1996): Pl. 31 [255]. Rautenstrauch (1994): Pl. 43-44.

Taxonomy: See 11.007b *lepontinus*.

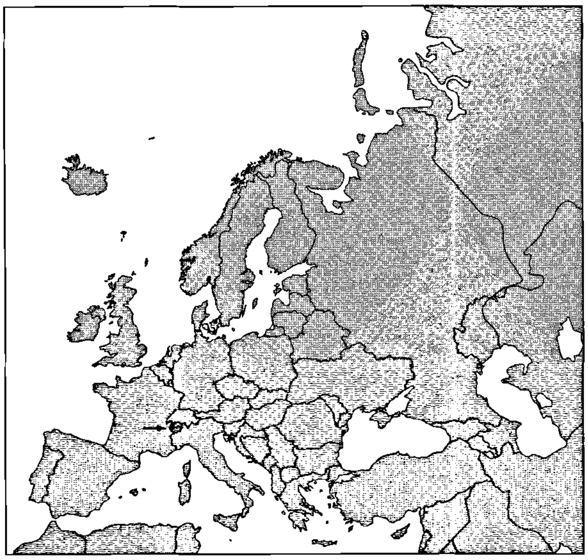
Geographical range: Endemic species of the W.C. Alps; Pennine, Lepontine Alps. **Chorotype:** SEU-ALPW. **Range characteristics:** Alpi(C). **Distribution in Europe**: **Switzerland/Italy/France** (Marggi, 1992; Casale *et al.*, 1982; Jeannel, 1941; see also the recent detailed map in Bisio, 2002) – Pennine Alps, from Mt. Bianco Massif and Mt. Rosa Massif on both French and Italian sides, E. to the Tessin Alps; in Switzerland S. Wallis and Lepontine Alps, in middle C. Alps in the N. to region of Obwalden (Engelberg). Coulon *et al.* (2000) place critical notes on the occurrence on the French records by Jeannel (*l.c.*); probably not present on the westside of the Mt. Blanc, but possibly to be found above Chamonix in the environments of Col de Balme.

Subspecies: Depressed, elongated specimens of the high Aosta Valley have been described as *bernhardinus* Kraatz, 1878; small high-altitude (2000-3000 m) specimens from Mt. Rosa Massif have been described as *alpinus* Dejean, 1826; large specimens with widened pronotum, from Biellese (Sessera and Sesia Valleys), have been described as *amplicollis* Kraatz, 1878. We consider that all these names must be interpreted as junior synonyms of *concolor* (*s.str.*). Due to constant and distinct features, such as the different shape of the aedeagus, and for the lack of intermediate forms, we consider the Italian endemic *C. lepontinus* (see: 11.007b) as a distinct species. This has recently been confirmed by findings of sympatric populations of *C. concolor* and *C. lepontinus* in Val Grande in the Lepontine Alps (Vigna Taglianti *et al.*, 1998), see Chapter 3, *Key to the adults*, p. 99).

Ecology: Stenotopic montane and alpine species. Alpine and subalpine pastures from 1600 to 3000 m; exceptionally, also in subalpine forests at 1300-1500 m (Casale *et al.*, 1982). It can be found under stones and vegetation, often near melting snow; it is the most abundant alpine *Carabus* species (Casale *et al.*, *l.c.*).

Transect: Chapter 8: T-88.

Biology: **Activity** – No data. **Periodicity** – The first peak of adult activity is from May to July, when reproduction takes place, followed by an aestivation diapause in August (Sturani, 1962). The eggs (size 3.3 x 1.5 mm) develop in ca 15 days. A certain proportion of the adult population becomes active before they enter hibernation from October until April. **Food** (Larochelle, 1990) – In the field, slugs (*Arion flavus* Nilsson), probably insect larvae and, occasionally, the flower of *Gentiana verna* L. In captivity, raw meat, caterpillars, small snails, fruits, bread soaked in sugared milk. Sometimes eating own eggs. **Larva**: Described by Vacher de Lapouge (1908), Sturani (1962) and Raynaud (1975). Food – in captivity, same as adults.



11 007a concolor + 11 007b lepontinus (Orinocarabus)

Conservation: Not endangered.

11.007b. C. (Orinocarabus) lepontinus
Born, 1908.

General literature: **Checklists and catalogues** – Breuning (1933): 741. Březina (1994): 35; (1999): 44. Deuve (1994): 160 [337]. Kleinfeld & Schütze (1999): 22. Lorenz (1998): 86. Turin *et al.* (1993): 25. **Iconography** – Ghiretti (1996): 172. Imura & Mizusawa (1996): not listed.

Taxonomy: By Březina (1994; 1999), Deuve (1994), Kleinfeld & Schütze (1999) and Lorenz (1998), treated as a subspecies of *C. concolor* Fabricius. The specific status was however recently confirmed by sympatric populations of *C. concolor* and *C. lepontinus* in Val Grande in the Lepontine Alps (Vigna Taglianti *et al.*, 1998).

Geographical range: Endemic species of the W. Alps. **Chorotype:** SEU-ALPC. **Range characteristics:** Alpi(CW). **Distribution in Europe**: **Switzerland/Italy** – W. Lepontine Alps, E. side of Toce Valley, Mt. Zeda, Mt. Limidario, Pizzo Marone, Cima Laurasca, Cannobina Valley.

Subspecies: No subspecies.

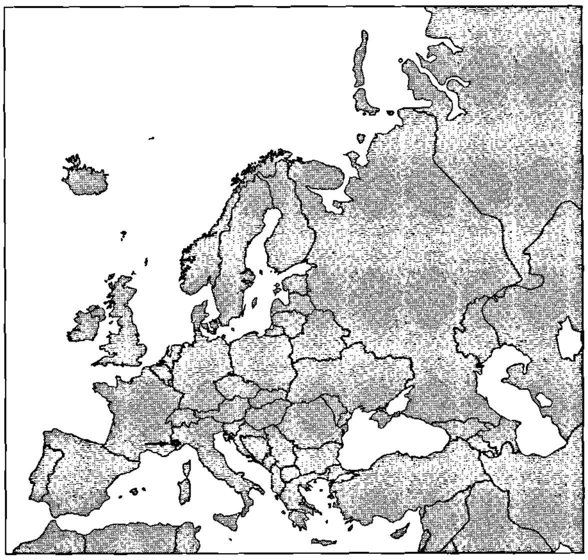
Ecology: Similar to *C. concolor*.

Biology: Similar to *C. concolor*.

Conservation: Not endangered.

11.008. C. (Orinocarabus) fairmairei
C. G. Thomson, 1875.

General literature: **Checklists and catalogues** – Breuning (1933): 749. Březina (1994): 35; (1999): 44. Deuve



11 008 fairmairei (Orinocarabus)

(1994): 159 [336]. Kleinfeld & Schütze (1999): 22. Lorenz (1998): 86. Turin *et al.* (1993): 25. **Iconography** – Casale *et al.* (1982): fig. 83. Forel & Leplat (1995): Pl. 21. Ghiretti (1996): 171. Imura & Mizusawa (1996): Pl. 31 [254]. Rautenstrauch (1994): Pl. 46.

Geographical range: Endemic of W. (Cottian) Alps. **Chorotype:** SEU-ALPW. **Range characteristics:** Alpi(C). **Distribution in Europe: Italy** (see the recent detailed map in Bisio, 2000) – Very restricted in the W. Alps, from Germanasca Valley to Maira Valley. **France** – A few populations are situated in the S.E., along the Italian border: Hautes Alpes (Masif de l'Iseran, Briancon, Queyras and perhaps Enchastraye Mts.).

Subspecies: See also remarks in the *Key to the adults* (p. 100) and Deuve, 2002 (Addendum). **a) subsp. fairmairei** – Monviso Massif, High Pellice Valley. **b) subsp. pelvicus** Cavazzuti, 1973 – High Varaita (Bellino) Valley and Maira Valley. **c) subsp. stecki** Born, 1902 – Cottian Alps on the transalpine (French) side, in Italy in high Germanesca Valley and in Varaita (Chianale) Valley.

Ecology: Alpine and subalpine pastures from 1500 to 2800 m (Coulon *et al.*, 2000); at the lowest altitudes inhabiting pine and larch (*Larix*) forests (Casale *et al.*, 1982). In contrast to *C. putzeysianus*, nearly absent from calcareous habitats and mainly found on acid soil (Casale *et al.*, 1982; Cavazzuti & Meli, 1999).

Biology: **Activity** – Active during the night; during daytime hidden under stones, sometimes rather abundant. **Periodicity** – Reproduction in June-July. The adults occur from June-September, but are rare in August (Du Chatenet, 1986), probably due to an aestivation diapause (Sturani, 1962). The species is especially active during rainy periods. The size of the eggs is 3 x 1.2 mm, and they develop in about 13 days. The larva develops in approximately 40 days. The adults make small cells for hibernation, in soil or under stones lying on sand. **Food** (Larochelle, 1990): In Italy, it accepted in the laboratory raw meat, snails, fruits and bread soaked in sugared water. **Larva**: Unknown, see Casale *et al.* (1982). Food – in captivity similar to the adults (Larochelle, *l.c.*).

Conservation: Not endangered.

11.009. C. (Orinocarabus) heteromorphus

K. Daniel, 1896.

General literature: **Checklists and catalogues** – Breuning (1933): 745. Březina (1994): 36; (1999): 44. Deuve (1994): 160 [336]. Kleinfeld & Schütze (1999): 22. Lorenz (1998): 86. Turin *et al.* (1993): 25. **Iconography** – Ghiretti (1996): 171. Imura & Mizusawa (1996): not listed. Rautenstrauch (1994): Pl. 44.

Taxonomy: In Březina (1994) and Deuve (1994) treated as a subspecies of *C. fairmairei* C. G. Thomson.

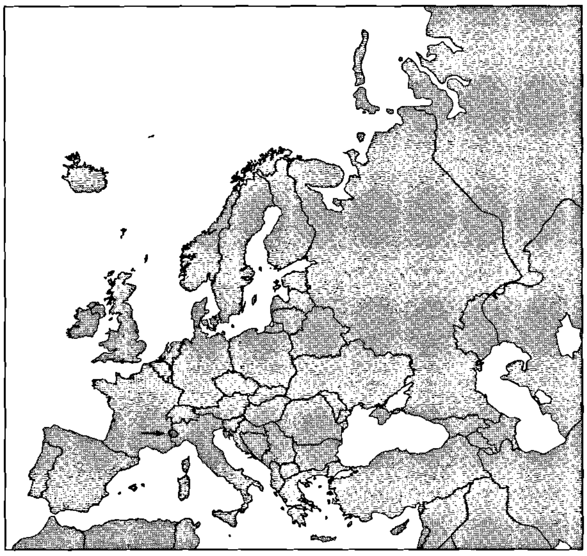
Geographical range: Endemic species of the W. Alps (N. Grajan Alps). **Chorotype:** SEU-ALPW. **Range characteristics:** Alpi(W). **Distribution in Europe**: **Italy** – N. Grajan Alps, in the Gran Paradiso Massif, from Colle del Nivolet in S.W. to Valgrisanche (Aosta) to the N. In Levanna Massif substituted by the closely related vicariant *C. (O.) cenisius* Kraatz, 1878. In part of its geographical range, sympatric with *C. latreilleanus*. Not on the French side: Jeannel, 1941. Detailed maps in Bisio (2000).

Subspecies: No subspecies.

Ecology: In alpine and subalpine pastures from 1700 to 3000 m.

Biology: **Activity** – No data. **Periodicity** – Adults are active from June to September; reproduction occurs in mid-June. Development of eggs (size: 3.5 x 1.5 mm) in 15 days. Duration of larval development ca. 30-40 days. **Food** – No data. **Larva**: Described in Casale *et al.* (1982). Food – No data.

Conservation: Not endangered.



11 009 heteromorphus (Orinocarabus)

11.010. C. (Orinocarabus) latreilleanus
Csiki, 1927.

General literature: **Checklists and catalogues** – Breuning (1933): 763. Březina (1994): 36; (1999): 44. Deuve (1994): 162 [341]. Kleinfeld & Schütze (1999): 23. Lorenz (1998): 86. Turin *et al.* (1993): 25. **Iconography** – Casale *et al.* (1982): fig. 86. Ghiretti (1996): 175. Imura & Mizusawa (1996): Pl. 32 [259]. Rautenstrauch (1994): Pl. 50.

Taxonomy: Recently placed in a separate subgenus, *Cavazzutiocarabus* Imura, 1998 (Březina, 1999); see remarks in the *Key to the adults* (p. 98-99). By Lorenz (1998) regarded as synonym of *C. bremii* Stierlin, 1881.

Nomenclature: *C. latreilleanus* is nomen novum pro *C. latreillei* Dejean, nec Fischer von Waldheim.

Geographical range: Endemic species of the W. Alps; N.E. Grajan and Peninne Alps. **Chorotype:** SEU-ALPW. **Range characteristics:** Alpi(W). **Distribution in Europe**: **(Switzerland)/Italy** (Marggi, 1992; Casale *et al.,* 1982, see also the recent detailed map in Bisio, 1999) – Endemic to the Pennine and N.E. Grajan Alps, in the Monte Rosa Massif (both on the Italian and Swiss sides) and in the E. Gran Paradiso Massif. Du Chatenet (1986) mentions the species for Alpes Bernoises, Alpes de Valais, Massif de Mont Blanc, Swiss side of Monte Rosa. However, the occurrence of the species could not be confirmed for Switzerland, because no evidence exists (see Marggi, 1992).

Subspecies: No subspecies.

Ecology: From montane (1400 m) to high altitude alpine pastures (2600-2800 m), under stones, near the snow. Sympatric in the M. Rosa Massif with *C. (O.) concolor*, and in Gran Paradiso with *C. (O.) heteromorphus.*

Transects: Chapter 8: T-88.

Biology: **Activity** – Mainly nocturnal (Assmann, *pers. observ.*). **Periodicity** – At lower altitudes active from the middle of May, generally appearing earlier than the sympatric *Orinocarabus* species, at the first melting of the snow. Montane adults occur especially in June-July, and enter aestivation diapause by August, when other species are still active, thus appearing rarer to collectors (Casale *et al.,* 1982; Sturani, 1962). **Food** – No data. **Larva**: Described by Busato & Giachino (1994). Food – No data.

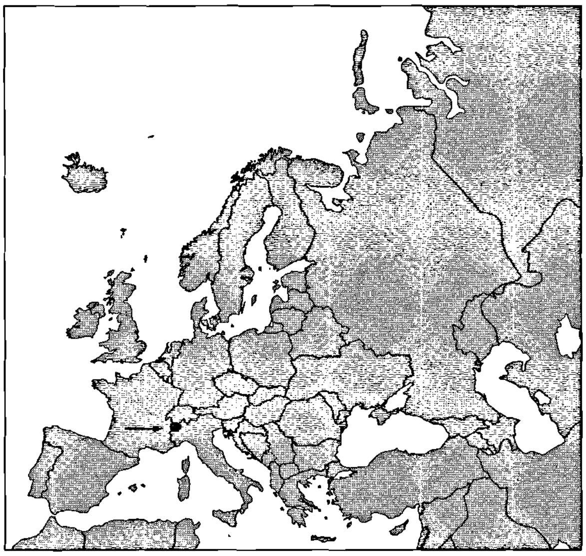
Conservation: Not endangered.

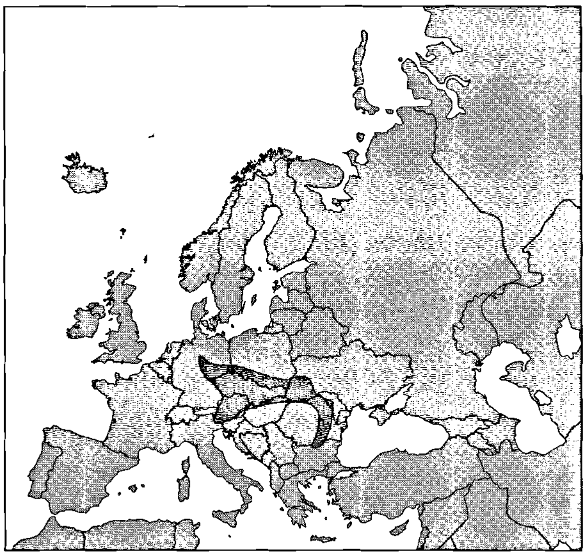
11.011. C. (Orinocarabus) linnaei
Duftschmid, 1812 (= *linnei* Panzer, 1813).

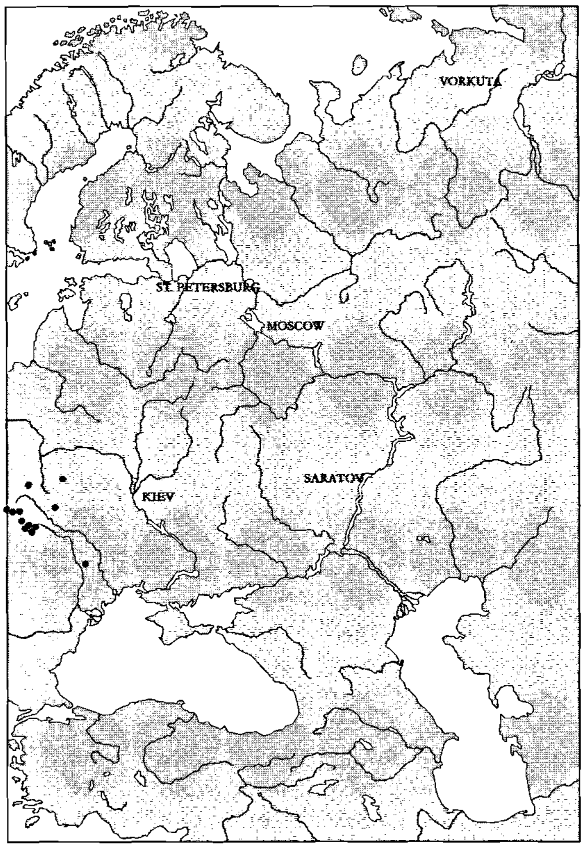
General literature: **Checklists and catalogues** – Breuning (1933): 733. Březina (1994): 36; (1999): 46. Deuve (1994): 162 [343]. Kleinfeld & Schütze (1999): 23. Kryzhanovskij *et al.* (1995): 44 [106]. Lorenz (1998): 86. Turin *et al.* (1993): 25. **Iconography** – Casale *et al.* (1982): 79. Ghiretti (1996): 173. Imura & Mizusawa (1996): Pl. 32 [261]. Rautenstrauch (1994): Pl. 43.

Taxonomy: By Březina (1999) placed in *Oreocarabus* Géhin.

Geographical range: C. and E. Europe mountains, from C. Germany, Switzerland and Austria via E. Alps, Bohemian Massif and Carpathian Mts. to W. Ukraine. **Chorotype:** SEU-ALCA. **Range characteristics:** CEur-EEur(W)-Balk(N). **Distribution in Europe**: **Germany** – Only mentioned for the Harz (near the borderline of Lower Saxony and Sachsen-Anhalt), but the record is doubtful, and it could not be found again in spite of intensive collecting (Assmann, *pers. comm.*; see also Horion, 1941). In Thüringen, Sachsen, and Bayern, locally common. In E. Germany only in the S. of the territory (Sachsen, Thüringen: Thüringerwald, Vogtland, Erzgebirge, Lausitzerbergland, Sächsischer Schweiz, Bohemian Forest) more common towards the E. (Arndt, 1989). **Poland** – Reported from the S. of the country, mainly in montane regions. **Russian Plain** – Ukrainian Carpathians


11 010 latreilleanus (Orinocarabus)


11 011 linnaei (Orinocarabus)



11 011 linnaei

and W. Ukraine, known from the provinces of Zakarpatye, Ivano-Frankovo, Lvov and Ternopol' (many localities – Ponomarchuk, 1956; Rizun, 1990; IZ; ZIN, MPGU). Found also in C. Moldova (Kodry) (coll. Khvylya – Makarov, *in litt.*), however this record needs confirmation. **Moldova** – Only reported from the N.-most region. **Czechia & Slovakia** – Occurring in montane regions of the territory; Bohemian Massif and Carpathians. **Hungary** – Restricted to the W., montane part (Kőszeg) of the country; in the N. only a single, doubtful record. **Romania** – Carpathians to the Banat. **Bulgaria** – Recorded from the Danube Plain (Pleven), however, this record needs confirmation. **Austria** – All parts of the Alps, except Vorarlberg. **Italy** – Only in the E. Alps, from E. Lombardia to the Venetian Alps and Prealps of Brescia.

Subspecies: No subspecies. Mandl mentions *linnaei s.str* for the lower parts of Austria (E. Oberösterreich, N. Niederösterreich) and *folgaricus* Bernau, 1913, for the sub- to high alpine parts in the rest of Austria.

Ecology: Stenotopic, hygrophilous, silvicol, montane and subalpine. Hoffmann (1907) mentiones it in C. Europe mainly from 500 m up to 2000 m. In E. Europe, this species is typical of forests of extensive mountain complexes showing a preference for montane to subalpine, wooded marshes, cool, humid forest and forest swamps, with a preference for forest brook ravines (Arndt, 1989; Hůrka, 1996). In Hungary in montane beech and coniferous forests. In Ukraine in dark coniferous forests of the W. forest-steppe, bordering upon the E. Carpathians, rare (Petrusenko, 1971). In Moldova in the dry cherry-oak forests in the N. (Neculiseanu & Matalin, 2000). In S. Europe in *Fagus, Picea* and *Abies* montane forests, at 800-1500 m, to alpine meadows up to 2000 m in the Italian Prealps and Dolomiti (Casale *et al.,* 1982; Brandmayr & Zetto-Brandmayr, 1988). Hůrka (1973) indicates the altitude of 2300 m as a maximum.

Transects: Chapter 8: T-34-35 and 63.

Biology: **Activity** – Nocturnal, during daytime hidden under pieces of wood (Du Chatenet, 1986). **Periodicity** – Reproduction in summer and early autumn with larval diapause (Hůrka, 1973; Brandmayr & Zetto-Brandmayr, 1988). Copulation was observed by Hůrka (1958) in the first half of July; fertilised eggs in the ovaria were found from the beginning of May until the end of August. Oviposition must be assumed to take place from June to July/August (Sturani, 1962). The development of the larvae lasts until the next summer when pupation takes place during a 10 days period (Arndt, 1989). Probably the L2 and (mainly) L3 larvae hibernate and have an obligatory winter diapause. Teneral adults occur in summer and late summer, and are active for a time during the autumn, before hibernating from October onwards, together with the larvae in groups in old trunks. They do not reproduce before the following May. There is no adult summer diapause. **Food** (Larochelle, 1990) – In captivity, minced meat, fish, apples. **Larva**: Described by Verhoeff (1921: L3), nec Vacher de Lapouge (1908, 1929)! (*variolosus*?), Casale *et al.* (1982: L1, L3), Hůrka (1971b), and key: Arndt (1985, 1991b). Food – earthworms in the laboratory (Arndt, *pers. observ.*).

Conservation: Like most montane species, not endangered.

11.012. C. (Orinocarabus) putzeysianus
Géhin, 1876.

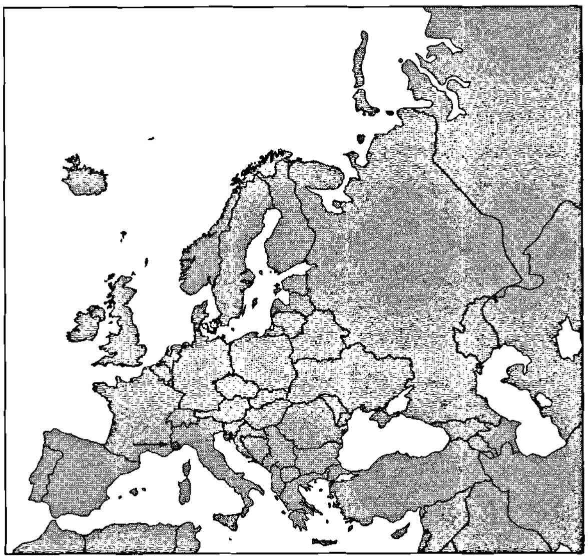
General literature: **Checklists and catalogues** – Breuning (1933): 751. Březina (1994): 36; (1999): 45. Deuve (1994): 159 [335]. Kleinfeld & Schütze (1999): 22. Lorenz (1998): 86. Turin *et al.* (1993): 25. **Iconography** – Casale *et al.* (1982): fig. 81. Forel & Leplat (1995): Pl. 20. Ghiretti (1996): 170. Imura & Mizusawa (1996): Pl. 31 [253]. Rautenstrauch (1994): Pl. 47.

Taxonomy: Revised by Deuve (2002) (see Addendum).

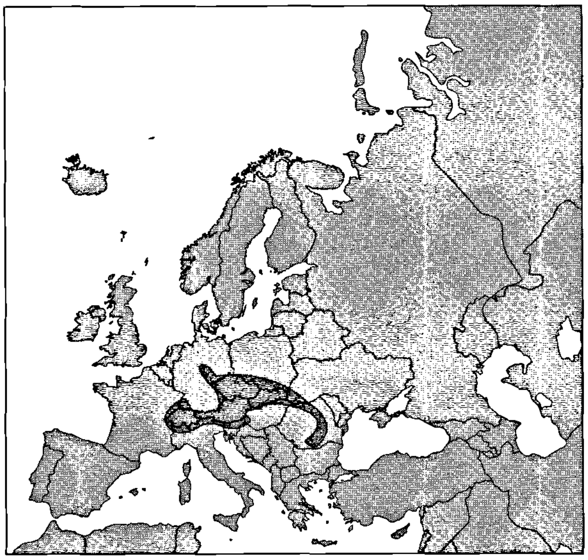
Geographical range: Endemic species of the W. Alps. **Chorotype:** SEU-ALPW. **Range characteristics:** Alpi(W).

Distribution in Europe: **Italy** – Ligurian, Maritime and S. Cottian Alps, Val Maira (see the recent detailed map in Bisio, 2000; Deuve, 2002). **France** – Restricted to some populations in the S.E., near the Italian border: Cottian and Maritime Alps (Col de Mirandol, de Pourriac, Colla Lunga, Haute Vésubie, Col de Tende and Mt. Saccarel).

Subspecies: a) subsp. putzeysianus (s.str) – Ligurian and Maritime Alps, from the Roya Valley to Stura di Demonte Valley on the Italian side, and the Vallée de la Vé-



11 012 putzeysianus (Orinocarabus)



11 013 sylvestris (Orinocarabus)

subie on the French side. **b) subsp. raynaudianus** Deuve & Simard, 1977 – Maritime Alps: Colla Lunga area. **c) subsp. germanae** Casale & Cavazzuti, 1976 – Ligurian Alps: Mt. Saccarello, M. Fronté and Mt. Bertrand. **d) subsp. omensis** Born, 1901 – Maritime and Cottian Alps, from the Stura di Demonte Valley and the Maira Valley. **e) subsp. pedemontanus** Ganglbauer, 1892 – Ligurian Alps, from Mt. Marguareis (Tenda Pass) to Pesio, Ellero and Corsaglia Valleys. **f) subsp. bisioi** Cavazzuti & Meli, 1999 – Cottian Alps at high altitude, 2750-3000 m between the Maira and the Varaita Valleys (see Chapter 3, p. 98).

Ecology: In subalpine and alpine landscapes, from 1700 to 2900 m, notably in calcareous landscapes (Casale *et al.,* 1982). Most abundant near melting snow; in dry and warm periods hidden in the *Rhododendron* zone in scrub or in fissures (Casale *et al.,* 1982).

Biology: **Activity**: Nocturnal, during daytime hidden under stones and vegetation. **Periodicity** – Reproduction from June to the beginning of August when adults enter a summer diapause (Casale *et al.,* 1982; Sturani, 1962). The size of the eggs is 3.5 x 1.6 mm and they develop in ca 15 days. Like most alpine species, hibernation can take place as adult or larva, depending on the speed of development (Forel & Leplat, 1995). **Food** (Larochelle, 1990): In captivity, raw meat, small snails, fruits and gingerbread. **Larva**: Described by Sturani (1962). Food – Same as adults (Larochelle, *l.c.*).

Conservation: Not endangered.

11.013. C. (Orinocarabus) sylvestris
Panzer, 1796 (= *silvestris* auct.).

General literature: **Checklists and catalogues** – Breuning (1933): 765. Březina (1994): 36; (1999): 45. Deuve (1994): 161 [340]. Kleinfeld & Schütze (1999): 22. Kryzhanovskij *et al.* (1995): 44 [107]. Lorenz (1998): 86. Turin *et al.* (1993): 25. **Iconography** – Casale *et al.* (1982): fig. 89. Forel & Leplat (1995): Pl. 21. Ghiretti (1996): 173-175. Imura & Mizusawa (1996): Pl. 32 [258]. Rautenstrauch (1994): Pl. 51-52.

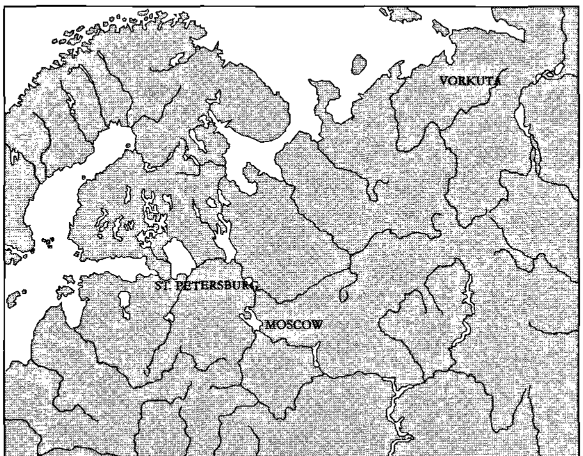
Taxonomy: The status of some populations as 'subspecies' is not clear yet (Březina, 1994, 1999; Deuve, 1994).

Geographical range: Species of C. Europe, from France (Vosges) and Switzerland (Jura) in the W., to Transylvania and Carpathian Ukraine in the E. Alpine chain on the N. side, in Italy only in some areas at the border with Switzerland and Austria. In some localities sympatric with *C. (O.) alpestris*. **Chorotype:** SEU-ALCA. **Range characteristics:** CEur. **Distribution in Europe**: **Germany** – Not in the W. and N.-most parts; reported from Lower Saxony, Sachsen-Anhalt, Sachsen, Thüringen, Bayern and Baden-Würtemberg, notably in montane regions such as Harz, Erzgebirge, Bavarian Forest. Widely distributed in the S. of E. Germany. Except for Sachsen and Bayern, noted as vulnerable or seriously endangered. **Poland** – Distributed along the whole S. border from the W. Sudety Mts. to the E. Beskydy Mts. **Russian Plain** – Only in the Ukrainian Carpathians, where it seems to be rare. Known from the Chernogora Mt. Range (Goverla Mt., Petros Mt. – MPGU; Pop Ivan – IZ). **Czechia & Slovakia** – Reported from Bohemia (especially border mountains), Tatra Mts., Moravia and Slovakia, locally common. **Romania** – Carpathians (Transylvanian Alps), Caraiman Mts. (the old 'Hungarian' localities are now situated in Slovakia and Romania). **Balkan Peninsula** – Restricted to the N.; Slovenia (Julian Alps). **Austria** – Distributed in all parts, except Burgenland. **Switzerland** – This montane species is widespread all over the Swiss Jura and the N. side of the C. Alps (all right side of the Rhône); it is almost absent from the N.E. Mittelland, Wallis and Tessin. **Italy** – Restricted to the Alps along the Swiss-Italian and Austrian-Italian border. **France** – In the E. restricted to two small areas near the Swiss border, one situated in the

Jura near Pontarlier and the other W. of Geneve (Coulon *et al.*, 2000). Not in the Vosges (Callot & Schott, 1993).

Subspecies: a) subsp. sylvestris (s.str) – From Vosges and Jura, Switzerland, C. Germany, eastward to mountains of Bohemia and Moravia, to the S. in Italy, in some localities of the C. and E. Alps. **b) subsp. kolbi** Breuning, 1927 – E. Alps, S.E. Austria, Slovenia. **c) subsp. redtenbacheri** Géhin, 1876 – S.E. Austria. **d) subsp. transylvanicus** Dejean, 1826 – Carpathian Mountains, to S. Poland, Slovakia, Ukraine and Romania, subalpine to high alpine. **e) subsp. haberfelneri** Ganglbauer, 1892 – S.E. Germany (Bavaria), N. and C. Austria, alpine subspecies.

Ecology: Mainly a montane species in C. and S. Europe, inhabiting moderately humid, coniferous (spruce) or mixed forests (also forest grasslands) and frequently also in the alpine zone, up to 2500 m (Czechia, Slovakia: Hůrka, 1973, 1996). Also according to Hoffmann (1907), in C. Europe mainly between 800 and 2500 m. In the Harz also found in peat bogs (Koch, 1989). In Switzerland in montane forests between 850 m and the timber line, and in alpine habitats up to a maximum of 2700 m (Marggi, 1992). In the S.-most part of the territory (N. Italy) it is found between 1800-2000 and 2900 m, strictly and most abundant in alpine steppe habitats (Casale *et al.,* 1982). In the Julian Alps (Slovenia) also above the timber line between 1500-2000 m (Drovenik, 1975). In C. Europe, where it also occurs in montane and subalpine forests, up to 2000 m; the lower limit situated at 700-1000 m, and in the N.-most area of distribution, e.g. in E. Germany and in the Harz at about 300 m (Arndt, 1989). In alpine prairies also at the border of melting snow (Koch, 1989).



11 013 sylvestris

Transects: Chapter 8: T-29-30, 77 and 79-80.

Biology: Activity – Usually a night active species, however, during the periods of reproduction also showing diurnal activity. **Periodicity** (Hůrka, 1973) – This species reacts very plastically according to environmental circumstances. In Italy, adults occur from April-May to September; reproduction can start immediately after hibernation, depending on altitude, and ends usually at the beginning of June, later at high altitudes. Under rearing conditions, copulations were already observed in March and April by Hůrka (*l.c.*), and in the field in May and June (Martius, 1972). Oviposition from June until August, the females of the new generation starting in July, laying eggs until September. Larvae develop during autumn and winter, with an obligatory winter diapause of the L3. Development of the eggs 9-10 days, L1 9-23 days, L2 15-27 days, L3 hibernates and pupates the following summer. For E. Gemany, Arndt (1989) reports that reproduction takes places in autumn and that the larvae are able to hibernate at all stages, subsequent to a period of pupation in spring (S. Europe) or summer (E. Europe). Teneral animals usually appear in July-August, sometimes in September; after a short period of activity they go into hibernation diapause, generally from September to April (Sturani, 1962). Both larvae and adults hibernate, often under trees, notably conifers (Casale *et al.,* 1982; Du Chatenet, 1986). **Food** (Larochelle, 1990) – In the field small slugs, also observed eating from the buds of *Vaccinium myrtillum.* In the field baited with beer, fruits and meat. In captivity, minced meat, earthworms, fish, chopped mealworms and fruits. **Larva**: Described by Letzner (1854: L3?), Hůrka (1971b: L1-L3) Raynaud (1976) and key: Arndt (1985, 1991b). Food – earthworms in the laboratory (Arndt, *pers. observ.*).

Conservation: Not endangered, except in the N. (Germany).

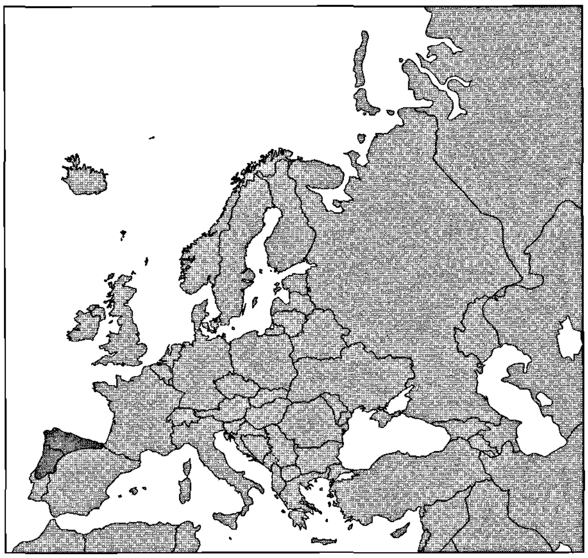
12. OREOCARABUS GÉHIN, 1876

12.001(+007). C. (Oreocarabus) amplipennis

Vacher de Lapouge, 1924
(including *C. pseudosteuarti* Vacher de Lapouge, 1924
and *C. getschmanni* Vacher de Lapouge, 1924).

General literature: Checklists and catalogues – Breuning (1933): 696+699. Březina (1994): 35; (1999): 45. Deuve (1994): 158+159 [332]. Kleinfeld & Schütze (1999): 21. Lorenz (1998): 85. Turin *et al.* (1993): 26. **Iconography** – Forell & Leplat (1998): fig. 32-34. Ghiretti (1996): 162. Imura & Mizusawa (1996): Pl. 31 [250]. Rautenstrauch (1994): Pl. 38-39.

Taxonomy: *C. amplipennis* has been treated by Lorenz (1998) as a subspecies of *C. luetgensi* Beuthin, 1886. *C. pseudo-*



12 001 amplipennis (incl. 12 007 pseudosteuarti) (Oreocarabus)

steuarti and *C. getschmanni* have been treated as proper species by Zaballos & Jeanne (1994). However, due to their morphological similarity and the lack of sympatric populations, we agree with Deuve (1994) and Březina (1994, 1999) and regard them as subspecies.

Geographical range: Endemic species of the Iberian Peninsula. **Chorotype:** WEU-IBEN. **Range characteristics:** Iber(NW). **Distribution in Europe**: **Iberian Peninsula** (Zaballos & Jeanne, 1994): Portugal, Spain, Cantabrian Mountains and C. Montane System: Sierra de Bussaco, de Lousa and de Estrella.

Subspecies: **a) subsp. amplipennis** – From N. Portugal (Serra do Marao) via Galicia to the Mts. W. and S. of Leon (Sierra de la Cabrera). **b) subsp. getschmanni** Vacher de Lapouge, 1924 – From the Cantabrian Mts. to the W. Basque Mts. **c) subsp. pseudosteuarti** Vacher de Lapouge, 1924 – (listed as species **12.007** in Turin *et al.* 1993) – C. Portugal: Serras do Bucaco, do Lousa and da Estrela.

Ecology: In forests and dry wasteland at middle altitudes (Zaballos & Jeanne, 1994). In montane and subalpine (rarely in alpine) zones, inhabiting coniferous and deciduous woodlands as well as open land (e.g. pastures with broom and gorse), often found in rocky and stony places (Assmann, *pers. observ.*). Most abundant between 800 and 1200 m (Forel & Leplat, 1998). Novoa (1979) and Alonso *et al.* (1988) collected the species more frequently in *Quercus pyrenaica* stands (up to about 1500 m) than in heathlands with ericaceous shrubs (mostly *Erica* species, including *Erica arborea*) or in meadows. In the W. part of the area of distribution (e.g. in the Serra do Marao), different proportions of red-legged individuals occur from place to place (cf. *Carabus granulatus*).

Transects: Chapter 8: T-95-98.

Biology: **Activity** – Predominantly nocturnal. **Periodicity** – Information on biology is poor. Probably close to that of *C. guadarramus*. Some females collected in May had chorionised eggs, probably a spring species. Adults of subspecies *amplipennis* have been recorded from April to September; recordings of the subspecies *getschmanni* and *pseudosteuarti* exist from June and August-September. Reproduction probably in early summer, the larvae developing over summer (Forel & Leplat, 1998). Teneral specimens occur at the beginning of autumn. **Food**: No data. **Larva**: Unknown.

Conservation: Not endangered.

12.002. C. (Oreocarabus) ghilianii
LaFerté-Sénectère, 1847.

General literature: **Checklists and catalogues** – Breuning (1933): 700. Březina (1994): 35; (1999): 45. Deuve (1994): 159 [334]. Kleinfeld & Schütze (1999): 21. Lorenz (1998): 85. Turin *et al.* (1993): 25. **Iconography** – Forel & Leplat (1998): fig. 40-41. Ghiretti (1996): 163. Imura & Mizusawa (1996): Pl. 31 [252]. Rautenstrauch (1994): Pl. 40.

Geographical range: Iberian endemic species. **Chorotype:** WEU-IBEC. **Range characteristics:** Iber(C). **Distribution in Europe**: **Iberian Peninsula** – Spain, C. Montane System: Sierras de Guadarrama and de Gredos (Zaballos & Jeanne, 1994; Du Chatenet, 1986).

Subspecies: **a) subsp. ghilianii** – Sierras de Guadarrama, de Ayllon and de Pela. **b) subsp. negrei** Breuning, 1966 – Sierra de Gredos and Sierra de Béjar.

Ecology: In damp montane bushes and forests, rather local, from 1200 to 1900 m; most abundant between 1600 and 1800 m in coniferous forest (Du Chatenet, 1986; Forel & Leplat, 1998).

Transects: Chapter 8: T-99.

Biology: **Activity** – No data. **Periodicity** – Spring breeder; reproduction starts in June; adults recorded during

12 002 ghilianii (Oreocarabus)

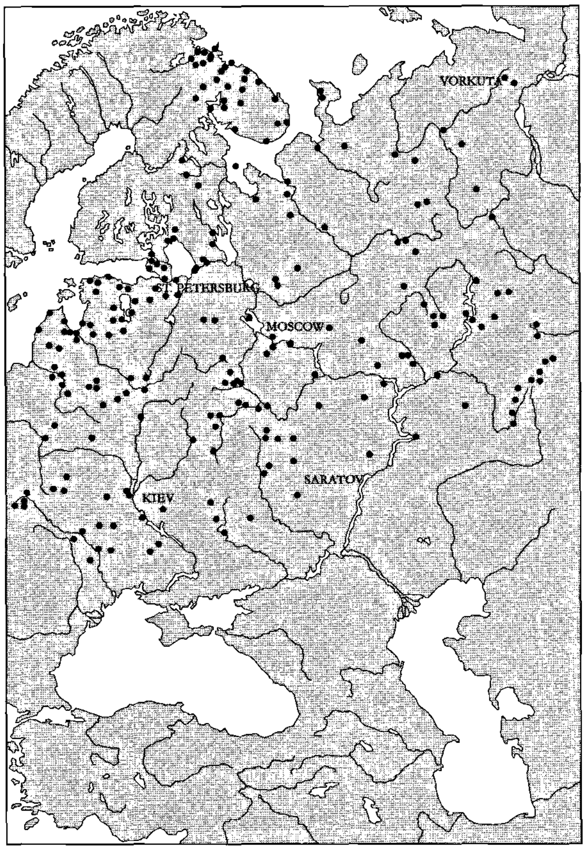
June-September (Novoa, 1975; Assmann, *pers. observ.*). **Food**: No data. **Larva**: Unknown.

Conservation: Not endangered.

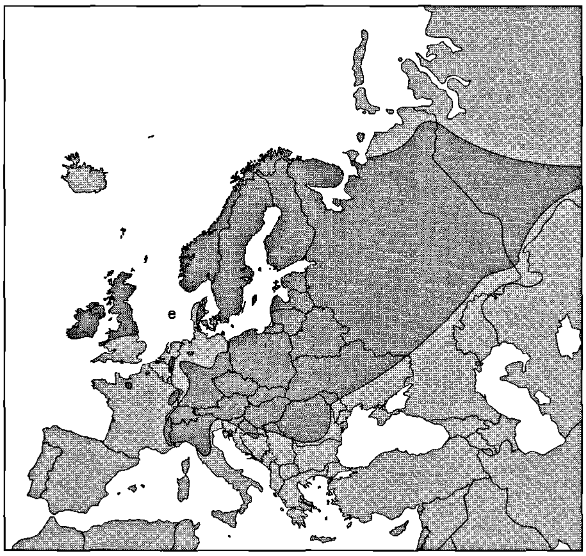
12.003. C. (Oreocarabus) glabratus
Paykull, 1790.

General literature: **Checklists and catalogues** – Breuning (1933): 723. Březina (1994): 36; (1999): 46. Deuve (1994): 163 [345]. Kleinfeld & Schütze (1999): 21. Kryzhanovskij *et al.* (1995): 45 [109]. Lorenz (1998): 85. Turin *et al.* (1993): 25. **Iconography** – Casale *et al.* (1982): fig. 74. Forel & Leplat (1995): Pl. 22. Ghiretti (1996): 163. Imura & Mizusawa (1996): Pl. 33 [265]. Jakobson (1905): Pl. 3. Pavicevic & Mesaros (1997): cd-rom. Rautenstrauch (1994): Pl. 42.

Geographical range: N. and C. Europe, from European Russia and W. Siberia to E. France and N.W. Italy (S. to Tuscany); N. England, and Fennoscandia. Absent from Iberia and the S.-most and S.E.-most parts of Europe. **Chorotype**: EUR. **Range characteristics**: CNEur-WSib. **Distribution in Europe (and adjacent areas)**: **Fennoscandia** – Generally distributed and common thoughout the area. **Denmark** – Scattered, but locally abundant in E. Jutland. **British Isles** – A strictly montane species in Britain and Ireland, most abundant in the N.; S. to Derby, widely distributed in Wales and Scotland. Widespread in Ireland, but local; mostly on high ground (Anderson *et al.,* 2000). **Netherlands** – Most records between 1890 and 1926, from the C. part of the country, which is the 'high' part of the Netherlands (up to about 140 m above sea level). Not found after 1948 and most probably now extinct. **Belgium** – Extinct, only few very old records in the E. **Germany** – Reported from nearly the whole area, however, mostly found in the montane areas, as single individuals. Only few records exist from the W. part of the N.-German plain (records from the lower part of the Rhine land – Koch, 1990; from the Westphalian Lowlands – Hanning & Drewnskus, 1995; from Lower Saxony – Assmann, 1994); in the E. parts of N. Germany more abundant (Arndt, 1989). A relict of old stands in N.W. Germany (Assmann, 1999). **Poland** – Widespread throughout the territory. **Baltic** – Known from all countries. **Byelorussia** – All the territory. **Russian Plain** – All of European Russia, except for the S. steppe regions. The N. range limit reaches 69°N and the species is known from several localities along the coast of the Kola Peninsula, Kanin Peninsula, Ust' Tsil'ma river basin and Polar Ural (ZIN; Poppius, 1905). The S. range limit coincides with the S. border of the large isolated forests in the forest-steppe zone (C. Moldova – Kodyma Forestry, N. of Odessa province (ZIN) – Znamenka nr. Kirovograd (ZM/KIEV, MPGU) – Kharkov (Medvedev, 1950) – Samara (ZIN) – Yuzhno-Ural Reserve (Kashevarov, 1986) – Irgizla (ZIN)). The species is rather common in the N. parts of the Russian Plain and becomes significantly rarer and more local towards the S. parts of the mixed forest zone. **Moldova** – Only found in the Kodry Hills. **Czechia & Slovakia** – Common throughout the territory. **Hungary** – Distributed in the montane areas, but never abundant. **Romania** – In the higher parts of the Carpathian mountans. **Balkan Peninsula** – Present in a small area in Slovenia, N.E. Croatia, and N. Bosnia. **Austria** – Distributed over the whole area. **Switzerland** – Widespread, except in the N.E. Mittelland and S. Wallis, where



12 003 glabratus



12 003 glabratus (Oreocarabus)

it is almost completely absent. Usually in the hills up to the montane or subalpine zone. In Tessin the most common *Carabus* species. **Italy** – In general common, mainly in the Prealps and Alps of N. Italy, the lowlands of the N.W. and the N. and C. Apennines. **France** – It has a scattered distribution in this territory. Isolated populations exist in the lowlands of the N.W. near Compiègne (N. of Paris) and near l'Aigle (W. of Paris); also isolated in the massifs of the Vosges (N.E. France: le Markstein, le Hohneck, le Hohwald, Wangenbourg and Saverne forest). Furthermore distributed in the high Alps in the S.E. (e.g. la Haute Ubaye, Vanoise and Mont Blanc massif); the last area is in connection with the main C. European area of distribution.

Subspecies: **a) subsp. glabratus** – C. and N. Europe. **b) subsp. extensus** Kraatz, 1885 – Carpathian Mountains. **c) subsp. lapponicus** Born, 1909 – British Isles, Lapponia to the Kola peninsula. **d) subsp. gibbosus** Heyden, 1866 – E. montane form of Austria, Balkans and Transylvania (alpine steppes). **e) subsp. latior** Born, 1895 – N. and C. Italy, from the Alps to Tuscany.

Ecology: Mesophilous forest species (Feoktistov, 1979). Rather eurytopic, characterised as silvicol by Mandl (1972). In W. Scotland, and Ireland, exclusively in montane regions, mainly in forests (Lindroth, 1974; Luff, 1998) but also on wet blanket peat and dwarf scrub heath (Anderson *et al.,* 2000). In the lowlands of N.W. Germany, *C. glabratus* is a relict species, restricted exclusively or mainly to ancient woodlands (Assmann, 1994, 1999). According to Hoffmann (1907), in C. Europe mainly from 300 m up to 1000 m. In the montane and subalpine zones, the species is also able to live outside forests, in montane heathlands (Westphalia – Balkenohl, 1981; Balkenohl & Grosseschallau, 1985; Lower Saxony – Assmann, 1994; Carinthia – Mandl, 1972). In lowlands only abundant in the N. of its distributional range (Fennoscandia; N. Russia), where it inhabits dark, spruce-mixed forest, rich in mosses (Lindroth, 1985). At least in N. Fennoscandia, it is able to live on permafrost. In Moscow province mainly in spruce forests, sporadic in other kinds of forest (Fedorenko, 1988). In the N. of C. Europe (Netherlands, N. Germany, Belgium, N. France), it seems to be restricted to coherent old forest areas that survived deforestation during last centuries; in this area a most stenotopic forest species that does not occur outside woodland (Assmann, 1999; Turin, 2000). In S. Europe rare in the lowlands and more abundant in foothills and montane habitats; in Switzerland from the foothills to 1300 m in the N. and to 1500 m in Tessin (Mt. Bar – Marggi, 1992). For the Swiss territory, the habitat on the N. side of the Alps is mainly deciduous or coniferous forest, in the S. mixed forest; it is almost never found in forest clearings or above the timber line (Marggi, *l.c.*). Coulon *et al.* (2000) mention it for the Rhône-Alpes from altidudes between 900 and 1200 m, occasionally higher. In contrast to this, Mandl (1972) characterises the (Austrian) lowland subspecies (*glabratus*) as silvicol, and the montane subspecies (*gibbosus*) as alpin-steppicol. In Hungary a characteristic species, however not in high densities, in closed beech, oak and coniferous forests in the mountains, mostly above 400 m, except in the W.-most part of Transdanubia, where it comes down to 200 m. In Italy rather thermophilic, in the lowlands notably in scrub or open country with at least some woody patches (Casale *et al.,* 1982), to montane forests (i.e. *Castanea* in S. Europe) in the middle mountain belt, subalpine and alpine pastures at 1200-1800 m (max. 2000 m). In the N. of the Balkan peninsula (former Yugoslavia), it is silvicol, inhabiting deciduous forests in hills and mountains (Pavicevic & Mesaros, 1997). In Ukraine, it inhabits the mixed or pine forests of the forest-steppe zone and the 'bairak' oak forests of the N. steppe subzone, but is never abundant (Petrusenko, 1971). In the Basegi reserve (Middle Ural), rare in mixed thinned forests and in forests with ferns on the forest floor (Esjunin *et al.,* 1995).

Transects: Chapter 1: I-1; Chapter 8: T-01-03, 05-06, 08, 10-11, 16-17, 21, 23-29, 32-36, 38-41, 44-45, 47-48, 58, 62-63, 76, 80-81 and 88.

Biology: **Activity** – Often mentioned as night active (e.g. Lindroth, 1985). Grüm (1966) and Weber & Thiele (1968) report a high percentage of day activity. Diurnal activity increases towards the N. (Neudecker, 1971; Thiele, 1977). In the S., it shows occasional day activity during rainy weather. **Periodicity** – The all-over picture is complex. In E. Germany, very similar to *C. hortensis* (Arndt, 1989). According to Lindroth (1985), it is an (nocturnal) autumn breeder with winter larvae in the S. and a (diurnal) spring breeder in the N. Sharova & Dushenkov (1979) report a one-year life cycle in Russia, and mention it to be a summer-autumn breeder with multi-seasonal activity of adults and autumn to spring activity of the larvae, which also applies to the C. Urals, where it is especially active during July and August (Kozyrev, 1989; Esjunin *et al.,* 1995). In N.W. Scotland, it breeds in summer (Luf, 1998). For Italy, where (in the lowlands) it appears generally in June-July, later than the other syntopic species, copulations have been reported from May until July (Casale *et al.,* 1982; Sturani, 1962); L1 larvae were found from July-October, L2 during August-October and L3 were found in October and December. Teneral animals were found in June and July (Denmark and Sweden – Larsson, 1939; Lindroth, 1945); furthermore, there are records from June, August and September (Germany – Henseler, 1938), until the beginning of October (Letland – Stiprajs, 1961). According to Sturani (*l.c.*), the adults enter aestivation diapause in August and are active again during September-October; this probably depends strongly on latitude and altitude. Several authors emphasise that the period of adult activity is relatively short, at least in some regions (Houston, 1981; Siebart, 1984; Puilliainen *et al.,* 1993; Assmann, 1994). Hibernating larvae and adults were found (France – Forel & Leplat, 1995; Italy – Casale *et al.,* 1982), in the soil and in mosses, very seldom in decaying wood (Casale *et al., l.c.*). Development in N. Europe with larval diapause, but without obligatory diapause of the adults. Duration of egg development: 8-10 days, L1: 16-21

C. putzeysianus putzeysianus Géhin
Italy, Maritime Alps (C. Lombarda).
Photo by A. Vigna Taglianti.

C. putzeysianus omensis Born
Italy, Cottian Alps (C. Valcavera).
Photo by A. Vigna Taglianti.

C. solieri clairi
Géhin
Italy, Maritime Alps
(C. Lombarda).
Photo by
A. Vigna Taglianti.

C. solieri
liguranus
Breuning
Italy, Maritime Alps
(M. Vaccia).
Photo by
A. Vigna Taglianti.

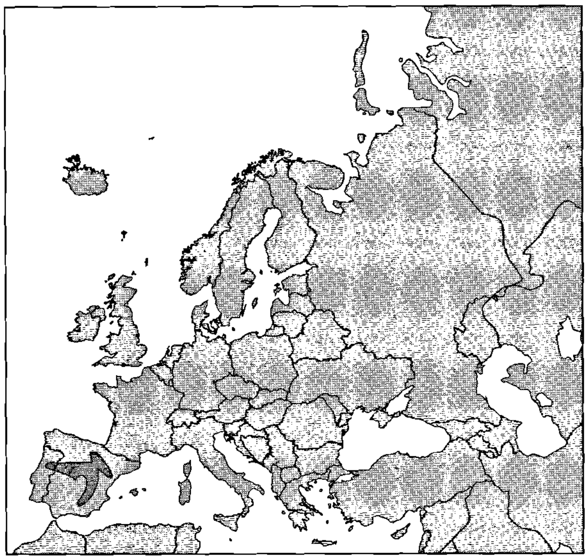
days, L2: 17 days, L3: up to 30 days. In N.W. Germany, where the species mainly inhabits old forest, the genetic structure of populations in the area is surprisingly homogeneous. This holds, even for sampling sites that are situated a few kilometers apart, especially if compared to other *Carabus* species, such as *C. arvensis*, *C. auronitens* and *C. granulatus*, which show greater genetic differences between sampling sites within a closed habitat (Assmann, 1999). **Food** (Larochelle, 1990): In the field caterpillars of *Dasychira* (Lymantriidae), larvae of Coleoptera, molluscs, various insect larvae and earthworms. In the laboratory, it accepts various kinds of meat, fruits (raspberries, apples), fish, chopped mealworms, and nectar of *Erica*; it is reported to be a frequent visitor of sugared baits for Lepidoptera. **Larva**: Described by Schiødte (1867: L3), Vacher de Lapouge (1905: L2; 1929: L1-L3), Hůrka (1971b), Raynaud (1976) and key: Arndt (1985, 1991b). Food – earthworms, pupae of large Diptera, Coleoptera (Arndt, *pers. observ.*). Feeding has also been investigated by serological methods (Gryuntal & Sergeeva, 1987), revealing that no clear preferences could be shown for the 10 tested groups of soil invertebrates. **Dispersal power**: The species shows a very low dispersal power and a low tendency to leave the forested habitat, which possibly is responsible for extinctions in areas where forested areas were fragmented and diminished (Assmann, 1999; Assmann & Günther, 2000).

Conservation: It disappeared completely from Belgium (Desender, 1986), the Netherlands, where it was present until ca. 1925 (Turin, 2000), and also from parts of W. Germany (Assmann, 1994; Gries *et al.,* 1973). Not endangered in the N. and E. of Europe. A most common and dominant species in the N. taiga zone. Also not endangered in the S. (Italy, N. Balkan). However, in a number of places in Germany, it survived the destruction of vast forested areas, that took place during the Middle-Ages and later centuries, in old stands that often belonged to aristocracy and ecclesiastic institutions (Assmann, 1999). The isolated populations in N. Germany, showed a remarkable differentiation according to allozyme studies, suggesting an ancient separation and low gene flow (Assmann & Günther, 2000). According to Blumenthal (1981), in C. Europe a good indicator of ancient areas of beech and spruce forest, especially of the large forest complexes. Also in S. Europe, e.g. in N. Italy, it can be the most abundant and dominant *Carabus* species in suitable places (deciduous bushes from 400-800 m – Casale *et al.,* 1982).

12.004. C. (Oreocarabus) guadarramus

LaFerté-Sénectère, 1847.

General literature: **Checklists and catalogues** – Breuning (1933): 699. Březina (1994): 35; (1999): 46. Deuve (1994): 159 [333]. Kleinfeld & Schütze (1999): 21. Lorenz (1998): 85. Turin *et al.* (1993): 26. **Iconography** – Forel & Leplat (1998): fig. 35-39. Ghiretti (1996): 162. Imura & Mizusawa (1996): Pl. 31 [251]. Rautenstrauch (1994): Pl. 39.



12 004 guadarramus (Oreocarabus)

Geographical range: Iberian endemic species. **Chorotype:** WEU-IBEC. **Range characteristics:** Iber(C). **Distribution in Europe**: **Iberian Peninsula** – Spain, C. Montane System: from Sierras de Gata, via de Sierras de la Peña de Francia, de Bejar, de Gredos, de Guadarrama, de Urbion and de la Demanda, to the Sierra de Moncayo, de Sagra; in the S. from the Sierras de la Cazorla and the Segura to the Sierras de la Sagra and de Alcaraz (Zaballos & Jeanne, 1994).

Ecology: In wasteland, bushes and forests of middle altitude, recorded from 1300 up to 2300 m (Du Chatenet, 1986; Assmann, *pers. observ.*). According to Forell & Leplat (1998), from 600 m upwards.

Biology: Generally having the same biological characteristics as *C. amplipennis* (Forel & Leplat, 1998). **Activity** – No data. **Periodicity** – Spring breeder. Adults were recorded during the periods April-June and August-September (after summer rain), teneral specimens in August and September. **Food**: No data. **Larva**: unknown.

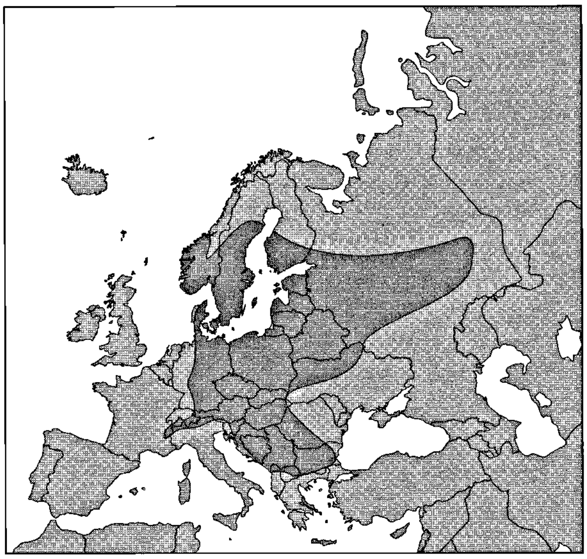
Conservation: Not endangered.

12.005. C. (Oreocarabus) hortensis

Linnaeus, 1758.

General literature: **Checklists and catalogues** – Breuning (1933): 701. Březina (1994): 35; (1999): 46. Deuve (1994): 162 [344]. Kleinfeld & Schütze (1999): 21. Kryzhanovskij *et al.* (1995): 45 [110]. Lorenz (1998): 85. Turin *et al.* (1993): 26. **Iconography** – Casale *et al.* (1982): fig. 74. Forel & Leplat (1995): Pl. 21. Ghiretti (1996): 163-164. Imura & Mizusawa (1996): Pl. 32 [262]. Jakobson (1905): Pl. 3. Pavicevic & Mesaros (1997): cd-rom. Rautenstrauch (1994): Pl. 41.

Geographical range: European species. N. and C. Europe; Alps; E. Europe to Russia; Balkan Peninsula to Bosnia, Montenegro and Bulgaria. Not in W. Europe. **Chorotype:** EUR. **Range characteristics:** NCEur-SEEur. **Distribution in Europe**: **Fennoscandia** – Distributed over the



12 005 hortensis (Oreocarabus)

entire area up to about 64°N; in Finland common in the N. and S. **Denmark** – Widely distributed and rather common, but not to the N. and W. of Jutland. **Germany** – Not in the C.W. (Rheinprovinz, Hessen, Westfalen; in Lower Saxony exclusively E. of the river Weser). Most records come from the S., however, widely distributed in most other parts of the territory; vulnerable in W. Thüringen, however for some parts of especially E. Germany, probably increasing locally and expanding its distribution. **Poland** – Widespread throughout the territory; not reported from the Beskydy Mts. in the S.E. **Baltic** – Present in all countries. **Byelorussia** – In all provinces. **Russian Plain** – Middle stretch of European Russia, N. to about 62°N (from S. Karelia to the N. of Perm' Province). To the E., this species extends to Kama river in Cisuralia (Perm' Province: Berezniki – Koz'minykh *et al.*, 1991b; Voronin, 1999; Chastye – Shilenkov & Voronov, 1973), from Bashkiria it is known only from literature (Matveev, 1990). E. border also in the Dnieper-Bug (right bank) forest-steppe (Medvedev, 1950). The S. range limit goes along the border between the deciduous forests and the forest-steppe – Zakarpatye (Ponomarchuk, 1956) – Kiev (Dolin, *in litt.*) – Bryansk (ZIN) – Mordov reserve (Feoktistov, 1979) – Raifa reserve nr. Kazan' (Zherebtsov, 1979) – Pavlovka nr. Bugul'ma (ZIN)). From the S. taiga subzone to the S. border of the subzone of deciduous forests. **Czechia & Slovakia** – Distributed over the whole area, very common in the forest zone. **Hungary** – One of the most common species in the hills and mountains, but absent from the Great Hungarian Plain. **Romania** – Present in hills and mountains in the W. **Bulgaria** – Distributed across the larger part of the territory, except the E. **Balkan Peninsula** – Distributed across the inland of former Yugoslavia: Slovenia (including Istria), E. Croatia, E. Bosnia-Herzegowina, Serbia and N.-most Macedonia. Not in the N. and and also not in the W. and S. of the peninsula, where it is replaced by *C. preslii* Dejean (Casale *et al.*, 1982). **Austria** – Reported from the whole area, but uncommon (Franz, 1971; Marggi, 1992). **Switzerland** – Distributed in the C.S. part of the territory, in Alp valleys (montane, rare in the hills), very scattered and in most places not common. **Italy** – Restricted to the N., Lombardia; distributed from Ticino through the valleys of the Orobian Alps, along N.E. Italian Alps and Venezian Prealps. **France** – Very restricted to the S.E. (Rhône-Alpes), near the Swiss-Italian and the W. Italian border: Alpes de Chamonix, de la Vanoise, de l'Oisans and Alpes de Queyras.

Subspecies: Despite its relatively large area of distibution, the species is very homogeneous and no forms merit a subspecific status.

Ecology: Eurytopic (mesophilous) forest species (Feoktistov, 1979; Fedorenko, 1988; Arndt, 1989), silvicol (Mandl, 1972). In bushes, light forests, river forests, forest hedges, forest clearings, parks and also open country; in N. Europe, especially on humus-rich rather dry soil (Lindroth, 1985). From lowlands in the N. and N.E to montane forests in the W. and S.; in Switzerland in spruce and river forests, rare in the hills and up to maximum 1500 m (Marggi, 1992); in Bulgaria from 300-2300 m (Guéorguiev & Guéorguiev, 1995); in N. Italy and S.E. France 700-2000 m, mostly in forests (Forel & Leplat 1995; Casale *et al.,* 1982). Arndt (*l.c.*) reports that it is locally a dominant species in moderately dry, coniferous forests in E. Germany and Poland (Casale, *pers. observ.*). In the Rhône-Alpes in higher places occasionally reaching alpine

12 005 hortensis

prairies (Coulon *et al.*, 2000). In woodlands S. of Hamburg, between the rivers Weser and Elbe, perhaps the most abundant *Carabus* species, in very different forest types (coniferous plantations with *Pinus* and *Picea*, deciduous forests with *Fagus*, *Quercus* and *Betula*), but lacking in some forests. In the N. restricted to deciduous or mixed forest on humus-rich, rather dry soil (Lindroth, 1985). In Latvia avoiding dry pine forest (Stiprajs, 1961). In Czechia and Slovakia common in both coniferous and deciduous forests (Hůrka, 1996). On the Balkan Peninsula also very eurytopic, occurring in several kinds of forest, but also in meadows, pastures from lowlands and hills, up to alpine regions (Pavicevic & Mesaros, 1997). In Ukraine in mixed forests of the forest-steppe zone and in 'bairak' oak woods of the N. steppe zone (Petrusenko, 1971). Marggi (*l.c.*) states that the range of this species almost matches that of the European spruce (*Picea abies*).

Transects: Chapter 1: I-1; Chapter 8: T-01, 03-05, 21, 23, 25, 31-33, 36-40, 55, 66-67, 69-71, 74-75, 77 and 79.

Biology: Activity – Nocturnal species. **Periodicity** (Hůrka, 1973) – Different life cycles have been reported. For N. and E. Europe, reproduction in autumn, August-September with autumn to spring activity of the larvae (Sharova & Dushenkov, 1979); according to Stiprajs (1961), maximum activity of adults in Latvia, in September. Biennial development in the N. of Fennoscandia (Lindroth, 1985) but also in many other parts of the continent; in this scenario, larvae hibernate, mostly as L1 (together with young first-year adults of the preceding generation). Teneral animals occur in the following year in June-August and after a short period of activity, these young adults hibernate under mosses (rarely in tree trunks – Geiler, 1980), before reproducing in the subsequent summer-autumn (Arndt, 1989). About 25% of the adults reproduce a second time (Schjøtz-Christensen, 1968). For C. Europe, Hůrka (*l.c.*) reports the following data: copulation and oviposition in autumn, from the end of August, during September and the first half of October (Schjøtz-Christensen, 1968; Stiprajs, 1961). Larvae were reported from February until July, and from October onwards, during the winter period (L1: October-July, L2 and L3: April-July). Pupae and fresh animals were found in June-July (Denmark) and July-August (Bohemia). This shift in occurrence might be linked with altitude and/or continentality. Development, according to Geiler (1980) and Larsson (1939), from egg to L3 ca 10 months (approx. 280 days in C. Europe); thus being a species with obligatory larval winter diapause and a short diapause of the adults during the summer (Hůrka, *l.c.*). For S. Europe, it is mentioned to be a spring reproducing species, with oviposition immediately after copulation in the period of April-May and adults remaining active until September without aestivation (Casale *et al.*, 1982; Sturani, 1962); the larvae remain active from May onwards, throughout the year and winter period, under mosses or tree trunks. In Italy, teneral adults appear regularly in August/September, but also in June when copulation and oviposition has taken place in autumn (Casale *et al.*, 1982). **Food** (Larochelle, 1990): In the field it preys on all kinds of insects and insect larvae (e.g. from Tipulidae, Coleoptera etc.), caterpillars of butterflies and moths, earthworms and slugs (e.g. *Arion* spec.). In captivity, it also accepts crushed snails, minced and raw meat, chopped mealworms, small or teneral beetles (even *C. violaceus*), fruits and bread soaked in sugared milk (Larochelle, 1990). Feeding has also been investigated by serobiological methods (Gryuntal & Sergeeva, 1987), revealing no clear preferences to the 10 tested groups of soil invertebrates. **Larva**: Described by Heer (1836: L3), Vacher de Lapouge (1908), Bentsson (1927: L1-L3), Hůrka (1971b), Raynaud (1976) and key: Arndt (1985, 1991b). Food – earthworms in the laboratory (Arndt, *pers. observ.*). **Dispersal power**: In the forests of N.W. Poland, the species walks longer distances in beech forests than in pine stands and generally the males are more active than the females (Szyszko & Gryuntal, *in litt.*). The species rarely climbs trees but also in this case the males show a more pronounced activity than the females. Climbing was only observed in beech forests and was seemingly restricted to September, for which no explanation has been found yet.

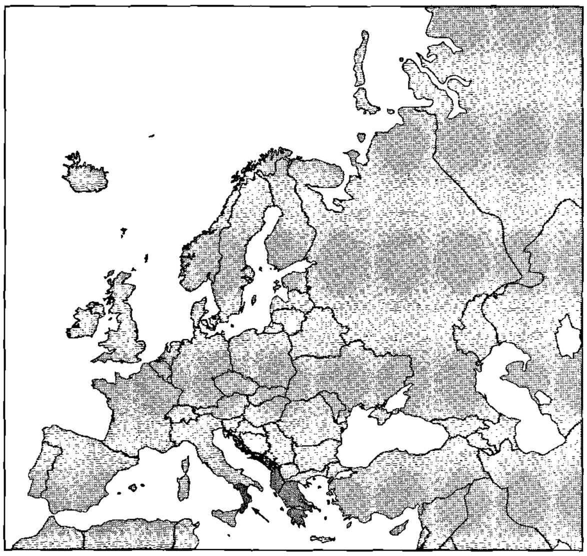
Conservation: Common and widespread, not endangered.

12.006. C. (Oreocarabus) preslii

Dejean & Boisduval, 1830.

General literature: Checklists and catalogues – Breuning (1933): 702. Březina (1994): 35; (1999): 46. Deuve (1994): 163 [344]. Kleinfeld & Schütze (1999): 21. Lorenz (1998): 85. Turin *et al.* (1993): 26. **Iconography** – Casale *et al.* (1982): fig. 74. Ghiretti (1996): 164. Imura & Mizusawa (1996): Pl. 32 [262]. Rautenstrauch (1994): Pl. 41-42.

Taxonomy: By Březina (1994, 1999) and Deuve (1994) treated as a subspecies of *C. hortensis*. Further studies are needed to clarify taxonomic status.



12 006 preslii (Oreocarabus)

Geographical range: A typical transadriatic-transionic element (Magistretti, 1965). S. Balkans: from Albania to Pelopponesos, S. Dalmatian coast and also in S. Italy. **Chorotype**: SEU-APDI. **Range characteristics:** Apen(SW)-Balk(W). **Distribution in Europe**: **Balkan Peninsula** – In the coastal region of Croatia (Dalmatia) and Bosnia; from N. Albania and S. Macedonia, also most of the Greek mainland to the E. coast. Also on Dalmatian and Ionian Islands. **Italy** – S. Apennines (from Campania and Lucania to Aspromonte).

Subspecies: **a) subsp. preslii** – Greece, Pelopponesos. **b) subsp. neumeyeri** Schaum, 1856 – Adriatic coast, from Montenegro to Croatian coast, N. and C. Greece. Italy: S. Apennines (Campania, Basilicata, Calabria). According to Deuve (1994), the (ssp.) *herzegowinensis* from Bosnia-Herzegovina, and (ssp.) *jonicus*, from Kerkyra, S. Albania and Pyndos (ssp.) *pindicus*, seem to be distinct from *neumeyeri*.

Ecology: In mediterranean bushes along the coasts and up to montane forest (rare in pastures); in Italy preferably in montane forest from 1000 to 1800 m. It occurs in deciduous (Fagetum) as well as in coniferous forests, but less in broad-leafed forests (Casale *et al.,* 1982). Also in forest clearings and plantations.

Transects: Chapter 8: T-68 and 86-87.

Biology: **Activity** – No data. **Periodicity** – No data. **Food** – Similar to *C. hortensis* (Casale *et al.,* 1982). **Larva:** Described by Sturani (1962) on the basis of specimens from Peloponnesos). Food – No data.

Conservation: Extremely abundant in forests, both in Greece and in S. Italy (Casale, *pers. observ.*); not endangered.

(12.007. C. (Oreocarabus) pseudosteuarti)
Vacher de Lapouge, 1924 (see **12.001** *C. amplipennis*).

13. TOMOCARABUS REITTER, 1896

(13.001. ? C. (Tomocarabus) antipai Panin, 1942)

General literature: **Checklists and catalogues** – Březina (1994): 93; (1999): 33. Deuve (1994): 145 [278]. Lorenz (1998): 80. Turin *et al.* (1993): 26.

Taxonomy: Described from a single male from Romania (probably an aberrant specimen of *C. convexus* ssp. *conciliator* Géhin, 1885; see Březina, 1994 (only in index); Deuve, 1994). Březina (1999) lists it as a synonym of *C. convexus convexus* Fabricius. A highly doubtful species (Kryzhanovskij, *in litt.*). **Iconography** – Not available.

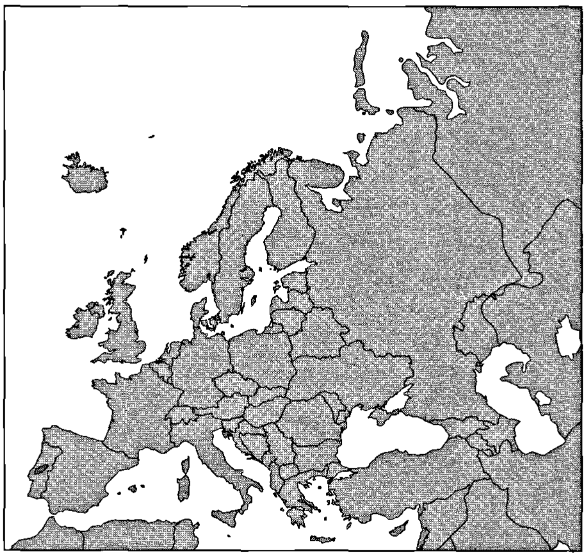
Distribution in Europe: Romania (Panin, 1952): N.E. Romania: Piatra Neamt: Varatec.

Subspecies, **Ecology**, **Biology** and **Conservation**: No data.

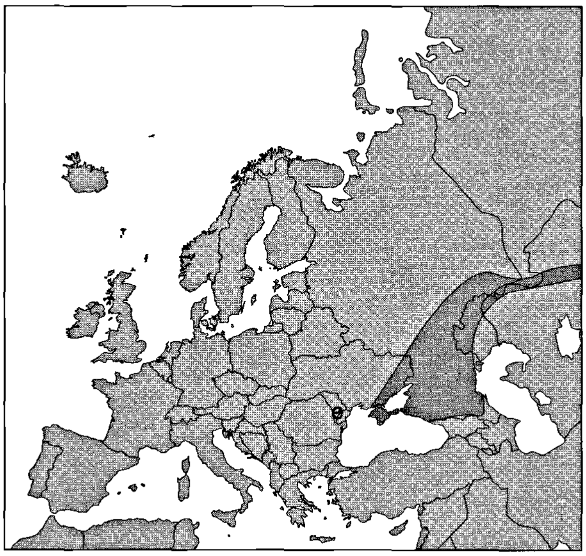
13.002. C. (Tomocarabus) bessarabicus
Fischer von Waldheim, 1823.

General literature: **Checklists and catalogues** – Breuning (1933): 884. Březina (1994): 41; (1999): 33. Deuve (1994): 146 [283]. Kleinfeld & Schütze (1999): 13. Kryzhanovskij *et al.* (1995): 46 [123]. Lorenz (1998): 80. Turin *et al.* (1993): 26. **Iconography** – Ghiretti (1996): 139. Imura & Mizusawa (1996): Pl. 24 [193].

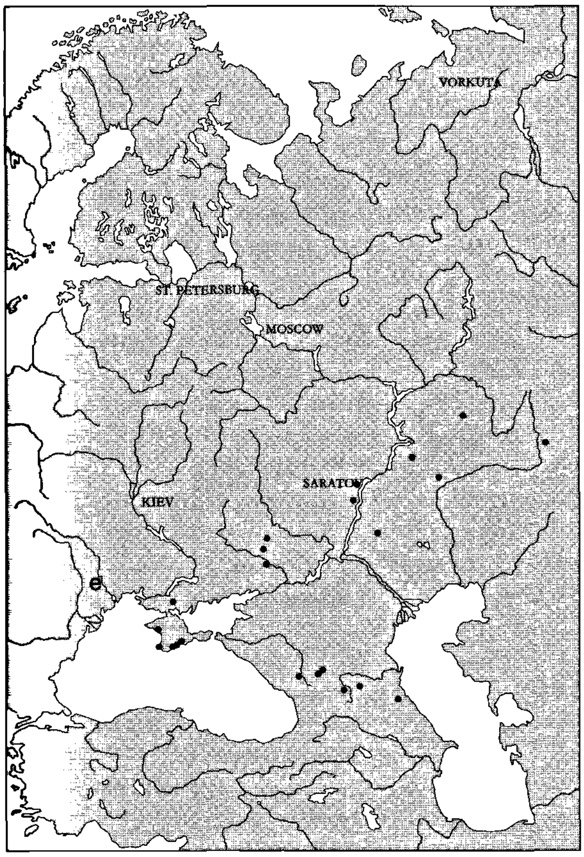
Geographical range: Ukraine, ?Moldova, Lower Volga, N. Caucasus, S.W. Siberia, Kazakhstan. **Chorotype:** SIE. **Range characteristics:** EEur(S)-Kaza. **Distribution in Europe**: **Russian Plain**: S. European Russia, S. Urals, Ciscaucasia. W. to Dnieper River and Crimea, the W.-most locality Bendery in Moldova (Fischer von Waldheim's type locality; to be checked according to Breuning (1933), but probably extinct there). In the N., it does not cross the N. limits of the steppe zone (the line Askania Nova Reserve –



12 007 pseudosteuarti (Oreocarabus)



13 002 bessarabicus (Tomocarabus)



13 002 bessarabicus

Derkul – Saratov – Belebei). Known from S. Ukraine (Kherson province, Askania Nova Reserve – Averin, 1938; Sharova, 1981; ZIN; Chernomorski Reserve – IZ; Rybalchye – MPGU); Crimea (Evpatoriya, Sevastopol, Ai-Petri, Agarmysh, Yalta, Sudak, Friedental – ZIN, ZM, IZ, Mal'tsev *et al.,* 1971); Lugansk province (Derkul, Strel'tsovskaya step', Proval'skaya step' – Medvedev, 1950, ZM, IZ). In S. European Russia recorded from Saratov province (Saratov, Sarepta (= Krasnoarmeisk) – ZIN), Samara (Pestravskii district – Utrobina, 1964), Volgograd (Ergeni upland – Komarov, 1986), Bashkiria (Aksenovo nr. Belebei – ZIN), Orenburg province (Bolotovsk – Sharova & Lapshin, 1971), Uralsk province (Uralsk – Zhuravlev, 1914; Dzhanybek – Arnol'di *et al.,* 1971 – MPGU). Several localities are reported from Ciscaucasia and N. Caucasus (Kumyska in Rostov province – Fomichev, 1983), Kislovodsk, Pyatigorsk, Teberda, Chervlennaya (Grozny province), Levash, Luchek Mt. (Dagesthan) – MPGU, ZIN, ZM. In N. Ossetia occurs only in arid montane valleys, not rare – Alekseev, *in litt.*). In the S. Dnieper region, only at the E. bank penetrating along Dnieper-Bug steppes into the forest-steppe; not on the W. bank (Medvedev, 1928, 1950). **Moldova** – Reported from S. Moldova and the lower Dnestr flood plains, however it seems to have never been reliably recorded for the last 80 years at least (Matalin, *in litt.*); most probably extinct. The record mentioned for Bessarabia by Jakobson (1905) is wrong according to Neculiseanu & Matalin (2000).

Subspecies: a) subsp. bessarabicus – Steppes of Ukraine including the Crimea, Moldova. Extinct in the major part of area. **b) subsp. concretus** Fischer von Waldheim, 1826 – N. Caucasus, Lower Volga, S.W. Siberia, Kazakhstan.

Ecology: Typical species of pure and undisturbed steppes (Dolin, *pers. comm.*); according to Alekseev (*in litt.*), in N. Ossetia it occurs in arid montane basins, xerophilic habitats and montane steppes from 800 up to about 1000 m.

Transects: Chapter 8: T-51-52 and 59-61.

Biology: **Activity** – No data. **Periodicity** – One year life cycle with reproduction in spring (Sharova & Dushenkov, 1979). The larvae are active during the summer period and the young adults appear in autumn, being active for some time before hibernation. **Food** (Larochelle, 1990) – In the field (Russia), caterpillars, various insects, e.g. larvae of Coleoptera. **Larva**: Described by Sharova (1958: L2-3; 1964: L2-3). Food – Same as adults.

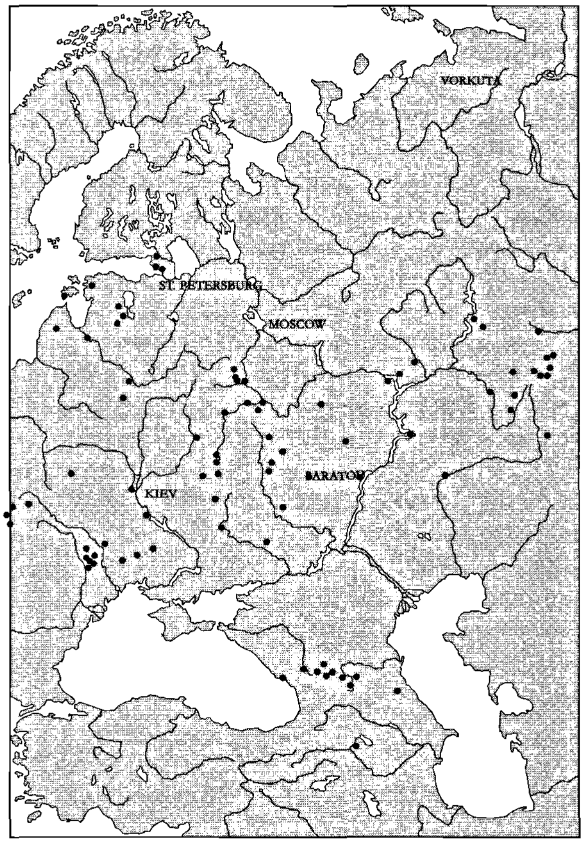
Conservation: Threatened in several areas, by agricultural methods, such as ploughing.

13.003. C. (Tomocarabus) convexus
Fabricius, 1775.

General literature: **Checklists and catalogues** – Breuning (1933): 861. Březina (1994): 41; (1999): 33. Deuve (1994): 144 [278]. Kleinfeld & Schütze (1999): 13. Kryzhanovskij *et al.* (1995): 46 [120]. Lorenz (1998): 80. Turin *et al.* (1993): 26. **Iconography** – Casale *et al.* (1982): fig. 64. Forel & Leplat (1995): Pl. 22; (1998): fig. 30-31. Ghiretti (1996): 134-137. Imura & Mizusawa (1996): Pl. 24 [195]. Jakobson (1905): Pl. 3. Pavicevic & Mesaros (1997): cd-rom. Rautenstrauch (1994): Pl. 60-61.

Geographical range: W.-palaearctic species. Europe in the N to 60°N; absent however, from the British Isles,

13 003 convexus (Tomocarabus)



013 003 convexus

N.W. France and most of the Iberian peninsula S. of the Pyrenees. In the E. to the Balkan peninsula, Turkey, the Caucasus and W. Siberia, further to Altai and N. Kazakhstan. **Chorotype:** SIE. **Range characteristics:** Eur-Anat-Wsib. **Distribution in Europe (and adjacent areas): Fennoscandia** – Norway, only in the S.W.; Sweden, scattered in the S., rare and decreasing after 1950; Finland, only in the extreme S., locally not rare. **Denmark** – Widely distributed but uncommon on the islands; absent from the W. part of the country. **Netherlands** – Mainly older records; it probably disappeared completely from the C. localities and was for a long time only reported from limestone grasslands in the S. Now probably also extinct there (last record from 1981). **Belgium** – Many old records exist from the C. part of the country and Flandria, where it now seems to be extinct. Restricted to the S.-most part and Luxembourg. **Germany** – Reported from all over the area, except the N.W.; rare in Schleswig-Holstein, Berlin, Sachsen-Anhalt and a decline is mentioned for Brandenburg and Bayern. In E. Germany widely distributed and in many places rather common (Arndt, 1989). **Poland** – All over the territory, locally common. **Baltic** – Scattered distribution over the whole area. **Byelorussia** – Only very few records in the W. and N. Provinces. **Russian Plain & Caucasus** – The middle stretch of European Russia, range 'narrowing' to the E., like in many other nemoral species, connected to the zone of deciduous forests. In the W. part of the range, reaches to the N. to Vyborg (61°N), however in the C. and E. regions of European Russia not exceeding the 57-58°N (Moscow province – Kazan' – Perm') and Pskov province (8 km N.W. of Zabelye Station – MPGU). The S. range limit coincides with the line Kishinev – Lugansk – Uralsk – S. Bashkiria. There is a disjunction in the range in the S.-most parts of the Russian Plain, where *C. convexus* is absent, but it appears again on the N. Caucasus where it is known from several localities (Daghestan, Luchek Mt.; Georgia, Daryae Gorge, Borzhomi (MPGU)). Rather common in zones of mixed forests and forest-steppe, penetrates to the S. taiga subzone in the N., and to the insular forests of the N. steppes in the S. **Moldova** – Reported from the C. and S. (Kodry, S. Moldova, Budzhak). **Czechia & Slovakia** – The nominate race is rather abundant in Czech and Slovak Republik. **Hungary** – Widespread, mainly in the montane areas. **Romania** – Common throughout the entire territory, both in the lowlands and in mountains. **Bulgaria** – Widespread and common. **Turkey** – European part, N. Anatolia. **Balkan Peninsula** – Most of the territory; widespread in all of former Yugoslavia and Albania. Distributed over most of the Greek mainland except the extreme S. of the Peloponnisos (in Greece only in high mountains); not reported from the Aegean islands and Crete. **Austria** – Widespread and common throughout the territory. **Switzerland** – Most widespread and common in the warm areas near Geneva, in the W. and Tessin; almost absent from the C. Alps and the N.E., rare in Graubünden. Mostly in hills and the montane zone, only in Tessin up to 1950 m (Mt. Tamaro). **Italy** – Widespread in most parts of the mainland; present in N. Sicily and absent from Sardinia. **France** – Widespread in most of montane France; absent from most of Brittany and W. Normandy, as well as from Landes and a coastal area in the S.E. from the Camargue to the foothills of the Alpes Maritimes. **Iberian Peninsula** – Only penetrating the territory from the N., to the E. Pyrenees and the N.-most part of the Catalonian Mts., Navarra, Huesca, Lerida, Gerona and Barcelona (Herrera & Arricibita, 1990). Generally rare.

Subspecies: a) subsp. convexus – Inhabits most of the species area. **b) subsp. pyrenaeicola** Csiki, 1927 – Pyrenees and Catalonian Mts. **c) subsp. dilatatus** Dejean, 1826 – S.E. Austria, N.E. Italy, whole Balkan peninsula except S. Greece. Guéorguiev & Guéorguiev (1995) mentions the form *gracilior* Géhin, 1885 from the lowlands of Bulgaria, and Pavicevic & Mesaros (1997) indicate this form for N.E. and S. Serbia, N. and E. Macedonia. **d) subsp. moreanus** Reitter, 1896 – S. Greece: Peloponnesos, island Euboea.

Ecology: Eurytopic and mesophilous in many places in E. Europe, however behaving as a typical thermophilic species in the N. and W. part of its area. Generally characterised as a forest species, of thin, humid deciduous and pine forests, forest clearings, parks and gardens, particularly for the C. and E. Europe in lowlands and middle montane belt, mainly between 500 and 1200 m (Hoffmann, 1907). In the S. also in bushes along shores and mediterranean forests. Most common in regions with a continental climate. In the C. and E. European mountains, exceptionally present but less abundant at high altitudes; in Italy up to 2000 (occasionally to 2200 m – Casale *et al.,* 1982) and on the S. slope of the Pyrenees in N. Spain, up to 1500 m (Forel & Leplat, 1998). In Bulgaria up to 2600 m (Guéorguiev & Guéorguiev, 1995). In the C. Balkans (former Yugoslavia), it is a typical forest dweller in the inland, reported from deciduous and coniferous forests in hilly and montane areas, sometimes even up to alpine steppes, while in the coastal regions it also inhabits meadows and pastures (Pavicevic & Mesaros, 1997). In Hungary occurs in various forest associations and in forest edges; preferably in the hills and mountains, inhabiting the S.-facing slopes and sandy areas in the lowlands. In Moscow province rare, restricted to anthropogenous habitats (parks, gardens), avoiding mature forests (Fedorenko, 1988). In N. Ossetia, where it is one of the most common *Carabus* species, from deciduous forests in the lowlands (avoiding dry pine forests), to alpine meadows and steppes at 2500 m (Alekseev, *in litt.*). In the Ukraine mainly in oak-hornbeam forests of the forest-steppe zone and 'bairak' oak woods of the N. steppe zone (Petrusenko, 1971). Also Forel & Leplat (1995, 1998) mention it for France and N. Spain predominantly as a forest species that occurs only exceptionally in marshy alpine prairies to a maximum of 1800 m. For Czechia and Slovakia, mentioned as being common in various shaded places, especially at lower altitudes (Hůrka, 1973, 1996). Mandl (1972) characterises for Austria the nominate subspecies *convexus* as silvicol, and *dilatatus* as alpin-steppicol. The species can be very abundant in its optimum habitat, but is never found aggregated in hibernation (Casale *et al.,* 1982). It seems to avoid intensively cultivated (manured and fertilised) habitats. In N.W. Europe more stenotopic, e.g. in the Netherlands, where it is probably extinct now, it occurred mainly on warm limestone grasslands and extensively managed fields in the S. (province of Limburg), however, close to forest edges (Turin, 2000). Also Lindroth (1985) characterises the species for Scandinavia as an inhabitant of warm and dry places, such as sun exposed hills, where it occurs on grassland and (not intensively) cultivated land. In N. Germany, besides on calcareous soil, also observed in moist heath on peaty soil (Mossakowski, 1970a), and dry heath on sandy soil (Koch, 1989). Arndt (1989) states that the species can resist cold very well. In N.-most Spain in forests and montane and subalpine grasslands (Herrera & Arricibita, 1990).

Transects: Chapter 1: I-1, 2; Chapter 8: T-05, 18, 20-21, 23, 25-31, 33-35, 39, 44, 46-51, 53-58, 61-76, 78-79, 81-90 and 93-94.

Biology: **Activity** – Mainly a nocturnal species, only occasionally diurnal (Burmeister, 1939). **Periodicity** – In C. Europe, it reproduces in early spring, and becomes active during the first half of April (Hůrka, 1973) or in February/March (Blumenthal, *pers. comm.*). In C. Italy, the new (autumn) generation is also active in winter when it is intensively predated by owls (Casale *et al.,* 1982: results by A. Vigna Taglianti from pitfall trapping). In general, from the middle of April onwards, oviposition takes place (egg size 3 x 1.5 mm); and after egg development of about two weeks, the first larvae appear at the end of the same month (Arndt, 1989; Kozyrev, 1989). The larval development, without diapause, takes 30-40 days until June-July; L1 are seen from May to July, L2 from June-July (C. Europe: Hůrka, *l.c.*). Raynaud (1967) reports a L3 by the end of June in the French Pyrenees. Teneral animals appear from the end of July to the beginning of August. The young adults are very active before they go into hibernation diapause from November, lasting until March (Forel & Leplat, 1995). Duration of development, eggs: 14 days (Sturani, 1962), L1: 7-15 days, L2: 8-16 days, L3: no data; pupa: 10-12 days, with a total of approximately 60 days under captive breeding conditions (Stiprajs, 1961) and about 3 months in the field in N. Europe (Larsson, 1939). Sturani (1962) reports a first period of adult activity from April to July and a period of aestivation during August. From September until the beginning of November, at least in the S., the adults show a renewed period of activity and enter hibernation in November until March (this could not be confirmed by data from N.W. Europe, Netherlands). **Food** (Larochelle, 1990): In the field, insects and insect larvae, earthworms, snails, slugs and carrion. In captivity also chopped mealworms, raw meat, gingerbread, fruits (apple), fish, minced and raw meat. **Larva**: Described by Vacher de Lapouge (1908), Bentsson (1927), Vacher de Lapouge (1929) and Hůrka (1971b). Food – earthworms and larvae of Coleoptera (Arndt, *pers. observ.*). The L3 shows canibalism (Stiprajs, 1961).

Conservation: Arndt (1989) states that the occurrence and distribution of this species in many cases is underestimated, because it is difficult to find with the traditional method of sampling by hand. Moreover, in C. Europe, the most important period of activity takes place in early spring, and ends by the second half of April. However in Greece, and in some parts of Italy, in rather dry oak-forests, it can be extremely abundant during July-August and if there are rains, teneral specimens may occur (Casale, *pers. observ.*). Probably the species is commoner in many places in Europe than expected and known so far. The best way to catch it, is by pitfall sampling. Desender & Turin (1989) noted a severe decrease for N.W. Europe, which is probably caused by the loss of (xero)thermic places, due to fertilisation of poor and limestone grasslands. Chumakov (1988) reports that it disappeared from many polluted areas in Byelorussia. Blumenthal (1981) consideres it an unsuitable bioindicator, especially because of its eurytopy. Up until now, it seems not endangered in most of its S. populations, except perhaps in S.E. Bosna and S. Montenegro (Pavicevic & Mesaros, 1997).

13.004. C. (Tomocarabus) marginalis
Fabricius, 1794.

General literature: **Checklists and catalogues** – Breuning (1933): 892. Březina (1994): 43; (1999): 34. Deuve (1994): 144 [277]. Kleinfeld & Schütze (1999): 18. Kryzhanovskij *et al.* (1995): 46 [122]. Lorenz (1998): 80. Turin *et al.* (1993): 26. **Iconography** – Ghiretti (1996): 134. Imura & Mizusawa (1996): Pl. 24 [196]. Rautenstrauch (1994): Pl. 63.

Taxonomy: Previously (Breuning, 1933; Březina, 1994) placed in the monotypical subgenus *Callistocarabus* Reitter, 1896, nowadays listed in *Tomocarabus* (Deuve, 1994; Březina, 1999).

Geographical range: Poland, Romania, Byelorussia, N. Ukraine, Russia, in the N. almost to 54°N, and E. to Middle Ural and SW Siberia. **Chorotype:** EEU. **Range characteristics:** EEur(C)-WSib. **Distribution in Europe (and adjacent areas)**: **Germany** – Noted as extinct from Sachsen-Anhalt (authentic old records exist from glacial valleys of the Oder-Weichsel: Muldeaue near Jessnitz, 1824, 1948, 1968; Magdeburg, 1890); no further records. **Poland** – Formerly widespread in the N. from the coast to the E.; in the S. it was absent from most areas; nowadays restricted to and rare in pine woods in the E.; this species has showed a marked decline during the last decades (Szyszko, *in litt.*). **Byelorussia** – Now only from the S.E.-most area (see below), in former days probably also more to the W. (compare Poland and Germany). **Russian Plain** – A species with a disjunct distribution in the Russian Plain, known from Ukraine, C. European Russia and the Urals. To the N., *C. marginalis* is distributed to S. Byelorussia (Gomel' – Molodova, 1990) and, according to old data, to Mogilev (Jakobson, 1905) and Lithuania (ZIN). Most literature data and specimens in the collections are from the region between the rivers Dnieper and Don (provinces of Kiev, Chernigov, Bryansk, Gomel', Cherkassy, Poltava, Sumy, Kharkov, Dnepropetrovsk, Lugansk, Belgorod, Kursk, Voronezh, Ryazan' – ZIN; ZM; IZ; MPGU; Medvedev, 1950; Arnol'di, 1956). There are old records also from W. Ukraine (provinces of Podolsk – Jakobson; provinces of Volyn' and Zhitomir – Breuning) and Crimea (Averin, 1938; ZIN). Isolated populations occur in the Urals (Perm' – ZIN; Chikali in Kishert district – Koz'minykh *et al.,* 1991b; Uktus nr. Ekaterinburg – ZIN) and the Altai (ZIN), the last one, however, doubtful. From mixed forests to the N. steppe subzone. **Moldova** – Only found in the Kodry Hills. **Czechia & Slovakia** – Not occurring in the territory; erroneously recorded from Kojsovská in the Slovenské Rudohorie Mts. **Hungary** – Only known from very few localities in Transdanubia: Somogy county, Bakony Mts. (Kutasi, 1997). **Romania** – N.E. territory, Siebenbürgen: Ratosnva. Re-discovered in Transylvania (Varghis Valley – Harghita county) in 1997 by Máthé; old records are known from Sibiu, Cristian-Sibiu, Rastolita (formerly Ratosnya), Turda (Lie & Máthé, 2000).

13 004 marginalis

13 004 marginalis (Tomocarabus)

Subspecies: Except nominate, no subspecies in Europe.

Ecology: In deciduous or pine forests, mostly in forests-steppe zone. Probably an inhabitant of old glacial river valleys (Arndt, 1989). Rare in pine forests in Poland

(Hůrka, 1996). Arnol'di (1956) mentioned it a mesophilous forest species prefering especially oak woods. In Hungary, the records come from forests and forest margins (Pinetum, Robinietum) and acid, sandy biotopes. In Ukraine, it lives in the 'bairak' oak woods of the N. steppe zone and the oak woods of the forest-steppe zone (Petrusenko, 1971). According to Grechanichenko (2000), in the Central-Chernozem Reserve in various biotopes, preferring open places in forests (where it may have up to 30% of all *Carabus* specimens) and non-mown steppes; there a relatively dominant or subdominant species, also in upland oak groves and forest-steppe ravines.

Transects: Chapter 1: I-2; Chapter 8: T-47, 49, 53 and 55-57.

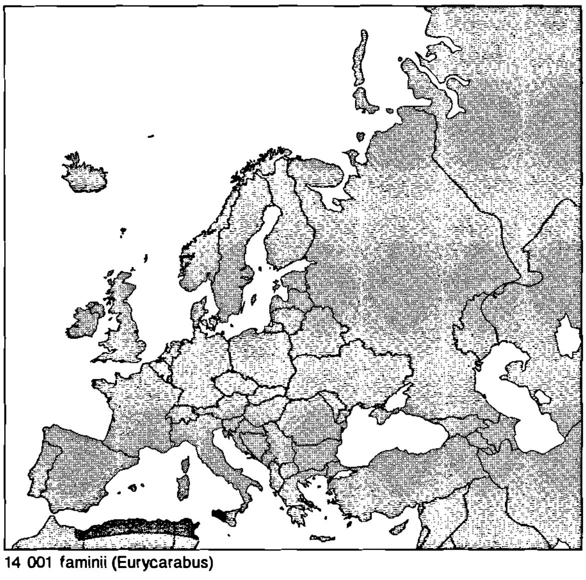
Biology: **Activity** – No data. **Periodicity** – One year life cycle; autumn breeding and autumn to spring activity and development of larvae (Sharova & Dushenkov, 1979). **Food** – No data. **Larva**: Described by Sharova (1958: L1-L3; 1964: L1-L3), Hůrka (1971b: L1-L3), Arndt (1991b): L1-L3). Food – No data.

Conservation: According to Szyszko (*pers. comm.*), the species has declined heavily in Poland during last decades and is in fact now restricted (and very rare) to the E.-most part of the country, whereas in former days the W. border was situated in E. Germany. This decline is probably due to climatic changes, possibly in combination with intensive forest cleaning.

14. EURYCARABUS GÉHIN, 1885

14.001. C. (Eurycarabus) faminii
Dejean, 1826.

General literature: **Checklists and catalogues** – Breuning (1933): 898. Březina (1994): 18; (1999): 36. Deuve (1994): 98 [142]. Kleinfeld & Schütze (1999): 19. Lorenz (1998): 82. Turin *et al.* (1993): 26. **Iconography** – Casale *et al.* (1982): fig. 55. Ghiretti (1996): 56-57. Imura & Mizusawa (1996): Pl. 28 [228]. Rautenstrauch (1994): Pl. 64-65.


14 001 faminii (Eurycarabus)

Geographical range: Siculo-maghrebinian species (Casale *et al.* 1982), distributed across N. Africa (E. Morocco, Tunisia, Algeria) and W. Sicily. **Chorotype**: NAF. **Range characteristics**: NAfr-Sici. **Distribution in Europe (and adjacent areas)**: **Italy** – Distributed only in the W. and S. part of Sicily (provinces of Agrigento, Trapani and Palermo). **North Africa** (Antoine, 1957; Casale *et al.*, 1982) – In the N. coastal, mediterranean region from E. Morocco to the N.E. part of Tunisia.

Subspecies: In the European area (Sicily) only the typical form occurs; some highly distinct subspecies exist in E. Morocco, Tunisia and Algeria (*lucasi* Gaubil, *numidicus* Castelnau; see Casale *et al.*, 1982).

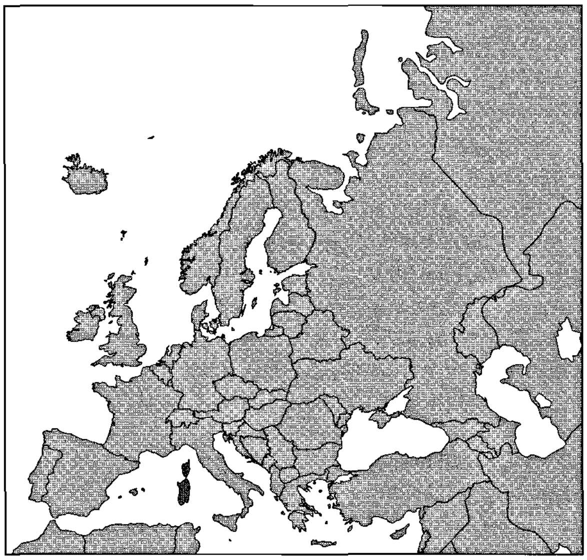
Ecology: In open country, mediterranean scrub or oasis-forests, in Sicily not in montane forests. Mostly on calcareous soil (limestone). From sea level up to 1000 m, especially inhabiting humid places; under stones and debris (Casale *et al.*, 1982).

Biology: **Activity** – No data. **Periodicity** – The adults occur from November to March and are particularly active in winter, being most numerous in December (Casale *et al.*, 1982). Oviposition also in winter and early spring. During January they have a period of relative inactivity, and become active again from February until March-April followed by an aestivation period from April/May to the end of October (Sturani, 1962). Korell (1975) was not able to find the species during spring at several well-known Sicilian localities. Hibernation during the coldest period in the soil (Korell, *l.c.*). In N. Africa, reproduction from November/December (copulation, egg-laying, larval hatching) to February/March (larval development); first instar takes ca 10-14 days (Arndt, *pers. observ.*). In Sicily, adults emerge from the pupa in April (M. Romano, *pers. observ.*). **Food** (Larochelle, 1990; Casale *et al.*, 1982) – In the laboratory snails. **Larva**: Described by Vacher de Lapouge (1905) and Casale & Sturani (1976). Food – earthworms in the laboratory (Arndt, *pers. observ.*) and small larvae of Coleoptera.

Conservation: In Sicily probably endangered in some places by the loss of original mediterranean vegetation, due to urbanisation.

14.002. C. (Eurycarabus) genei
Gené, 1939.

General literature: **Checklists and catalogues** – Breuning (1933): 828. Březina (1994): 19; (1999): 37. Deuve (1994): 98 [141]. Kleinfeld & Schütze (1999): 19. Lorenz (1998): 82. Turin *et al.* (1993): 26. **Iconography** – Casale *et al.* (1982): fig. 55. Forel & Leplat (1995): Pl. 2. Ghiretti (1996): 58. Imura & Mizusawa (1996): Pl. 28 [229]. Rautenstrauch (1994): Pl. 63.



14 002 genei (Eurycarabus)

Geographical range: Endemic species of Corsica and Sardinia. **Chorotype:** SEU-SACO. **Range characteristics:** Sard-Cors. **Distribution in Europe**: **Italy** – Scattered distribution all over Sardinia (Casale *et al.*, 1982; Casale & Vigna Taglianti, 1996); also on several small islands near Sardinia. **France** (Bonadona, 1971; Forel & Leplat, 1996): Corsica, widespread, all over the island.

Subspecies: No subspecies.

Ecology: Mostly in open country, sometimes in scrubland, from the sea level to 1200 (exceptionally to 1500) m, preferably on cool, moist places in open as well as wooded country; most abundant in the lowlands and the foothills (Casale *et al.,* 1982; Magistretti, 1965). In Corsica, particularly encountered in montane patches where snow remains for a long time during spring, which is not the case in Sardinia. Recorded on Col de Vizzavona and Mont d'Oro in the middle of May, directly at the snow border (Arndt, *pers. observ.*). Both in the laboratory and in the field, adults have been observed to stay submerged in the water under stones for 4 minutes (Casale *et al., l.c.*).

Biology: **Activity** – No data. **Periodicity** – According to Sturani (1962) and Casale *et al.* (1982), it is a spring breeder, the first period of activity takes place from March to June, followed by aestivation diapause during July-September and a new period of activity that lasts until January when the species (only at high altitude) enters hibernation until February. In the mountains of Sardinia, L2 larvae and teneral adults have been recorded in May (Casale, *pers. observ.*). The development is poorly known. **Food** – Snails, insects, worms and all kinds of larvae (Forel & Leplat, 1995). **Larva**: Described in Casale & Sturani (1976). Food – No data.

Conservation: Not endangered.

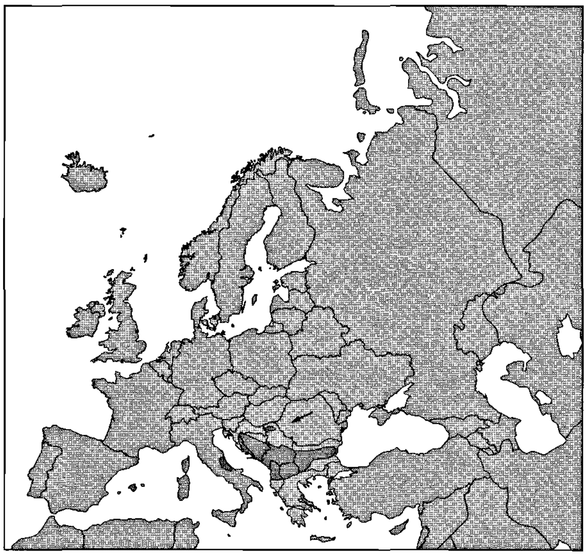
15. PACHYSTUS MOTSCHULSKY, 1865

15.001. C. (Pachystus) cavernosus
Frivaldszky, 1837.

General literature: **Checklists and catalogues** – Breuning (1933): 797. Březina (1994): 40; (1999): 35. Deuve (1994): 148 [292]. Kleinfeld & Schütze (1999): 19. Lorenz (1998): 82. Turin *et al.* (1993): 27. **Iconography** – Casale *et al.* (1982): fig. 61. Ghiretti (1996): 144-145. Imura & Mizusawa (1996): Pl. 27 [227]. Pavicevic & Mesaros (1997): cd-rom. Rautenstrauch (1994): Pl. 54.

Geographical range: A true transadriatic species; S. Italy and Balkan peninsula. **Chorotype:** SEU-APDI. **Range characteristics:** Apen(CW)-Balk(WC). **Distribution in Europe**: **Bulgaria** – Species of the C. and W. mountains (Stara Planina, Osogovska Planina, Rila Mt., Slavyanka Mt., W. Rhodope Mts.). **Romania** – A single specimen of *C. cavernosus* was collected in the Transylvanian Mts. in July of 1998. The exact locality is Torockó: Székelykő (in Hungarian) and Rimetea: Piatra Sacuesc (in Romanian). The locality lies on the plateau of a limestone mountain, the vegetation is limestone rock sward, the collecting methods was singling at day. This record is very interesting, because the species is new for the Carpathian Basin (Kutasi *et al.*, 2000). **Balkan Peninsula** – Montane areas of Croatia, E. Croatia, Bosnia-Herzegovina, Alpine Montenegro, C., E. and SW Serbia, W. Macedonia, Kosovo and Albania (except the S.); not in Greece (although the occurrence in W. Macedonia is close to the Greek border – Pavicevic & Mesaros, 1997), or European Turkey. **Italy** – Scattered occurrences in the Abruzzi Mts.

Subspecies: **a) subsp. cavernosus** – Bosnia, Herzegovina, Serbia, Macedonia, Albania, Bulgaria. **b) subsp. variolatus** O.G. Costa, 1839 – C. Italy: Abruzzi, Gran Sasso, Bagno, Velino and Greco Mts., and Sibillini Mts.



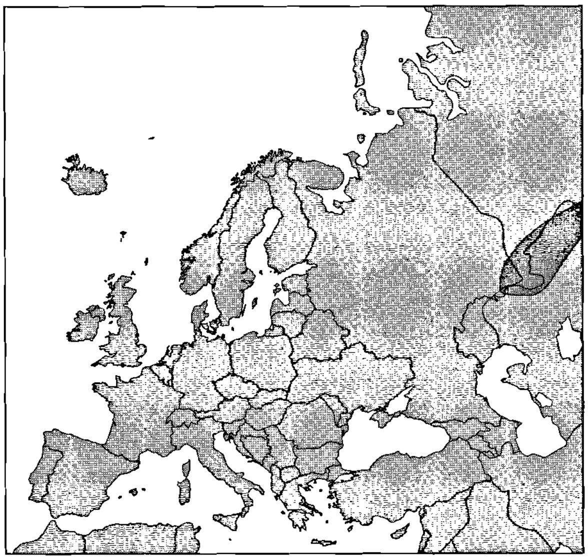
15 001 cavernosus (Pachystus)

Ecology: In Italy in dry montane prairies on limestone, especially between 1500 and 2300 m (Casale *et al.,* 1982). In Bulgaria 800-2300 m (Guéorguiev & Guéorguiev, 1995). For the C. parts of the Balkan peninsula, characterised as a praticol-silvicol species, inhabiting open habitats in hills, mountains, up to the alpine belt. In Romania, the above mentioned new locality lies on the plateau of a limestone mountain, the vegetation is limestone rock sward (Kutasi *et al.,* 2000).

Transects: Chapter 1: I-3; Chapter 8: T-65-66, 70 and 84-85.

Biology: **Activity** – Sometimes diurnal (Casale, *pers. observ.*; Du Chatenet, 1986). **Periodicity** – Adults recorded from May to September (Casale *et al.,* 1982), most abundant during June-July (Du Chatenet, 1986), probably followed by a long period of inactivity from September to June, at least at high altitudes (Sturani, 1962). **Food** (Larochelle, 1990) – In the field, Orthoptera, small dead Coleoptera, plants and fruits. Often under dead birds, reptiles and mammals. In captivity, fruits, raw meat, small slugs (*Limax* species), and crushed snails (*Helix* species), caterpillars of moths, earthworms, bread soaked in milk. According to Sturani (after Larochelle, 1990), the adults are strongly cannibalistic. **Larva** – Described by Casale *et al.* (1982). Food – In captivity, same as adults.

Conservation: Not endangered, on the contrary, in many places apparently increasing! Nevertheless, the history of the subspecies *variolatus* in Italy is almost as famous as that of *C. olympiae.* It was considered to be 'extinct' for several decades, due to overcollecting, with the help of local shepherds (exactly as for *C. olympiae*). It 're-appeared' more abundantly in the late sixties, and now it is apparently increasing, at least in the Gran Sasso Massif (Tassi, 1969). Speculations about the reason for this phenomenon vary from climatic changes to the more simple influence of a new road at Campo Imperatore at 1800-2000 m, which created a lot of stones and many new micro-environments, as well as better opportunities for entomologists to check this population. It is striking that at other places than Gran Sasso, the species remained 'rare', especially in populations situated several hours walking from some collectors residencies.



15 002 cribellatus (Pachystus)

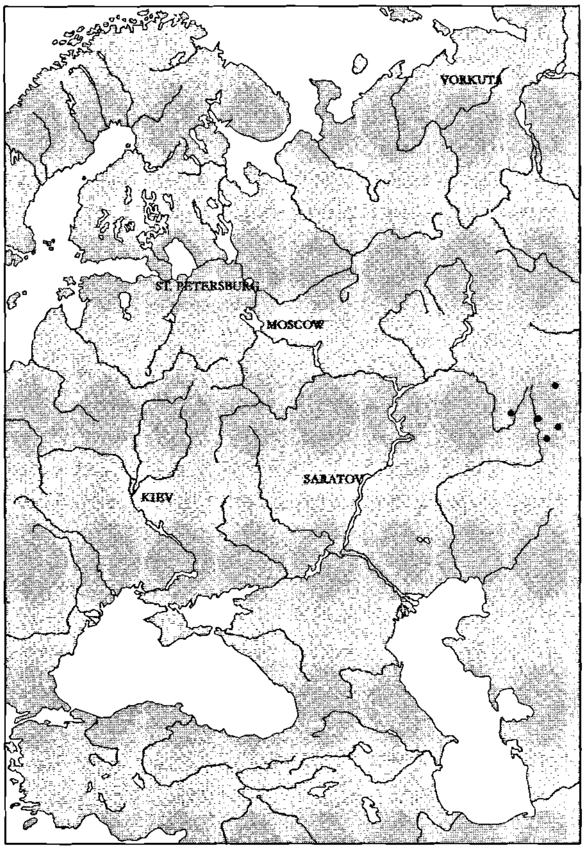
15.002. C. (Pachystus) cribellatus

Adams, 1812 (= *perforatus* Dejean, 1826).

General literature: **Checklists and catalogues** – Breuning (1933): 792; Březina (1995): 40; (1999): 36. Deuve (1994): 148 [291]. Kleinfeld & Schütze (1999): 19. Kryzhanovskij *et al.* (1995): 47 [128]. Lorenz (1998): 82. Turin *et al.* (1993): 27. **Iconography** – Ghiretti (1996): 144. Imura & Mizusawa (1996): Pl. 27 [226]. Rautenstrauch (1994): Pl. 53.

Taxonomy: In Březina (1994, 1999) and Deuve (1994) treated as a subspecies of *C. hungaricus* Fabricius.

Geographical range: S.W. Ural, Siberia (to Jakutsk and Transbaikalia), N. and C. Kazakhstan. **Chorotype:** SIB. **Range characteristics:** EEur(E)-CSib(S). **Distribution in Europe**: **Russian Plain** – In European Russia this Siberian species is known only from the S. Urals Mts.: S. Urals (Uzun-Kul – ZIN); Bashkiria (Bashkir Reserve – Koz'minykh, *in litt.*), Chelyabinsk province (Troitsk Reserve – Esjunin & Koz'minykh, *in litt.*; Bredy, Magnitogorsk, Glugorag Lake – IERZ) and Orenburg province (Orenburg, Verkhnyaya Karagalka river – ZIN; Bolotovsk – Lapshin, 1969 – MPGU). A steppe species.



15 002 cribellatus

Subspecies: Except nominate, no subspecies in Europe.

Ecology: In Europe only in steppes (S. Ural). For Yakutia it is recorded from dry meadows and pastures (Shilenkov & Averenskii, 1991).

Transects: Chapter 8: T-51-52.

Biology: **Activity** – No data. **Periodicity** – One-year life cycle. It breeds in autumn. The larvae are active from autumn to spring. Young adults occur at the end of spring and are active during summer and autumn (Sharova & Dushenkov, 1979). **Food** (Larochelle, 1990; Casale *et al.*, 1982) – In the field caterpillars and various insect species, e.g. larvae of *Leptinotarsa decemlineata* (Coleoptera). **Larva**: Described by Sharova (1958: L2-L3). Food – No data.

Conservation: No data.

15.003. C. (Pachystus) graecus
Dejean, 1826.

General literature: **Checklists and catalogues** – Breuning (1933): 799. Březina (1994): 40; (1999): 36. Deuve (1994): 149 [293]. Kleinfeld & Schütze (1999): 19. Lorenz (1998): 82. Turin *et al.* (1993): 27. **Iconography** – Ghiretti (1996): 145-146. Imura & Mizusawa (1996): Pl. 27 [225]. Pavicevic & Mesaros (1997): cd-rom. Rautenstrauch (1994): Pl. 54-55.

Geographical range: S. and E. parts of Balkan peninsula, Turkey. **Chorotype: EME. Range characteristics:** Balk-Anat. **Distribution in Europe (and adjacent areas)**: **Bulgaria** – Mainly C. and S.E. (Stara Planina Mts., Thracia, E. Rhodope Mts., Black Sea coast). **Balkan Peninsula** – N. C. and S.E. Macedonia, S. Albania, Greece (most of area: Macedonia, Salokini, Thessaly, Aegina, Euboea, Peloponnisos). **Turkey** (Apfelbeck, 1904; Darge, 1990) – European part, Bosporus (Guéorguiev & Guéorguiev, 1995). Also present in Anatolia (Casale & Vigna Taglianti, 1999).

Subspecies: a) subsp. graecus – Greece, S. Albania. **b) subsp. morio** Mannerheim, 1830 – E. part of Balkan peninsula from S.E. Romania to Macedonia and Asian Turkey to Ankara and Baiburt.

Ecology: Greece, lowlands and mountains to 1900 m (Mt. Veluchi – Apfelbeck, 1904), in Bulgaria between 0-1300 m (Guéorguiev & Guéorguiev, 1995). In the Balkan peninsula, it is praticol, inhabiting open habitats, lowlands and hills (Pavicevic & Mesaros, 1997).

Transect: Chapter 8: T-64.

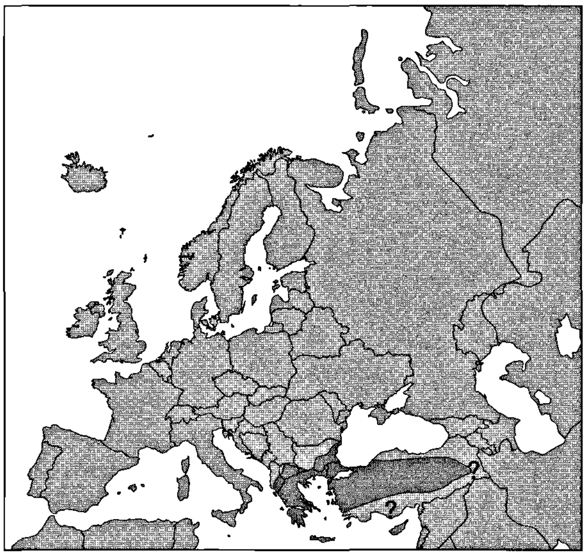
Biology: **Activity** – No data. **Periodicity** – In Bulgaria, adults have been recorded from March to June and from September to November (Guéorguiev & Guéorguiev, 1995). This applies also to Greece and Turkey (Casale, *pers. observ.*). **Food** (Larochelle, 1990) – In captivity, raw meat, small crushed snails and fruits. **Larva**: Unknown. Food – Same as adults (Larochelle, 1990).

Conservation: Not endangered.

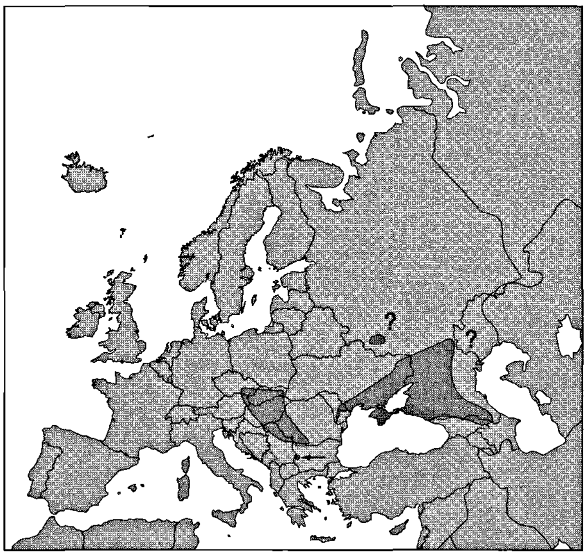
15.004. C. (Pachystus) hungaricus
Fabricius, 1792.

General literature: **Checklists and catalogues** – Breuning (1933): 790. Březina (1994): 40; (1999): 36. Deuve (1994): 148 [292]. Kleinfeld & Schütze (1999): 19. Kryzhanovskij *et al.* (1995): 47 [127]. Lorenz (1998): 82. Turin *et al.* (1993): 27. **Iconography** – Ghiretti (1996): 144. Imura & Mizusawa (1996): Pl. 27 [226]. Jakobson (1905): Pl. 2 Pavicevic & Mesaros (1997): cd-rom. Rautenstrauch (1994): Pl. 53.

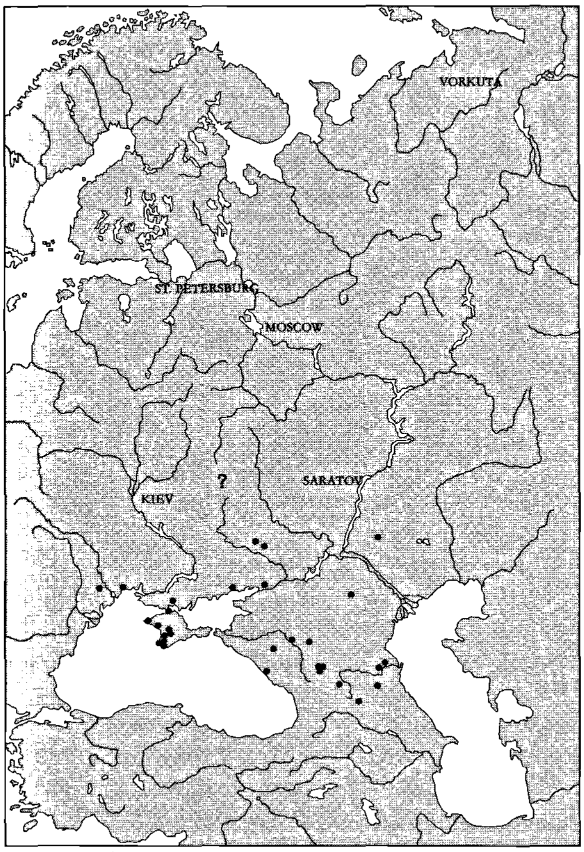
Geographical range: W.-palaearctic species. Disjunct distribution: 1) Steppes of SE Europe and 2) steppes of the Russian Plain and Caucasus. **Chorotype:** EEU-SEEU. **Range characteristics:** **Pann-EEur(S). Distribution in Europe (and adjacent areas)**: **Russian Plain and Caucasus** – Ukraine, Crimea, W. and S.W. Russia and the E. Caucasus: S.



15 003 graecus (Pachystus)



15 004 hungaricus (Pachystus)



15 004 hungaricus

regions of European Russia and Caucasus, N. to 50°N. The W.-most locality on the Russian Plain seems to be Odessa (ZIN), the E.-most– Tinguta. To the S.E., it reaches Dzanybek Field Station (Arnol'di, 1952). To the N. extending to the Derkul steppes in the Lugansk province (ZM), the N.-most record from the C.-Chernozem reserve nr. Kursk (Gusev *et al.,* 1987) is probably based on an erroneous determination. Recorded from the provinces of Odessa, Kherson (Askania Nova reserve – Pavlova, 1974), Kharkov (Starobelsk steppes – Averin, 1938), Lugansk (Derkul), Volgograd (Komarov, 1986), Uralsk (Dzanybek), Rostov, and the Kalmyk republic (Sovkhoz Prudovyi – MPGU, Ergeni Upland – Komarov, 1986). Reported also from several localities in the Crimea, Ciscaucasia (provinces of Krasnodar and Stavropol), and the N. Caucasus, to the E. to Daghestan. A steppe species, which does not exceed the border of the steppe and semi-desert zones; it occurs however in arid montane habitats. **Moldova** – Only reported from the S. (Budzhak). **Czechia & Slovakia** – Recorded from S.E. Moravia and W. Slovakia, very rare and local in steppe habitats. **Hungary** – A characteristic species of the Hungarian steppes and hills. **Romania** – S.W. Romania; rediscovered in Transylvania in 1993 in a *Robinia* forest in environs of Jamu Mare (Banat, Temes county) (Lie, 1994). Apart from this, thre are only 3 old transylvanian records (Timisoara, Masloc and Remetea Mica, Banat). **Bulgaria** – W. Bulgaria (Dragoman, Petarch). **Balkan Peninsula** – Serbia; a small isolated occurrence in the Banat. **Austria** – Restricted to the E. (E. Niederösterreich, Burgenland, region of Neusiedler See); endangered.

Subspecies: a) subsp. hungaricus – S.E. Austria, S.E. Moravia, S. Slovakia, Hungary, W. Romania (Banat), W. Bulgaria. **b) subsp. mingens** Quensel, 1806 – Crimea, the N. Caucasus, C. and Lower Volga region, in lowlands and montane steppes to 1800 m. **c) subsp. scythus** Motschulsky, 1847 – Lived in the XIX century in the steppes between Dniester and Don, now nearly extinct, survived in several reserves of E. Ukraine and in middle Volga region.

Ecology: A specialised species of steppe habitats (Hůrka, 1973; 1996), living on limestone as well as on 'löss' soil; in C. Europe more xerophilous (Koch, 1989). In Hungaria a characteristic xero-thermophilic species of the dry, sandy steppe habitats of the plains and of the S.-facing slopes of hills with dolomitic, sparsely vegetated rocks. In Serbia (Deliblato) mainly a xerophilic-silvicol species, inhabiting deciduous forests in the lowlands (Pavicevic & Mesaros, 1997). In W. Bulgaria between 500 and 800 m (Guéorguiev & Guéorguiev, 1995). According to Alekseev (*in litt.*), in N. Ossetia, where it occurs between 400 and 2200 m, it avoids dry steppes and meadows, and prefers the moister and richer grass-herb steppes of foothills and mountains.

Transects: Chapter 8: T-59-60, 72 and 78.

Biology: **Activity** – No data. **Periodicity** – Almost no data are known from the literature (Hůrka, 1973). Adults occur from April to September (Du Chatenet, 1986). Ripe eggs were found in the ovary on October 18th. L3 larvae were found in April and May. A fresh animal was found at the end of May (Sharova, 1958). Reproduction takes place most probably in late summer, with a maximum of recorded adult activity in August. The species shows an obligatory larval diapause and probably no adult dormancy. **Food** (Larochelle, 1990) – In captivity, it accepted minced meat, earthworms, fish and apples. **Larva**: Described by Sharova (1958: L1-L3; 1964: L1-L3), Hůrka (1970, 1971b: L3), and key: Arndt, 1985, 1991b. Food – No data.

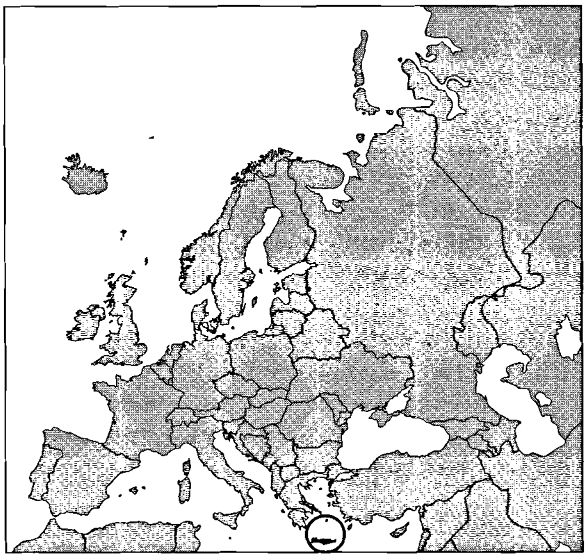
Conservation: In many places (almost) extinct due to ploughing of virgin steppes (Arnol'di, 1956). In Austria endangered, nearly extinct (Franz, 1983). Also in the N. Balkans (Banat) probably endangered (Pavicevic & Mesaros, 1997).

15.005. C. (Pachystus) trojanus
Dejean, 1826.

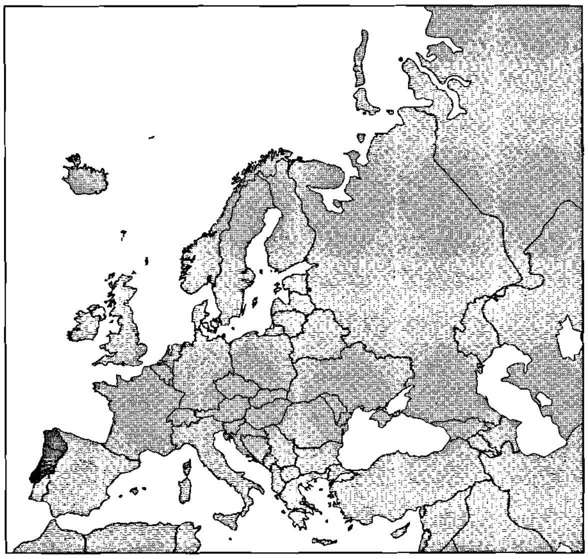
General literature: **Checklists and catalogues** – Breuning (1933): 804. Březina (1994): 41; (1999): 36. Deuve (1994): 149 [293]. Kleinfeld & Schütze (1999): 19. Lorenz (1998): 82. Turin *et al.* (1993): 27. **Iconography** – Ghiretti (1996): 145. Imura & Mizusawa (1996): Pl. 27 [225]. Rautenstrauch (1994): Pl. 52, 55.

Taxonomy: Probably an insular subspecies of *C. graecus* Dejean (see Deuve, 1994 and Lorenz 1998).

Geographical range: Endemic species of Greek islands. **Chorotype:** SEU-CRET. **Range characteristics:** Balk(S).



15 005 trojanus (Pachystus)



16 001 galicianus (Ctenocarabus)

Distribution in Europe: **Balkan Peninsula** – Greece: Kikladhes (Milos, Naxos, Santorini, Syra, Tinos), Crete.

Subspecies: No subspecies.

Ecology: No data.

Biology: **Activity** – No data. **Periodicity** – In Kikladhes (Cyclads) active in winter, from November to April-May (Casale, *pers. observ.*). Development of eggs (size 5 x 2 mm) about 12 days; larvae, including 2 weeks prepupal stage, about 50 days and pupal stage about 14-18 days (Sturani, 1962). **Food** (Larochelle, 1990) – In the field found on a dead bird. In captivity raw meat, crushed snails, earthworms, fruits and gingerbread. **Larva**: Described by Raynaud (1975). Food – In captivity, same as larvae.

Conservation: No data.

16. CTENOCARABUS C. G. THOMSON, 1875

16.001. C. (Ctenocarabus) galicianus

Gory, 1839.

General literature: **Checklists and catalogues** – Breuning (1935): 1170. Březina (1994): 45; (1999): 54. Deuve (1994): 176 [395]. Kleinfeld & Schütze (1999): 31. Lorenz (1998): 94. Turin *et al.* (1993): 27. **Iconography** – Forel & Leplat (1998): fig. 94-95. Ghiretti (1996): 196. Imura & Mizusawa (1996): Pl. 56 [458]. Rautenstrauch (1994): Pl. 78.

Geographical range: Endemic species of the N. Iberian Peninsula. **Chorotype: WEU-IBEC. Range characteristics:** Iber(W). **Distribution in Europe: Iberian Peninsula** – N. Spain: Galicia, to river Navia in the E. and Mts. de León; mountains of N. and C. Portugal to the river Aviz in the S., Serras do Geres, de Lousa, De Bussaco and Port d'Estrella.

Subspecies: No subspecies.

Ecology: Highly hygrophilous species, mostly near streams, in which it dives and hunts. It can stay under water for ca. 10 minutes; in reedbeds, sometimes hidden under stones (Du Chatenet, 1986; Forel & Leplat, 1998). Mostly in middle altitudes, between 500 and 1200 m, but locally up to 2000 m (Peña Trevinca – Assmann, *pers. observ.*).

Transect: Chapter 8: T-95.

Biology: **Activity** – Nocturnal, during the day hidden under stones, even if submerged (Assmann, *pers. observ.*; Forel & Leplat, 1998). **Periodicity** – Adults occur from March-September (Du Chatenet, 1986; Alonso *et al.*, 1987-1988; Novoa *et al.*, 1989). Probably a spring breeder with reproduction in May and June (cf. also catching rate of Alonso *et al.*, *l.c.*). **Food**: Tadpoles, aquatic insect larvae (e.g. Trichoptera) and aquatic molluscs. **Larva**: Described by Andrade Malde (1977). Food – No data. **Dispersal power**: Very agile species and a fast runner (Du Chatenet, 1986; Assmann, *pers. observ.*).

Conservation: A declining species, endangered by water pollution and modifications to the natural habitat (especially of river banks).

17. RHABDOTOCARABUS SEIDLITZ, 1887

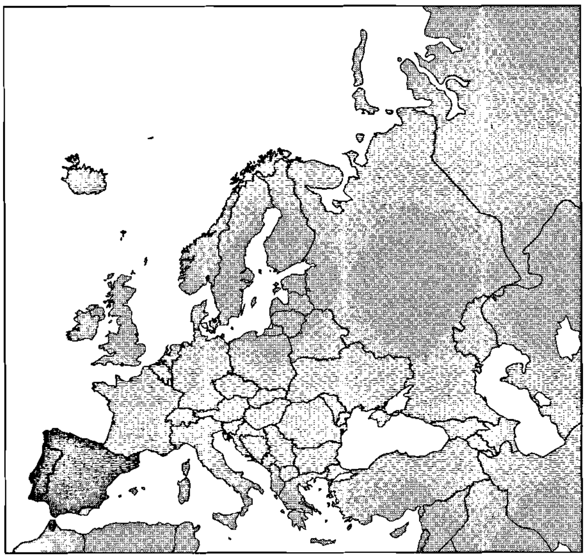
17.001. C. (Rhabdotocarabus) melancholicus

Fabricius, 1798.

General literature: **Checklists and catalogues** – Breuning (1935): 1172. Březina (1994): 45; (1999): 54. Deuve (1994): 176 [396]. Kleinfeld & Schütze (1999): 31. Lorenz (1998): 94. Turin *et al.* (1993): 27. **Iconography** – Forel & Leplat (1995): Pl. 26; (1998): fig. 96-98. Ghiretti (1996): 196. Imura & Mizusawa (1996): Pl. 56 [459]. Rautenstrauch (1994): Pl. 80.

Taxonomy: By Deuve (1994), Březina (1999), Kleinfeld & Schütze (1999) and Lorenz (1998), placed in *Ctenocarabus* C. G. Thomson.

Geographical range: Iberian Peninsula, except S.E. Spain; S. France (Pyrenees), N. Morocco. **Chorotype: WEU-IBER. Range characteristics:** Iber-NAfr. **Distribution**



17 001 melancholicus (Rhabdotocarabus)

in Europe and adjacent areas: **France** – The species occupies a small area in the Dept. Pyrénées Orientales, from Perpignan throughout the valleys of the Tech and Tet, W. to the Tour de Carol. **Iberian Peninsula** – Distributed over most of the peninsula. From Cadiz and Andalucia in the S. to the E. and W. Pyrenees. **North Africa** (Antoine, 1957) – Restricted to the N.-most area of Morocco, opposite Gibraltar (W. of Rif Mts.; N. of line Rabat – Fès).

Subspecies: (ssp. *melancholicus* – only in N. Africa: N. Morocco. **a) subsp. submeridionalis** Breuning, 1975. In Europe only present in S. Portugal and S.W. Spain, from Cadiz to Almeria; Andalusia and S. Guadalquivir. **b) subsp. costatus** Germar, 1824 – Rest of Iberian Peninsula, S. France.

Note: Zaballos & Jeanne (1994) and Březina (1994) recognise a third subspecies (*submeridionalis* Breuning 1975), from S.E. Spain. Deuve (*in litt.*) believes that the populations from the Caceres province (*dehesicola* Gracia-Paris & Paris, 1996), are markedly distinct and merit a status of subspecies.

Ecology: Hygrophilous, near marshes, in reedbeds and along (montane) streams, able to dive; from the lowlands (sea level) to 1500 m in the Pyrenees and up to 2000 m in the mountains (Sierra Nevada – Du Chatenet, 1986; Peña Ubiña – Assmann, *pers. observ.*). The habitat is limited to wet and marshy places, preferably bordered by vegetation with *Juncus* that provides places to hide during diapause. The beetles live in direct contact with the water line, and are, like the larvae, able to hunt in the water and stay submerged (Sturani, 1961). At high altitudes sometimes in moist prairies.

Transects: Chapter 8: T-95-100.

Biology: **Activity** – Nocturnal. **Periodicity** – The species has two generations per year, in spring and autumn; this probably depends on the places where development takes place, directly near the water or at the deposits that are created during the (autumn) river floods (Forel & Leplat, 1995). The female lays about 12 eggs (size 5 x 2 mm); the larvae hatch after 15 days and pupate in a cell in the soil. This cell is made of clay from along brooks or pools and it is able to resist a pressure of 20 cm water for more than two weeks, during hibernation diapause (Forel & Leplat, *l.c.*). **Food** (Larochelle, 1990): In the field, aquatic and terrestrial snails, slugs and larvae of Neuroptera and Coleoptera, especially of riparian and water insects, as well as fallen fruit. During the hunt, it can stay under water for more than 15 minutes (Sturani, 1961). In captivity, the adult accepted aquatic molluscs, earthworms, raw meat, ripe fruits, gingerbread and bread soaked in sugared milk (Larochelle, 1990). **Larva**: Described by Raynaud (1975) and key: Arndt (1994). Cárdenas & Hidalgo (1998) describe in detail all instars and the pupa for subspecies *dehesicola* Garcí & Paris, 1995 (see note above). Food – In the laboratory, it accepted prey items similar to adults; a larva was succesfully reared to the adult stage with a diet of flies (Sturani, *l.c.*).

Conservation: Not endangered.

18. HYGROCARABUS C. G. THOMSON, 1875

18.001. C. (Hygrocarabus) nodulosus

Creutzer, 1799.

General literature: **Checklists and catalogues** – Breuning (1935): 1167. Březina (1994): 45; (1999): 54. Deuve (1994): 177 [398]. Kleinfeld & Schütze (1999): 26. Lorenz (1998): 90. Turin *et al.* (1993): 28. **Iconography** – Casale *et al.* (1982): fig. 109. Forel & Leplat (1995): Pl. 26. Ghiretti (1996): 197. Imura & Mizusawa (1996): Pl. 41 [345]. Pavicevic & Mesaros (1997): cd-rom. Rautenstrauch (1994): Pl. 79.

Taxonomy: Many authors regard *C. nodulosus* as a subspecies of *C. variolosus* (e.g.: Březina, 1994, 1999). Further systematic study on this topic is needed.

Geographical range: W. part of C. Europe: E. France, Switzerland, Austria, Germany (mostly in the W. and S.),

18 001 nodulosus (Hygrocarabus)

N.E.-most of Italy, W. Hungary, Slovenia, Croatia, Bosnia-Herzegovina. **Chorotype:** CEU. **Range characteristics:** CEur. **Distribution in Europe: Belgium** – Only one old record. **Germany** – Reported from Lower Saxony (N. to Hamburg), Westfphalia, Rhineland, Baden-Württemberg and Bayern. Heavily endangered in the whole territory or extinct (compare Weber & Weber, 1966). In E. Germany a single, old record (Arndt, 1989). **Czechia & Slovakia** – Not yet recorded for the territory, but very close to Czechia in the mountains of the Bayerische Wald. **Hungary** – Very rare and sporadic in the W. part (Transdanubia) only. **Balkan Peninsula** – Distributed across the W. part of former Yugoslavia towards the N. of Albania; Slovenia, N.W. Croatia, C., E., and S. Bosnia, W. Serbia and disjunct in Kosovo and N.W. Macedonia. **Austria** – Reported from most parts, except Vorarlberg; seriously endangered. **Switzerland** – Old records exist from the neighbourhood of Geneva; not reported in the 20th century. **Italy** – A marginal and very restricted distribution in Friuli -Venezia Giulia, near Trieste, today apparently extinct. **France** – Formerly it was reported from several regions in the E.: Morvan, Savoie and Dauphiné, but no recent records exist. Nowadays it is restricted to a small and isolated area in the C. part of the Vosges (Callot & Schott, 1993), a locality in département de l'Ain, and possibly a population in the Massif central (Coulon *et al.*, 2000).

Subspecies: No subspecies (see under *Taxonomy*).

Ecology: Stenotopic, silvicol and extremely hygrophilous (Weber & Weber, 1966; Koth, 1974; Arndt, 1989; Koch, 1989), exclusively living along the shores of small, stony, mostly montane, rivers and brooks, in marshy and wooded places, where it hides under submerged stones or branches (Sturani, 1963; Casale *et al.,* 1982). In Tyrol, in well moors (Koch, *l.c.*). In general, the habitat preference is similar to that of *C. variolosus*. Also for the Balkan (former Yugoslavia) characterised as an inhabitant of wet places in different types of forest in hills and mountains (Pavicevic & Mesaros, 1997).

Transects – chapter 1: I-1; Chapter 8: T-25-26 and 79.

Biology: **Activity** – Nocturnal and partly sub-aquatic (Thiele & Weber, 1968). After Sturani (1962), the beetles can stay submerged for more than 20 minutes. Air is held by thoracical stigmata. **Periodicity** – Reproduction during April-June; oviposition in N. Italy in spring, the eggs being deposited in single small cells in the soil (Sturani, 1962); the eggs (size 5 x 2 mm) hatch after 10 days and larval development of L1-L3, lasts for approximately 60 days (Casale *et al.,* 1982). According to Arndt (1989), larval development takes place very rapidly, and fresh animals can be found in August; no activity before hibernation from August until March, in heaps of reed or in trunks of *Alnus*. Some females from the Vosges have been collected from decaying wood during hibernation, and show a *corpus luteum*, indicating that the tenerals are active in this habitat and leave the pupal cell. Additionally, this result indicates that the breeding population probably consists of young and 'old' individuals (that have already reproduced the year before) (Assmann, *pers. observ.*). **Food** (Larochelle, 1990): The species hunts (in the water) during the night; in captivity, it accepted earthworms, small fishes, larvae of amphibians and aquatic insects, aquatic molluscs, raw meat, milk, sugared water, gingerbread and fruits (Sturani, 1962, 1963). **Larva**: Described by Sturani (1962, 1963) and Hůrka (1971b), compare Casale *et al.* (1982). Food – Same as adults (Sturani, *l.c.*).

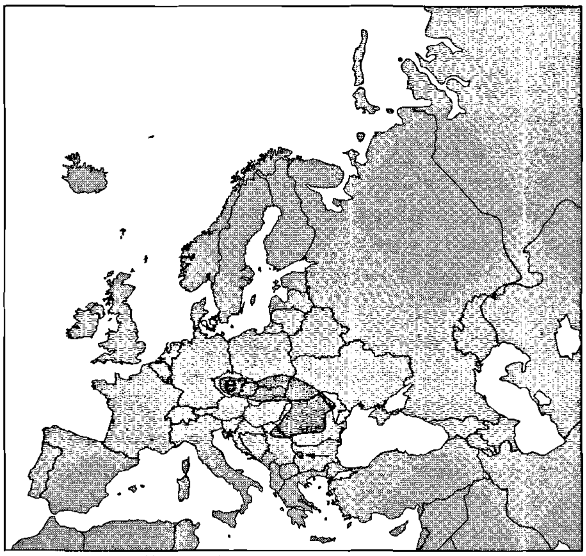
Conservation: Apparently extinct or strongly reduced near Trieste due to over-collecting and changes of the habitat. Also many populations in the N. seem to have disappeared, e.g. from N. Germany, the regions of Hamburg, Westphalia and Lower Saxonia (see Chapter 9 and Weber & Weber, 1966). The same seems to be the case in France (Coulon *et al.*, 2000). Endangered in the whole of its range (many places in France, Germany, Austria, Balkans etc.). It is an excellent indicator of undisturbed forest brooks.

18.002. C. (Hygrocarabus) variolosus
Fabricius, 1787.

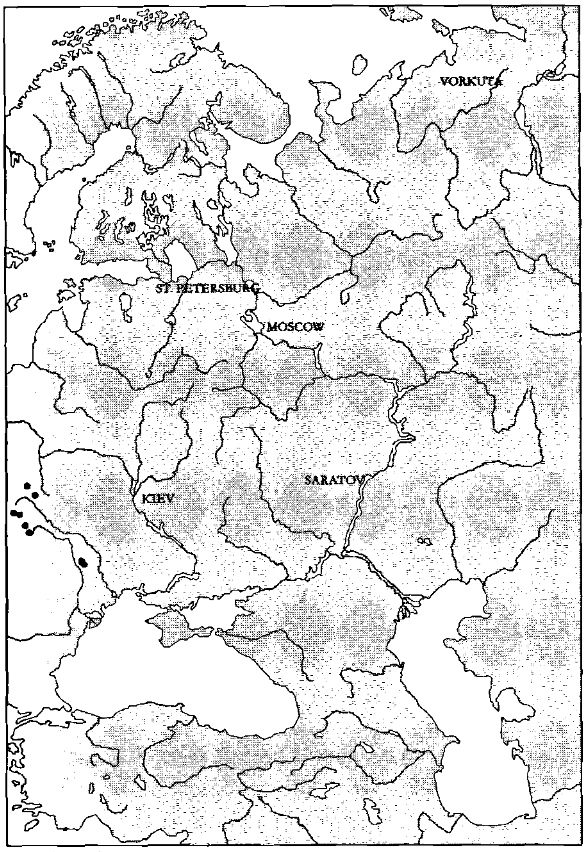
General literature: **Checklists and catalogues** – Breuning (1935): 1166. Březina (1994): 45; (1999): 54. Deuve (1994): 177 [397]. Kleinfeld & Schütze (1999): 26. Kryzhanovskij *et al.* (1995): 47 [129]. Lorenz (1998): 90. Turin *et al.* (1993): 28. **Iconography** – Ghiretti (1996): 197. Imura & Mizusawa (1996): Pl. 41 [344]. Pavicevic & Mesaros (1997): cd-rom. Rautenstrauch (1994): Pl. 79.

Taxonomy: See under *C. nodulosus*.

Geographical range: E. part of Europe: Czechia, Slovakia, S. Poland, Ukrainian Carpathians, Moldova, Romania, Bulgaria, N.E. Serbia, N.W. Bulgaria. **Chorotype:** EEU-PANN. **Range characteristics:** CEur-SEEur. **Distribution in Europe**: **Germany**: (Arndt, 1989) – A single old



18 002 variolosus (Hygrocarabus)



18 002 variolosus

and unreliable record refers to *C. nodulosus*. **Poland** – Mainly in the S.E., very rare. **Russian Plain** – Only in W. Ukraine and Moldova, the E.-most and S.-most localities seem to be Kodry reserve in C. Moldova (Neculiseanu, 1988) and Kalarashovka (MPGU). In Ukraine, it occurs in the Carpathians and the adjacent areas and is known from several localities in the provinces of Zakarpatye, Lvov, Ivano-Frankovo and Ternopol' (ZIN; Ponomarchuk, 1956; Rizun, 1990). In the zones of the forest-steppe and deciduous forests. **Moldova** – In the N. and in the Kodry Hills. **Czechia & Slovakia** – Probably extinct in Bohemia; rare in Moravia and in Slovakia mostly rare, but sometimes locally relatively common. **Hungary** – Only in the Zempléni Mts., rare. **Romania** – Carpathians, Transylvania. **Bulgaria** – Known from the W. Stara Planina Mts. (Varshets). **Balkan Peninsula** – Only reported from the N.W. of Serbia (Banat and Srem; Fruska Gora near Novi Sad).

Subspecies: By many authors, *C. nodulosus* Creutzer is regarded as a subspecies of the present species.

Ecology: Hygrophilous, paludicol, semiaquatic (Koch, 1989), generally associated with swamps and water meadow forests along rivers. It inhabits surroundings of brooks and small ponds, especially in montane forests of C. Europe up to 1000 m (Hoffmann, 1907; Hůrka, 1973; 1996). In N. Serbia in wet, deciduous forests in hilly regions (Pavicevic & Mesaros, 1977). In Bulgaria found up to 300 m (Guéorguiev & Guéorguiev, 1995). In Ukraine recorded from floodland forests (Petrusenko, 1971). In Moldova also found in the dry cherry-oak forests in the N. and in the Kodry Hills (Neculiseanu & Matalin, 2000).

Transects: Chapter 8: T-35, 62-63 and 72-73.

Biology: In general very similar to *C. nodulosus*. **Activity** – Active during daytime, probably also during the night. Behaviour in water, see *C. nodulosus*. **Periodicity** (Hůrka, 1973) – Reproduction in spring, in Bulgaria in May (Guéorguiev & Guéorguiev, 1995); oviposition in June. Copulations were reported by Jeannel (1941), who observed in spring the mating behaviour in a few decimeters of water, in N.W. Romania. In E. Slovakia, especially in June (Hůrka, *l.c.*). L1 larvae were observed at the end of July in decaying wood near water. L2 and L3 also in July, always close to water. Development of the larvae, without diapause, takes only a short time, eggs: 10 days, L1: 8 days, L2: 7 days, all together about 35 days (conditions of captive breeding: Sturani, *l.c.*), and the young adults appear in August (Arndt, 1989). After Hůrka (1973), pupation takes place close to the water side, and the young adults do not leave their pupal cells before next spring. There is therefore an obligatory adult winter diapause. **Food** – (Larochelle, 1990) – In the field, adults and larvae of Trichoptera, larvae of *Agabus* (Coleoptera, Dytiscidae). By Jeannel (1941) baited with dead fish placed under stones at the border of streams. *Note*: Many of the records mentioned in the works of Hůrka (1973) and Sturani (1962) concern *C. nodulosus*. **Larva**: Described by Hůrka 1961 (1961: L2-L3), Sturani (1963: L1), Hůrka (1971b: L1-L3) and key: Arndt (1985, 1991b). Food – Same as adults.

Conservation: Very much like *C. nodulosus*, an indicator of undisturbed forest brooks in E. Europe. In many places endangered due to habitat destruction and pollution, for instance in the Balkans (Pavicevic & Mesaros, 1997). In Transylvania, abundant in undisturbed forests (Casale, *pers. observ.*).

19. CHAETOCARABUS C. G. THOMSON, 1875

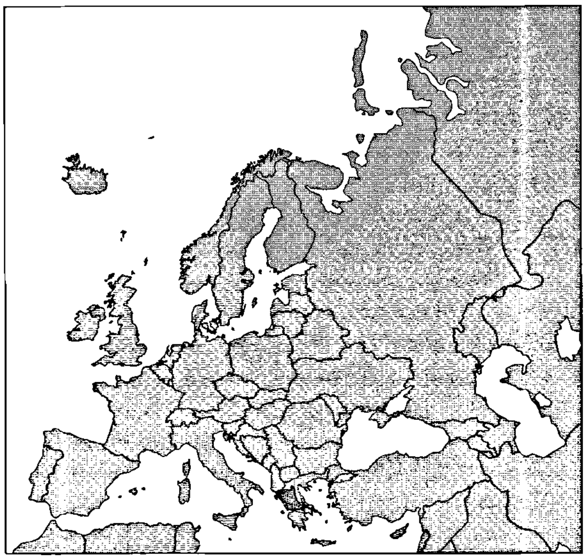
19.001. C. (Chaetocarabus) arcadicus
Gistel, 1850.

General literature: **Checklists and catalogues** – Breuning (1934): 1037. Březina (1994): 47; (1999): 53. Deuve (1994): 181 [405]. Kleinfeld & Schütze (1999): 25. Lorenz (1998): 89. Turin *et al.* (1993): 28. **Iconography** – Ghiretti (1996): 205. Imura & Mizusawa (1996): Pl. 41 [341]. Rautenstrauch (1994): Pl. 71.

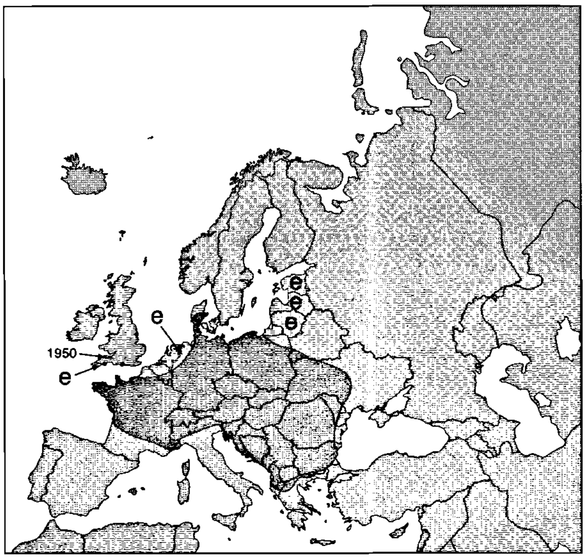
Taxonomy: The taxon *C. merlini* is frequently regarded as subspecies of *C. arcadicus*, but it is treated as a good species in the present work.

Geographical range: Endemic species of the S. Balkan peninsula. **Chorotype**: SEU-GRNC. **Range characteristics**: Balk(S). **Distribution in Europe**: **Balkan peninsula**: Greece: From Pyndos in the N.W. to Olympus in the E. and C. Greece (Parnassos, Elikon, Korax, Iti, Veluchi Mts.).

Subspecies: No subspecies, see under *Taxonomy*.



19 001 arcadicus (Chaetocarabus)



19 002 intricatus (Chaetocarabus)

Ecology: Montane and forest-dwelling species. Mainly in pine and deciduous forests, from 600 to 1600 m, sometimes in alpine pastures, at 2000-2200 m (Casale, *pers. observ.*).

Transect: Chapter 8: T-68.

Biology: **Activity** – No data. **Periodicity** – The species reproduces in spring. Teneral specimens occur in autumn. Hibernation under bark (mostly of pine), sometimes in the soil; normally in aggregations of many individuals. Also hibernating larvae have been recorded. **Food** – No data. **Larva**: Described by Lo Pinto (1998). Food – No data.

Conservation: Not endangered.

19.002. C. (Chaetocarabus) intricatus
Linnaeus, 1761.

General literature: **Checklists and catalogues** – Breuning (1934): 1034. Březina (1994): 47; (1999): 53. Deuve (1994): 180 [404]. Kleinfeld & Schütze (1999): 26. Kryzhanovskij *et al.* (1995): 47 [130]. Lorenz (1998): 89. Turin *et al.,* (1993): 28. **Iconography** – Casale *et al.* (1982): fig. 134. Forel & Leplat (1995): Pl. 27-28. Ghiretti (1996): 203-205. Imura & Mizusawa (1996): Pl. 41 [342]. Jakobson (1905): Pl. 3. Pavicevic & Mesaros (1997): cd-rom. Rautenstrauch (1994): Pl. 69.

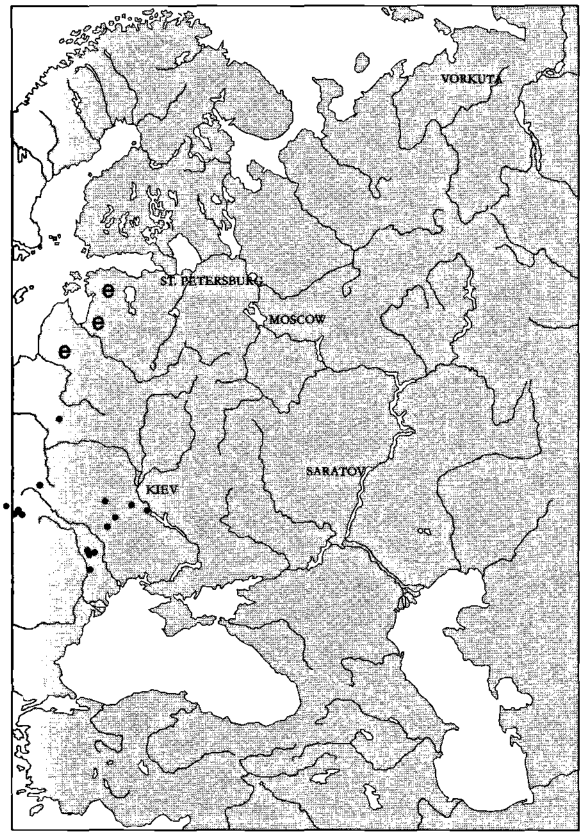
Taxonomy: Two taxa, regarded as subspecies by several authors, have been treated as valid species in the present work: *C. kruepeni* and *C. lefebvrei* (incl. subsp. *bayardi*).

Geographical range: Europe, except the N. and S.W.; from the Pyrenees and N. Italy to Poland; Balkan Peninsula to the S. (Bulgaria, N. Greece); Belgium, C. Germany to the N. with isolated (mostly, recently extinct) populations in S. England, the Netherlands, W. Germany and S. Sweden. **Chorotype:** EUR. **Range characteristics:** CEur-SEEur. **Distribution in Europe**: **Fennoscandia** – Not in Norway; in Sweden only in the S.E. area of Skåne, local and rare, but found several times after 1950, not in Finland. **Denmark** – C.E. Jutland, mainly older records. On Bornholm several records after 1950, however getting rarer. **British Isles** – Endangered: very local and restricted to a small area in S.W. England (Devon), before 1970 also in Cornwall and one specimen from 1950 has recently been identified from Somerset. Unconfirmed reports exist from the highlands of Scotland. **Netherlands** – Rarely collected from the C. part of the country; not after 1941, most records are much older. Probably extinct now. **Belgium** – From the C. area only records before 1950 and one locality from N. Flandria (1980). Recent records are restricted to E. Belgium and Luxembourg (Ardennes). **Germany** – Not in Sachsen-Anhalt and the region of Bremen. From several regions reported as endangered or nearly extinct, especially in the N. and W. areas. Completely extinct from the Westphalian lowlands. However, Arndt (1989) reports many new localities from E. Germany, probably due to increasing collecting intensity after 1960, especially in the E. and S. of the territory. **Poland** – Reported from all areas except Kotlina Nowotarska near the Tatra. **Baltic** – Collected in all countries (Spuris, 1983). Present in Latvia according to the latest checklist (Barsevskis, 2002), but probably extinct now. **Byelorussia** – Very sporadically in the W. near the Polish border (see below), probably old records. **Russian Plain** – Restricted to the S.W.-most area of the C. and S. Russian Plain, Ukrainian Carpathians and Transcarpathia, to the W. of Dnieper river. Reported from several localities in Moldova (Adashkevich *et al.,* 1973; ZIN; IZ), and the Ukrainian provinces of Zakarpatye, Ivano-Frankovo and Lvov (several localities – Ponomarchuk, 1956; Rizun, 1990), Podolsk (Voronovitsy – ZIN), Vinnitsa (Rechera – IZ), Cherkassy (Kanev reserve; Sinyava – IZ; MPGU), Kiev (Kozhanka – ZIN). The N.-most localities seem to be Belovezha Forest in Byelorussia (ZIN, MPGU) and the records from the Baltic states. Occurs in the zones of deciduous and mixed forests and the forest-steppe. **Moldova** – In the W. (Prut River flood plains), C. (Beltz, Kodry) and S. (Budzhak). **Czechia & Slovakia** – Sporadic in the Czech and

Slovak republics, only nominate subspecies. **Hungary** – A characteristic species from the montane areas; only one doubtful record from the Great Hungarian Plain. **Romania** – Scattered occurrences across the territory, mostly found at relatively warm sites. **Bulgaria** – Found in most parts of the country, except the E. Rhodopes. **Balkan Peninsula** – Occurring nearly all over the area (Pavicevic & Mesaros, 1997). Widely distributed throughout Slovenia, Croatia, Bosnia-Herzegowina, Serbia, Montenegro, Macedonia. In Albania and Greece N. of 41 °N. **Austria** – Distributed all over the country, but absent from the high Alps. **Switzerland** – In general, it follows the same pattern as mentioned for Austria; most common in the Rhône area and Ticino. **Italy** – Present in the Alps and Prealps of N. Italy, often common. Notably in the foothills along the alpine chain from Maritime Alps to Venezia Tridentina. **France** – Widespread in N. and C. France; S. to Limousin, Cevennes and S.E. to Maritime Alps. Not S. of the Garonne and the line Toulouse – Hyères. Very rare in the N. and N.E.

Subspecies: Rather homogeneous over most of its area of distribution. Only some populations from S. Balkans, such as *macedonicus* Jurecek, 1928, *starensis* Born, 1918, *subrhodopensis* Blumenthal, 1976 and *weiratheri* Breuning, 1932 probably merit a subspecific status.

Ecology: Silvicol (Mandl, 1972). A thermophilic forest-dwelling species that can be found from lowland to montane forests at middle altitudes from 300 to 800 m (Hoffmann, 1907); for Italy and France, especially coniferous and *Castanea* forests are mentioned (Casale *et al.,* 1982; Forel & Leplat, 1995), and for C. Europe, mixed forests of *Pinus-Betula* (Arndt, 1989). Preferably in older and larger forests of various age and composition. In E. Germany especially in hills along river valleys (Arndt, 1989), with a clear preference for S. slopes. Also in Belgium significantly found mostly in localities above 300 m (Desender, 1986a). In Czechia and Slovakia, a species typical of relatively warm, open forests, from 200-1500 m; in Prague not rare in parks, and villa quarters (Hûrka *et al.,* 1973; 1996). In Hungary a characteristic species of dense deciduous forests (beech, oak-hornbeam) in hills and mountains. For the Balkan Peninsula (former Yugoslavia), denoted as praticol-silvicol, occurring in deciduous and coniferous forests in hills and mountains in the N. and C. parts. In the S. (Montenegro and Macedonia) also up to alpine pastures (Pavicevic & Mesaros, 1997). In Ukraine it was found in hornbeam and oak-hornbeam forests of the forest-steppe zone (Petrusenko, 1971). It seems to prefer forests with a thick, humid layer of humus or mosses, where it is active in warm weather, shortly after rain (Hyman, 1992). The species is most abundant in S.C. Europe, in hills and the lower mountains (France up to 1200 m, Forel & Leplat, *l.c.*); Switzerland up to 1300 m (Marggi, 1992), rare above 1500 m (Du Chatenet, 1986); in Austria at middle altitudes, not in the lowlands and not in high mountains (Mandl, 1956-1958). More to the S. at higher altitudes, Val d'Aosta and Piedmont up to 1600-1700 m, sometimes (rare) up to 2000 m (Casale *et al.,* 1982); in Bulgaria up to 2000 m (Guéorguiev & Guéorguiev, 1995). In the N. of its distribution usually scattered and rare. Very common in some places of N.W. Italy (Casale, *pers. comm.*) as well as in France (Drôme) and the Balkan peninsula. Compared to C. and S. Europe, rather diverse habitat preferences have been reported for the British Isles: moist hardwood forests with a thick humus layer (Lindroth, 1974), and for Scandinavia: ravine (beech) forest, moist and shaded, rich in litter (Lindroth, 1985).

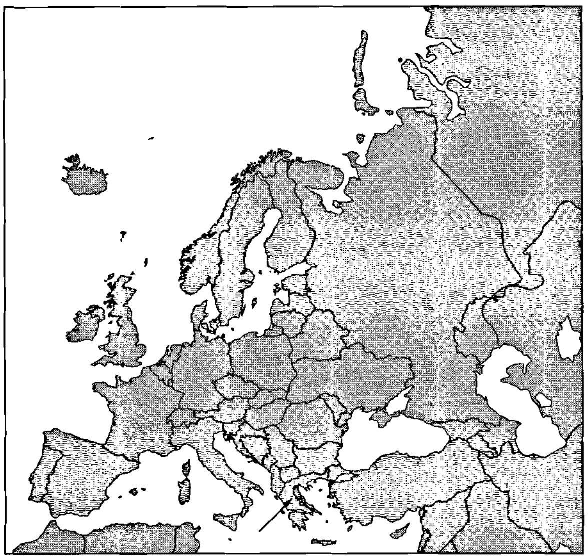


19 002 intricatus

Transects: Chapter 1: I-1; Chapter 8: T-05, 17, 26-27, 30, 33-34, 39, 58, 62, 65, 67-76, 80-81 and 88-91.

Biology: **Activity** – Mainly diurnal according to Wachmann *et al.* (1995), but Forel & Leplat (1995) call it a nocturnal species. Mostly nocturnal in N. Italy (Casale, *pers. observ.*), although an early specimen from this area was reported walking in the sun on February 11th 2002, after a cold winter (Burattini, *pers. comm.*). Adults are able to climb trees for several meters. **Periodicity** (Hûrka, 1973) – A spring reproducing species, active from April/May until September and hibernating as adult. Reproduction mainly in May-June, but occasionally copulations have been observed in autumn (Burmeister, 1939). The eggs (size 6 x 3 mm) are laid in the period April-June, in separate cells in the soil or without any protection under mosses. Larvae were reported from June-August; Luff (1969) mentioned a L1 from August and L3 from April. The larval development, which takes place without diapause, lasts for about 35-50 days and the pupal stage takes 15-18 days. At low altitudes and under very warm conditions, an aestivation of 6-8 weeks may occur during July-August (Sturani, 1962); teneral beetles appear in summer and early autumn (Forel & Leplat, *l.c.*). Total duration of development lasts 2 to 2.5 months (Casale *et al.*, 1982; Hůrka, 1973): eggs: 12 days, larvae (including 5-8 days prepupal stage): 35-45 days and pupae: 14-18 days (Sturani, 1962). The young adults emerge in summer and late summer, and can be active until October before they hibernate under mosses or in tree trunks, until next April (Arndt, 1989; Du Chatenet, 1986). **Food** (Larochelle, 1990): In the field, earthworms and snails. The adult mainly hunts insects; in autumn also observed eating fallen fruits. In captivity, it accepts snails (*Helix* species), slugs (*Arion* and *Limax* species), minced meat, larvae, earthworms, beef hearts, caterpillars, fruits (when no other food is available) and bread soaked in sugared milk or sugared water. **Larva**: Described by Schiödte (1867: L3), Vacher de Lapouge (1906: L2-L3) and Verhoeff (1921: L1-L3). Food – in the laboratory, snails, earthworms and much of the food that is accepted by adults including chopped mealworms (Arndt, *pers. observ.*; Larochelle, 1990). *Note*: The adults stridulate (Casale *et al.*, 1982). Other species that stridulate are: *C. depressus*, *C. planatus* and especially some Anatolian and Caucasian *Tribax* species.

Conservation: The species has disappeared from many regions in the N.W. part of its former territory, e.g. the Netherlands, C. Belgium and the W. and N. parts of Lower Saxony (W. Germany) (see Desender & Turin, 1989 and Turin, 2000). In many other regions in N. and W. Europe, and partly also in C. Europe, the numbers of observations have been severely reduced. An explanation can be found in the loss of broad-leafed woodland with old trees, clear-felling and coniferisation (Hyman, 1992). Also forest hygiene, leading to removal of fallen trees and trunks, has been mentioned. The presence of ancient trees and rotting trunks with bark are important sites for hibernation, not only for *C. intricatus*, but also for many other beetle and insect species. Therefore it is important that there are no large gaps in age structure of the tree populations, within single forest sites (Desender *et al.*, 1995). Another explanation for the decline in N.W. Europe might be found in a shift to a more atlantic climate, especially in the period until 1930 (Gries *et al.*, 1973). Due to changes in forestry and habitat fragmentation, the species could probably not recover and recolonise the lost territory. In general, it can be stated that it is a good indicator for ancient temperate forests (Blumenthal, 1981) and of vast, well-structured and complex woodland areas. In S. Europe there are in general no problems, except in and near cities, where it disappears due to forest hygiene practices and urbanisation. For former Yugoslavia, only the form *montenegrinus* Kraatz, has been mentioned as endangered (Pavicevic & Mesaros, 1997), however this is unlikely, because it has always been very common in the large forests of Montenegro (Casale *pers. observ.*).


19 003 krueperi (Chaetocarabus)

19.003. C. (Chaetocarabus) krueperi
Reitter, 1896.

General literature: **Checklists and catalogues** – Breuning (1934): 1038. Březina (1994): 47; (1999): 54. Deuve (1994): 180 [404]. Kleinfeld & Schütze (1999): 26. Lorenz (1998): 90. Turin *et al.* (1993): 28. **Iconography** – Ghiretti (1996): 205. Imura & Mizusawa (1996): Pl. 41 [342]. Rautenstrauch (1994): Pl. 69.

Taxonomy: By Březina (1994; 1999) and Deuve (1994) listed as a subspecies of *C. intricatus*, which could be correct; however, further investigation of this topic is needed.

Geographical range: Endemic species of the Balkan peninsula. **Chorotype:** SEU-THES. **Range characteristics:** Balk(S). **Distribution in Europe**: **Balkan Peninsula** – E. Greece, Ossa and Pelio Massifs.

Ecology: In *Pinus*, *Castanea* and *Fagus* forests, mostly from 500 up to 1500 m (Casale, *pers observ.*).

Biology: Most similar to *C. intricatus*.

Conservation: Although the species occurs very locally, it seems not to be endangered.

19.004. C. (Chaetocarabus) lefebvrei
Dejean, 1826.

General literature: **Checklists and catalogues** – Breuning (1934): 1038. Březina (1994): 47; (1999): 54. Deuve (1994): 180 [404]. Kleinfeld & Schütze (1999): 26. Lorenz (1998): 90. Turin *et al.* (1993): 28. **Iconography** – Casale *et al.* (1982): fig. 134. Ghiretti (1996): 204. Imura & Mizusawa (1996): Pl. 41 [342]. Rautenstrauch (1994): Pl. 70-71.

Taxonomy: Listed as a subspecies of *C. intricatus* Linnaeus (Březina, 1994, 1999 and Deuve 1994). Also by many early authors regarded as a subspecies of *C. intricatus*. It is undoubtedly related to the Balkanian *intricatus*-populations (*macedonicus*, *weirathen*), as a transadriatic-transionian element, and not to the alpine populations.

Geographical range: Endemic species of C. and S. Italy: Apennines. **Chorotype:** SEU-APPE. **Range characteristics:** Apen. **Distribution in Europe**: **Italy** – Restricted to C. and S. Apennine chain down to Calabria (Aspromonte) and the mountains of N. Sicily.

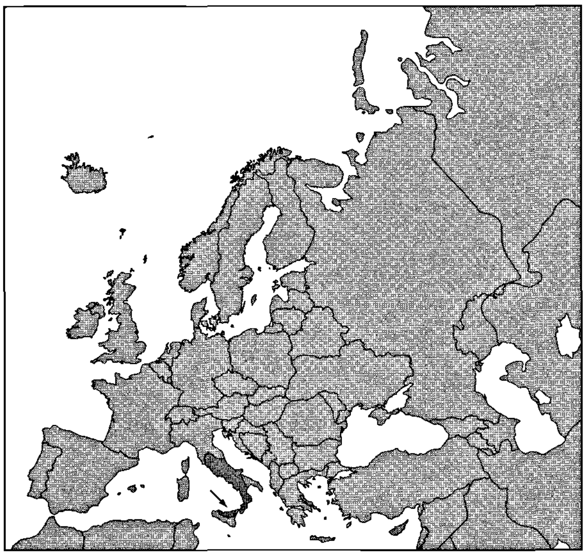
Subspecies: a) subsp. lefebvrei – Sicily, Calabria (Aspromonte). **b) subsp. bayardi** Solier, 1835 – C. and S. Apennines.

Ecology: The ecology of this species is very similar to that of *C. intricatus* and other *Chaetocarabus* species (Casale *et al.,* 1982). It inhabits forests and forest edges (Korell, 1975), from sea level (*Quercus*), and foothills (*Castanea*) to montane forests (*Fagus* at 800-1800 and coniferous stands at 900-2000 m).

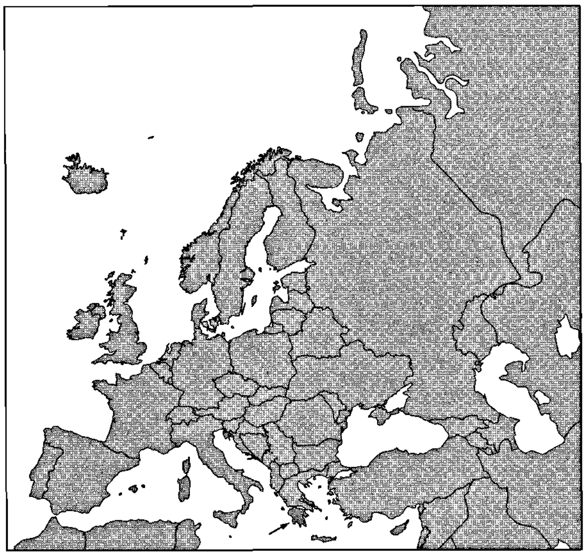
Transects: Chapter 1: I-3; Chapter 8: T-83-87.

Biology: **Activity** – Nocturnal, during the day hiding under stones (Korell, 1975). **Periodicity** – The first animals start their activity half March (Sicily, see Korell, 1975). Activity increases in April and the animals stay active until the summer. Development of eggs (size 6 x 3 mm) in about 12 days; larvae (including 8 day prepupal stage): 36 days and pupae: 17 days (Sturani, 1962). Hibernation (mostly) aggregated in old tree trunks; sometimes as single behind dry bark at about 1.5 m above soil level (Korell, *l.c.*). **Food** (Larochelle, 1990) – In the field, snails, slugs and larvae of *Gnorimus decempunctatus* (Helf) and *Rhizotrogus* spp. (Coleoptera, Scarabaeidae). **Larva**: Described by Casale *et al.* (1982). Food – No data. **Dispersal power**: Like *C. intricatus*, adults often climb trees to a height of several meters above soil level (Casale *et al.,* 1982).

Conservation: Not endangered. A population of subspecies *lefebvrei* introduced near Florence, from Lazio (described as *lombardii* Luigioni, 1924) disappeared after a few years (Casale *et al.,* 1982).



19 004 lefebvrei (Chaetocarabus)



19 005 merlini (Chaetocarabus)

19.005. C. (Chaetocarabus) merlini
Schaum, 1861.

General literature: **Checklists and catalogues** – Breuning (1934): 1037. Březina (1994): 47; (1999): 53. Deuve (1994): 181 [406]. Kleinfeld & Schütze (1999): 25. Lorenz (1998): 90. Turin *et al.* (1993): 28. **Iconography** – Ghiretti (1996): 205. Imura & Mizusawa (1996): Pl. 41 [341]. Rautenstrauch (1994): Pl. 70.

Taxonomy: By Březina (1994, 1999) and Deuve (1994) listed as a subspecies of *C. arcadicus.*

Geographical range: Endemic species of the Balkan Peninsula. **Chorotype:** SEU-PELO. **Range characteristics:** Balk(S). **Distribution in Europe**: **Balkan Peninsula** – S. Greece, mountains of the Pelopponesos peninsula.

Subspecies: No subspecies.

Ecology: Mainly in pine forests at 1000-1500 m, but also at altitudes up to 2000 m, in montane pastures near snow (Casale *pers. observ.*).

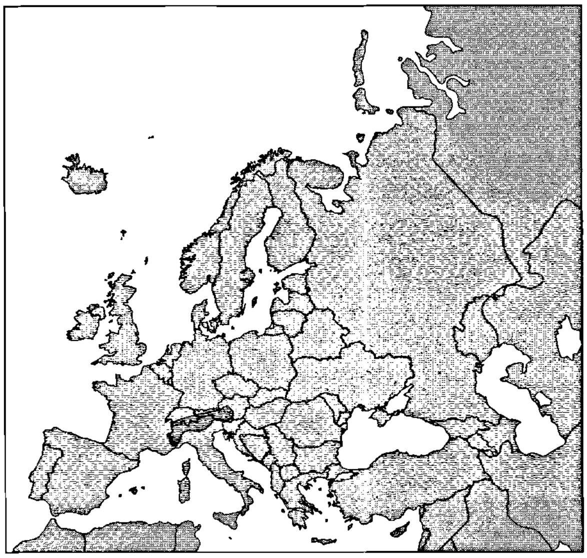
Biology: Most similar to *C. arcadicus.*

Conservation: Not endangered.

20. PLATYCARABUS MORAWITZ, 186

20.001. C. (Platycarabus) depressus
Bonelli, 1810 (= *bonellii* Dejean, 1828).

General literature: **Checklists and catalogues** – Breuning (1934): 1059. Březina (1994): 46; (1999): 52. Deuve (1994): 177 [399]. Kleinfeld & Schütze (1999): 25. Lorenz (1998): 89 (*lucens* Schaum, 1857). Turin *et al.* (1993): 28. **Iconography** – Casale *et al.* (1982): fig. 138, 144. Forel & Leplat (1995): Pl. 27. Ghiretti (1996): 197-198. Imura & Mizusawa (1996): Pl. 40 [337]. Rautenstrauch (1994): Pl. 74.



20 001 depressus (Platycarabus)

Taxonomy: Lorenz (1998) notes that strict application of I.C.Z.N. would change the nomenclature of this well-known alpine taxon and its synonyms so strongly, that we adopted for it the right indication by Deuve (1994). The name *depressus* should in fact be substituted by *bonellii* because of primary homonymy (Silfverberg, 1977), however, the name has been recommended to be maintained as 'nomen conservandum' (Deuve, 1994; Březina, 1999).

Geographical range: Europe, Alpine chain on the N. and S. sides, from Ligurian Alps to Carinthia. **Chorotype:** SEU-ALPI. **Range characteristics:** Alpi(N). **Distribution in Europe**: **Austria** – Widely distributed in the W. part, from Vorarlberg to Carinthia; not known from Niederösterreich, Steiermark and Burgenland. **Switzerland** – Widespread and rather abundant in the Alps; rare in the E. of Graubünden; absent from Säntisgebiet. **Italy** – Widely distributed in the Alps around the French-Swiss border, from Piedmont and W. Liguria to Venetia Tridentina. **France** – Distributed in the high Alps along the Italian border, from the Maritime Alps to N. of the Cottian Alps and the Mont-Blanc massif.

Subspecies: a) subsp. depressus – From W. (Cottian) Alps (Monviso), Mt. Blanc to E. Alps. **b) subsp. lucens** Schaum, 1857 – W. Alps, from S. slope of Monviso Massif, via Maritime Alps, S. to the Ligurian Alps (Casale *et al.*, 1982).

Ecology: Species of high montane forests and the alpine zone, from 1000 (sometimes 800) to 2500 m (Coulon *et al.*, 2000), with an optimum in altitudes between 1600 and 2100 m; preferably in poor alpine grasslands, often along roads or at eroded spots, under stones or woods (Marggi, 1992). It is especially active at places near melting water from glaciers or after rainfall (Forel & Leplat, 1995). According to Du Chatenet (1986), normally between 1700 and 2500 m in alpine prairies but rare at lower altitudes in beech forest between 800 and 1200 m, however, in Italy, very common in the same environment (Casale *et al.*, 1982). In some *Fagus* forests of the N.W. Alps, at 1200-1400 m, it is the dominant species (Casale, *pers. observ.*). It is strictly acidophilous, and vicariant on acid soils (although sympatric) of *C. creutzeri*, in the Eastern Alps (Dolomiti) (Brandmayr & Zetto-Brandmayr, 1988).

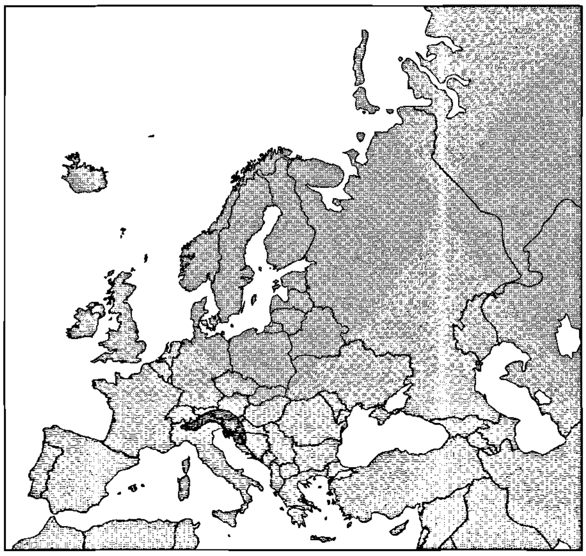
Transects: Chapter 8: T-79, 81 and 88.

Biology: **Activity** – Exclusively night active (Thiele & Weber, 1968). **Periodicity** – Adults are active from March/April until July/August followed by aestivation from August to September. Spring breeder, oviposition in the period May-July. Larvae (above 2000 m) of various stages were observed from July until the beginning of September. Development of eggs (size 4.5 x 2 mm) takes about 10 days. Larval development in the summer, without diapause, about 30-40 days, pupa 8-10 days; all stages together 45-55 days (Hůrka, *l.c.*; Sturani, 1962). A short, second period of adult activity can occur during September-October. Hibernation from October to April-May (Forel & Leplat, 1995; Sturani, *l.c.*). **Food** (Larochelle, 1990): In captivity, it accepted snails, earthworms and caterpillars without hair, liver and apples. In the field, snails (Assmann, *pers. observ.*). **Larva**: Described by Heer (1836), Schaum (1856), Vacher de Lapouge (1906, 1929), Sturani (1962), Hůrka (1971b) and key: Arndt (1985, 1991b). *Note*: The adults can stridulate (Casale *et al.*, 1982). Other species that stridulate are *C. intricatus*, *C. planatus* and especially some Anatolian and Caucasian *Tribax* species.

Conservation: Not endangered in the major part of its range.

20.002. C. (Platycarabus) creutzeri
Fabricius, 1801.

General literature: **Checklists and catalogues** – Breuning (1934): 1075. Březina (1994): 46; (1999): 52. Deuve (1994): 178 [402]. Kleinfeld & Schütze (1999): 25. Lorenz (1998): 89. Turin *et al.* (1993): 28. **Iconography** – Casale *et*



20 002 creutzeri (Platycarabus)

al. (1982): fig. 138 & 146. Ghiretti (1996): 199-200. Imura & Mizusawa (1996): Pl. 40 [336]. Pavicevic & Mesaros (1997): cd-rom. Rautenstrauch (1994): Pl. 76.

Geographical range: Endemic species of the C. and E. Prealps and Alps on the S. side. **Chorotype:** SEU-ALPE. **Range characteristics:** Alpi(CE). **Distribution in Europe**: **Balkan Peninsula** – Slovenia (Julian Alps, Karawanks) and W. Croatia: from Istria along the N. Dalmatian chain; down to N.W. Bosnia. **Austria** – Restricted to C.E. Austria (Kärnten, mainly in the S.). **Switzerland** – Only in the high parts of Monte Generoso. **Italy** – In the S. Alps along the N. border of Italy from the mountains N. of Lake of Como to Mts. of Friuli (Lombardia, Veneto, Ticino, Venezia Tridentina, Venezia Giulia).

Subspecies: **a) subsp. creutzeri** – N.E. Italy (Venezia Giulia) to W. Slovenia and S. Austria. **b) subsp. heros** Vacher de Lapouge, 1924 – Carinthia, N. Slovenia. **c) subsp. humilis** Berneau, 1911 – Croatia, along the N. Dalmatian chains. **d) subsp. kircheri** Germar, 1824 – C. and C.E. Alps and Prealps (high altitudes), W. vicariant of *creutzeri* (*s.str.*). **e) subsp. baldensis** Schaum, 1857 – Italy (Veneto and W. Trentino), vicariant of *kircheri* in the mountains E. of the Garda Lake.

Ecology: A typical montane species. In bushes and forests, occasionally also at low altitude (200-300 m in few places in Veneto: Casale *et al.,* 1982), mostly in the forest to the alpine zone (2000-2300 m: Hůrka, 1973). According to Hoffmann (1907), in C. Europe mainly between 800 and 2000 m. In Switzerland from the low valley forests (200 m) to open country at high altitudes (2500 m – Marggi, 1992). This characterisation also holds for the N.W. Balkans (Pavicevic & Mesaros, 1997). Like *C. depressus* in other areas in alpine habitats in the summer (Brandmayr & Zetto-Brandmayr, 1986). It is exclusively found on calcareous soil in all parts of its area of distribution (Brandmayr, 1972; Brandmayr & Zetto-Brandmayr, 1988; Casale *et al.,* 1982; Müller, 1926).

Transects: Chapter 8: T-74 and 81-82.

Biology: **Activity** – Nocturnal. **Periodicity** (Hůrka, 1973) – Depending on altitude, reproduction in spring or summer. Copulations have been observed at the end of June. Females lay their eggs after hibernation in spring; oviposition under conditions of captive breeding, from the middle of April onwards. L2 and L3 larvae have been found in the first half of July (at 2000 m) and L3 in the middle of August (Raynaud, 1968). Aestivation diapause may take place during July-September, depending on altitude (Sturani, 1962). Teneral animals appear in the forest zone in autumn and in the alpine zone after the melting of snow, in the spring (Breuning, 1934; Burmeister, 1939). Under captive breeding conditions, Raynaud (1968) observed emerging animals from the end of June. Duration of development, which takes place without larval diapause; eggs (size 3.5 x 2 mm): 8-10 days, L1: 9 days, L2: 8 days, L3: 21 days and pupa 30 days; about 75-80 days in total. Adults can be active during September-October, before entering hibernation from November onwards. It hibernates, often in groups of many individuals, under bark (*Pinus*), and in the soil at lower altitudes (Casale *et al.,* 1982). **Food** – (Larochelle, 1990; Casale *et al.,* 1982): In captivity, snails (*Helicigona*, *Helix*), slugs (*Arion*, *Limax*), earthworms, caterpillars (without hairs), raw meat, gingerbread and omelette. Fruit was accepted when no animal food was offered (Hölzel, 1942). Also cannibalistic. **Larva**: Described by Sturani (1962: L1) and Raynaud (1968: L3 ssp. *kircheri*). Food – Same as adults. Like the adults, the larvae are prominent cannibals (Hölzel, 1942).

Conservation: In Switzerland (Mt. Generoso), it seems to be seriously endangered by tourism (Marggi, 1992). No data are available about threats in similar situations from other areas. In the Italian Alps, normally very abundant, not endangered. Pavicevic & Mesaros (1997) mention only the form *humilis* Berneau as possibly endangered, however without presenting evidence for this statement. Also *humilis* was observed as one of the most common *Carabus* species (Casale, *pers. observ.*).

20.003. C. (Platycarabus) cychroides

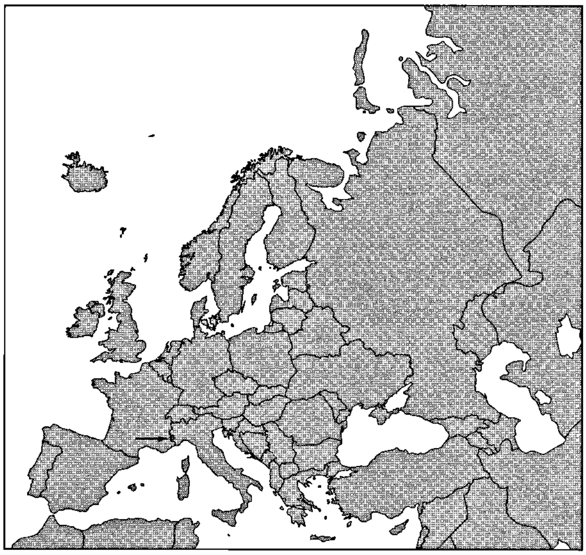
Baudi di Selve, 1864.

General literature: **Checklists and catalogues** – Breuning (1934): 1066. Březina (1994): 46; (1999): 52. Deuve (1994): 178 [400]. Kleinfeld & Schütze (1999): 25. Lorenz (1998): 89. Turin *et al.* (1993): 28. **Iconography** – Casale *et al.* (1982): fig. 139. Ghiretti (1996): 198. Imura & Mizusawa (1996): Pl. 40 [339]. Rautenstrauch: Pl. 75.

Geographical range: Endemic species of the N.W Italian Alps. **Chorotype:** SEU-ALPW. **Range characteristics:** Alpi(W). **Distribution in Europe**: **Italy** – Cottian Alps, on the high mountains in Val Chisone and Val di Susa (Mt. Orsiera-Rocciavré, Mt. Albergian).

Subspecies: No subspecies.

Ecology: In small alpine and subalpine areas at high altitude (1800-2000 to 2400 m). It is strictly confined to



20 003 cychroides (Platycarabus)

alpine prairies and moraine zones where it lives under stones and between *Rhododendron* and *Alnus* roots (Casale *et al.,* 1982; Sturani, 1962). It prefers a very moist environment, near snow.

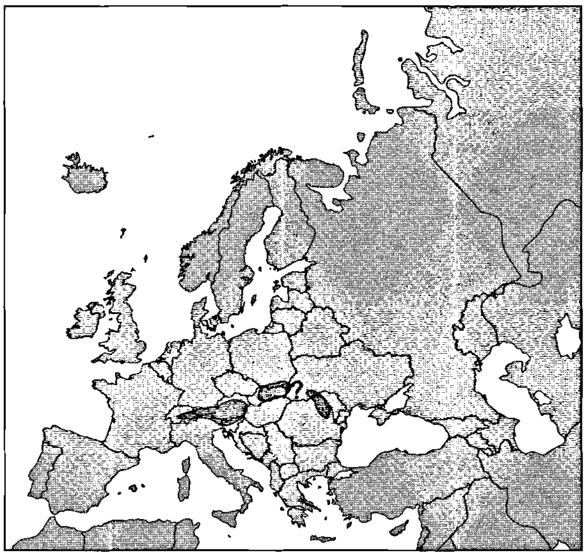
Biology: **Activity** – Nocturnal. **Periodicity** – A very early species, mainly active during May-June; the adults disappear in summer (July-August) and there is no adult activity until next spring, not from 'old' adults, nor from freshly emerged specimens. Spring/summer breeder with a very quick larval development: eggs (size 3.5 x 1.2 mm): about 5 days; larvae, including 4 days prepupal stage: 21-25 days and pupae 6 days (Sturani, 1962). Probably the teneral adults do not leave their pupal chambers until the following spring. **Food** – (Larochelle, 1990; Casale *et al.,* 1982): Helicophagous species; in the field, specialised on the snail *Helix (Helicigona) glacialis* Thoms. In captivity, live snails, raw meat, fruits and sugared water. **Larva**: Described by Sturani (1962); see Casale *et al.* (1982) and key: Arndt (1985). Food – Same as adults.

Conservation: Along with the better known *C. olympiae,* it is one of the most local *Carabus* species in Europe. A protected species in the Orsiera-Rocciavrè Natural Park.

20.004. C. (Platycarabus) fabricii
Duftschmid, 1812.

General literature: **Checklists and catalogues** – Breuning (1934): 1067. Březina (1994): 46; (1999): 52. Deuve (1994): 178 [401]. Kleinfeld & Schütze (1999): 25. Kryzhanovskij *et al.* (1995): 47 [131]. Lorenz (1998): 89. Turin *et al.* (1993): 29. **Iconography** – Casale *et al.* (1982): fig. 142. Ghiretti (1996): 198-199. Imura & Mizusawa (1996): Pl. 40 [338]. Jakobson (1905): Pl. 4. Rautenstrauch (1994): Pl. 74-75.

Geographical range: Distributed in many small isolated populations on the N. side of the C. and E. Alps, Carpathian Mountains and Tatra. **Chorotype:** SEU-ALCA. **Range characteristics:** Alpi-Carp. **Distribution in Europe**: **Germany** (Trautner & Müller-Motzfeld, 1995): only found in Bayern; rare. **Poland** – Restricted to Beskydy and Tatry Mts. **Russian Plain** – Ukrainian Carpathians (Chernohora Mts.). **Czechia & Slovakia** – Moravia (Beskydy Mts.); Slovakia (Low & High Tatry Mts., Malá & Velká Fatra Mts., Oravské Beskydy Mts.). **Romania** – Carpathians: N. Romania, Rodna, Caliman Mts., rare. **Austria** – Widespread from Vorarlberg to low Austria and Styria; not in Burgenland and also not reported from Osttirol. **Switzerland** – C.E. of the country: restricted to a relatively small, coherent area, from Mürren to the E. via the chain N. of the Vorderrhein; Alpes Bernoises and Alpes Grisons. In the N. roughly bordered by the line Interlaken – Luzern (St. Gallen). **Italy** – A most marginal fauna element, restricted to a small part of the E. Alps along the N.E. border from Val dell'Isarco to Pusteria.


20 004 fabricii (Platycarabus)

Subspecies: a) subsp. fabricii – C. and E. Alps, Czechia (only old records in Beskydy mountains), Slovakia, Austria, Switzerland, N.E. Italy, E.-ward to the Tatra. **b) subsp. koralpicus** Sokolar, 1910 – Austria, S. vicariant of the typical form. **c) subsp. malachiticus** C. G. Thomson, 1875 (?= *ucrainicus* Lazorko, 1951) – Carpathians of N. Romania (Rodna Mts., Caliman Mts.), Slovakia (Tatry Mts.); *ucrainicus* from W. Ukraine (Hoverla massif) is questionable.

Ecology: Subalpine to high alpine species (Hůrka, 1973); petrophil (Mandl, 1972). From 1600 m, in the upper zone of montane forests, but most abundant in the open habitats of the alpine zone, up to 2700 m. In the alpine prairies under stones. According to Hoffmann (1907), in C. Europe mainly between 1500 and 2500 m.

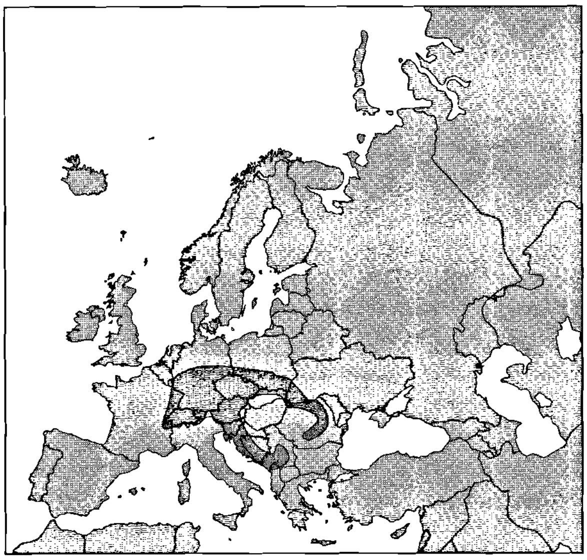
Transects: Chapter 8: T-34-35 and 77.

Biology: **Activity** – No data. **Periodicity** (Hůrka, 1973) – Reproduction in spring and early summer. Larval development takes place without diapause. L1 can be found in June-July and L3 in August-September. Teneral animals were reported from autumn and spring, in the last case they probably hibernated as pupae or as teneral adults in their pupal chambers (Breuning, 1934; Burmeister, 1939). The adults occur regularly from May/June until August (Sturani, 1962); animals that emerged in autumn are not active before hibernation which occurs from August onwards. A large proportion of the adult individuals hibernate and reproduce in the next year. **Food** – No data. **Larva**: Described by Vacher de Lapouge (1906: L2), Hůrka (1970: L1-L2) and Hůrka (1971b: L1-L3); see Casale *et al.* (1982) and key: Arndt (1985). Food – Earthworms in the laboratory (Arndt, *pers. observ.*).

Conservation: Not endangered.

20.005. C. (Platycarabus) irregularis
Fabricius, 1792.

General literature: **Checklists and catalogues** – Breuning (1934): 1086. Březina (1994): 46; (1999): 53. Deuve (1994): 179 [403]. Kleinfeld & Schütze (1999): 25. Kryzh-



20 005 irregularis (Platycarabus)

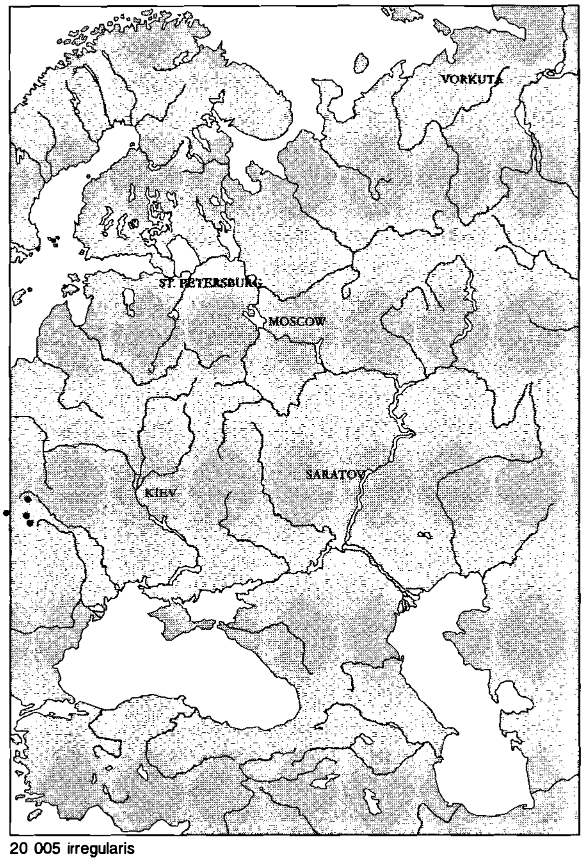
anovskij *et al.* (1995): 47 [132]. Lorenz (1998): 89. Turin *et al.* (1993): 29. **Iconography** – Casale *et al.* (1982): fig. 148. Forel & Leplat (1995): Pl. 27. Ghiretti (1996): 200-202. Imura & Mizusawa (1996): Pl. 40 [340]. Jakobson (1905): Pl. 3. Pavicevic & Mesaros (1997): cd-rom. Rautenstrauch (1994): Pl. 77-78.

Geographical range: C. and E. Europe; C. and E. Alps, Carpathians, W. Balkan Mts. to N. Albania. **Chorotype:** EUR. **Range characteristics:** CEur-SEEur. **Distribution in Europe**: **Belgium** – Very few, old records from E. Belgium; now extinct. **Germany** – Not in the N. and N.W. (Schleswig-Holstein, Mecklenburg-Vorpommern, Berlin, Brandenburg); it just reaches the N. of Weser Mts. near Osnabrück, Hannover and Harz (Du Chatenet, 1986; Arndt, 1989), in Germany not below 220 m (Weber, 1966c). Few records, scattered throughout the country; in many places rare or threatened (Sachsen, Thüringen, Bayern, Baden-Würtemberg). **Poland** – Restricted to the S. (Sudety, Beskydy, Tatry Mts.). **Russian Plain** – Only in the Ukrainian Carpathians (Zakarpatye, Ivano-Frankovo and Lvov provinces: Chernogora Mt., Poradya Mt., Pop Ivan, districts of Uzhgorod, Rakhov, Skole, Drogobych, Kamenets – Ponomarchuk, 1956; Rizun, 1990; IZ). **Czechia & Slovakia** – In Bohemia, Moravia and Slovakia, sporadically throughout all territory, in primary forests sometimes quite common. **Hungary** – Only in the W.-most part, in the Kőszeg Mts., very rare and sporadic. **Romania** – Carpathians, N.W. upland, Krain, Rarau Mts. N.E. Romania. **Balkan Peninsula** – W. mountain chain; Slovenia (Julian Alps), N.W. Croatia, S.E. Bosnia-Herzegowina (Dinaric Alps), W. Serbia, N. and C. Montenegro (to N. Albania?). **Austria** – Distributed throughout the entire territory. **Switzerland** – Widespread but scattered over the N.W. part of the country; N. side of the Alps, Jura. Single records exist from Graubünden and Wallis. No recent records near the Italian border (compare Casale *et al.,* 1982). **Italy** – An extremely marginal fauna element; restricted to isolated locatities in the N.W. Alps (Val Sarentina, Croce Pass). Erroneously cited from the Gran San Bernardo Pass, in Aosta Valley. **France** – Widespread in the N.W., along the Swiss border from the Savoie PreAlps, throughout the Jura, up to the N. part of the Vosges.

Subspecies: **a) subsp. irregularis** – S. Belgium, N.E. France, C. and S. Germany, Switzerland, C., S. and W. Austria, Czechia, Hungary, N.E. Italy. **b) subsp. bucephalus** Kraatz, 1879 (= *ramanus* Sokolar, 1909) – Dinaric chain and Balkan Peninsula, from Slovenia, Serbia, Croatia to S. Bosnia. **c) subsp. montandoni** Buysson, 1882 – Carpathian Mountains of Slovakia, Romania and W. Ukraine.

Biogeography: According to Weber (1966c), it is a recent coloniser of N.W.-C. Europe, that probably arrived with the beech (*Fagus silvatica*), and that survived the medieval forest felling of the lowland forests.

Ecology: Silvicol (Mandl, 1972), mainly in montane forests of C. Europe and of the Carpathian chain, not in W. Europe. According to Hoffmann (1907), in C. Europe mainly between 300 and 2000 m. Especially in cool and shadow-rich beech forests situated on moist N. slopes, less frequently in mixed or coniferous forests (Weber, 1966c; Giers, 1973; Arndt, 1989). In E. Europe from 300-400 m to about 1000 m, occasionally in low densities to the upper forest region, 1900-2000 m (Hůrka, 1973). In Hungary only in dense mon-



20 005 irregularis

tane forests of the spruce and beech belt, preferring wet places. In the terrirory of former W. Yugoslavia, it occurs in deciduous and coniferous forests in montane regions (Pavicevic & Mesaros, 1997), mostly on limestone (Casale, *pers. obseru*). In Switzerland in foothills and submontane forests to about 500 m (Marggi, 1992). In France found in the E. Rhône-Alpes especially between 700 and 1200 m (Coulon *et al.*, 2000; Forel & Leplat, 1995), rarely higher to 1500 or 1700 m in prairies; this also applies to the E. Alps and the Balkans.

Transects: Chapter 1: I-1; Chapter 8: T-27, 31-32, 34-35, 74, 77 and 80.

Biology: **Activity** – Nocturnal, but during the reproductive period also day active (Thiele & Weber, 1968); usually hidden during daytime under tree trunks. **Periodicity** (Hůrka, 1973) – Reproduction in spring; copulations observed from March onwards (Vacher de Lapouge, 1908; Raynaud, 1943). Oviposition depending on altitude from March/April until the beginning of July. Larval development without diapause. Larvae were mainly found in the period July-September (Hůrka, *l.c.*). In the S. of its distribution (Karawanks), third instar larvae were found in mid-September, and fresh adults in the first half of October (Hölzel, 1942). Duration of development for all stages 9-10 weeks (eggs: 8-12 days, L1: 5-9 days, L2: 10-14 days and L3: 15 days; the larval period on total takes about 45-50 days and pupation another 20 days. After emerging in autumn (August – first half of October), the young adults may have a short period of activity before they hibernate (in decaying tree trunks, but also under mosses or in the soil) around the end of September (C. Europe: Arndt, 1989; Forel & Leplat, 1995). According to Sturani (1962), adults are only active during the period June-August. **Food** – At least in the woodlands near Osnabrück (Lower Saxony) a specialised snail hunter. The short but strong asymetric mandibles are used for cracking shells, like members of the genus *Licinus* (cf. Brandmayr & Zetto Brandmayr, 1986). *Trichia hispida*, *Ena montana*, *E. obscura* and some clausiliid snails are common prey. It hunts snail species on the bark of trees. The fluctuations of the population density seem to be great (Barner, 1937). **Larva**: Described by Letzner (1850: L3?), Vacher de Lapouge (1906: L2-L3), Hůrka (1971b: L1-L3) and key: Arndt (1985). Food – Earthworms in the laboratory (Arndt, *pers. obseru.*). *Note*: The adult beetles stridulate when disturbed. Biological significance of this phenomenon is unknown. The stridulatory structures have been described by Bauer (1975). **Dispersal power**: The beetle is a good tree-trunk climber (cf. the catches in tree falls of Martius, 1986; Assmann, *pers. obseru.*).

Conservation: In Germany, in tall, old forests above 220 m (Weber, 1966c); in Czechia and Slovakia an indicator of primary forest in hills and mountains (Hůrka, 1996). Blumenthal (1981) concludes that on a European scale, the significance of the species as an indicator is low, because of a N.-S. shift in habitat preference. However, on a local scale, the species seems – in agreement with Hůrka (1996) – to be a good indicator of unfragmented habitats. For the W. Balkan, mentioned as vulnerable (Pavicevic & Mesaros, 1997), which is not in agreement with the actual status of the species, because it is in fact very common and widespread (Casale, *pers. obseru.*).

21. HETEROCARABUS MORAWITZ, 1886

21.001. C. (Heterocarabus) marietti
De Cristoforis & Jan, 1837.

General literature: **Checklists and catalogues** – Breuning (1934): 982. Březina (1994): 47; (1999): 54. Deuve (1994): 181 [406]. Kleinfeld & Schütze (1999): 26. Lorenz (1998): 90. Turin *et al.* (1993): 29. **Iconography** – Ghiretti (1996): 205-207. Imura & Mizusawa (1996): Pl. 41 [343].

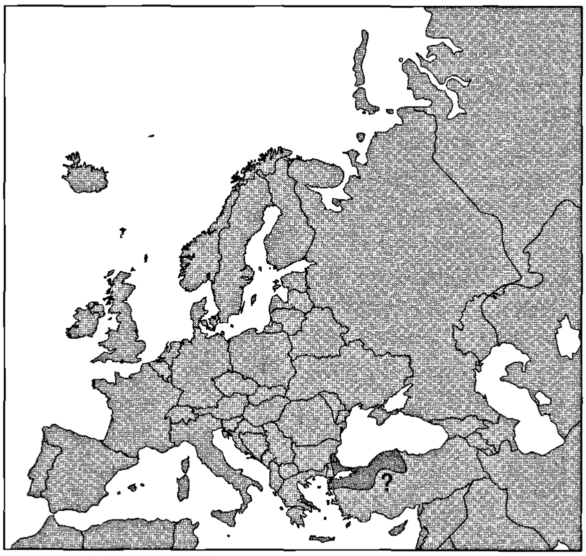
Taxonomy: A complex of several (semi)species of this subgenus exists in the forests of Turkey, including *C. marietti marietti* (by Deuve, 1994, treated in *Chaetocarabus).*

Geographical range: S.E. Bulgaria, N. part of European Turkey and N.W. part of Asiatic Turkey. **Chorotype**: ANAT. **Range characteristics:** Balk(SE)-Anat(N). **Distribution in Europe (and adjacent areas)**: **Bulgaria** – Recorded from the S. Black Sea coast and Strandhza region. **Turkey** (Apfelbeck, 1904; Darge, 1990) – European part, Bosporus. Also present in NW. Anatolia (Casale & Vigna Taglianti, 1999).

Ecology: A forest species. In Bulgaria up to 200 m (Guéorguiev & Guéorguiev, 1995). In Anatolia, up to 1000-1500 m.

Biology: **Activity** – No data. **Periodicity** – Like other *Heterocarabus,* an early-spring breeding species. In Bulgaria reported from May-June (Guéorguiev & Guéorguiev, 1995). Rather common in beech forests of Strandhza Mt. in early spring (IV-V) and autumn (IX-XI); prefers forest ravines covered by *Rhododendrom ponticum* (Kodzhabashev, *pers. obseru.*). In Asiatic Turkey hibernating under bark (Casale, *pers. obseru.*). **Food** – No data. **Larva**: No data.

Conservation: Not endangered.



21 001 marietti (Heterocarabus)

22. SPHODRISTOCARABUS GÉHIN, 1885

22.001. C. (Sphodristocarabus) varians
Fischer von Waldheim, 1823 (= *janthinus* auctt.).

General literature: Checklists and catalogues – Breuning (1934): 995. Březina (1994): 48; (1999): 61. Deuve (1994): 186 [423]. Kleinfeld & Schütze (1999): 30. Kryzhanovskij *et al.* (1995): 50 [157] (*armeniacus* Mannerheim, 1830). Lorenz (1998): 93. Turin *et al.* (1993): 29. **Iconography** – Ghiretti (1996): 214-215. Imura & Mizusawa (1996): Pl. 55 [452].

Taxonomy: Generally known and cited as *C. janthinus* Ganglbauer, 1887. About 20 species of this subgenus live in Turkey and the Caucasus. Treated as a subspecies of *C. adamsi* Adams, 1817 by Březina (1994) and Deuve (1994). By Březina (1999) finally listed as a subspecies of *C. varians* Fischer von Waldheim, 1827 and this treatment is accepted here.

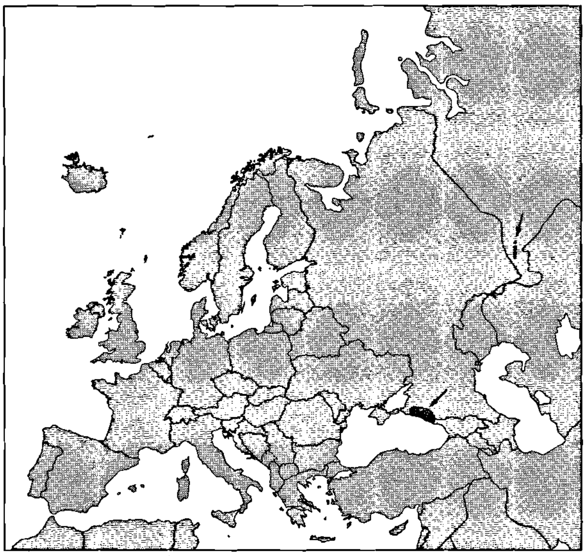
Geographical range: Endemic species of W. Caucasus and Ciscaucasia. **Chorotype:** CAUC. **Range characteristics:** Cauc(W). **Distribution in Europe: Russian Plain & Caucasus** – W. Caucasus in the limits of Krasnodar region and Abkhasia. The species is included in the present book, because it was recorded from the Ilmen reserve in the S. Ural; this record is probably based on an accidental introduction, as seems to be the case with another Caucasian species, *C. exaratus*, also found near the Ilmen reserve (Lagunov & Novozhenov, 1996).

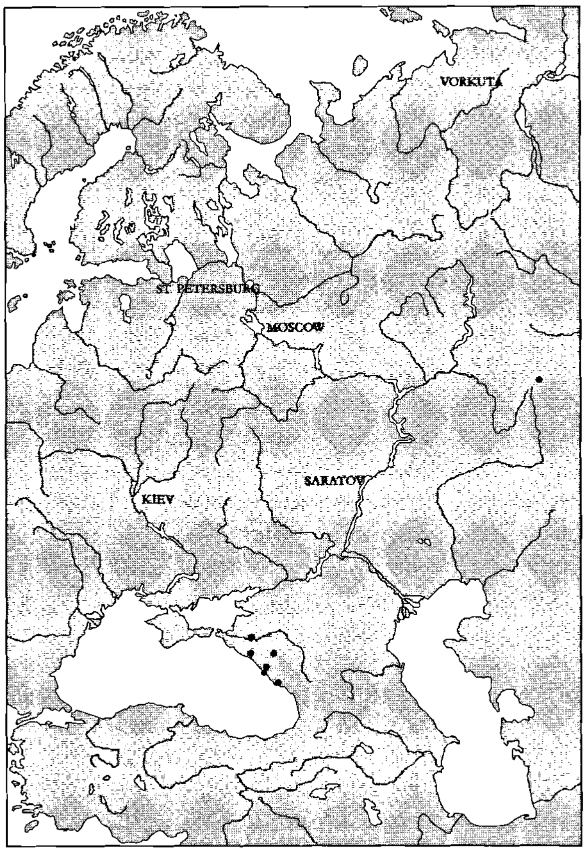
Subspecies: Several subspecies have been described. Subsp. **janthinus** inhabits the N. part of the species area (in the S. to Sotchi and Krasnaja Poliana).

Ecology: Lives in forests of lower and middle montane belts.

Biology: No data. A very common species.

Conservation: Not endangered.


22 001 varians (Sphodristocarabus)



22 001 varians

23. MEGODONTUS SOLIER, 1848

23.001. C. (Megodontus) aurolimbatus
Dejean, 1829.

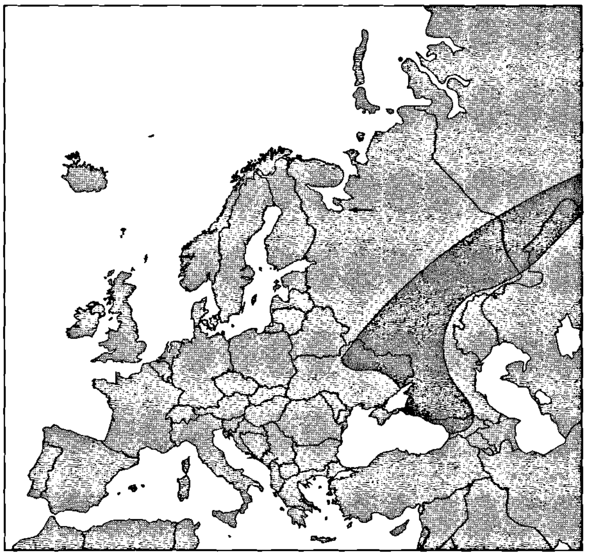
General literature: Checklists and catalogues – Breuning (1935): 1237. Březina (1994): 73; (1999): 77. Deuve (1994): 255 [681]. Kleinfeld & Schütze (1999): 38. Kryzhanovskij *et al.* (1995): 48 [140]. Lorenz (1998): 100. Turin *et al.* (1993): 29. **Iconography** – Ghiretti (1996): 336. Imura & Mizusawa (1996): Pl. 71 [577].

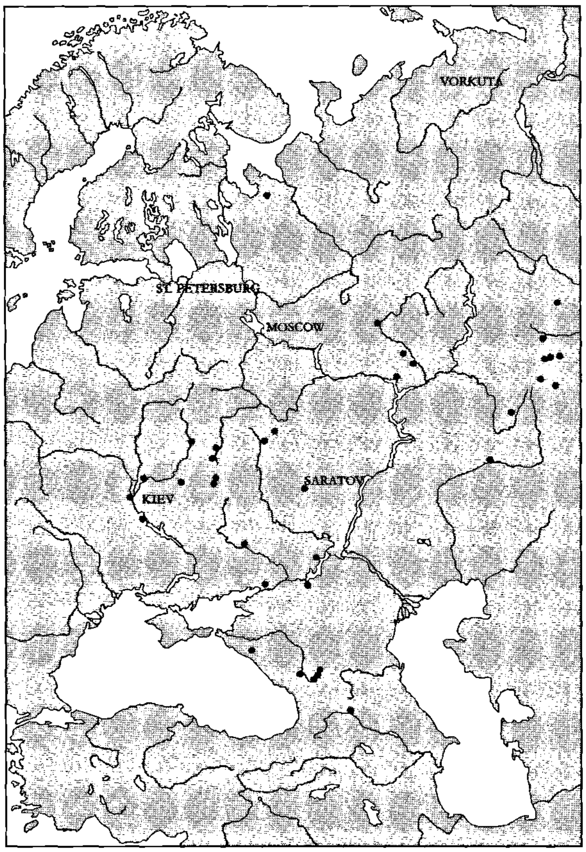
Taxonomy: Many authors united this form with *C. violaceus* as its subspecies (e.g.: Březina, 1994, 1999), but Russian entomologists (Jakobson, 1905; Semenov-Tian-Shanskij, 1932; Kryzhanovskij, in the present *Key to the adults*) considers it a distinct species. K. Makarov (*in litt.*) recently corroborated this opinion on the basis of larval characters.

Geographical range: E. part of European Russia (except dry steppes), forest steppe zone of W. and C. Siberia (to Krasnoyarsk) and N. Kazakhstan (Kokshetau), mountains of the N. Caucasus (to 2000 m). **Chorotype:** SIE. **Range characteristics:** EEur(S)-CSib. **Distribution in Europe (and adjacent areas): Russian Plain & Caucasus** – Middle stretch of European Russia, W. to Dnieper River, N. to the line Chernigov – Bryansk – Skopin (Ryazan Province) – Kotelnich – Turinsk, one isolated locality, however is known from the far N. island of Mudyug (Archangelsk region – MPGU). S. to the Caucasus, E. to S.W. Siberia and N. Kazakhstan. The N. limit of the range generally coincides with the S. margins of the mixed forest subzone. Known from C. and E. Ukraine (Kiev, Baturin, Chernigov, Kanev, Poltava province (Damontovo), Severskii Donets Valley (Svyatogosrk, Yarovaya) – ZIN, ZM), the provinces of Bryansk (Bryansk forest – Stark, 1926), Belgorod (Les-na-Vosrkle Reserve – Grin'feld, 1948), Kursk (Kazatskii Les, C.-Zhernosem Reserve – ZIN, ZM, Sharova, 1982), Orel (Orel – ZIN), Ryazan (Gremyachka and Alekseevskii les in Dankov District – ZIN, ZM), Voronezh (Borisoglebsk – Fomichev, 1983; Khoper Reserve – MPGU) Vyatka (Malmyzh, Nemda, Gol'tsy – Shernin, 1974, ZIN; Kotelnich – Yuferev, 1980), Kazan' District (ZIN). Widely distributed in the Urals: Bashkiria (Bashkir Reserve – Koz'minykh, *in litt.*), Orenburg (ZIN), village Larino in Ekaterinburg province – MPGU, Chelyabinsk province (Il'men Reserve, Kunashak, Miasskoe – Coll. Lagunov; Misyash – Voronin, 1987; Troitsk Reserve – Esjunin & Koz'minykh, *in litt.*; Saimonov dolina – ZIN; Bol'shoi Kuyash Lake – Field report of the Institute of Evolutinary Morphology & Ecology, Moscow, 1981), Ekaterinburg proivince (Koz'minykh, *in litt.*). In the S., it is known from Rostov province (Rostov, Volgodonsk, Oblivskaya – Fomichev, 1983) and Caucasus (Kislovodsk, Terskaya, Georgievskoye, Teberda, Elbrus, Baksan Gorge, Tbilisi – ZIN, ZM, MPGU). Khoper reserve in Voronezh province (MPGU) and Baksan in Kabarda-Balkaria in the Caucasus (Makarov, *in litt.*). From the S. limits of mixed-forest zone through the whole forest-steppe and steppe zones, but not common.

Subspecies: Morphologically very homogeneous, no subspecies.

Ecology: Mostly in open landscapes. Ecology similar to that of *C. violaceus.* In the Central-Chernozem Reserve (Grechanichenko, 2000), it is rare in forests (less than 1%), but common in forested ravines (11%) and steppe habitats (11% in mown steppes and 14% in non-mown steppes). In the N. tayga of the Archangelsk Province it rarely was trapped in a floodland willow shrub, but in higher numbers in a city park (Filippov, 2000).


23 001 aurolimbatus (Megodontus)



23 001 aurolimbatus

Transects: Chapter 1: I-2; Chapter 8: T-48.

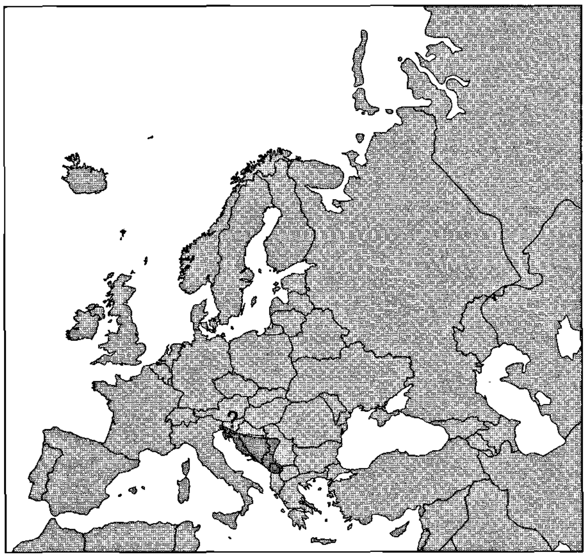
Biology: Generally similar to that of *C. violaceus.* **Activity** – No data. **Periodicity** – It has on average a two-year development (data after dissections). Eggs are mainly laid in July and it reaches 2nd or 3rd instar stages in September after wich they enter hibernation. Next July, development resumes and the juveniles appear at the end of the season (end of August, beginning of September) and hibernate sexually immature. **Food** – No data. **Larva**: No data.

Conservation: No data.

23.002. C. (Megodontus) caelatus
Fabricius, 1801.

General literature: Checklists and catalogues – Breuning (1935): 1291. Březina (1994): 70; (1999): 73. Deuve (1994): 257 [684]. Kleinfeld & Schütze (1999): 39. Lorenz (1998): 101. Turin *et al.* (1993): 29. **Iconography** – Casale *et al.* (1982): fig. 119. Darnaud (1984b): Pl. 17. Ghiretti (1996): 344-346. Imura & Mizusawa (1996): Pl. 72 [583]. Jakobson (1905): Pl. 2. Pavicevic (1997): cd-rom. Rautenstrauch (1994): Pl. 89-90.

Geographical range: N.E. Italy, S.E. Austria (?) and the W. parts of Balkan peninsula to Montenegro and N. Albania. **Chorotype:** SEU-CADI. **Range characteristics:** Balk(W).



23 002 caelatus (Megodontus)

Distribution in Europe: Balkan Peninsula – Slovenia-Croatia, from S. Istria and Julian Alps along Dalmatian coast, through Bosnia and Montenegro, to N.W. Macedonia and N. Albania (Velipoja, Vilajet, Alessio) and in the S.E. to the surroundings of Vishegrad (S.E. Herzegowina). **Austria** – Probably not indigenous; not mentioned by Mandl (1972), although reported from S. Steiermark (Trifail, Montpreis) by Breuning (1935). **Italy** – Only in the N.E.; Friuli-Venezia Giulia near borders of Slovenia, from Tarcento (Udine) to Gorizia and Trieste.

Subspecies: **a) subsp. caelatus** – S.E. Austria, N.E. Italy (Friuli), N.W. and C. Slovenia, N. Croatia to Zagreb. **b) subsp. schreiberi** Kraatz, 1877 – Widely distributed from the Alpi Giulie and Trieste in Italy through S. Slovenia and Croatia. **c) subsp. dalmatinus** Duftschmid, 1812 – Croatia, W. Bosnia, Herzegovina, Montenegro and N. Albania. Mostly along sea-shores and on the Adriatic islands, but also in mountains to middle forest zone. Large specimens with greenish or bluish elytra, from the S. Croatian and Montenegrine coasts, have been described as *procerus* Reitter, 1885. **d) subsp. sarajevoensis** Apfelbeck, 1890 – S. Croatia, Bosnia-Herzegovina, Montenegro, E. Albania, in mountains (along sea-shores, replaced by *dalmatinus*). *Note*: It seems that the areas of distribution of subspecies *sarajevoensis* and *dalmatinus* overlap in some parts (coastal chains), and this makes it probable that they are ecologically separated (Casale *et al.*, 1982).

Ecology: From the sea level to 2200 m; in the C. and W. of its distribution, it is most abundant in the middle forest zone and not present in alpine steppes (Casale *et al.*, 1982); subsp. *dalmatinus* occasionally occurs in open habitats in the littoral zone, up to 400 m (Pavicevic & Mesaros, 1997) and mediterranean maquis. In the E. of its distribution on the Balkans, it is mainly montane to alpine, e.g. subsp. *sarajevoensis* which is mainly found in forests in hills and mountains. Despite the indications given by Apfelbeck (1904), the species is rare at high altitudes. In general, in all Balkans, it is mainly a forest species, both in the montane and mediterranean parts (Casale, *pers. observ.*), and sometimes very common. The three main subspecies correspond with the three major forest zones: a) the mountain forest zone (*Fagus*) with *caelatus s.str.* b) karst zone (*Quercus*) with *schreibersi* and c) the mediterranean (Maquis) zone with *dalmatinus* (Müller, 1926b).

Transects: Chapter 8: T-70-71 and 74.

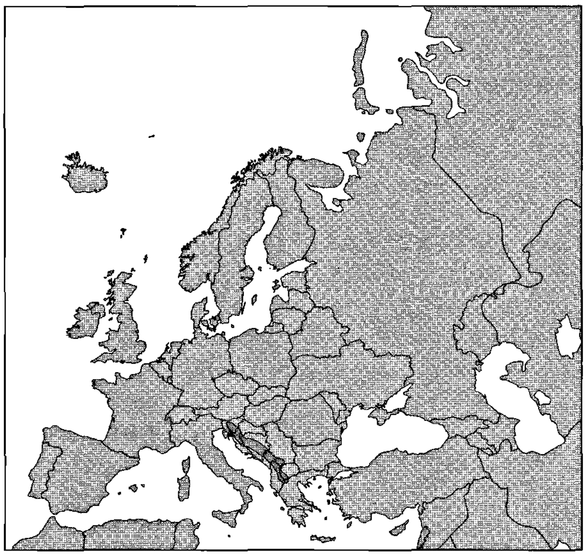
Biology: **Activity** – No data. **Periodicity** – Mostly autumn breeder (Brandmayr & Zetto-Brandmayr, 1986b). Adults occur from May to October; hibernation takes place in the soil, sometimes (infrequently) in rotten wood (Casale *et al.*, 1982; Du Chatenet, 1986). The eggs (10 x 3 mm) develop in 10-14 days and the larvae (including a 10-40 days prepupal stage): 40-85 days and pupae: 14-15 days (Sturani, 1962). Transition from autumn propagation to a two-years development due to increasing altitude is observed (Brandmayr & Zetto Brandmayr, 1986). **Food** (Larochelle, 1990) – In the field, carrion, snails. In captivity, live snails (*Helix* species), earthworms, caterpillars without hairs, raw meat, gingerbread, bread soaked in sugared milk. **Larva**: Described by Sturani (1962) and Raynaud (1976). Food – No data.

Conservation: Most forms are not endangered. Pavicevic & Mesaros (1997) mention however a few smaller populations as endangered or vulnerable, especially near the coast; probably due to tourism (Casale, *pers. observ.*).

23.003. C. (Megodontus) croaticus

Dejean, 1826.

General literature: **Checklists and catalogues** – Breuning (1935): 1283. Březina (1994): 71; (1999): 73. Deuve (1994): 257 [685]. Kleinfeld & Schütze (1999): 39. Lorenz (1998): 102. Turin *et al.* (1993): 29. **Iconography** – Casale *et al.* (1982): fig. 159. Darnaud (1984b): Pl. 17. Ghiretti (1996): 346-347. Imura & Mizusawa (1996): Pl. 72 [582]. Pavicevic & Mesaros (1997): cd-rom. Rautenstrauch (1994): Pl. 88-89.



23 003 croaticus (Megodontus)

Geographical range: Endemic species of the W. part of the Balkan peninsula. **Chorotype:** SEU-CADI. **Range characteristics:** Balk(W). **Distribution in Europe**: **Balkan Peninsula** – S.W. Slovenia, through Croatia and Bosnia-Herzegovina (not in the W.), S.W. Serbia to Albania and N.W. Macedonia, where it has an inland distribution; absent from the Adriatic shore. (**Italy** – erroneously reported from E.-most Venezia Giulia).

Subspecies: a) subsp. croaticus (incl. *frankenbergeri* Obenberger, 1914) – Krain, S.W. Slovenia, Croatia, W. Bosnia, N. Herzegovina. **b) subsp. kobingeri** Apfelbeck, 1904 – W. Bosnia: mountains near Foinice, Travnik, Kresov etc. Purplish-black form with narrow violet margins from Bosnia (Ostrelj, etc.) have been described as *pretneri* Kratschmer et Drovenik, 1977. **c) subsp. bosnicus** Apfelbeck, 1890 (= *zepcensis* Reitter, 1902) – C.N. Bosnia, Herzegovina; rather variable form. **d) subsp. durmitorensis** Apfelbeck, 1904 – Isolated mountainous race from Montenegro (Mt. Durmitor). **e) subsp. ljubetensis** Apfelbeck, 1919 – Mountains of S. Kosovo, N.W. Macedonia, N.E. Albania, S.E. Montenegro. **f) subsp. babinjensis** Apfelbeck, 1918 – Local race from the high altitudes of N. Albania (Babinje-Planina). It possibly does not deserve a status of subspecies.

Ecology: Mostly at middle and upper forest belts to alpine zone. The species is common and abundant in the great virgin forest complexes of S. Bosnia, especially in the high beech and spruce forests, often with single specimens of *C. caelatus* as company (Apfelbeck, 1904). In former Yugoslavia it is silvicol, occurring in both deciduous and coniferous forests. In the hills and mountains to praticol (in less density) in the alpine area. Found from 900 up to 2400 m, predominantly in the *Abies, Pinus* and *Fagus* forests from 1500 to 2000 m; still generally a common species (Casale *et al.,* 1982).

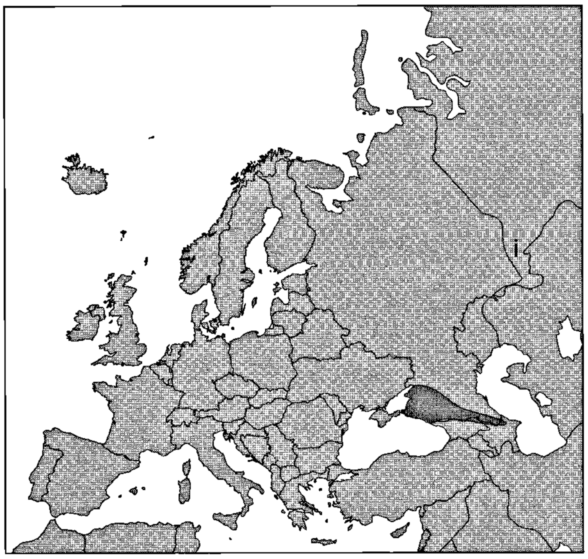
Transects: Chapter 8: T-70 and 74.

Biology: **Activity** – No data. **Periodicity** – Little is known about reproduction and development. Adults occur from May to September, but mainly in the period June-July (Du Chatenet, 1986; Sturani, 1962). Adults hibernate in rotten trunks and wood of *Abies* or *Fagus*, as well as under mosses (Casale, *pers. observ.*). **Food** – (Larochelle, 1990; Casale *et al.,* 1982): In the field, earthworms. In the laboratory, earthworms, caterpillars without hairs and bread soaked in sugared milk have been accepted. **Larva:** Described by Raynaud (1976); compare Casale *et al.* (1982). Food – No data.

Conservation: Not endangered in the inland montane populations such as the form *bosnicus* Apfelbeck, but Pavicevic & Mesaros (1997) consider endangered most other forms from former Yugoslavia. This is most probably incorrect; also in the large forests of Slovenia and Croatia common and abundant (Casale, *pers. observ.*).

23.004. C. (Megodontus) exaratus
Quensel, 1806.

General literature: **Checklists and catalogues** – Breuning (1935): 1215. Březina (1994): 71; (1999): 74. Deuve (1994): 253 [679]. Kleinfeld & Schütze (1999): 38. Kryzhanovskij *et al.* (1995): 48 [143]. Lorenz (1998): 101. Turin *et al.* (1993): 30. **Iconography** – Ghiretti (1996): 333. Imura & Mizusawa (1996): Pl. 70 [570].



23 004 exaratus (Megodontus)

23 004 exaratus

Geographical range: Endemic species of the N. Caucasus; during last decades expanding in N. direction, reaching Rostov regions (Kryzhanovskij, *in litt.*). **Chorotype:** CAUC. **Range characteristics:** Cauc-EEur(S).

Distribution in Europe: **Russian Plain & Caucasus** – A Caucasian species, very common on the N. slope of Caucasus Major range; from the Black Sea to C. Daghestan. Few localities are known from Rostov province (Rostov, Sal'sk, Sel'khoz Gigant – Fomichev, 1983), but still not found N. of the Don river. Individuals found in Vitebsk province and in the S. Urals (a rather strange but confirmed record: Bol'shoi Terenkul Lake in Chelyabinsk province – Lagunov & Novozhenov, 1996) are most probably introductions.

Subspecies: The various geographic races that have been described, can all be regarded as synonyms to the nominate form (Deuve, 1994).

Ecology: Mostly in forests, up to an altitude of 2000-2200 m, also in gardens and shelter belts, fairly common. In N. Ossetia from the dry lowland steppes to the alpine belt; it is the most common species of the middle mountain belt, with abundance 2-3x higher than all other *Carabus* species (Alekseev, *in litt.*). Also common in fields. In N. Ossetia rare in the alpine belt, but occasionally up to 3000 m.

Biology: **Activity** – No data. **Periodicity** – The adults have a short period of activity during May and June in the steppe, after which they disappear (Alekseev, *in litt.*). **Food** – (Larochelle, 1990): In the field, ticks (*Ixodes*, *Dermacentor* and *Boophilus* species), and dead rodents. **Larva**: Described by Sharova (1958, 1964: L2-L3). Food – No data.

Conservation: Apparently a very common species.

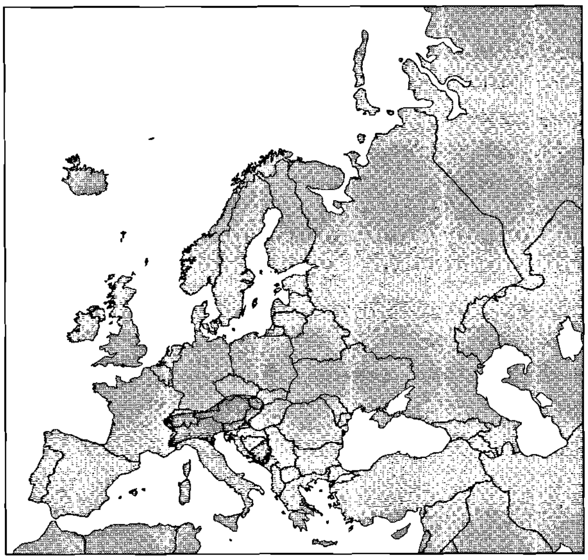
23.005. C. (Megodontus) germarii

Sturm, 1815 (= *exasperatus* auctt.).

General literature: **Checklists and catalogues** – Breuning (1935): 1227. Březina (1994): 73; (1999): 77. Deuve (1994): 255 [682]. Kleinfeld & Schütze (1999): 38. Lorenz (1998): 100. Turin *et al.* (1993): 30. **Iconography** – Casale *et al.* (1982): fig. 122, 124. Forel & Leplat (1995): Pl. 34. Ghiretti (1996): 342-344. Imura & Mizusawa (1996): Pl. 71 [576]. Rautenstrauch (1994): Pl. 86-88.

Taxonomy: By several authors regarded as a subspecies of *C. violaceus* L. (e.g.: Březina, 1994, 1999). To our knowledge, no hybrid zones exist between *C. germarii* and *C. violaceus*. Furthermore, in N.W. Italy the two species are parapatric, without introgressive forms. According to Lorenz (1998a), a neotype selection is needed for stabilization of the nomenclature in this case.

Geographical range: European species with a disjunct distribution: Alps from Savoie to Slavonia and from N. Apennines to N. Tirol and W. Hungary (to Buda Mts.); the second fragment of area in S. Bosnia, Herzegovina and Montenegro. **Chorotype:** SEU-ALPI. **Range characteristics:** CEur-SEEur. **Distribution in Europe**: **Germany** – Only mentioned from Bayern; rare. **Czechia & Slovakia** – Ranges from Austria into S. Moravia and S.W. Slovakia; not uncommon. **Hungary** – Restricted to Transdanubia, where it is rather distributed and abundant. **Balkan Peninsula** – Two disjunct areas: 1) Slovenia and N. Croatia (Slavonia), connected with the main distribution in adjacent countries, and 2) in the W. of former Yugoslavia, from S. Bosnia, via Herzegovina to Montenegro. **Austria** – Distributed across most parts of the country except Vorarlberg. **Switzerland** – S. Sopra-Ceneri (common in Mt. Generoso massif); except Graubünden, absent from the C. Alps, Wallis, and in the Rhône-Rhein area. **Italy** – Distributed across the N. (Piemonte, Liguria, Lombardia, Ticino, Veneto, Venetia Tridentino, Venezia Giulia), limited in the S. to the N. part of the Tosco-Emilian Apennines, scattering into a zone of vicariance with *C. violaceus picenus*. **France** – Restricted to the Alps of the S.E.: Alpes Maritimes and the area between Chamonix and Mt. Cenis.



23 005 germarii (Megodontus)

Subspecies: About 10 subspecies are known, from W. to E.: **a) subsp. fiorii** Born, 1901 (incl. *pedemontanensis* Breuning, 1935) – Italy: Piedmont, Alps to Mt. Generoso, N. Apennines of Liguria and Emilia (W. Padanian Plain); France: Savoie (Chamonix) and Haute Savoie; Switzerland: Tessin. Mostly in middle forest zone, rarely in lowland. **b) subsp. savinicus** Hammer, 1906 – Switzerland: Tessin S. of St. Gothard, Italy: Orobic, Lessinian, Venetian and Julian Alps, Dolomites (partly); Mts. of Slovenia; Austria: Carinthia, Karawanks, Dobratsch. Mostly in middle and upper forest belts and alpine zone. A small (22-26 mm), very narrow form of *savinicus* from Tessin, Trentino and Venetian Alps has been described as *rombonensis* Bernau, 1911, it has still more roughly sculptured elytra with strong purple tint. Some authors, including Casale *et al.* (1982) united subsp. *savinicus* with *germarii*, but their differences are fairly appreciable. **c) subsp. germarii** Sturm, 1815 – Italy: Environments of Venezia, Trieste, Trentino; Austria: Steiermark (Lichtenwald), Slovenia: Krain (loc. typ.), Dravgrad, environments of Ljubljana. Living in lowlands and valleys. **d) subsp. exasperatus** Duftschmid, 1812 (= *obliquus* Breuning, 1935, nec C. G. Thomson, 1875) – Inhabits the N.E. part of the species' area: Slovenia, N. Croatia, E. Austria (Lower Austria, Styria, Burgenland), W. Hungary, Czechia (Brno), Slovakia (Bratislava). Lives here and there sympatrically with *C. violaceus*. Several local forms have been described from this territory, but they probably do not deserve subspecific status. **e) subsp. styriensis** Breuning, 1932 (= *laevigatus* Dejean, 1826 nec Scriba, 1790) – Austria (Oberösterreich, Steiermark, Carinthia, Tirol). – From valleys to upper forest belt and sometimes in alpine zone. Probably, a mere synonym of f) subsp. *neesi*. **f) subsp. neesi** Hoppe & Hornschuch, 1825 – Alps of W. Austria, Switzerland (Graübunden) and N. Italy (Alto Adige, Dolomiti). Always in alpine zone. **g) subsp. scordiscus** Vacher de Lapouge, 1901 – S. Bosnia, Herzegovina; in middle forest zone. – Very large (31-35 mm) and narrow individuals have been described as *igmanensis* Eidam, 1927. **h) subsp. vlasuljensis** Apfelbeck, 1894 – Bosnia (Volujak, Maglic, Treskavica), Herzegovina (Plasa Planina), N. Montenegro. **i) subsp. prenjus** Eidam, 1927 – Mandl (1985b) considered this form from Prenj Mt. (Herzegovina) a distinct subspecies, but other authors doubt its status.

Ecology: Living from the lower forest belt to the alpine zone, e.g. subspecies *neesi* Hoppe, which can be characterised as alpin-steppicol (Mandl, 1972). Coulon *et al.* (2000) mention it to inhabit altitudes especially in montane prairies between 1600 and 1800 m. In Hungarian Transdanubia, mainly in the forest edges in mountains and hills, and in more open field biotopes in the plains. From lowland up to 2400 m; but most abundant at middle altitudes in various kinds of forest; rather eurytopic in Italy; also in cultivated habitats (Casale *et al.,* 1982).

Transect: Chapter 8: T-79, 88.

Biology: Very similar to that of *C. violaceus* (including *C. purpurascens*). **Periodicity** – Adults occur from April to September (Du Chatenet, 1986). *Note*: Most information was taken from sources where the taxon was not specifically distinguished from *C. violaceus*. **Larva**: Described by Sturani (1962), compare Casale *et al.* (1982). Food – No data.

Conservation: In general not endangered; only declining in intensively managed agricultural habitats.

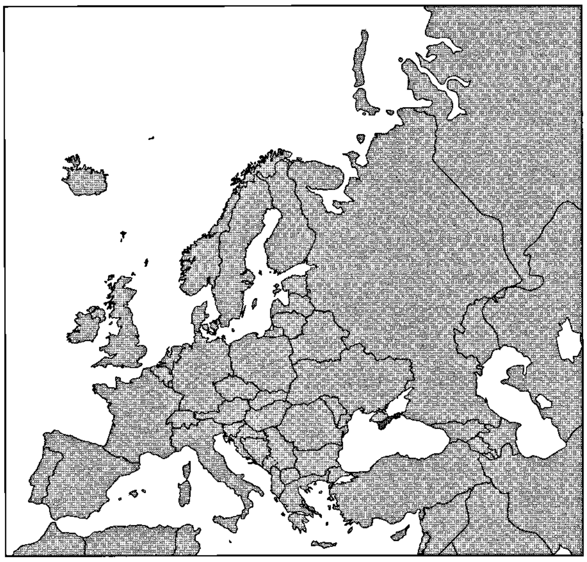
23.006. C. (Megodontus) gyllenhali

Fischer von Waldheim, 1827 (= *dejeani* Fischer von Waldheim, 1823, nec Fischer von Waldheim, 1822).

General literature: **Checklists and catalogues** – Breuning (1935): 1213. Březina (1994): 71; (1999): 74. Deuve (1994): 252 [678]. Kleinfeld & Schütze (1999): 38. Kryzhanovskij *et al.* (1995): 48 [142]. Lorenz (1998): 101. Turin *et al.* (1993): 30. **Iconography** – Ghiretti (1996): 332. Imura & Mizusawa (1996): Pl. 70 [572].

Taxonomy: The name *gyllenhali* should perhaps be substituted by *blackistoni* Newman, 1857 because of primary homonimy (Silfverberg, 1977; Lorenz, 1998; Březina 1999).

Geographical range: Endemic Ukrainian species. **Chorotype:** CAUC-CRIM. **Range characteristics:** Crim.



23 006 gyllenhali (Megodontus)

23 006 gyllenhali

Distribution in Europe: **Russian Plain** – Strictly endemic in the mountains of Crimea, known from more than 30 localities in the S. mountain coasts (ZIN, MPGU), absent in the N. steppe part of the peninsula.

Subspecies: No subspecies.

Ecology: Mesophilous forest species, predominantly inhabiting beech and oak forests (Apostolov *et al.,* 1981; Perrusenko *et al.,* 1973).

Transect: Chapter 8: T-60.
Biology: No data.
Conservation: No data.

23.007. C. (Megodontus) planicollis
Küster, 1846.

General literature: **Checklists and catalogues** – Breuning (1935): 1276. Březina (1994): 71; (1999): 74. Deuve (1994): 257 [683]. Kleinfeld & Schütze (1999): 38. Lorenz (1998): 101. Turin *et al.* (1993): 30. **Iconography** – Ghiretti (1996): 344. Imura & Mizusawa (1996): Pl. 70 [573]. Rautenstrauch (1994): Pl. 81.

Geographical range: Endemic species of the S. Carpathians. **Chorotype**: EEU-CARP. **Range characteristics:** Carp. **Distribution in Europe**: **Romania** – C.S. Carpathians from Retezat Mts. until Brasov Mts., including Sibiu Mts. (Cindrel and Codeanu Mts.), Fagaras Mts. and Bucegi Mts.

Subspecies: (ssp.) *verae* Csiki, 1905 was described on the basis of rather slightly sculptured and more shining individuals from S.E. Carpathes; apparently it does not deserve a subspecific rank. *C. deubeli* Reitter, 1896 from Transylvania is probably the hybrid of *planicollis* and *violaceus volffii* Dej. (= *wolffii*); one single specimen is known.

Ecology: Generally known as an uncommon montane species; local in the upper forest and alpine zones (usually higher than 1500 m). However, C. Ghittino and A. Casale (*pers. comm.*) report that it is rather abundant under flat rocks and fissures in the alpine environment. The majority of the records come from the *Pinus mugo* zone, especially localities with a lot of larger stones.

Transect: Chapter 8: T-62.

Biology: As a montane species, not endangered, but rare and scattered over most of its range.

Conservation: No data.

(**23.008.** See under 23.010 *C. violaceus*)

23.009. C. (Megodontus) septemcarinatus
Motschulsky, 1814.

Note: This species is not included in the *Key to the adults*, as its occurrencies in Europe can be due to introduction.

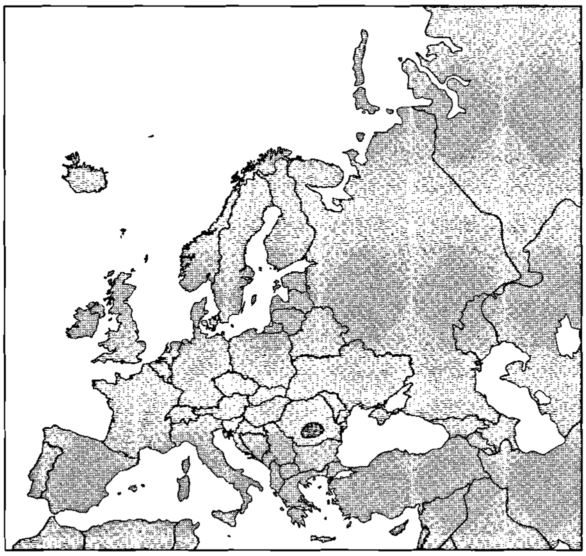
General literature: **Checklists and catalogues** – Breuning (1935): 1218. Březina (1994): 71; (1999): 75. Deuve (1994): 253 [680]. Kleinfeld & Schütze (1999): 38. Kryzhanovskij *et al.* (1995): 49 [144]. Lorenz (1998): 101. Turin *et al.* (1993): 30. **Iconography** – Ghiretti (1996): 332. Imura & Mizusawa (1996): Pl. 70 [571]. Jakobson (1905): Pl. 4.

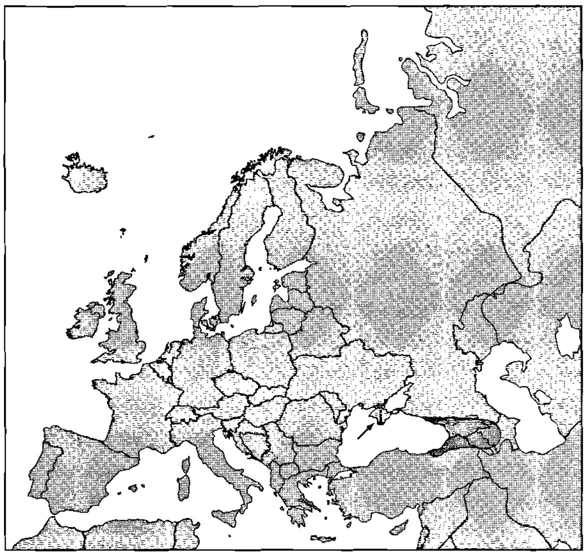
Geographical range: Endemic species of the W. Caucasus and N.E. Turkey. **Chorotype:** CAUC. **Range characteristics:** Cauc-Anat(NE). **Distribution in Europe (and adjacent areas)**: **Russian Plain & Caucasus** – Distributed across the W. and C. Caucasus, recently also recorded from Crimea (Belousov, *in litt.*), however its occurrence there is probably due to introduction.

Ecology: In N.E. Turkey (Anatolia), from Trabzon to the frontier with Georgia, in lowland and montane forests, rather localised.

Biology: **Activity** – No data. **Periodicity** – No data. **Food** (Larochelle, 1990) – In the field, *Cryptolaemus montrouzieri* (Coleoptera, Coccinellidae), and large snails. In captivity, mostly earthworms; also accepted meat and fish, but not slugs. **Larva**: Unknown. Food – No data.

Conservation: In the Caucasus apparently very common and not endangered.


23 007 planicollis (Megodontus)


23 009 septemcarinatus (Megodontus)

23 009 septemcarinatus

23.010. C. (Megodontus) violaceus

(Linnaeus, 1758) (including **23.008** *C.* Fabricius, 1787).

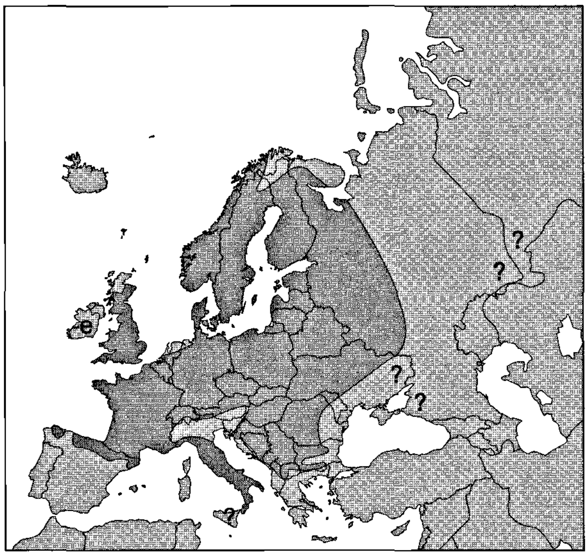
General literature: **Checklists and catalogues** – Breuning (1935): 1222. Březina (1994): 71,72; (1999): 75,76. Deuve (1994): 253 [681]. Kleinfeld & Schütze (1999): 38. Kryzhanovskij *et al.* (1995): 48 [139]. Lorenz (1998): 101. Turin *et al.* (1993): 30. **Iconography** – Darnaud *et al.* (1979b: *purpurascens*). Casale *et al.* (1982): fig. 122. Forel & Leplat (1995): Pl. 30, 34-35. (1998) fig. 105-116; Ghiretti (1996): 333-342 (*s.l.*). Imura & Mizusawa (1996): Pl. 71 [577]. Jakobson (1905): Pl. 3 and 5. Pavicevic & Mesaros (1997): cd-rom. Rautenstrauch (1994): Pl. 81-86.

Taxonomy: *C. violaceus* is the primary form of an extensive, manifold Euro-Siberian complex. For taxa that are frequently regarded to be subspecies of *C. violaceus*, see also *C. aurolimbatus* Dejean, *C. germarii* Sturm (here treated as separate species) and *C. purpurascens* Fabricius. An early revision of the *C. violaceus* subspecies in C. and W. Europe, was given by Cleu (1965, 1966 and 1969) and previous taxonomic discussions by Eidam (1941a) and Henseler (1941). Henseler (1940), Posinger (1950), Blumenthal *et al.* (1977) and Assmann & Schnauder (1998) present maps of distribution of *violaceus/purpurascens* in Germany, including chorological and taxonomical discussions. Mandl (1956-1958) and Marggi (1992) present similar maps for the 'subspecies' of *C. violaceus* in Austria, and Switzerland respectively, Casale *et al.* (1982) present maps for *C. picenus/C. germarii* in Italy. A discussion about morphological variation between *violaceus/germarii* in alpine areas has been given by Cleu (1965).

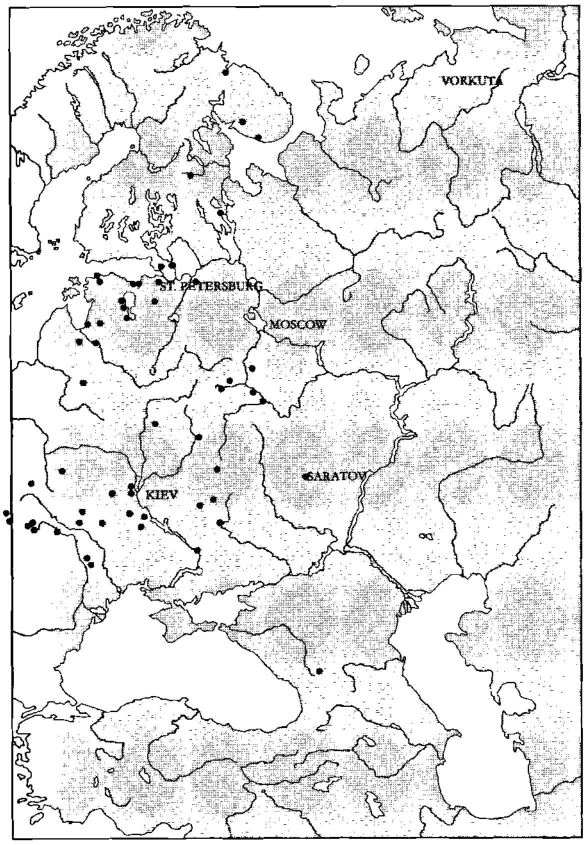
In many treatments, *C. purpurascens* has been regarded as a subspecies of *C. violaceus* (e.g. Březina, 1994, 1999; Deuve, 1994). The existence of broad hybrid zones in Switzerland (Marggi, 1992) and N.W. Germany (Assmann & Schnauder, 1998) are a strong argument for the subspecific status of *purpurascens* and *violaceus*. To include the maximum amount of information, we have taken a conservative standpoint and treat the most significant information concerning these forms in two separate units, until a thorough revision will be made. The subspecies have been numbered continuously over the units.

C. violaceus-complex:

Geographical range: European (sub)species. Widely distributed across Europe, except large parts of France (see *C. purpurascens*), Greece and Russia; not in the Netherlands, Belgium or the Iberian Peninsula. In older publications, *C. violaceus* has been treated as a huge complex of twin species, characterised as a trans-palaearctic element, reaching to Japan (see under *Taxonomy*). **Chorotype:** EUR. **Range characteristics:** CNEur. **Distribution in Europe**: **Fennoscandia** – Widely distributed and common. **Denmark** – In E. Jutland and the E. Islands; nearly absent from the W. part of the country. **British Isles** – A very common species throughout Britain, in fact the most common *Carabus* species, but absent from Ireland (see: Speight *et al.* 1982). **Germany** – Widely distributed and locally rather common. In the N. W.-wards up to the river Ems near Meppen and S.-wards to the Lüneburg Heath; not in Westphalia and the Rhineland; isolated populations in the Eifel and in the Black Forest (Assmann & Schnauder, 1998). Strictly vicari-



23 010 violaceus (incl. 23 008 purpurascens) (Megodontus)



23 010 violaceus

ant to *purpurascens*. In E. Germany generally distributed over the N. E. and S.; probably threatened in Sachsen-Anhalt and Thüringen. In the S. of E. Germany, overlap with *C. purpurascens* exists (Arndt, 1989). **Poland** – Distributed across the whole area. **Baltic** – Recorded from all countries. **Byelorussia** – All the territory. **Russian Plain** – W. and C. European Russia; the distribution is not well-defined due to mixing of data with those of *C. aurolimbatus*. It seems that the transitional zone between both species goes approximately along 40°E. The locality of Arkhangelsk (ZM) mentioned for *C. violaceus* concerns *C. aurolimbatus*. The E.-most are several localities in Moscow province (Orlov, 1983) and Ryazan province (MPGU). However, Gryuntal (*in lit.*), reports that it seems to be extinct from the Moscow region, where it was searched for a long time without results. From the N. coasts of Kola Peninsula (Kola nr. Murmansk – Poppius, 1905; Karelia (MPGU)) to the S. border of the forest-steppe zone (Kishinev (MPGU) – Kharkov (ZM) – Borisoglebsk district (MPGU)). The record of Petrusenko *et al.* (1971) from Crimea needs to be confirmed (Eidelberg *et al.,* 1988). From the forest-tundra to the forest-steppe, commoner in the subzones of S. taiga and mixed forests. **Moldova** – Only in the Kodry Hills. **Czechia & Slovakia** – All of the territory, rather common. **Hungary** – In the Great Hungarian Plain and in the N. Mts. excluding Transdanubia. Szél (*pers. comm.*) found, from examining male genitalia, that *C. violaceus* and *C. germarii* are vicariant species in Hungary. *C. germarii* lives (only) in Transdanubia, while *C. violaceus* occurs everywhere except for Transdanubia. **Romania** – Most of the territory, not rare. **Bulgaria** – Widespread and often common, in the S. to the S. Rhodopi Mts. **Balkan Peninsula** – Widely distributed in most of former Yugoslavia with a number of scattered occurrences: Slovenia, W., N. and C. Croatia, C. and S. Bosnia, N.W. and N. Herzegowina, N, N.E. and S.E Montenegro, Serbia and Macedonia; in Greece only in the N. (from Olympus, to W. Thrakia). **Austria** – Distributed in the W. and the N. (Vorarlberg, Tirol, Salzburg, Oberösterreich, Niederösterreich). **Switzerland** – Mostly distributed on the N.W. side of the Alps, abundant in hills and mountains; in the lowlands nearly replaced by *C. purpurascens*. Also recorded from parts of Tessin and Graubünden. **Italy** – Mainland, from Ligurian Alps to the S. of the peninsula; absent from the islands. **France** – Present in two small areas, one in the C. Jura, along the Swiss border near Pontarlier and the other isolated in the Alpes Maritimes in the S.E. (Vésubie, Authion, cime de Thueis, Mt. Ventabren); the latter concerns subspecies *picenus* Villa, which is often treated as a good species (see below).

Subspecies: A large number of subspecies have been described. The Fennoscandian and Balkan forms have been revised by Mandl (1962; 1985a,b), however, many named forms are of doubtful status. Although the subspecific division of this species is not yet elaborated sufficiently, it can be stated that some races differ distinctly from each other. The taxonomy of the Balkan forms is particularly complicated. At the moment it is not possible to separate *picenus* Villa at the specific level from *violaceus* L. In concordance with the *Key to the adults*, comments relating to the subspecies are in two sections: **SUB-COMPLEX I**: (*C. violaceus* **partim**: Relating to the subspecies of *picenus* Villa – Italy and the S. part of Balkan peninsula. **a) subsp. picenus** A. & G.B. Villa, 1838 – France, Maritime Alps, Italy from Ligurian Alps to the S. of the peninsula, absent in the plain of Po and to the N.; not in Sicily. From lowlands to mountain forests, also in the alpine zone. Small (20-25 mm), montane individuals from Abruzzi have been described as subsp. *bruschii* Tarrier, 1974. Casale *et al.* (1982) did not accept this form as a distinct subspecies. **b) subsp. bartoni** Mařan, 1930 – Mts. of S.W. Bulgaria: Sandanski, Begovica, the spurs of Pirin Mts., Mt. Slavianka (= Alibotush), near the frontier of Greece. Mostly between 1000 and 1600 m. Small individuals (22 mm) from the alpine zone of Pirin have been described as *pirinensis* Mandl, 1985; we consider it a variety of *bartoni*. *Note*: Probably m) subsp. *dryas* Gistel, 1857, described from N.E. Greece (Thessaloniki), is junior synonym of both b) *bartoni* and c) *marani*, having a nomenclatorial priority (Březina, 1999). **c) subsp. marani** Šterba, 1945 – Alpine race from S.W. Macedonia between Bitola and Ohrid lake (Jablanica, Golesnica, Peristeri, Popova Sapka, 1800-2500 m). According to Březina (1999), the preceding two taxa (*bartoni* and *marani*) have to be attributed to m) *dryas*, which has the priority. **d) subsp. rilvensis** Kolbe, 1887 – It was described from a single male, labelled 'Rumelia' but named after the Rila Mts., W. Bulgaria. – Another form of the *violaceus*-complex occurs in Rila Mts., i.e. the following n) *skombrosensis* Eidam, 1925. It is quite different from *rilvensis*. The specimens similar to the *rilvensis* holotype were collected later in S.W. Bulgaria (Kostenec, Camkurja, Kozhukh-Planina); they are 24-26 mm long, elongate, black with greenish tint and bright-green margins. Mandl (1985a) supposed that the type specimen of *rilvensis* either was labelled erroneously or, if it indeed really came from the Rila Mts., it was a hybrid form between *violaceus* subsp. *skombrosensis* and *picenus* subsp. *bartoni*. **SUB-COMPLEX II**: (*C. violaceus*, **partim**). – N., C. and S.E. Europe. **e) subsp. violaceus** – The nominate subspecies inhabits S.-most Sweden, Denmark, most of the N. European lowlands from river Ems to W. Poland, in the S. to N. Bavaria and Czechia. **f) subsp. candisatus** Duftschmid, 1812 – E. Austria and S.W. Czechia. Differences between *violaceus* (*s.str.*) and *candisatus* need thorough investigation. **g) subsp. salisburgensis** Kraatz, 1879 (= *meyeri* Born, 1898) – S. Germany, N. Switzerland, W. Austria, scattered occurrences in Jura Mts. and N. foothills of Alps. Very small (20-23 mm) individuals from alpine zone of Austria (Vorarlberg) and Switzerland (Simmentaler Alps) with almost smooth elytron sculpture, have been described as *muellerianus* Born, 1902. **h) subsp. sollicitans** Hartert, 1907 – British Isles; rather common. The population from the S. coast of England have more roughly granulate elytra with more distinct intervals. Raasay Island (Scotland) has a markedly isolated population, described as *browni* Deuve, 1999. **i) subsp. ottonis** Csiki, 1909 – most part of Fennoscandia (except the N.-most parts and high mountains). Slender specimens from S. Finland have been described as *lindbergi* Burkhard, 1921; individuals from Karelian isthmus as *carelicus* Hellen, 1934. Finally, a form very similar to *carelicus* was collected from the moors of Lüneburger Heide (N.W. Germany) and has been described as *blumenthali* Blumenthal, 1961. This population belongs probably to *violaceus* (*s.str.*). **j) subsp. lindrothi** Silfverberg, 1977 (= *arcticus* Sparre-Schneider, 1888; see also Silfverberg, 1977). Mountains and extreme N. of Norway, Sweden and Finnish Lapland and the Murmansk province of Russia. This subspecies probably derived from the populations that survived the last glacial period in the refugia of the Norwegian coast. **k) subsp. volffii** Dejean, 1826 (= *wolffii* auct.) – N.W., C., S.W. Romania (Banat), E. Hungary, S.E. Slovakia. **l) subsp. azurescens** Dejean, 1828 – Balkan peninsula: Croatia, Bosnia, Herzegovina, W. and N.E. Serbia, Montenegro, N. Albania. Individuals from the high mountains of Montenegro have been described as *zabljakensis* Eidam, 1927 and *durmitorus* Mandl, 1985. **m) subsp. dryas** Gistel, 1857 (=*merditanus* Apfelbeck, 1918) – small alpine form – N.C. Albania, Macedonia, N.E. Greece (Thessaloniki region). The subsp. *letellieri* Blumenthal, 1976, from Pangaeon Mt. is a synonym of *dryas*. **n) subsp. skombrosensis** Eidam, 1927 (= *balcanicus* Vacher de Lapouge, 1902, nec Born, 1899) – Bulgaria: Stara Planina, vicinities of Sofia, Rila. According to Březina (1999), this taxon is probably a synonym of d) subsp. *rilvensis* Kolbe, 1887. **o) subsp. andrzejuscii** Fischer von Waldheim, 1823 – C.E. Poland, C.W. Russia, N.E. Slovakia, N. Romania, Ukraine, Baltic states. This subspecies may be considered an aggregate of populations intermediate between *violaceus* subsp. *volffii* Dejean and *aurolimbatus* Dejean.

Note: Probably there are more forms that merit a distinct status, for instance the *violaceus* forms living in the Carpathian Basin show a high diversity which is not reflected above. *C. v. pseudoviolaceus* Kraatz, 1886 (Hungary: Northern Mts.; Slovakia: N. Carpathians); *C. v. carbonarius* Schaufuss, 1882 (Ukraine: NE. Carpathians); *C. v. mehelyi* Ganglbauer, 1896 (Transylvania, excl. Banat).

Ecology: Eurytopic, mesophilic, eurytherm with a dark preference; often on rather acid soil (Barndt *et al.*, 1991; Stiprajs, 1961; Thiele, 1977). According to Hoffmann (1907), in C. Europe occurs at all altitudes. In C. Europe, it lives mainly in moderately humid, coniferous, mixed or deciduous, mainly light forests, forest edges and clearings from lowlands to the subalpine zone (Arndt, 1989; Hůrka, 1996). In N.W. Germany, the species is able to reproduce in damp and acid woodlands (e.g. birch brooks with *Sphagnum*), wet meadows (with *Juncus* and *Sphagnum*) and dry and wet heathlands (with *Calluna vulgaris* and/or *Erica tetralix*) (Assmann & Schnauder, 1998). At least in N. Fennoscandia, it is able to live on permafrost (Lindroth, 1945). In S. Europe at high altitudes in the open landscapes of the alpine zone (Italy: up to 2000 m – Magistretti, 1965, but common also in lowlands and hills (ex. near Rome)); Bulgaria: from lowlands to 2300 m (Guéorguiev & Guéorguiev 1995). In former Yugoslavia silvicol, occurring in deciduous forests in hills and mountains (Pavicevic, 1997); however, some inland forms are praticol and go up to (sub)alpine and eualpine habitats. In Switzerland especially in upland and montane forests, very abundant between 700 and 1200 m (Marggi, 1992; compare with *C. purpurascens*, which lives in the same area, in the lowlands). In Italy (Liguria) parapatric, but not sympatric with *C. germarii* (Casale *et al.*, 1982). In W. Europe, and especially in Britain it inhabits more open habitats, especially gardens and parks, resembling the habitat preference of *C. nemoralis* on the continent (Hyman, 1992; Lindroth, 1974). In Hungary rather eurytopic, inhabiting various kinds of forest as well as dry and wet meadows. In Moscow province in forests, but rare (Fedorenko, 1988). In Ukraine in mixed forests of the forest-steppe zone and in 'bairak' oak woods in ravines of the N. steppe subzone (Petrusenko, 1971). Investigations in plots with other *Carabus* species present (especially with or without *C. glabratus* and *C. hortensis*) in N. Germany, learned that this 'competition' does not influence body length or body mass, but that there are slight shifts in seasonal activity, possibly caused by food competition (Günther & Assmann, 2000).

Transects: Chapter 1: I-1, 3; Chapter 8: T-01-05, 07-13, 17-18, 20-21, 23-36, 38, 48, 53, 55, 58, 62-63, 65, 67, 70, 74-77, 80-81, 83-85, 89-95 and 98.

Biology: **Activity** – Nocturnal, day activity less than 15% (Thiele, 1977). **Periodicity** – In Austria, the periodicity is highly synchronised with that of its most important prey, the slug *Arion lusitanicus* (Paill, 2000). The species becomes active from the beginning of July onwards (in the S. from April onwards – Sturani, 1962) and depending on altitude, reproduction takes place in summer and autumn (Hůrka, 1973). The eggs (size 5 x 1.5 mm) are laid in separate cells in the soil, from the second half of July until the beginning of September (Forel & Leplat, 1995); according to Vacher de Lapouge (1906), in France oviposition is occasionally delayed until March. L1 occurs in July-August, L2: August-October, and L3 have been observed from August-May, with an optimum during September-October (Arndt, 1989; Luff, 1969). Pupation takes place during spring (March-May: Larsson, 1939; Stiprajs, 1961) and fresh animals appear from May onwards (in Scandinavia in the summer – Lindroth, 1985); most of them reproduce in the same year, others hibernate first. Some adults hibernate and reproduce for a second time. Duration of development: eggs: 4-14 days; larval development, including a 5-45 days prepupal stage, in total 30-80 days with aproximately the following division: L1: 5-8 days, L2 1-2: weeks, and usually L3 hibernates; pupation in spring lasts about 2 weeks (Stiprajs, 1961; Sturani, 1962); all together (except duration of the larval diapause) 50-70 days. A certain proportion of the adult population hibernates (in trunks or in grassy tussocks) and reproduces for a second time (Arndt, 1989). According to Kozyrev (1989) and Sharova & Dushenkov (1979), in Russia, the species has a one-year life cycle, with multi-seasonal activity of the adults and autumn/spring activity of the larvae. **Food**: In the field, adults and larvae of various insects, young spiders, earthworms, live and dead snails and slugs, carrion, caterpillars, mushrooms, fruits, such as half-rotten apples; occasionally a pest in ripe strawberries. In captivity the same as in the field, and also gingerbread and bread soaked in sugared milk. In the field successfully baited with sugar or beer and fruits (Larochelle, 1990). In Austria, it is an effective slug predator that is able to reduce crop damage e.g. by the abundant slug species *Arion lusitanicus*. The amount of slugs in the diet of *C. violaceus* varied from 30% to 100% during July, whereas slugs comprised up to 80% of the larval diet (Paill, 2000). **Larva**: Described by Schiödte (1867: L3), Bengtsson (1927: L1-L3), Hůrka (1971b) and key: Arndt (1985, 1991b). Food – earthworms and snails in the laboratory (Arndt, *pers. observ.*). Slugs, see above. *Note*: Some information on the biology of this species comes from sources where no proper distinction between the closely related (sub)species, e.g. *C. purpurascens* and *C. germarii,* has been made.

Conservation: Sensitive to pollution (Chumakov, 1988). In most parts of Europe there are no serious problems. However, as for a number of other species, for former Yugoslavia, several forms have been indicated to be endangered (Pavicevic & Mesaros (1997). This has not been supported by data or other kinds of evidence; the species is generally extremely abundant everywhere!

C. purpurascens-complex

(**Taxonomy**: see above)

Geographical range: W.-European species; N. Spain, France, Belgium, Netherlands, W. Germany, N. Switzerland, W. Austria. Combined (*C. purpurascens*/*C. violaceus*) maps of distribution have been published by Blumenthal *et al.* (1977) and Assmann & Schnauder (1998). **Chorotype:**. WEU-CEU. **Range characteristics:** WEur-CEur. **Distribution in Europe**: **Netherlands** – Widespread and common in the S.-most and C. forested areas of the country. It also occurs in a few small localities along the coast (introduced) and in the E. along the German border. **Belgium** – Widespread and locally abundant, especially in the C. and E. **Germany** – This species replaces *C. violaceus* in the W. part (S.W. and S. parts of Lower Saxony (see also *C. violaceus*), Westphalia, Rhineland, Hessen and Rheinhessen), mainly W. of the river Weser. It penetrates into E. Germany from the S.W. (Südharz, Kyfhäuser) into Sachsen-Anhalt and Thüringen (where placed on the Red List) to Beelitz (S.W. of Potsdam) (Arndt, 1989). Also in Bayern and Baden-Würtemberg. **Czechia & Slovakia** – Probably missing; occurrence in the S.-most part of Bohemia not confirmed. In the collection of the Hungarian Natural History Museum (Budapest) is found one single *C. purpurascens* specimen labelled 'Zsolna, Ehmann, 1902.V.' (Zsolna is today Zilina – Slovakia). The origin of this specimen is uncertain, because Ehmann has reputedly never collected in Zilina, he got the specimen in question probably by change (Szél, *pers. comm.*). **Austria** – Restricted to Oberösterreich and W. Niederösterreich. **Switzerland** – Distributed throughout the N.W. lowlands, where it replaces the montane *C. violaceus.* Zones of sympatry exist. **France** – Generally found throughout the country. **Iberian Peninsula** – Distributed in the N. of Spain: Pyrenees, and from the Galician Mts. via the Cantabrian Mts., Sierra de la Demanda to Cataluña (river Noguerra Ribagorzana); S. to Montsant.

Subspecies: **p) subsp. aurichalceus** Kraatz, 1879 – N. Spain: mountains of Asturia (prov. Bilbao, Santander), at low or middle altitudes (Zaballos & Jeanne, 1994). – Small (18-24 mm) alpine specimens from Picos de Europa Mts. in Asturia have been described as 'morpha' *europae* Breuning, 1935. **q) subsp. asturiensis** Born, 1925 – Asturia: Prov. Oviedo – Los Cabos. From this region another forms has been described (*lugensis* Breuning, 1972). **r) subsp. muelleri** Haury, 1878 – N.E. Spain, Cataluña at low altitude (prov. Barcelona, Lerida, Gerona). Population from S. France, related to *muelleri*, with the pronotum distinctly narrowed towards the basis, are known as (ssp.) *baeterrensis* Vacher de Lapouge, 1901. Race *provincialis* Born, 1903 is closely related to *baeterrensis*, it is of the same length but more broad, coloured as *muelleri*, elytron intervals are slightly granulate. – S.E. France: Dep. Gard, Vaucluse, Basse Alpes, Isère, in the middle forest zone. **s) subsp. pseudofulgens** Born, 1905 – N. and S. foothills of Pyrenees in Spain (to prov. Santander, Burgos, Zaragoza) and France (to Dep. Gironde and Aude). **t) subsp. fulgens** Charpentier, 1825 – W. and C. Pyrenees of France and Spain, in upper forest and alpine zones. **u) subsp. purpurascens** Fabricius, 1778 (incl. *pseudopurpurascens* Breuning, 1935) – N and C. France, Belgium, Netherlands, W. Germany, N.W. Austria, N.W. Switzerland, mostly in lowlands. The population from E. France, Germany and Austria have more strongly punctured elytral striae, the sides of intervals are serrate. Some authors (Jeannel, 1941) mention this form as subsp. *crenatus* Sturm, 1815. **v) subsp. mixtus** Géhin, 1876 – The most distinct subspecies, endemic in the S.E. France: dep. Isère, Drôme, locally in upper forest and subalpine zones. This subspecies is treated as a proper species in some works (e.g. Forel & Leplat, 1995).

Ecology: In France, where it is widespread, predominantly a species of light, open forests, exceptionally at higher altitudes in alpine prairies, also in N. Spain (Forel & Leplat, 1995; 1998). In the lowlands also at forest edges, in gardens, cultivated land and even water meadows and marshy places besides fresh water (Koch, 1989). In W. Germany, it has been reported to show a preference for cultivated land with cereals, more than for hedgerows (Thiele, 1964b). In the Netherlands, where it approaches its N.W. fringe of distribution, it occurs mainly in thin, often coniferous, forests. In the S. it can be found on N. or N.W.-facing grassland slopes (Turin, 1983). In general, most abundant at low and middle altitudes, occasionally up to 2000 m in Pyrenees and Cantabrian Mts. (Zaballos & Jeanne, 1994). In comparison to *C. v. violaceus*, it is more thermophilic, preferring dryer habitats (Assmann & Schnauder, 1998).

Transects: See *violaceus*-complex.

Biology: **Activity** – Nocturnal. **Periodicity** (Hůrka, 1973) – In the lowlands active from May and at higher altitude from June onwards. Copulations have been observed in both spring and autumn. Oviposition of old, hibernated females can take place from June onwards, and of teneral animals in the course of summer and early autumn (egg size 5 x 1.5 mm). Similar to the biology of *C. violaceus*, the larvae develop from August onwards, and L3-larvae hibernate together with a proportion of the adult population. Despite the statement of Forel & Leplat (1995), hibernating adults can easily be found in bushes and forests in France, both in the soil and in rotten wood or under bark (Casale, *pers. observ.*). **Food** (Larochelle, 1990) – In the field, snails, larvae of different insects, earthworms and molluscs; the diet is in general similar to that of *C. violaceus*. In the field baited with earthworms, carrion, crushed snails and slugs, beer and gingerbread. In the laboratory, it accepted meat, fruits (apples, peaches and apricots). **Larva**: Described by Hůrka (1971b). Food – earthworms and snails in the laboratory (Arndt, *pers. observ.*). *Note*: Most information was taken from sources in which the taxon was not specifically distinguished from *C. violaceus*.

Conservation: Blumenthal (1981) regards it as a non suitable indicator of particular forest types. The species is rather abundant in a vast forested area in the Netherlands (Veluwe area), but nearly absent from adjacent forested areas, e.g. the forests of the Utrecht upland, separated by approximately 4 km of open peaty grassland. One can draw the conclusion that the species may be highly sensitive to fragmentation of forests and isolation.

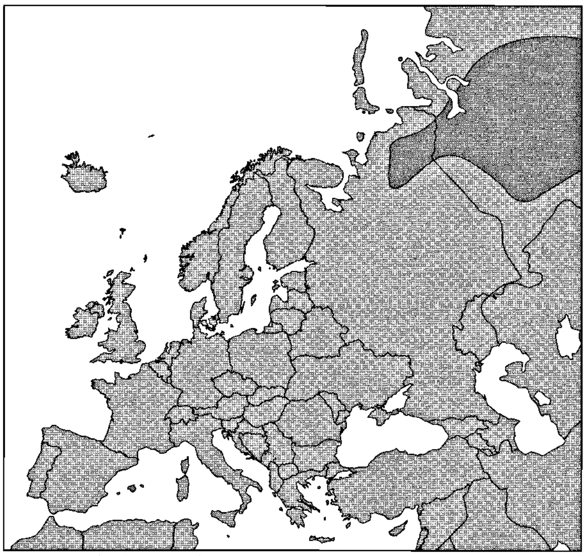
24. PACHYCRANION SOLIER, 1848
(= *CARABULUS* LUTSHNIK, 1924)

24.001. C. (Pachycranion) ermaki
Lutshnik, 1924 (= *amoenus* Chaudoir, 1852).

General literature: **Checklists and catalogues** – Breuning (1935): 1220. Březina (1994): 71; (1999): 74. Deuve (1994): 251 [673]. Kleinfeld & Schütze (1999): 39. Kryzhanovskij *et al.* (1995): 49 [152]. Lorenz (1998): 102 (*kantaikensis* Géhin, 1885). Turin *et al.* (1993): 30. **Iconography** – Ghiretti (1996): 331. Imura & Mizusawa (1996): Pl. 71 [580].

Taxonomy: Listed under *Megodontus* Solier, in Březina (1994, 1999), Deuve (1994), and Lorenz (1998).

Geographical range: N.E. of European Russia and N. Siberia, from the Malyi Yamal Peninsula to the mouth of the Lena river, Baikal environments and Western Sayan Mts.; the old records indicating 'Altai' in fact refer to the Sayan Mts. (Obydov, 2000). **Chorotype: SIB. Range characteristics:** EEur(NE)-WSib. **Distribution in Europe**: **Russian Plain** – Known from a few localities in N.E. European Russia, W. to 50°E, S. to 50°N: Lower Pechora river


24 001 ermaki (Pachycranion)

24 001 ermaki

(Poppius, 1910); Kuya river at the mouth of Pechora – ZIN; Usa, 6 km below Koliva – ZIN; Salekhard, Labytanangi – ZIN.

Subspecies: laetensis Obydov, 2000, has recently been described from Republic of Komi (Usa, Lek-Rogovaia).

Ecology: In forest-tundra and S. tundra subzones; also in alpine zone of Saian Mts.

Biology: No data.

Conservation: No data.

24.002. C. (Pachycranion) schoenherri
Fischer von Waldheim, 1822.

General literature: Checklists and catalogues – Breuning (1935): 1203. Březina (1994): 71; (1999): 75. Deuve (1994): 252 [675]. Kleinfeld & Schütze (1999): 39. Kryzhanovskij *et al.* (1995): 49 [148]. Lorenz (1998): 102. Turin *et al.* (1993): 30. **Iconography** – Ghiretti (1996): 331. Imura & Mizusawa (1996): Pl. 70 [569]. Jakobson (1905): Pl. 4.

Taxonomy: Listed under *Megodontus* Solier in Březina (1994), Deuve (1994) and Lorenz (1998).

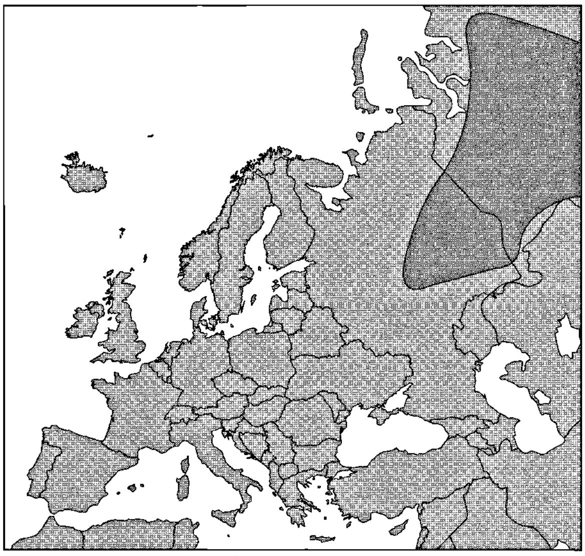
Geographical range: E. part of European Russia from Nizhnii Novgorod and Kostroma provinces to Urals; W. and C. Siberia to Irkutsk. **Chorotype: SIB. Range characteristics:** EEur(C)-CSib. **Distribution in Europe (and adjacent areas): Russian Plain** – E. regions of European Russia and the Urals. W. to 43-44°E (Manturovo district in Kostroma province (Eremin, *in litt.*) and the Mordov reserve (Feoktirstov, 1979)). To the E. it becomes more common and is known from several localities in the republics of Mari (Ioshkar-Ola district – MPGU), Tatar (Raifa – Zherebtsov, 1979) and Bashkiria (Yamantau Mt. – Kashevarov, 1986; Ai-River nr. Mesyagutovo – Zinovjev, 1991; Bashkir reserve and Shulgan-Tash – Koz'minykh, *in litt.*, Irgizla – ZIN), as well as the provinces of Nizhnii Novgorod (Anufriev *et al.,* 1989), Vyatka (Bebera, Medvedskii Bor, Sovetsk – Shernin, 1974), Perm' (Verkhnyaya Kvazhva – Shilenkov & Voronov, 1973; Predduralye, Perm', Nizhnyaya Kura – Koz'minykh *et al.,* 1991b), and Chelyabinsk (Il'men reserve – Lagunov *in litt.*, Troitsk reserve – Esjunin & Koz'minykh, *in litt.*). The N.-most record is known from the basin of Sinya river in the N. Ural (ZIN), the S.-most locality seems to be Irgizla in Bashkiria (ZIN). From the middle taiga to the S. border of the forest zone.

Subspecies: Except nominate, no subspecies in Europe.

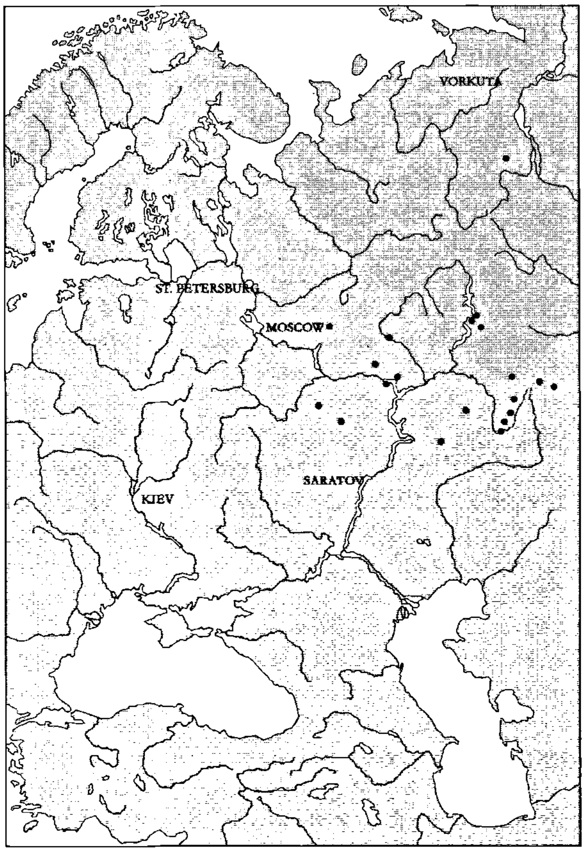
Ecology: In coniferous and mixed forests. In Krasnoturansky Bor (C. Siberia), it lives in *Betula* scrub on the N. slopes of bare mountains and hills (Anyushin, 1982). According to Tselischeva (2000), in Kirov province it is scarse in spruce and small-leaved forests, but rather common in Pine forests, where it may even reach the subdominant or predominant level. Feoktistov (1979) characterises it as a meadow species for the Mordov reserve (C.E. Russia). In the Baical region in montane forests up to 700 m, but rare (Berlov & Berlov, 1984).

Transects: Chapter 1: I-2; Chapter 8: T-44, 47-48 and 50.

Biology: **Activity** – No data. **Periodicity** – Reproduction in May-June, with oviposition during June-July (egg size 8.0 x 3.4 mm). The average number of eggs per female was 5-6, with a maximum of 10-13 eggs in the ovary (Tselischeva, 2000). Juveniles were mainly active during October.



24 002 schoenherri (Pachycranion)



24 002 schoenherri

Hibernation as third instar and as (older?) imago (Berlov & Berlov, 1984), as well as larvae. **Food** (Larochelle, 1990) – Preys mainly on molluscs (Kryzhanovskij, 1953). **Larva**: Described by Sharova (1958: L3); and by Berlov & Berlov (1984: L1-L3). Food – No data.

Conservation: No data from Europe, but in the Asian part of the Siberian taiga, apparently very abundant.

25. INIOPACHYS SOLIER, 1848

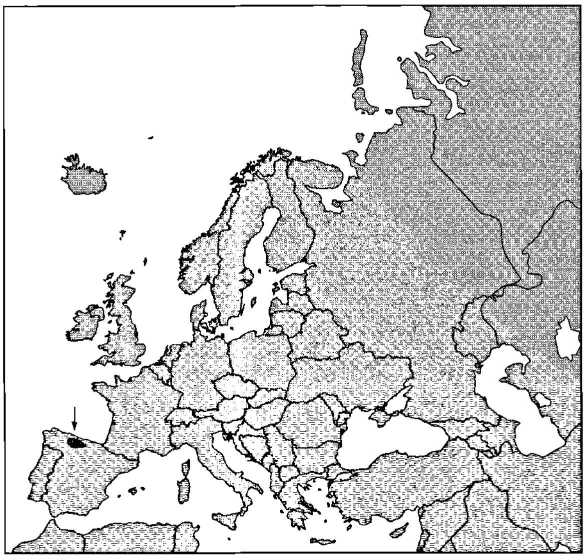
25.001. C. (Iniopachys) auriculatus

Putzeys, 1872.

General literature: **Checklists and catalogues** – Breuning (1934): 964. Březina (1994): 61; (1999): 76. Deuve (1994): 220 [574]. Kleinfeld & Schütze (1999): 28. Lorenz (1998): 91. Turin *et al.* (1993): 31. **Iconography** – Forel & Leplat (1998): fig. 101-104. Ghiretti (1996): 275. Imura & Mizusawa (1996): Pl. 45 [387]. Rautenstrauch (1994): Pl. 68.

Geographical range: Endemic species from the Iberian peninsula. **Chorotype: WEU-IBEN. Range characteristics:** Iber(N). **Distribution in Europe**: **Iberian Peninsula** – N. Spain, Cantabrian Mts.

Subspecies: a) subsp. auriculatus – C. Cantabrian chain: Picos d'Europa (Cornion, Urrieles, Andara). **b) subsp. ubinensis** Puissegur, 1955 – W. Cantabrian chain: Peña Ubiña Massif. Also in Peña de Oriniz ((ssp.) *ornizensis* Meyer, 1998).



25 001 auriculatus (Iniopachys)

Ecology: Subalpine and alpine zones; prairies from 1600 to 2500 m. The main habitat is snow field margins, especially on rocky and stony soil, where the beetles are able to move down to deeper layers if the upper stones get too hot in sunshine; very thermophobic and thus found most frequent near the surface during the early morning (Casale, Assmann, *pers. observ.*).

Transect: Chapter 8: T-98.

Biology: **Activity** – During the summer exclusively nocturnal, but in spring also day active (on sunlit rocks, whilst still surrounded by snow and ice (Hrusa, *pers. comm.*). **Periodicity** – Adults are found from May to September/October. Teneral adults are found from July to September (Assmann, *pers. observ.*; Du Chatenet, 1986). **Food** – Specialist in crushing shells of snails by means of the short but powerful mandibles (similar to *Licinus* species, cf. Brandmayr & Zetto Brandmayr, 1986). Most snails eaten belong to the genus *Pyrenaearia*. Other helicid species are rarely crushed (e.g. *Helicella* species). Snails with very thick and hard shells (e.g. cyclophorids of the genus *Chlochlostoma*) are not attacked. **Larva**: unknown.

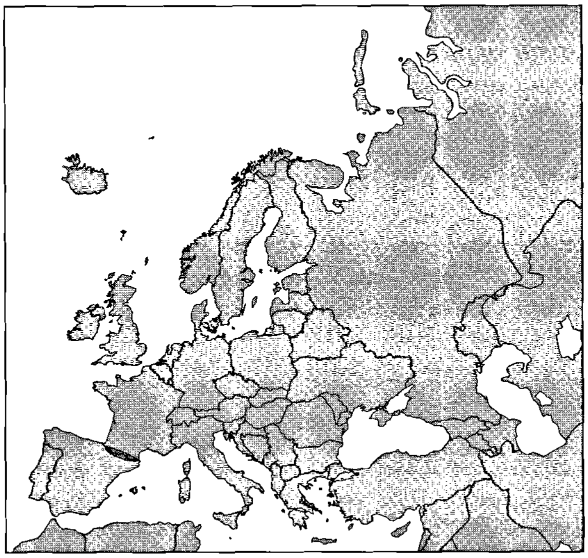
Conservation: Protected in the Picos de Europa National Park.

25.002. C. (Iniopachys) pyrenaeus

Audinet-Serville, 1821.

General literature: **Checklists and catalogues** – Breuning (1934): 960. Březina (1994): 61; (1999): 76. Deuve (1994): 219 [573]. Kleinfeld & Schütze (1999): 28. Lorenz (1998): 91. Turin *et al.* (1993): 31. **Iconography** – Forel & Leplat (1995): Pl. 28-29; (1998): fig. 99-100. Ghiretti (1996): 274. Imura & Mizusawa (1996): Pl. 45 [386]. Rautenstrauch (1994): Pl. 67-68.

Geographical range: Endemic species of the Pyrenees, both on the French and Iberian sides. **Chorotype:** WEU-



25 002 pyrenaeus (Iniopachys)

PYRE. **Range characteristics:** Iber(NW). **Distribution in Europe**: **France** – Only in the Pyrenees: from the Pyrénées Atlantiques (Pic d'Orhy) to the Pyrénées Orientales (Massif du Canigou, Lac du Laurenti). **Iberian Peninsula** – Restricted to the Pyrenees, distributed in most of the higher parts of the chain.

Subspecies: a) subsp. pyrenaeus (*s.str*) – W. Pyrenees, C. Pyrenees, present also in the E. Pyrenees (Andorra, Carlitte and Puigmal). Some forms have been maintained by Deuve (1994) as distinct subspecies: e.g. *cephalicus* Csiki, 1927, and the recently described **c) jeanneli** Deuve, 1994 – Hautes-Pyrénées, E. of Cauterets and in Haute-Garonne. **b) subsp. costulus** Géhin, 1885 – Very local in the French Aude, Canigou Massif.

Ecology: In the subalpine and alpine zones in gravelly places, generally above 1800 m. Exceptionally, in the W.-most populations it can be found above 1500 m; especially at moderately humid places with a thin and open vegetation of grasses, with shelter from the wind (Forel & Leplat, 1995; 1998). At the lowest altitudes found at the bottom of snow fields on N. slopes (Du Chatenet, 1986).

Transects: Chapter 8: T-93-94.

Biology: **Activity** – Predominantly nocturnal; probably similar behaviour as *C. auriculatus*. **Periodicity** – Active from the second half of June (sometimes the end of May) until the second half of September. Almost nothing is known about the development of the species; two larval stages were observed, both with a duration of 8 days, from which it may be concluded, that the total development of the species probably takes place in a relatively short period of time (Forel & Leplat, 1995). **Food:** arthropods and snails (Larochelle, 1990). A most oligophagous snail predator with asymmetric mandibles that have strong double teeth on the left mandible, thus forming a typical shell-cutting apparatus. The species lives syntopically with two abundant snail species: *Arianta xatarti* (Farines) (Helicidae), a species with rather thin shells, in the Canigou population, and the stronger *Pyrenaearia carascalensis* (de Férusac) (Helicidae) in most populations in the C. Pyrenees and the Atlantic Pyrenees; it was shown that the mouth-parts of the individuals in both areas were adapted to the thickness of the shells of the most abundant snail species (Assmann *et al.,* 2000; see also Fig. 6.10, 6.11 and colour photo in Chapter 6). **Larva**: Described by Raynaud (1975). Food – No data, but probably also snails.

Conservation: Not endangered; subspecies *costulus*, however, is rare and very local.

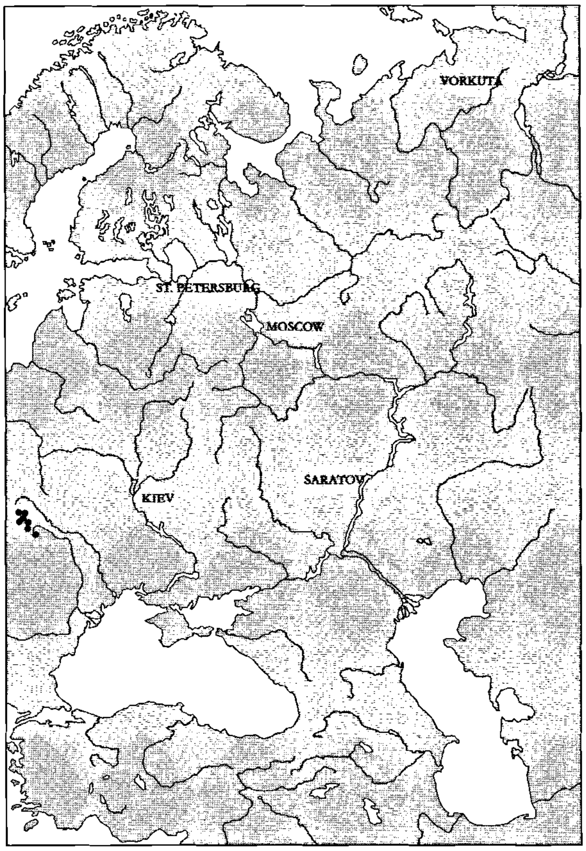
26 CHRYSOCARABUS C. G. THOMSON, 1875 (INCLUDING 27 *CHRYSOTRIBAX* REITTER, 1896).

Note: In many works, including Turin *et al.* (1993), *Chrysotribax* has been treated as a separate subgenus. Following the latest insights in the taxonomy of this species group, we regard *Chrysotribax* synonymous to *Chrysocarabus*, and therefore the respective species have been re-numbered successively as 26.006 for *C. hispanus* F. and 26.007 for *C. rutilans* Dejean (see also the *Checklist*, p. 59, and *Key to the adults*, p. 118). The taxonomically distinct species *C. olympiae* probably merits to be placed in a separate subgenus (see note on p. 270).

26.001. C. (Chrysocarabus) auronitens
Fabricius, 1792

General literature: **Checklists and catalogues** – Breuning (1936): 1462. Březina (1994): 75; (1999): 68. Deuve (1994): 263 [696]. Kleinfeld & Schütze (1999): 40. Kryzhanovskij *et al.* (1995): [49] 153. Lorenz (1998): 102. Turin *et al.* (1993): 31. **Iconography** – Casale *et al.* (1982): fig. 154. Darnaud (1977, 1978b, 1980b, 1981a): Pl. 1,3,11,12. Forel &

26 001 auronitens (Chrysocarabus)



26 001 auronitens

Leplat (1995): Pl. 42-52; (1998): fig. 148-149. Ghiretti (1996): 359-364 (*s.l.*). Imura & Mizusawa (1996): Pl. 75 [595]. Jakobson (1905): Pl. 3. Pavicevic & Mesaros (1997): cd-rom. Rautenstrauch (1994): Pl. 100-102.

Taxonomy: In most works (e.g. du Chatenet, 1986; Forel & Leplat, 1995) many forms have been regarded as valid subspecies, which makes this group one of the most complicated in all *Carabus* species. In many works, *C. punctatoauratus* (including all related forms) has been treated as a separate species (see under 'subspecies'). The results from recent works however reveal that this taxonomy, based on morphological characters, is not correct. Assmann & Weber (1997) studied allozyme polymorphism in *C. puntatoauratus* populations from across its whole range and constructed dendrograms by UPGMA cluster analysis, using four *auronitens* populations from the Montagne Noire (S. France, subsp. *festivus*) as a possible outgroup. Surprisingly, *festivus* does not behave as an outgroup. Rather, the analysed population from the Canigou (*punctatoauratus canigouensis*) branches off at a deeper position. However, they are probably too closely related to be an outgroup in terms of this tree. Allozymes are not going to vary much, the underlying genes may be more different (Clapp, *pers comm.*). In a DNA survey, Rasplus (*pers. comm.*) found a similar result, not in agreement with the division into two 'subspecies groups' (*punctatoauratus* and *auronitens*). The haploids from the E.-most and W.-most parts of the Pyrenees are more distant from a group formed by *auronitens* and C. Pyrenean *punctatoauratus* populations. Therefore, it is better to regard, at least at the moment, subspecies taxonomy in this group as provisional (cf. Assmann, 1995).

Geographical range: C. European mainland, in the W. from French Pyrenees and Atlantic coast (only in the N.W., e.g. Bretagne) to Poland, Romania and Ukraine (Carpathians) in the E., and from the Alpine chain in the S. to Germany in the N. **Chorotype:** CEU. **Range characteristics:** CEur. **Distribution in Europe**: **Netherlands** – It occurs in two relatively small and isolated areas in the C.E. part of the country; in the appropriate habitat rather abundant and possibly expanding W.-ward. **Belgium** – In the past it was distributed wider (Desender *et al., in prep.*; see *Conservation*), but nowadays distributed in the E. and the S. forested areas; mostly rare, usually restricted to altitudes above 200 m. In the Forêt de Soignes present with the notable, bicoloured form *putzeysi*, characterised by head and pronotum cupreous reddish and elytra dark violet to blackish. **Germany** – Most of Germany, but not in Schleswig-Holstein, Mecklenburg-Vorpommern and Brandenburg: in the lowlands of Lower Saxony, exclusively in the C. part of the region between the rivers Weser and Elbe (especially Lüneburger Heath, N.-wards to Hamburg and S.-wards to the montane areas). Within its range, especially in montane areas, generally rather abundant, e.g. in the mountains of E. Germany (Erzgebirge, Harz, Thüringer Wald) often the most abundant species. Also reaching the lowland forests of Westphalia, to the Dutch border, rather common (Gries *et al.,* 1993). **Poland** – Reported from most provinces except some areas in the N. and E. However reported from the area near the Baltic Sea, between Stettin and Dantzig (Mossakowski, *in litt.*). **Russian Plain** – Only found in the Ukrainian Carpathians; according to Medvedev (1950), the E. border lies in the adjacent Bessarabian-Podolian forest-steppe. **Czechia & Slovakia** – Distributed in all territory, throughout hills and mountains; the two subspecies *auronitens* and *escheri* are sporadic to common in forested hills and mountains. **Hungary** – A typical montane, however rare species in Hungary (subsp. *kraussi*), only in the W. in the Kőszeg and Sopron Mts. **Romania** – Restricted to the Carpathian upland. **Balkan Peninsula** – Only in the N.-most part of Slovenia (Kosenjak, Mozirska Planina, Pohorje Mts., Storzic) and E. Croatia (Pakrac); unconfirmed for Serbia (Banat?). **Austria** – Distributed all over the country except the lower parts in the E. where it is almost absent. **Switzerland** – Only N.W. of the line Zermatt – St. Gallen, widely distributed and, especially in the montane zone, locally common; not on the S. slope of the Alps and in the S. valleys of Tessin and Graubünden. **Italy** – Restricted to two small areas in the Alps in the N. of the country: 1) Val d'Aosta (Dora Baltea) in the N.W., and 2) in the N.E. close to the Austrian border (Trentino-Alto Adige, Carnian Alps, Val dell'Adige). **France** – Widely distributed throughout the territory except the W. *C. auronitens auronitens* (see below) is continuously distributed from the Belgium border in the N. to the Hautes-Alpes in the S.E. and to the Cevennes (Lozere and Tarn) in the S.; in the W. it is almost absent from the lowlands from Le Havre to Toulouse. The main area of distribution, however, includes in the W. the hills of the Normandie (E. Calvados, E. of Eure-et-Loire, area of the Orne), as well as the hills of Haute Vienne, near Limoges. S.-wards up to the environs of Rodez, the Montagne Noire (near Carcassone) and the Monts de Lacaune. It lives isolated in the W. of Brittany, and two very small areas (Forêts d'Écouves and de Cérisy (Normandie, Calvados)) the latter one occupied by the remarkable, black-bluish form *cupreonitens* Chevrolat (often regarded as a good subspecies); this form is rare in the Forêt d'Ecouves, where it lives together with the greenish nominate form. Isolated in the C. and E. Pyrenees, between river Neste in the W. and the Canigou massif, *C. auronitens punctatoauratus* lives (see below) in a complex of scattered and isolated populations. **Iberian Peninsula** – Limited in C. Pyrenees (only *punctatoauratus*), mainly in river valleys (e.g. Valle de Arán, de Segre).

Subspecies: See remarks under *Taxonomy*. Mossakowski (*in litt.*) believes that there is a clear distinction between the forms that have been attributed to *C. auronitens* and *C. punctatoauratus* Germar. In fact a complex, consisting of two semi-species, *auronitens* and *punctatoauratus*, which are regarded by several authors as separate species. However, although geographically isolated (see map), *punctatoauratus* (Malausa *et al.,* 1984; Puissegur, 1964), seems to be conspecific with *auronitens* from a genetic point of view (see also Březina, 1994, 1999; Deuve, 1994). All subspecies that are or were attributed to the *punctatoauratus*-group, live at altitudes between 500 and 2300 m (Forel & Leplat, 1995; Assmann, *pers. observ.*). The following subspecies have been mentioned in the key: **a) subsp. auronitens** – C. Europe (excluding E. Alps and Carpathians) to Belgium, the Netherlands, Germany, S. Poland, Czechia, N.W. Italy; **b) subsp. costellatus** Géhin, 1882 – C. and W. France: Auvergne, Bretagne. **c) subsp. kraussi** Vacher de Lapouge, 1898 (=*intercostatus* Gredel, 1854) – W. Hungary, E. Alps of Austria (except Vorarlberg) and N.E. Italy, Veneto and Venetia Tridentia. **d) subsp. festivus** Dejean, 1826 – S.W. France, Aude, Montagne Noire, Mts. de Lacaune, Tarn. **e) subsp. escheri** Palliardi, 1825 – Carpathian Mountains to W. Ukraine, Romania and isolated in E. Croatia. **f) subsp. punctatoauratus** Germar, 1824 – The most isolated taxon of the *auronitens*-complex. S.W. France, Pyrenees on both sides. Some local forms of *punctatoauratus* merit recognition as distinct subspecies (of a valid species) in the opinion of several authors (see Deuve, 1994; Forel & Leplat, 1995; Zaballos & Jeanne, 1994); the main 'subspecies' are: *montanus* Géhin, 1882 – C. and W. Pyrenees, on both French and Iberian sides; *farinesi* Dejean, 1826 – S.W. France, Ariège, Aude. *barthei* Barthe, 1912, close to *farinesi* – S.W. France: Belesta forest and vicinity and *canigouensis* Schaefer 1966, – S.W. France, Canigou massif.

Ecology: Silvicol (Mandl, 1972). Stenotopic species of forests in hills and mountains, but also in the larger lowland forest complexes in the atlantic zone (Thiele, 1977; Turin, 2000; Gries *et al.,* 1973). According to Hoffmann (1907), in C. Europe from 300 to 2500 m. It regularly inhabits forests of average moisture, preferably moist deciduous and mixed forests, especially montane Fagetalia. Generally, it seems to avoid open stands as well as pure *Pinus* and deciduous stands with *Betula* and *Quercus*, at least in the N. part of the territory and at low altitudes (Gries *et al.,* 1973; Thiele, 1977). However, in the Netherlands it was found in damp coniferous forest on sandy soil, although it seems to prefer loamy or clayish, often humus-rich soil. In W. Germany in many types of forest (Koch, 1989; Niehues *et al.,* 1996 (see below); Thiele, 1977). Apart from this 'silvicol' habitat preference, Mossakowski (*in litt.*) reports that some forms of *punctatoauratus* live exclusively in open stands, e.g. the populations of the Plateau Guillem in the W. part of the Canigou. In the upper part of the montane and in the subalpine zones, the species inhabits also open land (e.g. heathlands with *Calluna* and *Vaccinium*) (e.g. Hemmer and Terluter, 1987); this is also true for the heathlands in the Lüneburger Heath (altitude about 150 m – Assmann, *pers. observ.*), and for the Hochsauerland where many carabids can be found in anthropogenic heath, besides *C. auronitens* also *C. arvensis, C. glabratus* and *C. problematicus* (Grosseschallau, 1981; Weber *in lit.*). In the C. European mountains, it can be found up to 2400 m in the S. side of the Alps (Italy: Aosta Valley and Trentino); in N.E. exclusively montane, from 1000-1200 to 2200-2400 m; in Aosta Valley in *Pinus* forests and pastures (Fagetalia are not present in that area). Most abundant in forests of middle altitudes, and there it shows a preference for the cooler types of forest which are exposed to the N. or E. Rarely in the high alpine zone in open country. Also in Rhône-Alpes regularly above 700 m (Coulon *et al.,* 2000). In Hungary also a typical montane species and mainly found in the spruce belt (Bazzanio-Abietum prealpinum) but also in alder and beech forest. In E. Croatia also a forest dweller of lowlands and hills (Pavicevic & Mesaros, 1997). Moisture is obviously an important factor, because it avoids sites that are too dry. In spring, dispersing individuals can sometimes be found in open country at some distance from the nearest forest edge (> 50 m), even during daytime (Turin, observ. from Netherlands).

Transects: Chapter 1: I-1; Chapter 8: T-16, 20, 23, 25-35, 63, 73, 77, 79-80 and 89-94.

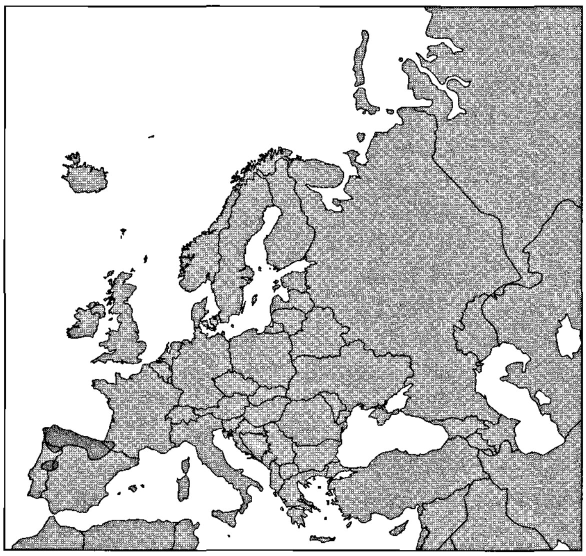
Biology: **Activity** – Mainly night active, but with an average of 30-45% day activity during the reproduction period (Thiele & Weber, 1968). **Periodicity** – Reproduction at lower altitudes in spring; development occurs without obligate diapause and both adults and larvae can be found in all seasons (Arndt, 1989; Hûrka, 1973; Stiprajs, 1964). In the Westphalian Lowlands (W. Germany), the species is strickly univoltine, with egg production, roughly, between the 2nd week of April and the 3rd week of May, pre-imaginal stages during summer and early autumn and young beetles hatching from the beginning of August until October (Weber & Heimbach, 2001). Schwöppe *et al.* (1998) carried out an allocation experiment by transferring specimens from the Westphalian highlands into enclosures in the lowlands and also here, strickt univoltism was observed. In the upper parts of the montane (and subalpine) zones, the reproduction period is in summer (mainly June-August), when the tenerals and larvae also occur (Hemmer & Terlutter, 1987), indicating a 2-year cycle of development for *C. auronitens* at higher altitudes. The adults hibernate in small to large groups under bark and in tree trunks, in the ground or in mosses. Attraction of the sexes during the mating season in spring, especially of males by females, was shown by pitfall experiments where almost three times more males were caught in female-baited traps than in male-baited traps. No sexual attraction of teneral specimens could be observed during the autumn season (Baumgartner, 2000). Copulation takes place after hibernation in March-May in the plain and a little later at higher altitude (Hůrka, 1973; Weber, 1999); at higher altitude in S. Europe, the main activity period is in June-July with an aestivation diapause during August (Sturani, 1962). The species seems to need relative high temperatures for successful reproduction; Weber (1987, 1999) observed that in case of an extreme cold spring, reproduction almost stops and the animals hibernated a second time, consequently reproducing next spring instead, without loss of large numbers, because the first year survival is invariably high (Hockmann *et al.*, 1998). The Westphalian populations consist of several age-cohorts each year, with survival probabilities of 65% from the 1st to the 2nd spring season, 60% from the 2nd to the 3rd spring, 55% from the 3rd to the 4th spring and about 40% from the 4th to the 5th spring (Hockmann *et al.*, *l.c.*). The oldest females observed were 6.5 years old (Weber & Heimbach, 2001). In E. Europe, copulations of young adults were observed in the autumn (Czechia – Niedl, 1969) and fertilised eggs were found in the ovaria of hibernating females in early spring (Hůrka, 1973). Oviposition from March until June in the N. of its distribution and from May until August in the S. (Italy – Casale *et al.*, 1982). Females lay approximately 30-50 eggs (size 5 x 1.5 mm). Larvae generally occur from May until October, L1: May-July, L2: June-August and L3: mainly from July until October. Pupae can be found from July onwards, but a proportion of the L3-larvae hibernate and pupate in the spring (Stiprajs, 1964); teneral animals from these larvae can be found in June-July. Others emerge in autumn during the period August-October and must forage actively before hibernation, while surviving old adults are dormant from the end of spring until the reproductive season in next spring (Weber, 1999). Individually marked, captured and regularly recaptured animals of a local enclosed population in Westphalia, showed over the years a remarkable constancy of activity-related and weight-related characters, which suggests that these characters such as phenotypic behaviour as well as egg-production/offspring and longevity might probably be determined genetically to a high degree (Baumgartner *et al.*, 1997; Baumgartner, 2002 (*in prep.*)). Hardening of the exoskeleton takes 40-50 days. In the N. of its area of distribution, the development takes 7-8 months including hibernation as larva, and about 2-3 months in the S. (without larval hibernation). Eggs: about 10-14 days, larvae all together, including 9-10 days prepupal stage, ca 65 days: L1: 10 days, L2: about 14 days, L3: 35-40 days and pupa about 14 days (Hůrka, *l.c.*; Sturani, *l.c.*). During the period of activity it is not easy to catch the animals, because they hide under stones or deep under mosses and in leaf litter. In contrast to this, they can very easily be found during hibernation from October onwards, when they hide under bark or in tree trunks, often in numbers, or in company of *Cychrus* and other *Carabus* species (Forel & Leplat, 1995; own observations). Weber (1999) investigated in detail the dynamics of populations in Westphalia (W. Germany), especially according to individual traits and survival. In general, small beetles that emerged early showed higher mortality, particularly during the first two weeks. Furthermore, the individual survival probability was higher the later a beetle was recorded for the first time during the spring season. **Food** (Larochelle, 1990) – In the field, various insects, caterpillars, myriapods and earthworms. In captivity, they accept live and crushed snails and slugs, raw meat, fish, liver, gingerbread soaked in milk or sugared water, ripe fruits (apples), banana skins and Gruyère cheese. **Larva** – Described by Heer (1936: L3), Vacher de Lapouge (1906: L1-L3), Bengtson (1927: L1), Hůrka (1971b) and key: Arndt (1985, 1991b). Food – earthworms and snails in the laboratory (Arndt, *pers. observ.*); in general, the same as the adults (Forel & Leplat, 1995). **Dispersal power** – The beetles are good tree climbers (Hockmann *et al.*, 1989), and they have been observed climbing plants and trees (Germany – Wachmann *et al.*, 1995; Italy – Casale, *pers. observ.*). According to Gries *et al.* (1973), forest type has no effect on its distribution (W. Germany, Westphalia), but in the Netherlands it was absent from several small forests patches within its distribution (E. Lam, *pers. comm.*). It is able, however, to cross at least small areas of open country (see *Ecology*).

Conservation: In the proper habitat *C. auronitens* is often a rather abundant species and it seems that it has the ability to resist severe ecological calamities through relatively high numbers and a good power of dispersal. Probably only endangered in case of serious deforestation and subsequent destruction of the landscape infrastructure. In Flanders, Belgium, results from genetic markers suggest a much wider distribution in earlier times, which was supported by archeological data (Desender *et al.*, *in prep.*). The species showed an extreme genetic variability over the isolated (relict?) populations. Blumenthal (1981) calls it a partly suitable indicator, being a real forest species and sensitive to barriers that might impede dispersal. Terlutter (1990) and Niehues *et al.* (1996) were able to re-construct the recent history of dispersal in a landscape in Westphalia (W. Germany) from the distribution of allele frequencies in a large meta population. Over a distance of more than 20 km, a gradual shift of more than 90% in the frequency was found. The authors conclude that *C. auronitens* survived the nearly complete deforestation of the area, that took place during the Middle Ages and early modern times, in a few small refugia S.W. of Münster. It is supposed that, in these refugia that are isolated from each other, the allele frequencies shifted in opposite directions, caused by 'random drift'. After regeneration of the semi-natural forests in the region, *C. auronitens* might have been able to recolonise the lost territory in a relatively short time, the populations from the different refugia combining in one metapopulation. When observing a number of populations of the Teutoburger Wald (Lower Saxony, W. Germany) over a 5-year period, largely synchronous fluctuations were observed, probably due to a unknow key (possibly climatic) factor that influenced the survival probability of adults and/or the reproduction rate (Giers-Tiedtke *et al.*, 1998). The fact that such a key factor even effects populations in rather stable habitats, such as the Melico-Fagetum of the Teutoberger Wald, is highly relevant for biomonitoring programs concerning forest species. The form *cupreonitens*, occurring in the Forêt de Cérisy, is protected by law in France. The statement of Pavicevic & Mesaros (1997) that some forms are endangered, for example the subspecies *escheri* Palliardi, is highly disputable; *escheri* is widespread and very common (Casale, *pers. observ.*).

26.002. C. (Chrysocarabus) lineatus

Dejean, 1826.

General literature: **Checklists and catalogues** – Breuning (1936): 1448. Březina (1994): 76; (1999): 71. Deuve (1994): 261 [694]. Kleinfeld & Schütze (1999): 40. Lorenz (1998): 104 (*basilicus* Chevrolat, 1837). Turin *et al.* (1993): 31. **Iconography** – Darnaud (1979a): Pl. 7. Forel & Leplat (1995): Pl. 40; (1998): fig. 117-141. Ghiretti (1996): 356-358. Imura & Mizusawa (1996): Pl. 75 [594]. Rautenstrauch (1994): Pl. 98-99.


26 002 lineatus (Chrysocarabus)

Geographical range: Endemic of W. Pyrenees and N.W. Iberia. **Chorotype**: WEU-IBEN. **Range characteristics:** Iber(N). **Distribution in Europe**: **France** (Jeannel, 1941; Bonadona, 1971) – Restricted to the S.W.-most part, close to the Spanish border, inhabiting an area in the French Pays Basque; montane W. part of the Pyréenées Atlantiques, between St. Jean-de-Luz and Larrau. **Iberian Peninsula** (Deuve, 1986; Zaballos & Jeanne, 1994) – The *C. lineatus-lateralis*-complex, as treated here (see below), is restricted to the N.W., including the W.-most part of the Pyrenees. It stretches from the Sistema C. in the S. (Serra da Estrella, Sierras de Gata, de Gredos, and de Béjar; Peña de Francia), to the N. Iberian chain (Galician and Cantabrian Mts., Mts. de León, Sierra de la Demanda) and to the W. Pyrenees. Disjunct in C.E. Portugal and C.W. Spain (Forel & Leplat, 1995).

Subspecies: Many infraspecific forms have been described: similar to *C. auronitens* (see below), two semi-species (*C. lineatus* and *C. lateralis*) belong to *lineatus* in the widest sense. They are maintained by several authors (see Zaballos & Jeanne 1994) as distinct species. **a) subsp. lineatus** – Cantabrian Mts. **b) subsp. troberti** Kraatz, 1860 – Mt. Ursui – W. Pyrenees, both on the French and Spanish sides; Navarra, from Puerto de Larrau to Vall. d'Oria and Sierra Urbassa. **c) subsp. lateralis** Chevrolat, 1840 – W. Cantabrian chain, Galician Mts., N. Portugal, Serra da Estrella. **d) subsp. leonensis** Born, 1918 – Mountains of Leon. **e) subsp. salmantinus** Bolivar, 1922 – Iberian C. chains: Sierra de Gata, Sierra de Francia and Sierra de Béjar.

Ecology: Eurytopic forest species. From lowland woodlands to the alpine zone, but especially at middle altitudes between 350 and 1800, sometimes up to 2000 m; inhabiting coniferous forest, Fagetalia, and *Castanea* forests and forest edges, rare in alpine prairies (Du Chatenet, 1986). It is rather tolerant to moisture and occurs in very dry as well as humid (but not too wet) places (Forel & Leplat, 1995); in general with a preference for N. expositions. A good example of the strong eurytopy is that it was able to settle the non-indigeneous *Eucalyptus* forests, a hostile habitat for many European surface-dwelling species (Casale, *pers. observ.*).

Transects: Chapter 8: T-95-98.

Biology: **Activity** – Nocturnal. **Periodicity** – The total period of activity is relatively short: 1-2 months (Forel & Leplat, 1995; 1998); oviposition from the end of April to the end of May (or later, depending on altitude), and the eggs (size 7 x 1.7 mm, white) hatch after 10-20 days. The larvae are extremely fast and voracious; the teneral adults appear after about 2 months, depending on individual constitution before entering aestivation diapause. They develop in a cell made by the adult, in the soil or under a thick layer of mosses at higher altitudes (Forel & Leplat, *l.c.*). Hibernation of adults mainly in trunks or under mosses, or in the soil (Du Chatenet, 1986). **Food** (Larochelle, 1990): captured in traps with bait consisting of gingerbread, raw meat, snails (*Helix* spp.), earthworms and beer. **Larva**: Described by Raynaud (1975).

Conservation: Not endangered. In Cantabria, it shows an ability to colonise even the non-indigenous *Eucalyptus* forests (Casale, *pers. observ.*).

026.003. C. (Chrysocarabus) olympiae
Sella, 1855.

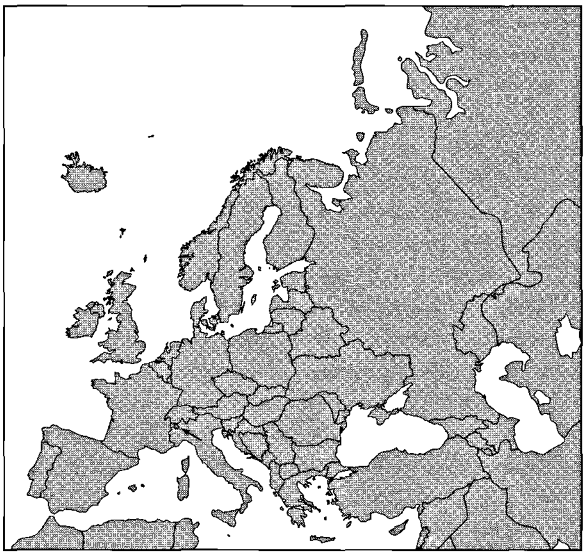
General literature: **Checklists and catalogues** – Breuning (1936): 1442. Březina (1994): 76; (1999): 71. Deuve (1994): 260 [692]. Kleinfeld & Schütze (1999): 40. Lorenz (1998): 102. Turin *et al.* (1993): 32. **Iconography** – Casale *et al.* (1982): fig. 150. Ghiretti (1996): 354. Imura & Mizusawa (1996): Pl. 74 [591]. Rautenstrauch (1994): Pl. 97.

Taxonomy: Some individual forms have been described (see Casale *et al.,* 1982). *Note*: According to the results of the DNA-analysis (Imura *et al.*, 1998), *C. olympiae* is very remote from the rest of *Chrysocarabus*-species, and its ranking in a separated subgenus (*Sellaecarabus* Sturani, 1947) seems reasonable (see also Casale *et al.,* 1982).

Geographical range: Endemic species of the Italian W. Alps. **Chorotype**: SEU-ALPW. **Range characteristics**: Alpi(W). **Distribution in Europe**: **Italy** – An extremely local species, endemic to the W. Alps (Piedmont: Biellese Prealps, Alta Val Sessera).

Subspecies: No subspecies.

Ecology: In forests (Fagetalia) from 850-900 to 1200 m, where it behaves as a true forest species, and in subalpine pastures, up to 1650 m, especially in the *Rhododendron* zone (Casale *et al.,* 1982).



26 003 olympiae (Chrysocarabus)

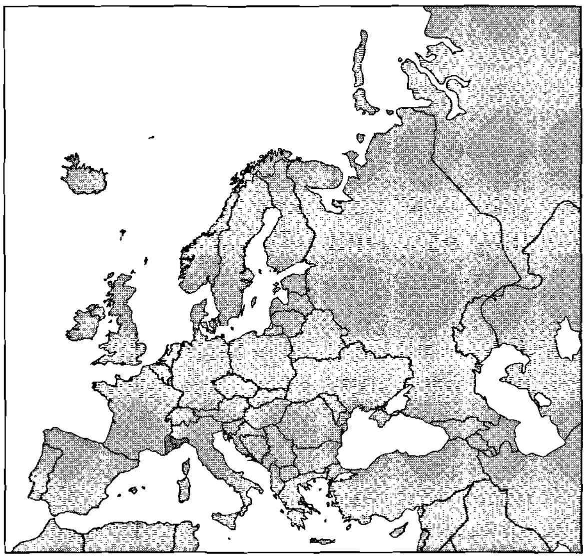
Biology: **Activity** – Night active. **Periodicity** (Malausa, 1978a; Sturani, 1947) – Reproduction in spring. Adults are mainly active from May to July after which they enter an aestivation diapause during August. There is a second period of adult activity in the end of August-September followed by hibernation from October until the following May (Sturani, 1962). Development of eggs (size 6.5 x 2 mm): 9-10 days; larvae, all together, including 10 days prepupal stage: 60-75 days and pupae: 15-18 days (Sturani, *l.c.*). Malausa found in experiments a second form that differs in reproductive strategy, with an imaginal diapause and reproductive success only after 5 months of low temperatures (<5°C). **Food** (Larochelle, 1990; Casale *et al.*, 1982) – In the field a specialised snail predator, notably hunting on a small, locally abundant, red slug *Arianta arbustorum* L. that lives on the Yellow Gentian. It also hunts on other slugs (*Arion* and *Limax* spp.). In the laboratory, it accepted red meat, earthworms, live slugs and snails (various *Helix* spp.), live insects of Orthoptera and Coleoptera, raw meat, cooked vegetables, potatoes, fruits and gingerbread. The adults are also reported to be cannibalistic (Sturani, 1947; 1962). **Larva**: Described by Sturani (1947) and Raynaud (1962). See Casale *et al.* (1982: L1-L2) also for pupa. Food – in captivity, same as adult.

Conservation: The species is a relict that probably survived the quaternary glacial period in some refugia, under favourable conditions. This extremely vulnerable species is protected by national and European law (also in CITES), but ineffectively. In the last years, however, the size of some populations (including the typical one) is increasing. The forest-dwelling populations are highly sensitive to forest cleaning (Casale, *pers. observ.*), due to the influence of light (sun) and high temperatures on eggs and larvae. The species was successfully reared in the laboratory (Malausa 1977, 1978a;) and subsequently introduced in the Mercantour National Park in France; however introduced 'populations' did not survive (Malausa, *pers. comm.*). In the Mercantour, one specimen was found that could probably be a hybrid between *C. solieri* and *C. olympiae.* It was also introduced near Grenoble.

026.004. C. (Chrysocarabus) solieri
Dejean, 1826.

General literature: **Checklists and catalogues** – Breuning (1936): 1444. Březina (1994): 74; (1999): 71. Deuve (1994): 260 [693]. Kleinfeld & Schütze (1999): 41. Lorenz (1998): 104. Turin *et al.* (1993): 32. **Iconography** – Casale at al. (1982): fig. 157. Darnaud (1978c): Pl. 4. Forel & Leplat (1995): Pl. 35-40. Ghiretti (1996): 354-356. Imura & Mizusawa (1996): Pl. 74 [592]. Rautenstrauch (1994): Pl. 97-98.

Taxonomy: Monographic contributions on this species were published for France by Bonadona (1973) and for Italy by Casale & Cavazzuti (1975). A detailed study of the



26 004 solieri (Chrysocarabus)

genetic composition of this species across much of its distribution was carried out by Rasplus *et al.* (2000). The results showed a distinct position of *C. solieri bonettianus* and the close genetic clustering of distant populations of *C. solieri liguranus* and *C. solieri solieri* as well as confirming the hybrid origin of the form *C. solieri curtii*. *C. solieri clairi* clustered with *C. solieri vesubiensis*, suggesting that the first is a melanistic form of the latter. This study is being extended to confirm these conclusions. Rasplus *et al.* (*l.c.*) assume that two Evolutionary Significant Units (see p. 428) (subspecies *bonnetianus* and *solieri*) survived the last glaciation within distinct refugia in France and Italy.

Geographical range: Endemic species of the W. Alps; S.E. France, N.W. Italy. **Chorotype:** SEU-ALPW. **Range characteristics:** Alpi(W). **Distribution in Europe**: **Italy** – N.W. Italy; Piemonte, Lombardia (a small area of the Apennines at the border of Liguria), Liguria (W. Alps, from Cottian to Ligurian Alps, N.-most Ligurian Apennines). **France** – Distributed in the Alps of the S.E.: from Var river through Hautes Alpes, Alpes Maritimes, Alpes de Haute Provence and Basses Alpes to Val d'Isère.

Subspecies: **a) subsp. solieri** – W. Alps, from the Cottian to the Maritime Alps, and Basses Alpes near Digne, both on the Italian and the French side, mostly at middle altitudes but in Ligurian Alps frequent in *Rhododendron* and *Alnus* at 1800-2000 m (Casale *et al.*, 1982). **b) subsp. liguranus** Breuning, 1932 – Ligurian Alps and N.W. (Ligurian) Apennines, S. Piedmont (Langhe region). **c) subsp. clairi** Géhin, 1885 – Maritime Alps, mostly on the French side (high alpine, in a wide area, with a hybrid zone with *solieri solieri*). **d) subsp. bonnetianus** Colas, 1937 – S.E. France: Tanneron-Esterel Massif. **e) subsp. bonadonai** Colas, 1948 – France, Alps of the Provence and S. Maritime Alps.

Ecology: In foothills with deciduous forests to montane forests (beech, chestnut and pine) and subalpine prairies, mostly from 200 to 2000 m; up to 2500 m in the Maritime Alps; it prefers silicat-stony and loamy soil which is rich in humus, leaf litter and mosses, and relatively moist. The habitat preference of the species is the forest belt with *Castanea* or *Fagus*, and also northerly exposed coniferous forests with *Pinus* and *Larix* (Casale *et al.*, 1982; Casale & Cavazzuti, 1975; Forel & Leplat, 1995). At high altitude, it lives in humid alpine prairies, preferably in gravel, close to snow fields, during day time hidden under stones, in *Rhododendron* scrub and around the stems of grape vines (Du Chatenet, 1986).

Biology: **Activity** – Predominantly nocturnal. **Periodicity** – At lower altitudes active from spring to autumn, with a first period of activity in May-July, followed by aestivation diapause during August and a second peak of adult activity during September-October (Sturani, 1962). At higher altitude, all activity concentrates in summer; the females lay 40-60 eggs (size 7 x 2 mm) in separate cells (Sturani *l.c.*). Eggs develop in 10-16 days; the larval stage, including 10-30 days of prepupal stage, lasts for 60-80 days and pupae ca 15 days (Sturani, *l.c.*). At high altitudes, the larvae hibernate as L2 or L3. Hibernation from October until April/May, usually under mosses or in the soil, rare in tree trunks (Casale *et al.*, 1982). **Food** (Larochelle, 1990): In the field, it was observed eating insects crushed by cars, dead and fresh fish, snails and earthworms. In captivity, it accepted the same food as adults, including live snails (*Helix arbustorum*, *H. pisana*, *H. variabilis*), Isopoda (*Armadillium* spp.), various larvae and fruits, raw and cooked meat, omlettes, cheese, gingerbead and bread soaked in water and sugared milk. **Larva**: Described by Bonadona (1966) and Raynaud (1976); compare Casale *et al.* (1982). Food – in captivity, same as adults. **Dispersal power**: A good tree climber (Rasplus, Assmann, *pers. observ.*).

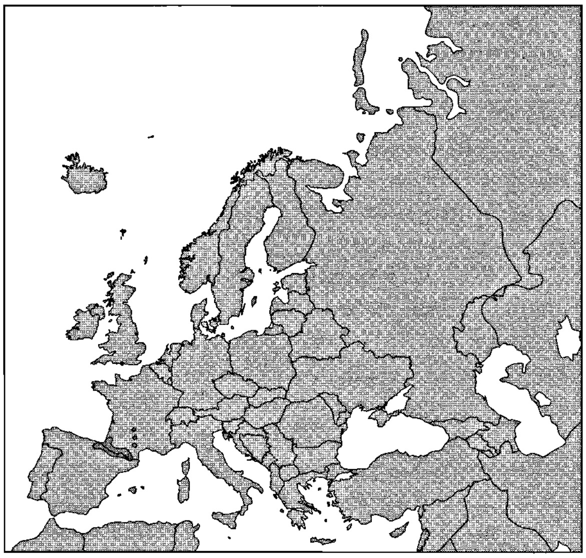
Conservation: The subspecies *bonnetianus* is endangered by loss of habitat (fire) and urbanisation. Although *C. solieri* is protected by law in France, the habitat, e.g. in parts of the Maritime Alps, has been affected by alpine tourism (ski-runs), and urbanisation near the coast. Nevertheless, many populations are abundant and apparently increasing.

26.005. C. (Chrysocarabus) splendens

Olivier, 1791.

General literature: **Checklists and catalogues** – Breuning (1936): 1455. Březina (1994): 77; (1999): 72. Deuve (1994): 262 [695]. Kleinfeld & Schütze (1999): 41. Lorenz (1998): 104. Turin *et al.* (1993): 32. **Iconography** – Forel & Leplat (1995): Pl. 41-42; (1998): fig. 142-147. Ghiretti (1996): 358-359. Imura & Mizusawa (1996): Pl. 74 [593]. Jakobson (1905): Pl. 3. Rautenstrauch (1994): Pl. 99.

Taxonomy: Forel & Leplat (1995) indicate that *C. splendens* interbreeds very easily with other *Chrysocarabus* species in most areas where they live in the same habitat; from the W. to the E. with *C. lineatus*, *C. auronitens* (subsp. *festivus*, subsp. *punctatoauratus*), *C. hispanus* and *C. ruti-*



26 005 splendens (Chrysocarabus)

lans; many natural hybrid forms are the result (see *Checklist*, p. 70-71). It is of course of great importance, whether these hybrids have fertile offspring or not (see Puissegur, 1964 and Allemand & Malausa, 1984 for an exact listing). A study of the distribution of two main haplotypes within the area covered by *C. splendens*, has opened several possibilities, for instance that the taxon comprises a complex of two sibling species, and that probably introgression has taken place between *C. splendens* and *C. auronitens punctatoauratus* in their sympatric area of distribution (Düring *et al.*, 2000).

Geographical range: S.W. France and E. Spain, Pyrenees. **Chorotype: WEU-PYRE. Range characteristics:** Iber(NW). **Distribution in Europe**: **France** – Distributed over a large area in the S.W., stretching from the Atlantic coast, where it occurs in the lowlands near Dax and Bayonne, throughout the Pyrenees to the Dep. Pyrénées Orientales. In the N. it reaches the line Oloron – Mt. Canigou. Absent from the mediterranean area near Perpignan. A few isolated populations exist more to the N.: a) Montagne Noire and Grésigne forest, b) forests of Najac and c) the N.-most one in the forests near Brive, where it has possibly been introduced by man. **Iberian Peninsula** – On the Iberian side restricted to the Basque mountains (Montes Vascos, Sierra de Urbasa, Sierra de Gorbea), W. and C. Pyrenees (Region de Bohí).

Subspecies: Morphologically (form of habitus) rather homogeneous, but highly variable in colour and size. Although some forty infraspecific forms have been described, e.g. *ammonius* of Mt. Noire, forêt de Grésigne, l'Aveyron and Montirat in Tarn, *lapurdanus* of Pays Basque, and *vittatus* of S. Landes and Chalosse, Low Valley de l'Adour, we agree with Deuve (1994) that none of them merits a subspecific status (see *Taxonomy*).

Ecology: In the lowland woodlands of Landes to montane forests in the Pyrénées Atlantiques, up to 1500 m, rarely in the alpine zone (up to 2000 m; Casale, *pers. observ.*); especially in humid forests with a N. exposure but also present in very moist scrub in the S. of Landes (Forel & Leplat, 1995). In N. Spain also found in grasslands and forest clearings at subalpine altitudes (Herrera & Arricibita, 1990; Assmann, *pers. observ.*).

Transects: Chapter 8: T-92-94.

Biology: Activity – Mainly nocturnal (Thiele & Weber, 1968). **Periodicity** – The period of activity depends strongly on altitude and starts in the second half of spring or in the summer (Forel & Leplat, 1995), at lower altitudes, adults are active from April-June, followed by a summer period of low activity and some activity of newly hatched animals in September (Mossakowski, *in litt.*). Development is very similar to that of other *Chrysocarabus* species: about 10 days after copulation in spring or early summer, the females deposit 30-40 eggs (size 6 x 1.8 mm) in separate cells at 2-5 cm deep in soil. Development takes in total about 40-60 days of which the eggs take ca 14 days and the larval stages about 30-40 days (Sturani, 1962). The adults hibernate (often in the company of other *Carabus* species, such as *Chrysocarabus* spp., *Megodontus* spp., *Mesocarabus* spp., *Archicarabus* spp. and even *Carabus* spp. *s.str.*), usually from September until April-May (Forel & Leplat, *l.c.*). Hibernation in soil, in mosses, under bark or tree trunks (Casale, *pers. observ.*; Mossakowski, *in litt.*). **Food** – In the field baited with gingerbread, snails, earthworms, raw meat and beer. In the laboratory, it accepted snails and various fruits (Larochelle, 1990). **Larva**: Described by Raynaud (1975). Food – In captivity, raw meat, small slugs, crushed snails and fruit (Larochelle, *l.c.*).

Conservation: Not endangered.

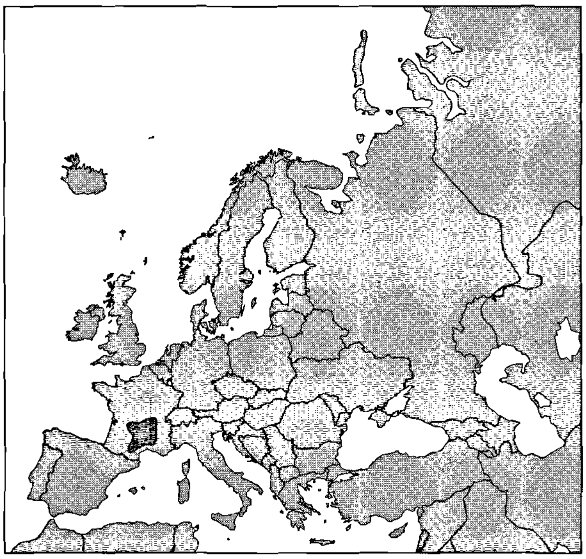
26.006 C. (Chrysocarabus) hispanus

Fabricius, 1787.

General literature: **Checklists and catalogues** – Breuning (1934): 1050. Březina (1994): 77; (1999): 67. Deuve (1994): 267 [697]. Kleinfeld & Schütze (1999): 41. Lorenz (1998): 105. Turin *et al.* (1993): 32. **Iconography** – Darnaud (1983a): Pl. 14. Forel & Leplat (1995): Pl. 52-53. Ghiretti (1996): 364. Imura & Mizusawa (1996): Pl. 75 [596]. Jakobson (1905): Pl. 3. Rautenstrauch (1994): Pl. 72.

Taxonomy: For discussion on the arrangement of *hispanus* and *rutilans* in *Chrysocarabus* and not in *Chrysotribax*, see *Key to the adults*.

Geographical range: Species endemic to France. **Chorotype:** SEU-FRAS. **Range characteristics:** WEur(W). **Distribution in Europe**: **France** – Distributed in a coherent central area in C.S. and S.W. France, in forests of Montagne Noire, C. Massif (Cantal, Haute-Loire to the N.), Cévennes and Drôme. It has two isolates, in the W. in the Corbières and in the E. in the Forêt de Saou (Drôme). In the W., S. and E. it is bordered by lowlands and river valleys, e.g. of Garonne, Aude and Rhône. The N. border is situated near



26 006 hispanus (Chrysocarabus)

the line Puy de Sancy – St. Etienne, the S. border near the line Toulouse – Carcasonne – Aude river.

Subspecies: The species is very homogeneous across its range, only *latissimus* Vacher de Lapouge, 1910, from Montagne Noire, in which the 4th article of male pro-tarsi is lacking the ventral lamellae, and *dromensis* Forel & Leplat, 1995 (formerly known as *boudeti* Beuthin, 1892; see Coulon *et al.*, 2000), isolated from the other populations on the E. side of the Rhône (Drôme, Forêt de Saou and neighbouring forests), perhaps merit the status of distinct subspecies.

Ecology: Forest species with often a clear preference for *Castanea* forests, however, in Forêt de Saou, very abundant in conifers but rare in beech (Casale, *pers. observ.*). In the Ardèche and Cevennes especially between 500 and 800 m (Coulon *et al.*, 2000), also in *Castanea*. Rare above 900 m (Forel & Leplat, 1995). It can occur in some other types of forest, but mostly in significantly lower numbers. The species prefers habitats exposed to the N. or E., exceptionally W. but never the S. It preferably inhabits humid places with loam and stones. Where the surface is rather dry, it is found deeper in the soil (Forel & Leplat, *l.c.*; Mossakowski, *in litt.*).

Transects: Chapter 8: T-89 and 91.

Biology: **Activity** – Nocturnal species. **Periodicity** – Spring breeder: the 40-50 eggs (size 8 x 2 mm) are laid after copulation, from May onwards and develop in about 16 days (Forel & Leplat, 1995; Sturani, 1962). The larval stage lasts for about 60-80 days (40-55 days after Sturani, *l.c.*), and pupal stage (including 3-4 days prepupa) takes 15 days. Hibernation takes place from the end of September to April under bark of old trunks or shallowly in the soil under mosses and among roots. **Food** (Larochelle, 1990): In the field, earthworms, snails (*Helix aspersa*) and various kinds of fruit. In captivity also gingerbread, soaked in water, softened Gruyère cheese, caterpillars without hairs, slugs and bread soaked in sugared milk. **Larva**: Described by Raynaud (1975). Food – only snails (Larochelle, *l.c.*). **Dispersal power**: The beetles are good tree climbers (Hockmann *et al.,* 1989; Assmann, *pers. observ.*).

Conservation: Not endangered; protected by law in France.

26.007 C. (Chrysocarabus) rutilans

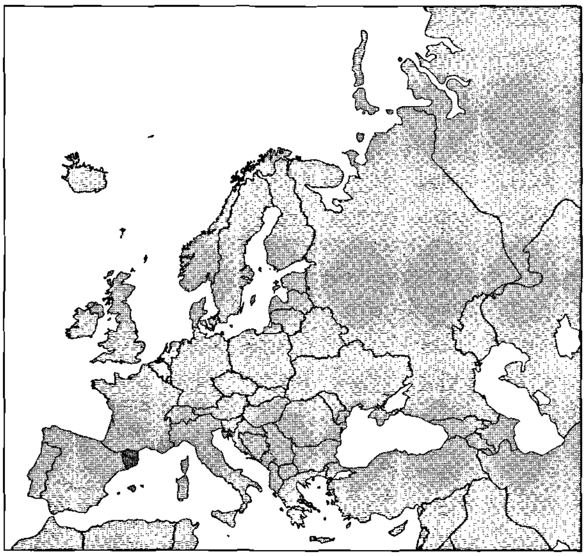
Dejean, 1826.

General literature: **Checklists and catalogues** – Breuning (1934): 1054. Březina (1994): 77; (1999): 67. Deuve (1994): 268 [698]. Kleinfeld & Schütze (1999): 41. Lorenz (1998): 105. Turin *et al.* (1993): 32. **Iconography** – Darnaud (1978a): Pl. 2. Forel & Leplat (1995): Pl. 54; (1998): fig. 150-160. Ghiretti (1996): 364-365. Imura & Mizusawa (1996): Jakobson (1905): Pl. 3. Pl. 75 [597]. Rautenstrauch (1994): Pl. 73.

Taxonomy: See *C. hispanus* and *Key to the adults*.

Geographical range: Endemic species of the E. Pyrenees and Cataluña. **Chorotype:** WEU-PYRE. **Range characteristics:** Iber(NW). **Distribution in Europe**: **France** – S.W. part of France, S. of the river Aude, but in the Pyrenees slightly more to the W., crossing the Aude to the upper stream of the Ariège: Corbières and Pyrénées Orientales. The area of distribution just reaches the S.-most part of the area of a small isolated population of *C. hispanus*. **Iberian Peninsula** – N.E. Spain: Cataluña, C. and E. Pyrenees. Found particularly in river valleys on the Spanish side (e.g. Noguera de Tor, Vallferrera, Llobregat, Ter), S. to the Ebro region.

Subspecies (Lequet, 1982): **a) subsp. rutilans** – E. Pyrenees on both sides (French and Spanish), all Catalunian chains to the Ebro river region. **b) subsp. perignitus** Reitter, 1896 – C. Pyrenees, Andorra and adjacent mountains on the Spanish and French sides. **c) subsp. opulentus** Oberthür, 1898 – Spain, C. Pyrenees: Val d'Aran; high basin of Noguera de Tor river. Subspecies *jeannei* is questionable (see *Checklist*, p. 66).



26 007 rutilans (Chrysocarabus)

Ecology: A rather eurytopic species, in lowland forests and scrub, at high altitude sometimes in open country; preferably in relatively humid beech or *Castanea* forests at middle altitudes, with a N. exposure, however, also in forests with cork oaks on very dry soil, in forests with oaks (*Quercus*), along reedlands, wooded road verges and gardens to subalpine prairies at high altitude (Du Chatenet, 1986; Forel & Leplat, 1995, 1998). According to Mossakowski (*in litt.*), mainly close to rivers or creeks, in the macchia as well as in the forest.

Transect: Chapter 8: T-92-93.

Biology: **Activity** – Nocturnal. **Periodicity** – The period of activity depends on altitude, starting in early spring (April) at sea level to the beginning of July at high altitude (Sturani, 1962). On the day, following the copulation, 40-60 eggs (size 9-10 x 2.5 mm) are laid in separate round cells, made with the hind legs and closed by the female after oviposition. After about 10-14 days, the larvae hatch and darken to black. In total, the length of the larval period lasts 35-60 days, including a prepupal stage of about 3 days, and the pupal stage takes another 14 days (Sturani, *l.c.*). During ecdysis, the larva hides in the soil. The third instar (ca 5 cm) makes a new oval cell of about 6 cm long for pupation, changing colour to white. Teneral adults appear in the lowlands around June; initially white, they darken to black and subsequently to brilliant golden green. After this, it takes the chitin exoskeleton a relatively long time to fully sclerotise (Forel & Leplat, *l.c.*). Some adults can be active until October or the beginning of November, however the autumn activity is mainly shown by freshly emerged animals (Casale, *pers. observ.*; Mossakowski, *in litt.*). They hibernate in the soil, in small holes in between rocks or tree roots, or under mosses. **Food** (Larochelle, 1990) – In the field, earthworms, snails (*Helix adspersa*) and caterpillars. In captivity, it also accepts slugs, fruits (apples, bananas), raw meat, gingerbread and bread soaked in sugared milk. **Larva**: Described by Raynaud (1975). Food – In general the same as the adults (Larochelle, 1990): earthworms, snails etc.

Conservation: Not endangered, however, like *C. hispanus* protected by law in France.

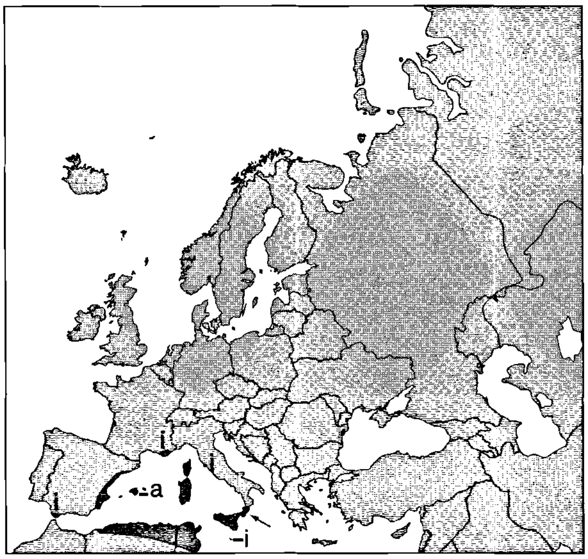
28. MACROTHORAX DESMAREST, 1850

28.001. C. (Macrothorax) morbillosus

Fabricius, 1792.

General literature: **Checklists and catalogues** – Breuning (1936): 1422. Březina (1994): 77; (1999): 66. Deuve (1994): 270 [701]. Kleinfeld & Schütze (1999): 40. Lorenz (1998): 102. Turin *et al.* (1993): 32. **Iconography** – Casale *et al.* (1982): fig. 115. Darnaud (1981b): Pl. 13. Forel & Leplat (1995): Pl. 54-55; (1998): fig. 169. Ghiretti (1996): 367-368. Imura & Mizusawa (1996): Pl. 74 [588]. Rautenstrauch (1994): Pl. 94-95.

Geographical range: W. Mediterranean species. **Chorotype:** WME. **Range characteristics:** NAfr-Sici-Iber(SE).



28 001 morbillosus (Macrothorax)

Distribution in Europe (and adjacent areas): *Note*: erroneous reports (Born, 1906; Vacher de Lapouge, 1929) exist from Switzerland (Tessin), Greece and Croatia (see Casale *et al.*, 1982; Marggi, 1992). **Italy** – S. Italy (Calabria: Aspromonte Massif), in the main Tyrrhenian islands (Sardinia, Sicily) and in several small islands near Sardinia and Sicily, Lampedusa, Malta. In C. Italy (Tuscany) and several small islands probably introduced recently by cork shipping (Casale *et al.*, 1989), but also possibly autochtonous (Vigna Taglianti, *pers. comm.*). **France** – Probably introduced on the mainland of S.E. France; nowadays it is found in a very small area near Le Muy and Fréjus (Var). Furthermore, it inhabits the C.E and S.E. part of Corsica. **Iberian Peninsula** – S.E. part of the peninsula (Murcia, from Cartagena in the coastal area up to S. Cataluña (environments of Tarragona). Also on the Baleares (Menorca, Mallorca). Introduced near Cadiz. **North Africa** (Antoine, 1957; Casale *et al.*, 1982) – Present in Maghreb (N. Algeria and N. Tunisia).

Subspecies: Casale *et al.* (1982) included the populations of Corsica and Sardinia in subsp. *morbillosus* in the widest sense. Recently, Deuve (1994) limited the typical form to the W. Maghrebinian populations, restoring the name *constantinus* for the E. Maghrebinian and Corsico-Sardinian populations. **a) subsp. morbillosus** – N. Algeria. Specimens introduced in S.E. France, probably from Kabylia, have been described as subsp. *cheminorum* Deuve, 1988. **b) subsp. constantinus** Vacher de Lapouge, 1899 – N.E. Algeria, N. Tunisia, C. Italy (Tuscany), Sardinia, Corsica, Lampedusa. Specimens introduced to S.E. France, probably from Corsica, were described as *galloprovincialis* Vacher de Lapouge, 1910. **c) subsp. alternans** Palliardi, 1825 – Sicily, Calabria (Aspromonte), Malta. **d) subsp. macilentus** Vacher de Lapouge, 1899 – S.E. Spain (Murcia, Catalonia); recently introduced in Torredembarra (Tarragona) and in the region of Cadiz presumably from the Baleares (described as *balearicus* Vacher de Lapouge, 1913).

Ecology: Eurytopic, rather frequent in open country, also in cultivated land and gardens in cities at low altitude, but in some areas frequently found in mediterranean scrub and forests from littoral habitats at sea level to 1000, occasionally 1200 m (Casale *et al.,* 1982). In Sicily, *C. morbillosus alternans* is rather numerous during March-April in fields and pastures under stones, from 50 up to 1000 m, but it was not found in the montane forests (1000-1600 m) of the Nebrodi and Madonie (Korell, 1975).

Biology: **Activity** – In Sardinia, normally nocturnal, but diurnal in rainy days (Casale, *pers. observ.*). **Periodicity** – Winter active and winter breeding, starting in autumn until next spring; most abundant from January to April (Casale *et al.,* 1982). Copulations occur in autumn and oviposition takes place until January. Average development of the egg 11 days; of the larva 29 days, including pre-pupae of 10 days (Sturani, 1962); in N. Africa, the first instar occurs from early November until December, the second and third instar in December; a last instar was found on Corsica at the end of May (Arndt, *pers. observ.*). Pupation takes 7-8 days, which brings the duration of development to about 45-50 days. The coloration of the adult takes 1 more day to attain full development. In N. Africa the development to adult is concluded in March, on the European side this can take until May (Arndt, *l.c.*). **Food** (Casale *et al.*, 1982; Larochelle, 1990) – The species is a pronounced snail eater; in Europe, *Helix* spp. (e.g. *H. pisana* Müller) and *Hybalus biggiber* (F.); in Tunisia, *Helix* spp. and *Stenogyra decollata* L. In the field also small slugs (*Limax* spp.). In captivity, crushed snails, raw meat, fruits, cooked vegetables, omelettes, gingerbread and bread soaked in sugared milk. See also Boettger (1921) for morphological adaptations of the *morbillosus* populations to different prey (snails of the genus *Otala* in N. Africa). **Larva**: Described by Vacher de Lapouge (1905, as *Calosoma auropunctatum*), Vacher de Lapouge (1906, 1929), Sturani (1962) and Raynaud (1975). Food – earthworms and snails (*Helicella*) in the laboratory, same as adults (Larochelle, *l.c.*) and in the field earthworms and snails (Arndt, *pers. observ.*).

Conservation: A common and sometimes very abundant, eurytopic species; not endangered.

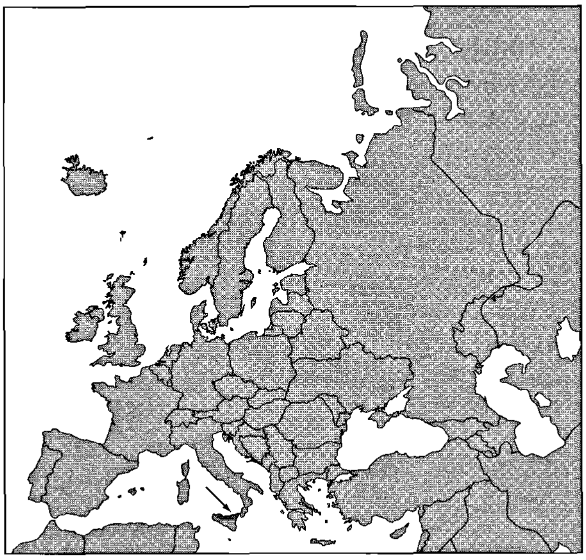
28.002. C. (Macrothorax) planatus

Chaudoir, 1843.

General literature: **Checklists and catalogues** – Breuning (1936): 1420. Březina (1994): 78; (1999): 66. Deuve (1994): 270 [700]. Kleinfeld & Schütze (1999): 40. Lorenz (1998): 103. Turin *et al.* (1993): 32. **Iconography** – Casale *et al.* (1982): fig. 115. Darnaud (1981b): Pl. 13. Ghiretti (1996): 369. Imura & Mizusawa (1996): Pl. 74 [589]. Rautenstrauch (1994): Pl. 96.

Geographical range: Endemic species of N. Sicily. **Chorotype**: SEU-SICI. **Range characteristics:** Sici. **Distribution in Europe**: **Italy** – Sicily: Madonie Mts., Nebrodi Mts. Not on Sardinia, as erroneously was reported by Porta (1923).

Subspecies: No distinct subspecies (Korell, 1975).



28 002 planatus (Macrothorax)

Ecology: A strictly montane species with very local populations, inhabiting cool, damp and foggy (*Fagus*-) forest in the middle mountain belt between 1300 and 1800 m (Casale *et al.,* 1982).

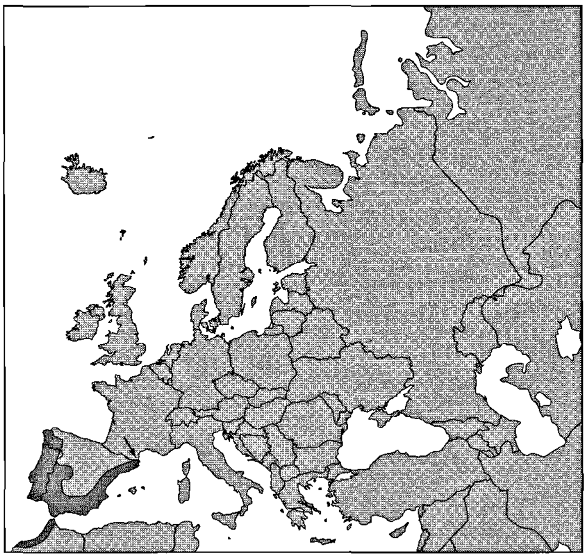
Biology (Casale *et al.,* 1982): **Activity** – No data. **Periodicity** – The animals are active in spring and summer, from April/May to July when they have a short aestivation. From August/September onwards, the adults become active again and reproduce. Occasionally, the animals start their activity even during the end of March (see phenological data in Korell, 1975). From November to March/April, the adults hibernate in roots and old beech trunks. The first non-alpine *Carabus* species with two-years development type (Brandmayr & Zetto Brandmayr, 1986). **Food** (Larochelle, 1990; Casale *et al.,* 1982) – In the field, snails (*Helix pisana* Müller, *H. rufa* Pffr., *Daudebardia nivalis* L., *D. brevis* Drap. and *Vitrina pelluciduala* Müller). In captivity, fruits, raw meat, slugs (*Limax* spp.), crushed snails and gingerbread. **Larva**: Described in Casale *et al.* (1982). Food – No data. *Note*: The adults can stridulate when disturbed; probably one of the most strikingly (*Cychrus*-like) sridulating *Carabus* species (Casale, *pers. observ.*). The biological meaning of this behaviour is not yet clear. Some other species that stridulate are *C. depressus*, *C. intricatus* and especially Caucasian *Tribax* species.

Conservation: According to Bruno (1968), this endemic could be seriously endangered, but it seems to have a good chance to survive in the remaining beech forests remnants, provided that further exploitation (especially tourism) of the Nebrodi area stops (Korell, 1975). In the Nebrodi Natural Park (Italy, Sicily), it is a protected species.

28.003. C. (Macrothorax) rugosus

Fabricius, 1775.

General literature: **Checklists and catalogues** – Breuning (1936): 1412. Březina (1994): 78; (1999): 66. Deuve



28 003 rugosus (Macrothorax)

(1994): 270 [699]. Kleinfeld & Schütze (1999): 40. Lorenz (1998): 103. Turin *et al.* (1993): 32. **Iconography** – Darnaud (1981b): Pl. 13. Forel & Leplat (1998): fig. 161-168. Ghiretti (1996): 366-367. Imura & Mizusawa (1996): Pl. 74 [590]. Rautenstrauch (1994): Pl. 93-94.

Geographical range: C. and N. Morocco, Iberian Peninsula, S.W. France (introduced). **Chorotype:** WEU-IBER. **Range characteristics:** Iber(S)-NAfr. **Distribution in Europe (and adjacent areas)**: **France** – Restricted to a very small area in the S.W.: Albères Mts. in the E. Pyrenees. **Iberian Peninsula** – Distributed in the W., C. and E. part of the peninsula. From Galicia and Portugal through the C. 'sierras' (de Gata, de Béjar, de Gredos, de Guadelupe, de Tudia, Guadalquivir valley, sierras de Cazorla and de Segura) and through the S. (most of Andalucia) to E. Spain, up to the E. Pyrenees (Deuve, *in litt.*). **North Africa** – N. and C. Morocco, down to the Moyen Atlas and the hills of the Grand Atlas near Marrakèch.

Subspecies: **a) subsp. rugosus** – (Only C. and N. Morocco). **b) subsp. celtibericus** Germar, 1824 – C. and N.W. Spain, C. and N.W. Portugal. Small, highly polychromous specimens from the Sierra de Gata, were described as *laufferi* Breuning, 1927; large specimens with very strong, convex elytron sculpture, from W. C. Spain, were described as *brannani* Schaufuss, 1871. **c) subsp. boeticus** Deyrolle, 1852 – S. Spain, from Andalusia to Catalonia and Guadalquivir valley. S.W. France (introduced). Small specimens from Sierra de Segura, Sierra de Cazorla, Sierra del Pozo, Sierra de la Sagra and Sierra de Alcaraz, were described as *seguranus* Lauffer, 1905; large specimens with tertiary intervals complete or scarcely broken, from Catalonia, were described as *levantinus* Lauffer, 1905. Other local forms from Guadalquivir valley, were described as *pseudobaeticus* Branes, 1985 (= *pseudoboeticus* Lassalle, 1986).

Ecology: A species from lowland and middle altitudes, mostly in moist and marshy places; also in pine forests (Du Chatenet, 1986). In the Iberian peninsula, rather eurytopic, from forest edges to grassy prairies, as well as relatively dry places along river shores (Forel & Leplat, 1998).

Transects: Chapter 8: T-97, 100.

Biology: **Activity** – Nocturnal. **Periodicity** – Very similar to *C. morbillosus* (Mossakowski, *in litt.*). Forel & Leplat (1995, 1998), mention that the form *vermiculosus* Fons *et al.* (1993; also regarded as a subspecies) from the Pyrénées Orientales, shows in rearing experiments a very long oviposition period. In the field, there is a peak of adult activity at the end of spring and in the late autumn. The white-yellow eggs (6 x 2 cm) are laid during a eight month period, from autumn onwards. The development of the eggs (5-15 days) and the larva (40-50 days) of this species in France is very similar to that of *C. morbillosus* (Forel & Leplat, *l.c.*); concerning the larval stage in N. Africa, Arndt (*pers. comm.*) made similar observations for *C. rugosus* and *C. morbillosus*. In the Iberian Peninsula, it is also active in late autum (especially October-November when reproduction takes place) and it disappeares nearly completely during January-March (Cárdenas & Bach, 1992). From April to the end of June, there is a peak in the activity of young beetles. Details on the shape of the (assymetric) mandibles for young and old beetles were given by Cárdenas & Bach (1992). **Food** (Larochelle, 1990) – In the field in Morocco, larvae of *Ocnogyna boetica meridionalis* Seitz (Lepidoptera, Arctiidae). Forel & Leplat (1995) mention snails, earthworms and other invertebrates. **Larva**: Described by Raynaud (1975). Food – earthworms and snails (*Helicella* spp.) in the laboratory and field (Arndt, *pers. observ.*).

Conservation: Apparently vulnerable in coastal localities, due to urbanisation (Casale, *pers. observ.*).

29. LAMPROSTUS MOTSCHULSKY, 1865

29.001. C. (Lamprostus) torosus

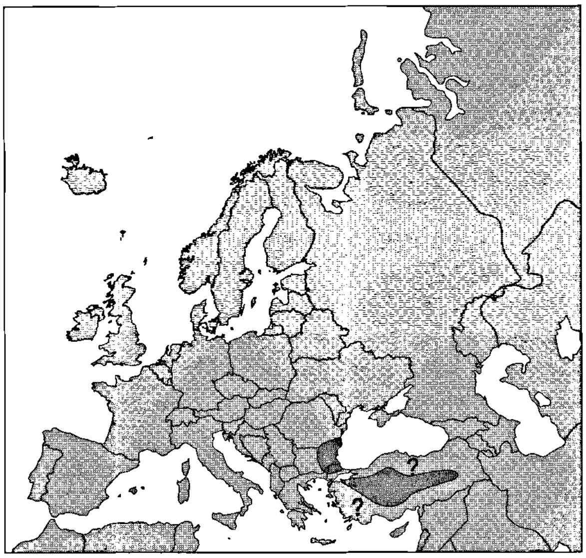
E. Frivaldszky, 1835.

General literature: **Checklists and catalogues** – Breuning (1935): 1343. Březina (1994): 62; (1999): 65. Deuve (1994): 221 [575]. Kleinfeld & Schütze (1999): 43. Lorenz (1998): 105. Turin *et al.* (1993): 33. **Iconography** – Cavazzuti & Ghiretti (1992). Ghiretti (1996): 279-280. Imura & Mizusawa (1996): Pl. 78 [611]. Rautenstrauch (1994): Pl. 90.

Taxonomy: The subgenus is represented by only this species in S.E. Europe (E. part of the Balkan peninsula).

Geographical range: Endemic of S.E. Europe and W. Turkey: S.E. Romania (Dobrudja), E. Bulgaria, Greece, European and Asiatic Turkey. **Chorotype:** ANAT. **Range characteristics:** Balk(SE)-Anat. **Distribution in Europe (and adjacent areas)**: **Romania** – S.E. Romania, Black Sea coast, Dobrodja. **Bulgaria** – Danube Plain near Russe, C. and E. Stara Planina, Dobrudja, Black Sea coast. **Turkey** – European part, widespread in Anatolia.

Subspecies: Several subspecies; in Europe only the nominate subsp. *torosus* (*s.str.*); the other subspecies in the W., C. and S. part of Asiatic Turkey.


29 001 torosus (Lamprostus)

Ecology: In the plain and foothills, rather xerophilous. **Transect**: Chapter 8: T-64.

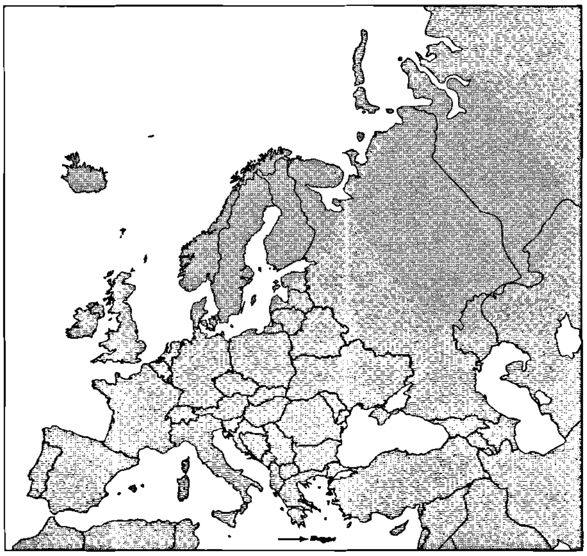
Biology: **Activity** – No data. **Periodicity** – No data. **Food** (Larochelle, 1990) – In captivity, live snails, raw meat, fruits and gingerbread. **Larva**: Described by Sturani (1962). Food – The larvae refused all food in captivity (Larochelle, 1990).

Conservation: No data.

30. PROCRUSTES BONELLI, 1809

30.001. C. (Procrustes) banoni
Dejean & Boisduval, 1829.

General literature: **Checklists and catalogues** – Breuning (1936): 1384. Březina (1994): 63; (1999): 61. Deuve (1994): 228 [595]. Kleinfeld & Schütze (1999): 41. Lorenz (1998): 105. Turin *et al.* (1993): 33. **Iconography** – Ghiretti (1996): 294. Imura & Mizusawa (1996): Pl. 76 [603].


30 001 banoni (Procrustes)

Geographical range: Endemic species of Crete. **Chorotype:** SEU-CRET. **Range characteristics:** Balk(S). **Distribution in Europe**: **Balkan Peninsula** – Greece: Isle Creta and the small Isle Dia, N. of Iraklion.

Subspecies: No subspecies.

Ecology: Found in hills and mountains in scrub and open country.

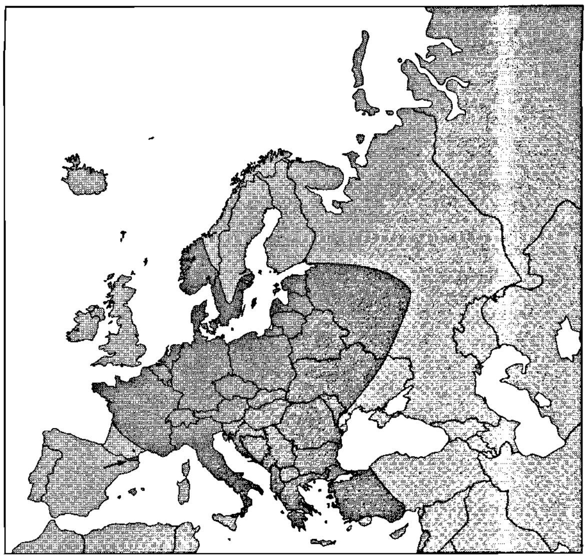
Biology: **Activity** – Nocturnal. **Periodicity** – Little is known about reproduction and development. From breeding experiments, Sturani (1962) mentions some data on larval development: L2: 14 days and L3: 30 days. **Food** (Larochelle, 1990) – They prey on molluscs, insects and earthworms. In captivity, it accepted live snails, raw meat, fruits and sugared water. **Larva**: Described by Raynaud (1975). Food – in captivity, same as adults.

Conservation: Very common and not endangered.

30.002. C. (Procructes) coriaceus
Linnaeus, 1758.

General literature: **Checklists and catalogues** – Breuning (1936): 1389. Březina (1994): 63; (1999): 62. Deuve (1994): 226 [593]. Kleinfeld & Schütze (1999): 41. Kryzhanovskij *et al.* (1995): 58 [270]. Lorenz (1998): 105. Turin *et al.* (1993): 33. **Iconography** – Casale *et al.* (1982): fig. 129. Forel & Leplat (1995): Ghiretti (1996): 288-293. Pl. 29-30. Imura & Mizusawa (1996): Pl. 77 [607]. Jakobson (1905): Pl. 2. Pavicevic & Mesaros (1997): cd-rom. Rautenstrauch (1994): Pl. 91-93.

Geographical range: Euro-Anatolian species. Widespread in Europe, W. and S. Anatolia, locally abundant. Absent from the British Isles, N. Fennoscandia and the Iberian peninsula. Distributed from S. France, S. Italy and the Balkan Peninsula, N. to 64°N (Sweden: 61°). In the E. to Jaroslavl, Moscow, Tula and Nizhnii Novgorod provinces, Moldova, C. Ukraine; in the S.E. including the islands of the Jonian and Aegean seas, to W. and S. Turkey (except N.E. districts). **Chorotype:** EUR. **Range characteristics:** Eur-Anat(W). **Distribution in Europe and adjacent areas: Fennoscandia** – Norwegian S. coastal region, up to 64°N; scattered inland occurrences in S. Sweden up to 61°N, absent from Finland. **Denmark** (Bangsholt, 1983; Jørum, 1996) – Scattered in W. Jutland; rather widely distributed in Zealand and the other E. Islands; locally abundant. **Netherlands** – Mainly along the big rivers in the S. and C. part of the country; only old records from the S.W. area. During the last decade frequently recorded from the N. part of the country in a coherent area. In the right habitat rather abundant. **Belgium** – It was found in the C. and E. parts, but greatly declined in the C. area. After 1950 only collected from 11 10x10 km UTM-squares in Flandria (before 1950 – 36 squares). **Germany** – Reported from nearly all over the country, perhaps lacking in some minor regions



30 002 coriaceus (Procrustes)

of N.W. Germany. No significant changes in occurrence during the last decades; in E. Germany one of the most common *Carabus* species, even penetrating deeply into urban habitats (e.g. C. of Leipzig). **Poland** – Reported from all provinces. **Baltic** – Reported from all countries. **Byelorussia** – All the territory. **Russian Plain** – Mainly restricted to the W. Ukraine. W. and C. regions of European Russia; N. to the province of Sankt Petersburg (60°N), the range 'narrows' to the E. along the line Sankt-Petersburg – Yaroslavl' – Nizhnii Novgorod. The E.-most localities seem to be Dryazga in Nizhnii Novgorod province, where the species does not occur to the E. of the Volga river (Anufriev *et al.,* 1989); the Mordow Reserve (Feoktistov, 1979), and Elniki District, Mordov Republic (MPGU). The S. range limit goes from S. Moldova through S. Ukraine (Chernyi Les near Znamenka; Kharkov) to the Tambov province. It seems to be rather common in the middle stretch of the Russian Plain, from the S. taiga subzone to the isolated forests of the N. steppes. **Moldova** – In most of the territory W. of Dnestr river. **Czechia & Slovakia** – Recorded from most of the territory, locally common. **Hungary** – One of the most widely distributed and common *Carabus*-species in the country (*coriaceus* in the N. Mts. and N. Transdanubia; *banaticus* in S. Transdanubia and *rugifer* in the SE part of the Great Hungarian Plain). **Romania** (Csiki, 1946; Panin, 1952) – Locally common across the territory. **Bulgaria** – Widely distributed throughout the country. **Turkey** (Darge, 1990; Casale & Vigna Taglianti, 1999) – European part, W. and S. Anatolia. **Balkan Peninsula** – Distributed all over the peninsula, including the islands. Found in Slovenia, Croatia, Bosnia-Herzegowina, Montenegro, Serbia, Macedonia, Albania, Greece. According to Pavicevic & Mesaros (1997), absent from N. and C. Croatia, N. and S. Serbia, Kossovo and most of C. Macedonia. **Austria** – All over the country, except the highest Alp regions. **Switzerland** – Mainly restricted to Ticino, the N.W. lowlands and wide valleys. Not in the high Alps. **Italy** – Widespread over most of the mainland. A few records exist from Sardinia and Sicily (probably introduced). **France** – Widespread in most of N. and C. France, but absent from a large area S. of the Garonne and the line Toulouse – Perpignan. There are some isolated localities in the E. Pyrenees (Montagne d'Alaric and the Roussillon plain).

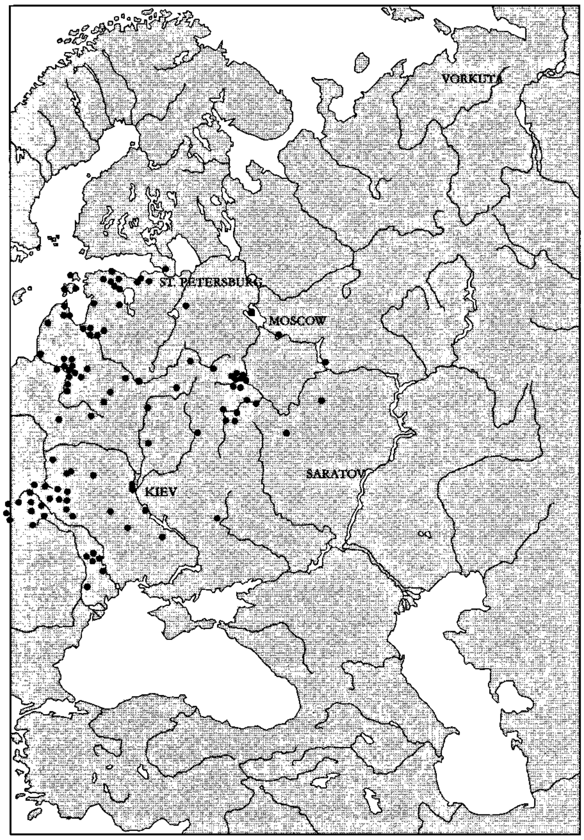
Subspecies: **a) subsp. coriaceus** – The N. and C. parts of species area; in the S. to S. France, Italy (also in Sicily; reported from Sardinia: introduced?), Slovenia, Serbia, C. Hungary, Czechia, N. slope of Carpathian Mts., C. Ukraine. **b) subsp. rugifer** (Kraatz, 1877) – Carpathian Mts. of Slovakia (widely distributed – Hůrka, 1996), Poland, Ukraine, Romania; also in the forests of Moldova and W. Ukraine. **c) subsp. excavatus** Charpentier, 1825 – Adriatic region (Casale *et al.,* 1982): N.E. Italy (Trieste), W. parts of Balkan peninsula from Croatia to C. Albania, in the E. to W. Bosnia. **d) subsp. mediterraneus** Born, 1906 – S. Albania, Jonian islands, S. Italy (Calabria, Puglia). A transadriatic-transionian element. **e) subsp. kindermanni** Waltl, 1838 – E. Bulgaria (lowlands to 400 m), European and the N.W. part of Asiatic Turkey. **f) subsp. cerisyi** Dejean, 1826 – C. parts of Balkan peninsula, from Serbia and S. Romania, through Macedonia, W. and C. Bulgaria to Greece (including Peloponnisos), islands of the adjacent archipelagos, and widely distributed in Asiatic Turkey, up to N.W. Syria. Many local forms, especially in islands.

Note: Another form is *C. c. banaticus* Redtenbacher, 1849, living in the Banat Mts. (Mehadia, Baile Herculane).

Ecology: Mesophilic species from snail-rich habitats, in the N. and C.N. areas especially from the lowlands and hills (Arndt, 1989; Feoktistov, 1979; Hůrka, 1973). According to Hoffmann (1907), in C. Europe mainly under 1000 m. Rather thermophilic (Thiele, 1977), however, with a preference for cool types of mountain forest at higher altitudes (Thiele & Kolbe, 1962). In general, living in moderately humid broad-leafed Quercetalia or Fagetalia, mixed or pine forests, sometimes in more open stands, such as hedgerows, orchards and vineyards (Koch, 1989; Stiprajs, 1961). In N.W. Europe known as an eurytopic forest species; the adults also occur in gardens and meadows on clay or silt soils, preferably near rivers and especially in more or less shaded places (Turin *et al.,* 1991). It prefers soil rich in humus (Lindroth, 1985). In Hungary rather eurytopic, with a preference for warm forest edges, but also in various forest associations and in the neigbourhood of waters. Also in the territory of former Yugoslavia, eurytopic, occurring in meadows, pastures, deciduous and coniferous forests in hills and mountains, in the inland up to alpine habitats (Pavicevic & Mesaros, 1997). In the Moscow province also mainly a forest species (Fedorenko, 1988). In the Ukraine, it occurs in the hornbeam and oak-hornbeam (Querco-Carpinetum) forests of the forest-steppe zone and the 'bairak' oak woods in ravines of the N. steppe (Petrusenko, 1971). In dense forest types, such as oak-hornbeam forests, mainly abundant at the forest edge (Turin, 2000), and also on limestone grasslands in the Netherlands which are exposed to the N., most abundant along forest edges (Turin, 1983) where also the highest diversity of surface dwelling snails, slugs, worms and arthropods was found; probably the most suitable place for foraging. In Scandinavia and Denmark more stenotopic than in C. Europe, usually confined to beech forest (Lindroth 1945, 1985). In France in nearly all biotopes, such as forests, fields, gardens and even rather abundant in grasslands, however avoiding agricultural pastures (Forel & Leplat, 1995; Jeannel, 1941). It occurs from lowland to ca 1500 m, but rarely higher (in Bulgaria up to 1900 m – Guéorguiev & Guéorguiev, 1995). It is found in several types of forest (Marggi, 1992; Thiele, 1977). Also in S. Europe rather eurytopic: in Italy, the habitat includes various field biotopes in the lowlands and hills, including urban habitats, such as parks and gardens (Casale *et al.,* 1982). In Greece, common in mediterranean scrub, oak-forests and open country; rare at high altitudes, over 1500 m (Casale, *pers. observ.*).

Transects: Chapter 1: I-1, 3; Chapter 8: T-03-05, 17-18, 21, 24-33, 35, 38-39, 48, 55, 58, 61-78, 80-82 and 86-90.

Biology: **Activity** – According to many authors, strictly nocturnal (Lindroth, 1985; Thiele, 1977; Weber, 1968b), but Riecken & Raths (1996) found that it was both diurnal and nocturnal, with a preference for night activity. Arndt (*pers. observ.*) recorded daytime activity in May and June. In Italy, it is even mostly diurnal in autumn (September-October), especially during rainy days (Casale, *pers. observ.*). **Periodicity** (Hůrka, 1973) – It is an autumn breeding species with, in most places, a biennial development (Arndt, 1989) and therefore it shows a peak of adult activity during the spring. Copulation and oviposition take place from the second half of August until November. The females lay 14-20 eggs (size 8 x 3 mm, sometimes up to 10 mm (Sturani, 1962)) separately in subterranean cavities, over a period of 20-30 days (Casale *et al.,* 1982). The eggs hatch after about 14 days (Sturani, 1962). The L1 and/or L2 hibernates, but in the S. they stay active and hunt also during the winter; the L3 (with maximum activity in May-June) needs a long period of maturation and the larvae pupate not earlier than next June-July. A period of 50-60 days for larval development is mentioned by Sturani, which includes the pre-pupal stage of 5-10 days; the pupa takes another fortnight. Teneral animals appear in the summer and early autumn, and they hibernate before reproducing in the next year. The hibernated adults become active in spring and reproduce after aestivation dormancy (July-August – Sturani, *l.c.*). Adults can be found in C. Europe throughout the year, but mainly from April to October, with a small peak in spring and the main one in August. In the N., it occurs mainly in summer (Lindroth, 1949). Hůrka (1973) concludes that, for C. Europe, it is a species that needs a larval as well as an adult diapause. In N. parts of its range, the development may last 3 years; a significant proportion of adults hibernate for a second time and reproduce again after aestivation dormancy (Lindroth, 1985; see also Malausa, 1978b). **Food** (Larochelle, 1990) – It is a specialised snail eater (especially *Cepaea* spp.), that is able to cut the shells along their spiral (Sturani, 1962). Bigger snails, such as *Helix* spp., however, are eaten by entering the shell opening, similar to the method of *Cychrus* species. Furthermore the diet consists of slugs (*Arion* spp.), earthworms and caterpillars. In the Netherlands, it was repeatedly found in 'empty' potato-chip bags, left in the field. In captivity, it accepted also minced meat, fish, ripe fruits, many species of live and crushed snails (*Helix pomatia*, *H. nemoralis*, *H. vermiculata*, *H. pisana*, *H. variabilis* etc. and slugs (*Arion* and *Limax* spp.) and chopped mealworms (Coleoptera, *Tenebrio*). Despite its obvious preference for a diet of molluscs, it is surprising that serobiological methods (Gryuntal & Sergeeva, 1987) revealed that no significant preferences could be shown for the 10 tested groups of soil invertebrates. **Larva** – Described by Audoin & Brullé (1835: L3), Vacher de Lapouge (1905: L1-L3), Hůrka (1971b) and key: Arndt (1985, 1991b) as well as most detailed in Cavazzuti (1989). The larvae are probably more confined to shaded habitats than the adults (Arndt, 1989). Food – Snails (*Deroceras*, *Cepaea*), earthworms and carrion, in the laboratory as well as in the field (Arndt, *pers. observ.*). **Dispersal power**: The species walks very well. Making use of small transmitters, it was shown that in a dense grassland vegetation a maximum distance of ca 20 m/day was covered, but in the open field much more (Riecken & Raths, 1996). The species uses linear elements in the landscape for orienta-



29 002 coriaceus

tion, such as forest edges and vegetated ditches (Riecken & Raths, 1996; Van Zuijen & Van Dijk, 1997).

Conservation: The species recently declined heavily in Belgium, while, in the same period during the last decades, it florished in the N. part of the Netherlands and even seems to expand nordwards in the province of Friesland (Van Zuijen, 1995; Van Zuijen & Van Dijk, 1997). This does not necessarily mean that this seemingly 'shift' can be explained by climatic changes, such as global warming. The reason for a decline can probably be found in general environmental conditions, such as humidity, habitat fragmentation and use of fertilisers and pesticides. In larger parts of W. Europe (S. and C. Netherlands, Belgium, W. Germany), and in N. Italy, this species was, without doubt, negatively influenced by current agricultural methods. It has greatly declined or disappeared completely from heavily urbanised and cultivated regions along rivers, and especially where forested areas have been fragmented or drained. However, it appears to possess an excellent ability to recover in case of nature restoration and improved landscape infrastructure (if there are not too many ecological barriers and if there is a certain presence of linear structures). Most probably due to its well-developed locomotory power, the species can survive well in fragmented cultivated landscape with hedges and forest edges providing shadow and shelter. These linear structures are preferred both for orientation and foraging (Riecken & Raths, 1996; Van Zuijen, 1995; see *Dispersal power*). It is, at least in N.W. and C. Europe, a useful indicator of shaded habitats rich in edaphic fauna (Blumenthal, 1981; Turin, 1983). In these regions and certainly in the C. Balkans, there are no problems concerning this species (Casale, *pers. observ.*). Generally, a limiting factor seems to be the availability and density of snails, and for this very reason the populations of *C. coriaceus* are most numerous on limestone soil where calciphilous snails are more abundant. In Italy, for instance, it is common in the N.E. but rare in the N.W. On the other hand, precipitation, does not seem to be a limiting factor: in some parts of Greece and Turkey with a low annual amount of rain, it is common.

31. PROCERUS DEJEAN, 1821

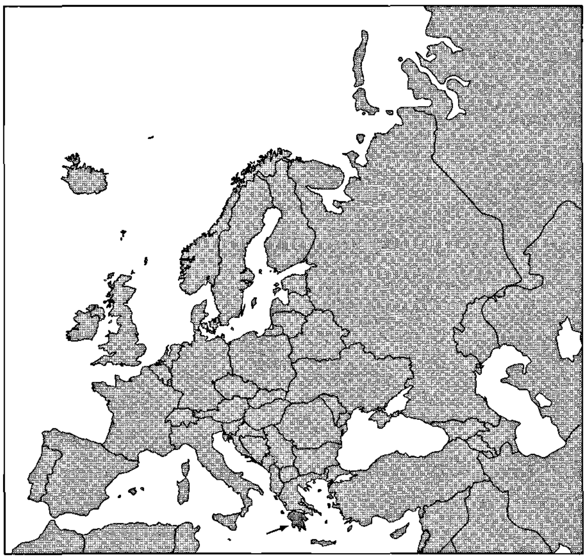
31.001. C. (Procerus) duponchelii

(Dejean, 1831).

General literature: Checklists and catalogues – Breuning (1935): 1333. Březina (1994): 74; (1999): 72. Deuve (1994): 259 [689]. Kleinfeld & Schütze (1999): 39. Lorenz (1998): 102. Turin *et al.* (1993): 33. **Iconography** – Casale *et al.* (1982): fig. 127. Cavazzuti (1989): Pl. 2. Darnaud (1984a): Pl. 16. Ghiretti (1996): 350. Imura & Mizusawa (1996): Pl. 72 [585].

Taxonomy: In the checklists of Deuve (1994, 1999) and Březina (1994), treated as a subspecies of *C. gigas*.

Geographical range: Endemic species of the S. Balkan peninsula. **Chorotype: SEU-PELO. Range characteristics:** Balk(S). **Distribution in Europe**: **Balkan Peninsula** – S. Greece: restricted to the Peloponnisos (Stemnitza, Mt. Kyllene, Mt. Chelmos, Mt. Taygetos, Evrostina, Trikala, Mt. Erimanthos, Mt. Bostika).



31 001 duponchelii (Procerus)

Subspecies: No subspecies.

Ecology: Preferably on limestone soils; on N. slopes especially in forest with oak (*Quercus*) or pine (*Pinus*), but also on S. slopes in the low parts in bushes of mediterranean maquis (Cavazzuti, 1989). In favourable conditions from the montane forests up to 2000 m (Chelmos, Erymanthos, Taygetos).

Biology: **Activity** – Nocturnal (Cavazzuti, 1989: see *C. gigas*). **Periodicity** – No data. **Food** – A specialized mollusc-eater. **Larva**: Described by Cavazzuti (1989). Food – Same as adults.

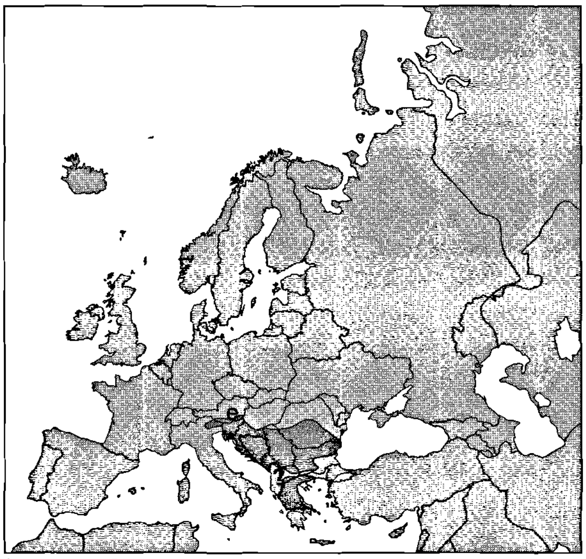
Conservation: In general, it is a rare species which is poorly represented in collections (Cavazzuti, 1989); no data on conservation.

31.002. C. (Procerus) gigas

Creutzer, 1799.

General literature: Checklists and catalogues – Breuning (1935): 1331. Březina (1994): 74; (1999): 72. Deuve (1994): 259 [689]. Kleinfeld & Schütze (1999): 39. Lorenz (1998): 102. Turin *et al.* (1993): 33. **Iconography** – Casale *et al.* (1982): fig. 127. Cavazzuti (1989): Pl. 1-2; Darnaud (1984a): Pl. 16. Ghiretti (1996): 350. Imura & Mizusawa (1996): Pl. 72 [585]. Pavicevic & Mesaros (1997): cd-rom.

Geographical range: S.E. Austria (possibly extinct), N.E. Italy, S. Hungary, S.W. Romania, Balkan peninsula except its S.W. part, probably Albania (but never cited) and N. and C. Greece. **Chorotype: SEU-DIBA. Range characteristics:** SEEur. **Distribution in Europe**: **Romania** (Csiki, 1946; Panin, 1952) – The N. margin of the distribution approaches the S. Hungarian border, but it does not occur in Hungary. The old 'Hungarian localities' are found



31 002 gigas (Procerus)

mainly in todays Romania, Banat Mts. (Domogled, Baile Herculane, Bocsa); also recently found in the Cerna valley. In S. Romania it penetrates from the N. of Bulgaria into Walachia, up to the S. Carpathians, very rare. **Bulgaria** (Cavazzuti, 1989; Hieke & Wrase, 1988; Guéorguiev & Guéorguiev, 1995) – Mainly reported from the S.W. (Sofia region; Pirin Mts. Macedonia) and S. (Rhodope Mts.); locally not rare. Also single reports from the Danube plain, Staraplanina Mts., and the Black Sea coast. **Balkan Peninsula** (Apfelbeck, 1904; Cavazzuti, 1989; Drovenik, 1995) – Widespread; in the N. from Slovenia along the Hungarian border to Beograd and Bulgaria. According to the above mentioned references, not in Vojvodina, but on the map that has been presented by Pavicevic & Mesaros (1997), the entire territory of former Yugoslavia is covered, except the coastal region along the Adriatic Sea. Most of the mainland, down to N. and C. Greece; not in the Peloponnisos. Not reported yet from C. Macedonia and Albania. Most records come from Slovenia and the S. of Austria; the relatively low number of Balkan records (see maps in Cavazzuti, 1989), can be explained by the low frequency of collecting over a long period. **Austria** – Only reported from Steiermark and Kärnten; heavily endangered or possibly extinct. **Italy** (Casale *et al.,* 1982; Cavazzuti, 1989) – Distributed but scattered in N.E. Italy (Veneto and Friuli-Venezia Giulia); from the Slovenian-Austrian border, through Friuli and the Prealps to Summano Mt. (Vicenza), and Valsugana in the W.

Subspecies: Cavazzuti (1989) mentions *parnassicus* as valid subspecies from Epyros and C. Greece.

Ecology: The most eurytopic among the European species of the subgenus (*C. scabrosus and C. sommeri* are more eurytopic in Asian Turkey), occurring in various types of pure or mixed forests and bushes, as well as in rather cultivated habitats such as gardens, parks, along road verges and in arable fields, mostly on limestone soils (Cavazzuti, 1989). It can be expected in many kinds of humid and shadowrich forests, however also well adapted to S. exposed mediterranean scrub, even if very dry, the most important condition being the presence of snails (*Helix* spp.). It can be quite abundant along shores of streams in forests. In C. Europa from lowlands to 1500 m, most abundant between 500 and 800 m; in Bulgaria up to 2000 m (Guéorguiev & Guéorguiev, 1995). Especially on wooded hills in humid beech forest. Also on rocky prairies (Du Chatenet, 1986). Preferably on limestone soil. In the lower parts mainly in hilly country (Magistretti, 1965).

Transects: Chapter 8: T-62, 64, 67-74 and 79.

Biology (Cavazzuti, 1989): **Activity** – Active during the night and especially at dawn, in the early morning (to 9/10 a.m.) and late afternoon (after 5 p.m.), preferably during rainy weather (Cavazzuti, 1989; Casale, *pers. observ.*). **Periodicity** (Hölzel, 1955; Hůrka, 1973) – Reproduction in spring and autumn. The eggs are among the largest in all *Carabus*, up to 12 mm (Sturani, 1962; Cavazzuti, 1989). Adults are active from the end of April to October/November (Sturani, 1962). Copulations of the young adults (emerged in the previous summer) from July onwards, during late summer and autumn. Old females, that take part in reproduction for a second time, copulate in the spring, from the second half of April onwards. Oviposition was observed in C. Europe between the second half of May and the end of August. In Italy, Sturani (1962) observed oviposition from the end of May until mid-October. Hibernation from November/December to April. **Food** (Larochelle, 1990) – In the field, snails (*Helix pomatia*), earthworms, carrion. In the laboratory, it accepted all kinds of snails, minced meat, raw meat, earthworms, fish, omelettes, gingerbread, bread soaked in sugared milk and apples. **Larva**: Described by Vacher de Lapouge (1905), Hölzel (1955), Sturani (1962), Hůrka (1971b), Raynaud (1976) and most detailed in Cavazzuti (1989). Food – exclusively snails (Zetto-Brandmayr & Brandmayr, 1998).

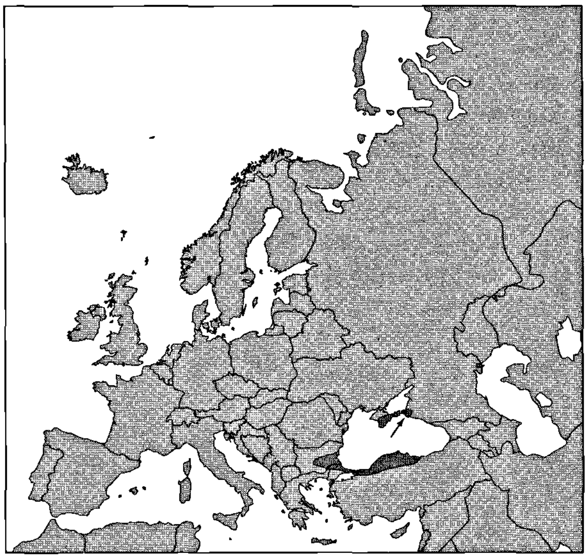
Conservation: In general not endangered, except in some ancient localities that are recently urbanised.

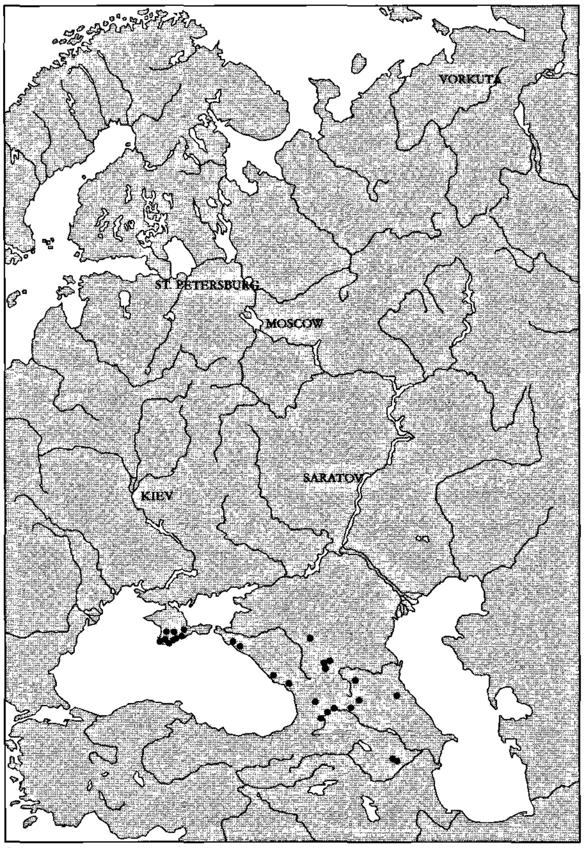
31.003. C. (Procerus) scabrosus

Olivier, 1789.

General literature: **Checklists and catalogues** – Breuning (1935): 1318. Březina (1994): 74; (1999): 72. Deuve (1994): 259 [690]. Kleinfeld & Schütze (1999): 39. Kryzhanovskij *et al.* (1995): 59 [292]. Lorenz (1998): 103. Turin *et al.* (1993): 34. **Iconography** – Cavazzuti (1989): Pl. 8-11. Darnaud (1984a): Pl. 16. Ghiretti (1996): 352. Imura & Mizusawa (1996): Pl. 73 [586].

Taxonomy: In contrast to the checklists of Březina (1994), Deuve (1994) and Turin *et al.* (1993), *C. scabrosus* is taken here in the narrow sense excluding *C. sommeri* which was separated by Cavazzuti (1989).


31 003 scabrosus (Procerus)



30 003 scabrosus

Geographical range: S.E. part of Balkan peninsula, the Crimea, Asiatic Turkey and W. Caucasus. **Chorotype:** POCA. **Range characteristics:** Balk(SE)-Crim-Cauc-Anat. **Distribution in Europe (and adjacent areas)**: **Russian Plain & Caucasus** – In the mountains and the S. coast of Crimea, Ciscaucasia and the Caucasus. It seems to be very common and locally abundant, for example in the collections of ZIN are preserved specimens from more than 25 localities in Crimea. In Ciscaucasia, its range does not go beyond the N. of Kuban river; the N. range margin, both in Crimea and Ciscaucasia coincides with 45°N. **Bulgaria** – C. and E. Stara Planina, Sredna Gora Mts., Tracian lowlands, Strandzha Mts., and S. Black-Sea coast (Guéorguiev & Guéorguiev, 1995). **Turkey** – European part (Cavazzuti, 1989), Bosporus and N.W. Anatolia.

Subspecies: Only European subspecies have been keyed: **a) subsp. scabrosus** – N. part of European Turkey and S.E. Bulgaria. **b) subsp. tauricus** Bonelli, 1810 – The Crimea except its steppe part.

Ecology: 0-1300 m (Guéorguiev & Guéorguiev, 1995).

Transects: Chapter 8: T-60.

Biology (Cavazzuti, 1989): **Activity** – No data. **Periodicity** – Berlov & Berlov (1997c) observed in the laboratory copulations and oviposition in April (egg size 9.1 x 4.2 mm. **Food** (Larochelle, 1990) – In the field, big snails. In the laboratory, mostly live snails (*Helix pisana*, *H. pomatia*, *H. vermiculata*), but it also accepted raw, minced and cooked meat, earthworms, fruits (apples, raisins, bananas and strawberries), cooked vegetables, omelettes, gingerbread and bread soaked in sugared milk. **Larva**: Described by Schaum (1864: L3), Sharova (1958: L1-L3) and Cavazzuti (1989). Food – in captivity, same as adults.

Conservation: No data.

31.004. C. (Procerus) sommeri
Mannerheim, 1844.

General literature: **Checklists and catalogues** – Breuning (1935): 1321. Březina (1994): 74; (1999): 73. Deuve (1994): 259 [690]. Kleinfeld & Schütze (1999): 39. Lorenz (1998): 103. Turin *et al.* (1993): 34. **Iconography** – Cavazzuti (1989): Pl. 4-8. Ghiretti (1996): 351-352. Imura & Mizusawa (1996): not listed.


31 004 sommeri (Procerus)

Taxonomy: By Deuve (1994), Lorenz (1998) and Březina (1999) listed as a subspecies of *C. scabrosus* Olivier.

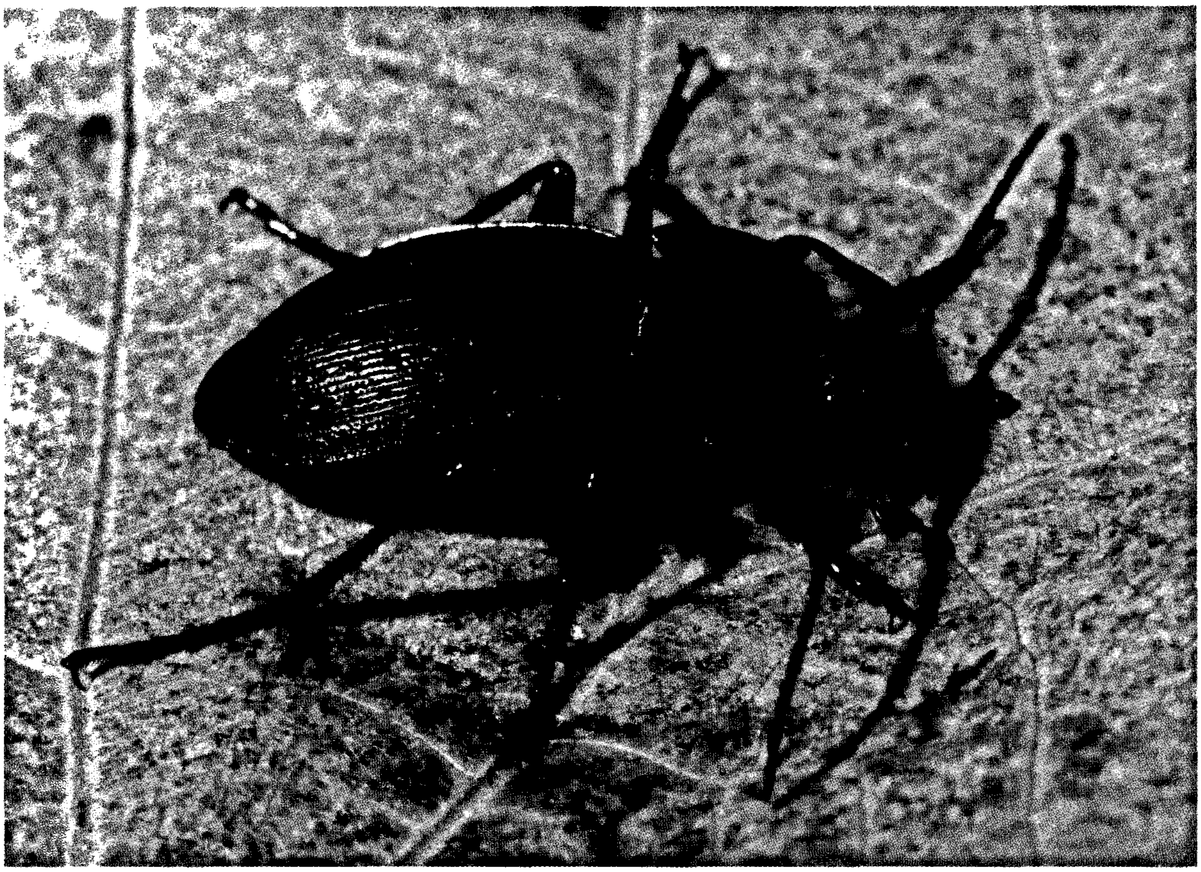
Geographical range: S.E. part of Balkan peninsula, Asiatic Turkey (C. and S.W. parts). **Chorotype:** ANAT. **Range characteristics:** Balk(S). **Distribution in Europe (and adjacent areas)**: **Bulgaria** (Guéorguiev & Guéorguiev, 1995) – Rhodope Mts. **Turkey** (Casale & Vigna Taglianti, 1999; Darge, 1991) – European part, Anatolia. **Balkan Peninsula** – Greece: N. of Xanthi.

Subspecies: In Europe only: **a) subsp. bureschianus** Breuning, 1928 – Bulgaria: C. Rhodopes: Asenovgrad, Backovo, Cepelare, Djovlen; S. Rhodopes – N.E. Greece: Xanthi region, Rhodopes at the Bulgarian border.

Ecology: In Bulgaria especially in forests with beech (*Fagus*) or oak (*Quercus*) at low and middle altitudes, up to 1500 m (Cavazzuti, 1989). In N. Greece, in association with mixed deciduous stands with *Quercus*, *Carpinus*, *Corilus* and/ or *Castanea*. At the Bulgarian border mainly in Fagetalia (Casale & Cavazzuti, *pers. observ.*).

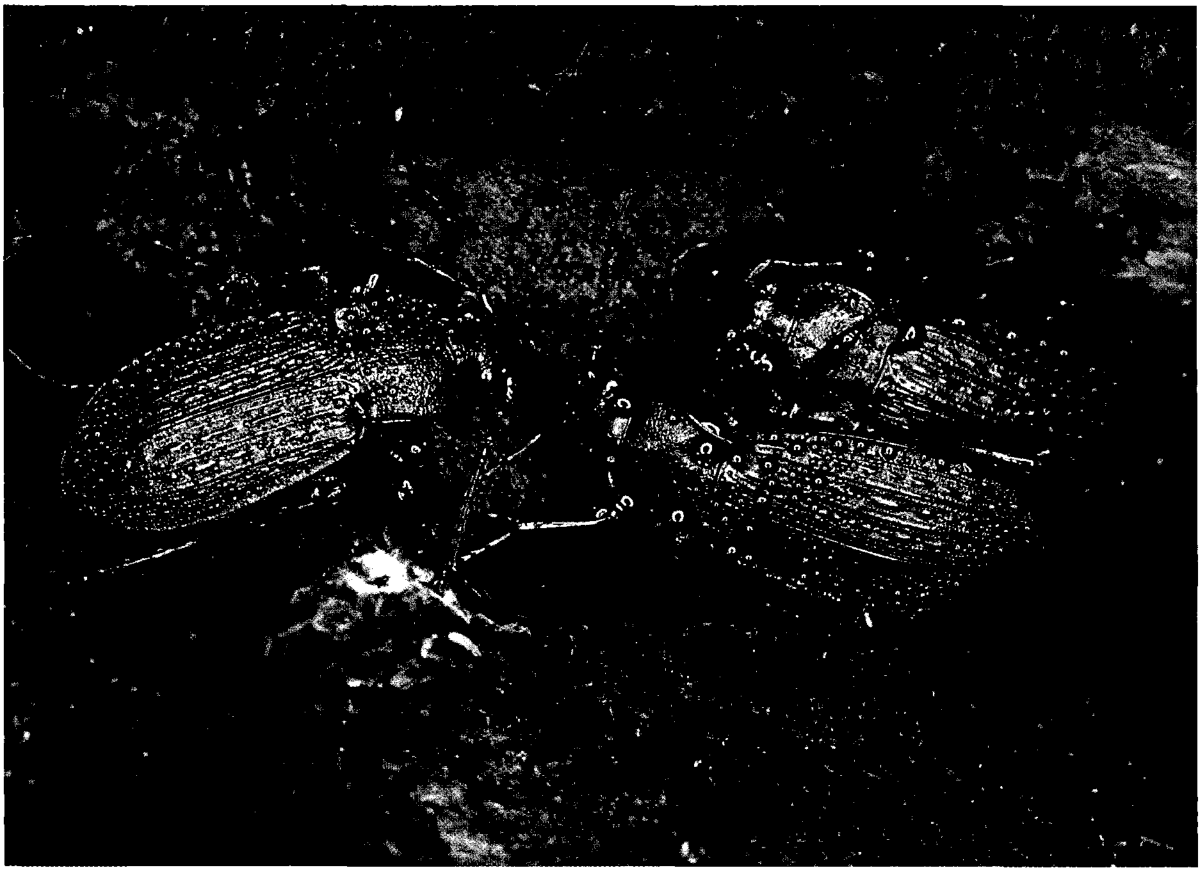
Biology: **Activity** – Night active, following same pattern as *C. gigas*. **Periodicity** – No data. **Food** – Snails (*Helix* spp.). **Larva**: Described by Cavazzuti (1989). Food – Snails.

Conservation: No data.



C. marietti
De Cristoforis & Jan
SW Bulgaria, Strandzha Mt. (Kachul). Photo by N. Kodzhabashev.

C. coriaceus
Linnaeus
Poland, Człuchowska Forest (Puszcza Człuchowska). Photo by J. Skłodowski.



C. granulatus interstitialis
Duftschmid
Italy, Latium (Central Apennine). Photo by A. Vigna Taglianti.

General Part

Chapter 6 Biology and ecology

Th. Assmann

6.1. INTRODUCTION

Millions of species, including an enormous number of insects, inhabit the earth. But biological research concentrates on just a few groups or species. This has resulted in a tremendous amount of knowledge focusing on a few groups or species. In most cases, these are characterised by special features (e.g. simple breeding, such as with *Drosophila* or *Escherichia coli*). The biological principles that have been found in the well-studied organisms are often also realised in many other taxa. It is therefore justified to work on such so-called 'model organisms'. The genus *Carabus* clearly belongs to the more intensively studied taxa of the insects. One important reason for the extensive knowledge of this genus is its attractive exoskeleton, which encourages many hobby-entomologists to study the distributions and morphological variation of these animals. Moreover, *Carabus* species are distinguished from most other insects by a number of characteristics which predestine these beetles to be studied from certain scientific approaches, and therefore to be model organisms. The aim of this chapter is to give an insight into the special morphological, physiological, ecological, population biological and evolutionary biological aspects of the genus *Carabus*.

6.2. THE LIFE FORM OF THE GENUS *CARABUS*

Systematic and taxonomic criteria already enable a definite delimitation of the genus *Carabus* within the ground beetles (cf. Chapter 1), but also the life form of this taxon allows a good characterisation of these insects. The significant or conspicuous features include: (1) medium to large body length, (2) small morphological differentiations (which can be interpreted – at least partly – as adaptive, e.g. 'cychrisation', 'licinisation'), (3) mainly epigeal locomotory activity (some species also ascend trees), (4) extra-intestinal digestion, (5) as a rule, constant brachyptery and hence the inability to fly which, in conjunction with stenotopy among many species, leads to (6) a marked differentiation of the populations in many ways, e.g. morphological, genetic and habitat preference.

6.3. REPRODUCTION AND DEVELOPMENT

6.3.1. Reproductive systems

The most important parts of the reproductive system in female *Carabus* species consist of a pair of ovaries (each containing several ovarioles), two lateral oviducts converging posteriorly of the ovaries, and a median oviduct opening posteriorly to the exterior at the gonopore. In addition to the primary parts, there are a large bursa copulatrix and a receptaculum seminis together forming the vagina. In the genus *Carabus* the bursa copulatrix shows strong sclerotisation on the ventral side.

The ovary is of the polytrophic type, i.e. the egg tubes of the ovarioles contain an alternating succession of an oocyte and several trophocytes (nurse cells), which are descendants, along with the oocytes from the oogonia (primary female germ cells), of the germarium. The follicle epithel is formed out of the mesodermal cells of the germarium, and surrounds the oocytes. The development of the oocytes shows two stages: (1) During previtellogenes there is an increased protein introsusception, which leads to the multiplication of the cytoplasma. At this stage the oocytes are transparent in translucent microscopy. (2) The yolk proteins, which are synthesised in the fat body, are incorporated during the vitellogenesis. After completion of vitellogenesis, the chorion (egg shell) is secreted by the follicle cells and the eggs are ready for oviposition. After oviposition the remnants of the follicle cells probably form the corpus luteum, which is obvious by its yellow to yellow-brown colour. In contrast to many other insects (e.g. Saltatoria: Singh, 1958) the corpus luteum is not resorbed but preserved much longer (at least for many months).

The male genitalia consist of a pair of testes (each containing a series of testicular tubes in which spermatozoa are produced), a pair of lateral ducts (vasa deferentia), and a median ductus ejaculatorius, the exit tube, which transports the semen to the gonopore. Accessory glands (formed as diverticula of the vasa deferentia) produce secretions, which form the spermatophore, the package that surrounds the spermatozoa. The aedeagus (penis or median lobe) contains the endophallus (internal sack), an inner chamber invaginated at the end of the aedeagus, into

◀ ***C. granulatus*** Linnaeus. The Netherlands, with mites. Photo by Th. Heijerman which the ductus ejaculatorius opens. The aedeagus is flanked at its base by a pair of differently formed and strongly sclerotised stalklets, called parameres.

Additional information about the female and male genitalia is given by Kern (1912), Franz (1929), Jeannel (1941), Hieke (1966), Meurgues & Ledoux (1966), Ishikawa (1973, 1978), Casale *et al.* (1982), and Deuve (1993, 1994).

6.3.2. Sexual attraction and the power of aggregation

The ability of both sexes to find each other is an important prerequisite for reproduction. In numerous insects, the males of any given species are able to detect pheromones produced and emitted by the females (Gullan & Cranston, 1994). In *C. auronitens*, almost three times more males were found in female-baited pitfalls than in male-baited or unbaited ones (Baumgartner, 2000). This attraction was detected during the reproductive season, but not during the autumn season when teneral beetles were active. A computer simulation indicated that the attraction range of a female was about two metres. *Carabus nemoralis* males were also attracted by *C. auronitens* females. – In *C. hortensis*, *C. glabratus*, *C. problematicus* and *C. violaceus*, pitfalls baited with females or males attracted significantly more individuals of either sex of the given species than did unbaited traps (Rosenkranz & Assmann, *in prep.*). This result indicates a power of aggregation in the species studied, as has already been described by Luff (1986) for another ground beetle, *Harpalus rufipes*. Extreme aggregation behaviour has evolved in *Brachinus* species, which form groups of about a dozen individuals. Wautier (1971) showed that the aggregations of these ground beetles depend upon olfactory stimuli (pheromones). The pheromones affecting sexual attraction and/or aggregation within/or between *Carabus* species are still unknown.

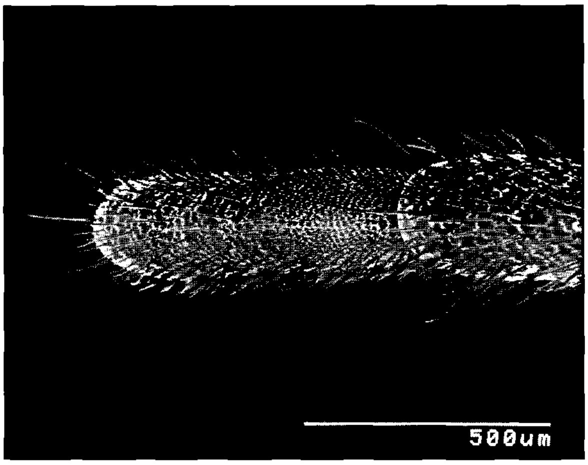


Fig. 6.1. Last segment of antenna, *C. auronitens punctatoauratus*, male. um: micrometres (photo: J. Lange & T. Assmann).

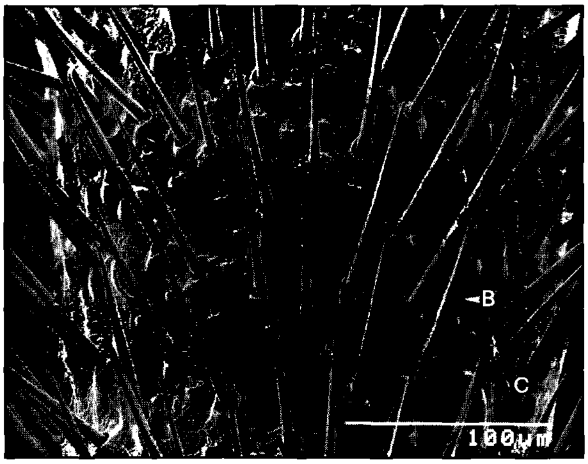


Fig. 6.2. Two different types of sensillae of the antennal segment 9, *C. a. punctatoauratus*, male. Long sensillae: sensillae chaeticae; short sensillae: sensillae basiconicae; um: micrometres (photo: J. Lange & T. Assmann).

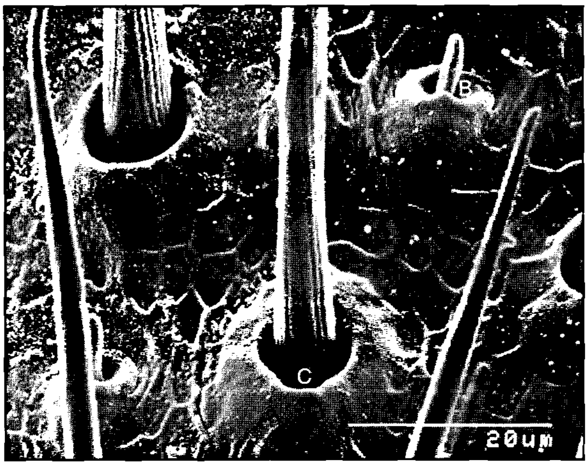


Fig. 6.3. Sensillae of the antennal segment 9, *C. a. punctatoauratus*, male. Long sensillae: sensillae chaeticae; short sensillae: sensillae basiconicae; um: micrometres (photo: J. Lange & T. Assmann).

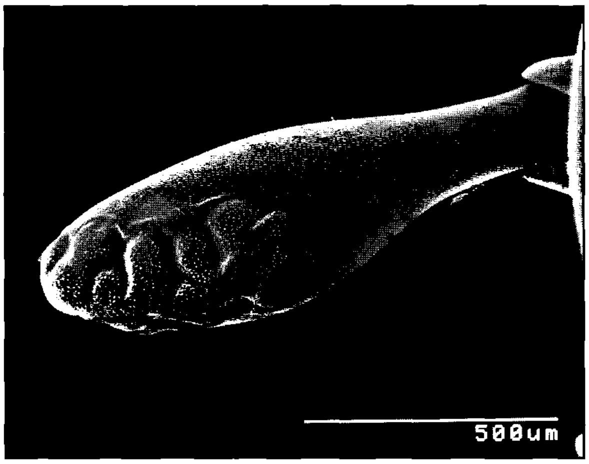
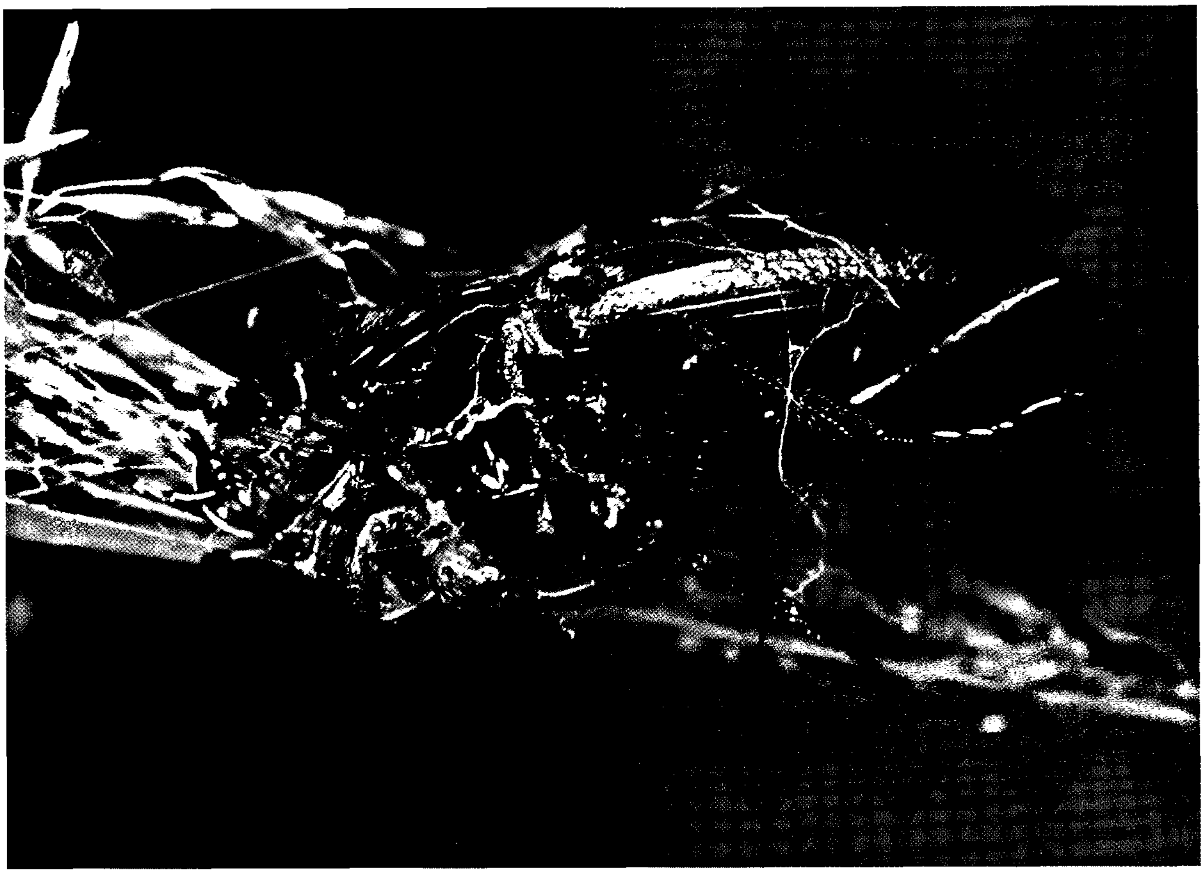
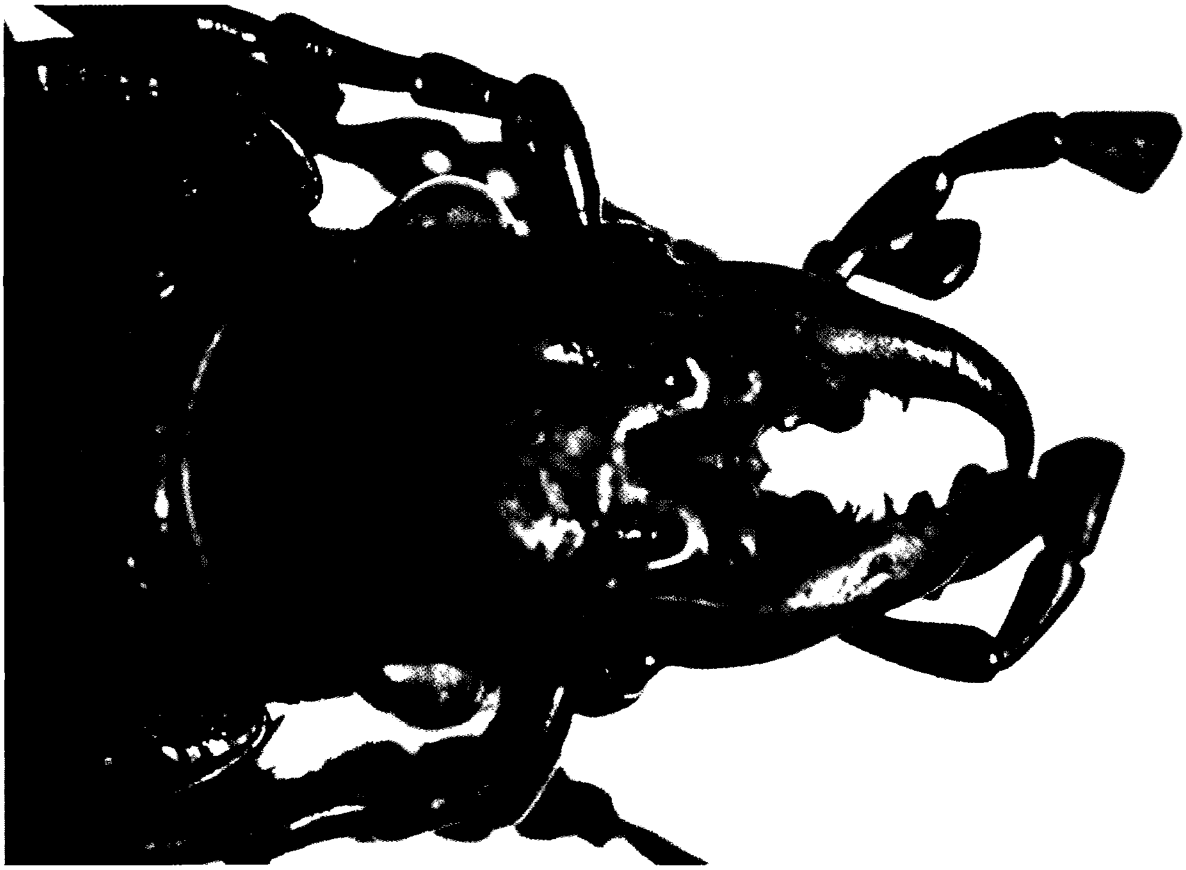


Fig. 6.4. Distal segment of the labial palp, *C. a. punctatoauratus*, male. um: micrometres (photo: J. Lange & T. Assmann). Notice the sensillae at the end of the segment.

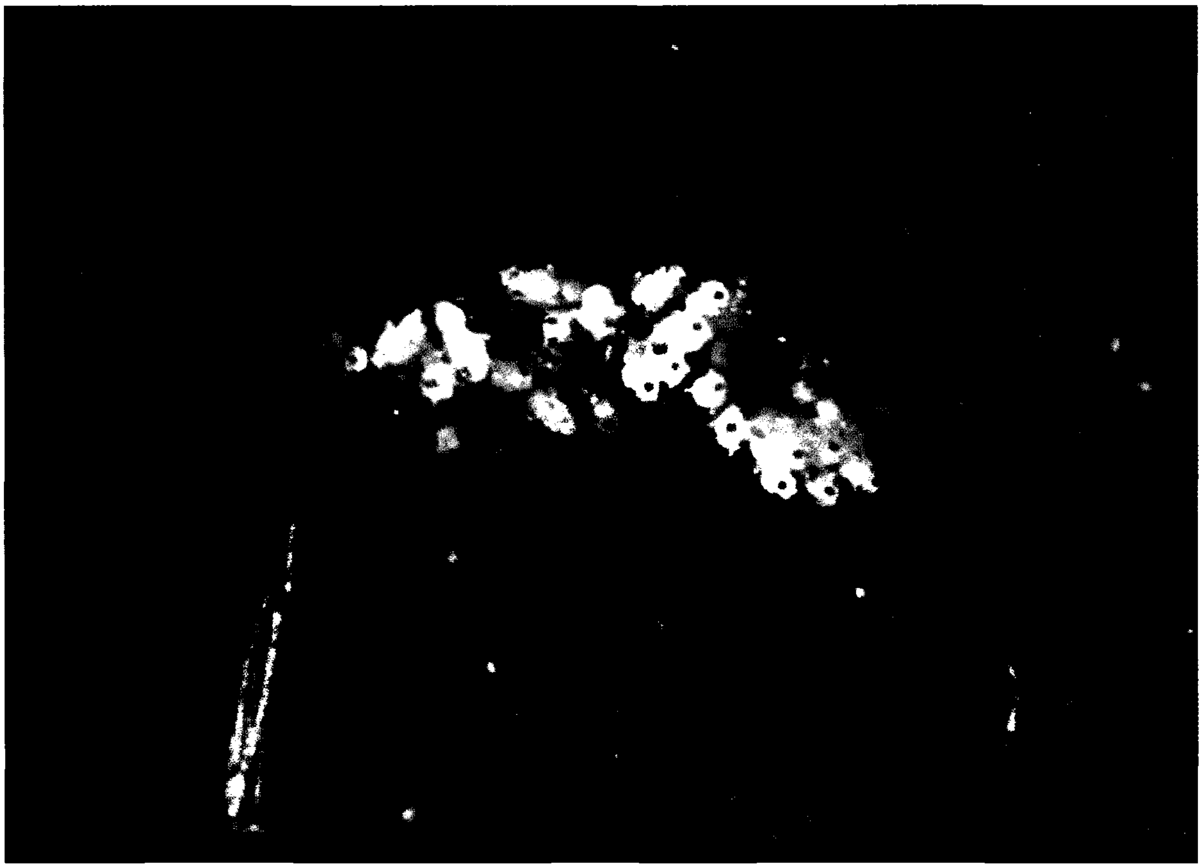


C. auronitens
Fabricius
The Netherlands, in spiders web.
Photo by
Th. Heijerman.

Pyrenaearia carascalensi shells, crushed by
C. pyrenaeus
Audinet-Serville
Canigou, France.
Photo by
Th. Assmann.



C. pyrenaeus
Audinet-Serville
France.
Photo by
Th. Assmann.



Puppae of
Phaenoserphus sp.
(Hymenoptera:
Proctotrupidae),
parasiting on
C. nemoralis
O.F. Müller
Moscow Province.
Photo by
K. Makarov.

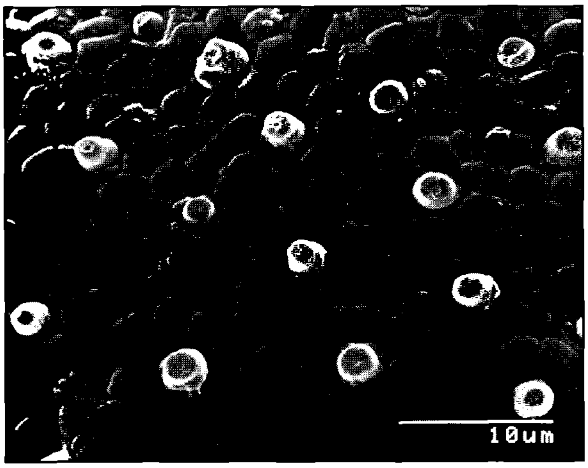


Fig. 6.5. Sensillae of the labial palp, C. *a. punctatoauratus*, male. um: micrometres (photo: J. Lange & T. Assmann).

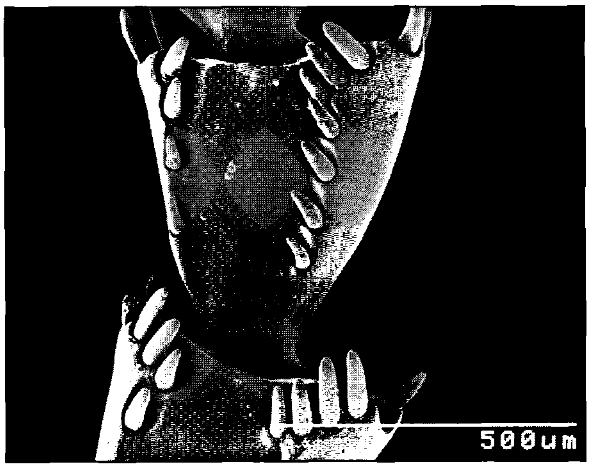


Fig. 6.7. Inferior side of protarsus 3, *C. a. punctatoauratus*, female. um: micrometres (photo: J. Lange & T. Assmann).

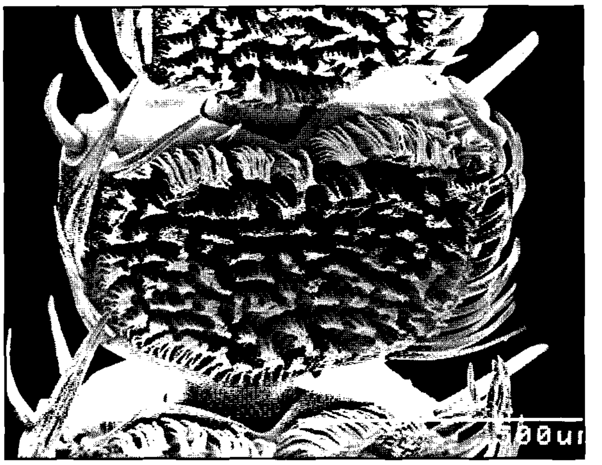


Fig. 6.6. Inferior side of protarsus 3 with adhesive setae, *C. a. punctatoauratus*, male. um: micrometres (photo: J. Lange & T. Assmann).

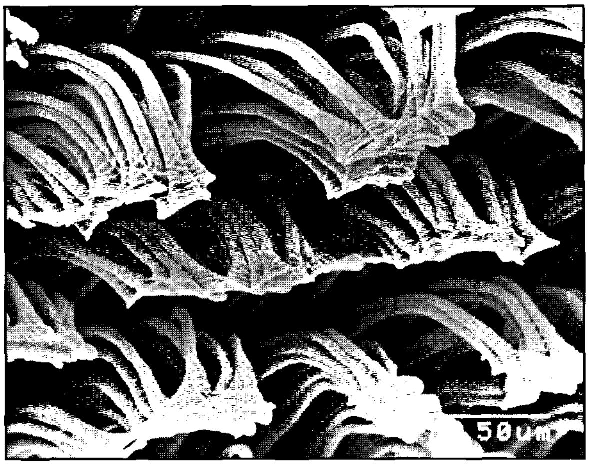


Fig. 6.8. Adhesive setae of protarsus 3, C. *a. punctatoauratus*, male. um: micrometres (photo: J. Lange & T. Assmann).

6.3.3. Copulation

Copulation has been described by some authors (e.g. Kern, 1921; von Lengerken, 1921). In most cases, the male approaches the female from the side or the back and feels her with his antennae, the segments 5-11 of which contain numerous sensillae (cf. Figs 6.1-6.3)[1]. The male then moves forwards so that the mandibles (and palpi, respectively) of both sexes touch each other (cf. Figs 6.4, 6.5). Sometimes the female raises her head during this period of precopulation. Subsequently, the first two pairs of legs of the male are wrapped around the thorax of the female. In males, a variable number of protarsal segments (2-4) are enlarged and possess adhesive articulo-setae (cf. Figs 6.6-6.8), which are supposed to hold the female during copulation (Stork, 1980). Following insertion of the penis, the endophallus is turned out in the female vagina and the copulatory piece (an apophysis of the endophallus) is inserted into a vaginal appendix. The duration of copulation ranges from a few minutes to a few hours. In few species the copulatory piece is reduced to a pigmented field (Franz, 1929; Ishikawa, 1973). External form and structure of the endophallus are important characters for reconstructing phylogeny (cf. Chapter 7).

The exact 'interaction' of the male and female genitalia parts may be important to prevent interspecific copulation and therefore to realise reproductive isolation. This 'lock-and-key' hypothesis has been criticised in many cases due to the lack of evidence that differences in genital morphology of closely related species actually affect copulatory success (e.g. Eberhard, 1985; Shapiro & Porter, 1989; Goulson, 1993). Within the genus *Carabus*, at least two character pairs are perhaps of importance as parts of a 'lock-and-key' mechanism: the endophallus and bursa copulatrix, as well

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[1] The distal part of the labial palp also contains numerous sensillae (Figs 6.4, 6.5).

as the copulatory piece and vaginal appendix, may correspond to each other. Sota & Kubota (1998) demonstrated experimentally that the genital characters of the copulatory piece and vaginal appendix impose a direct cost on interspecific copulation of the closely related species *C.* (*Ohomoptera*) *maiyasanus* and *C.* (*O.*) *iwawakianus* from Japan. Mortality of females increases significantly after heterospecific mating, due to the rupture of their vaginal membranes. Males of one species (*C. maiyasanus*) often show broken copulatory pieces following interspecific copulation. The fertilisation rate of eggs laid after interspecific copulation was reduced. These results indicate that the fitness cost of interspecific mating was very large. Therefore genital lock-and-key appears to exert significant selection against hybridisation in these *Carabus* species. Meurgues & Ledoux (1966) demonstrated the conspicuous congruence of the external form of the endophallus, and the internal form of the bursa copulatrix for *C. violaceus purpurascens*. A test for the lock-and-key hypothesis in this case, as in any other *Carabus* species, is still lacking.

Observations on laboratory specimens show that females can copulate with different males several times during their period of activity (e.g. Kern, 1921; von Lengerken, 1921; Sturani, 1962). It is not yet known whether a spermatophore is passed on with each copulation. Neither is it known whether the offspring of a female during a period of activity are the progeny of one or more males. Investigations of another carabid beetle (*Poecilus lepidus*) prove that the descendants of a female can originate from more than one male (up to 4 males proved by genetic analysis: de Vries, 2000).

6.3.4. Eggs

With the apex of their abdomen, the females dig a small hollow in the substrate, in which they deposit their eggs. All eggs are laid separately (Kern, 1921). The females of some *Carabus* species dig themselves into the ground completely before deposition of eggs (e.g. *C. auratus*; von Lengerken, 1921), whereas females of other species remain above the ground and introduce only the abdomen into the soil to form the egg chamber (e.g. Sturani, 1962). Huk & Kühne (1999) interpret the laying of single eggs, which is a feature of the genus *Carabus*, as a mechanism to reduce the risk of cannibalism. Larval cannibalism is frequently documented during the rearing of *Carabus* larvae (e.g. Kern, 1921) and is considered a possible mechanism to regulate population densities in another ground beetle (*Pterostichus oblongopunctatus*: Brunsting & Heessen, 1984).

The number of eggs laid per female is only known from captivity, and fluctuates greatly according to the individual and the species. Scherney (1957) and Huk & Kühne (1999) give values of between 56 for *C. auratus* and 9 for *C. clatratus*. It remains to be seen whether such numbers do also occur under natural conditions. In order to gain a better understanding of the reproductive and population biology, it is furthermore important to know whether there is a correlation between the number of ovarioles and the number of eggs laid, and whether the number of ovarioles fluctuates within a certain species. Such relationships and intraspecific variability have been determined for, e.g. *Drosophila melanogaster* (Wayne *et al.*, 1997).

The egg size is highly significantly and positively correlated with the body length of the imagines (Fig. 6.9). Small eggs are laid by, e.g. *C. convexus* (2.7 mm); the largest eggs are found among in *C.* (*Procerus*) *gigas* (12 mm) and *C. coriaceus* (10 mm) (Sturani, 1962; Cavazzuti, 1989). However, it must be emphasised that variation between species is considerable. Thus *C. catenulatus*, which on average is over 3 cm long, lay eggs of just 3.5 mm length, whilst those of the *C. coriaceus basilicatus*, which is of the same length, are approx. 8 mm long. The reasons for these differences are as yet unknown. The proportions of the eggs (in particular in comparison with other insects) are regarded as extraordinarily large (cf. Gullan & Cranston, 1994). Thus, the investment in a single egg with its high yolk content is great among members of the genus *Carabus*.

In view of the low number and large size of eggs the place of their deposition is of special importance. In the laboratory, Huk & Kühne (1999) showed that females of *C. clatratus* changed their substrate selection behaviour after copulation. Oviposition experiments revealed a distinct preference for wet peat (in contrast to dry peat and peat mixtures with sand). Egg mortality does not seem to be influenced by soil conditions (less than 7 % under both wet and dry conditions), but mortality of third instar larvae and pupal stage as well as deformations of the exosk-

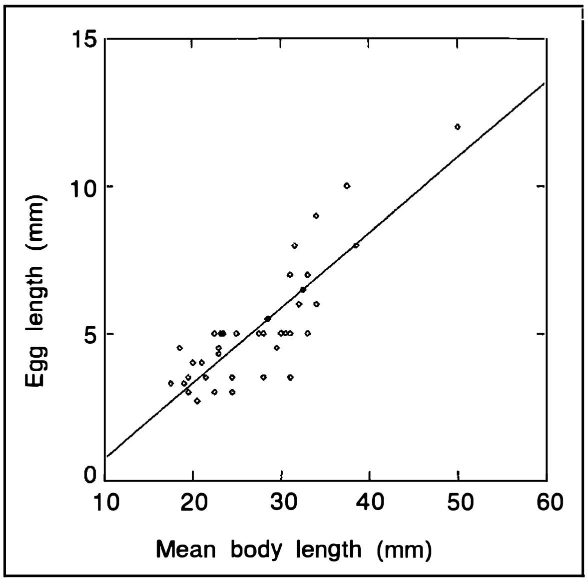

Fig. 6.9. Relationship between mean body lenght of imagines of 38 European *Carabus* species and subspecies (after Breuning, 1932-1937) and the egg length (after Sturani, 1962 and Cavazzuti, 1989)(multiple r=0.848, p<<0.001).

eleton increase, and the mean body size of immature adults decrease strongly under dry conditions. Therefore substrate selection for oviposition seems to be an important strategy of parental care[2] ('Brutfürsorge').

6.3.5. Larvae

The larvae hatch after an embryo development of several days (at 18°C: *C. auratus*: 5-6 days; *C. nemoralis*: 21 days; see Sturani, 1962 for a detailed description). As with many other ground beetles, larval development comprises three larval stages (e.g. Luff, 1993). On the basis of morphological characters, Bengtsson (1927) and Lapouge (1929) divided the larvae into three groups. These have gained acceptance from numerous other authors (e.g. Turin *et al.*, 1993): (1) the *Archeocarabus* group (= *Carabes serrilabres*) with larvae characterised by small tergites and short legs, (2) the *Neocarabus* group (= *Carabes rostrilabres*) with larvae showing very broad tergites projecting from the body and relatively long legs, (3) and the *Metacarabus* group (= *Carabes quadricuspides*) exhibiting intermediate characters (for a more detailed description of the 3 groups see Chapter 4). The different habitus of the larval groups is interpreted in the light of (presumably) divergent habitats: the *Archeocarabi* may be able to dig burrows into the soil, and prefers to live in open land. The *Neocarabi* may be more adapted to living in the litter stratum of woodlands.

In order to compare the larval behaviour of *C. granulatus* and *C. clatratus* in the field, Huk & Kühne (1999) used pitfall samples on different meadows. Both species have larvae of the *Archeocarabus* type. Whereas no larvae of the latter species were found, *C. granulatus* larvae were frequently caught. The legs of *C. granulatus* larvae are significantly longer than those of *C. clatratus* (Huk, 1998). This is perhaps an incidence for the more endogeic life of *C. clatratus* during larval development. The epigeic active larvae of *C. problematicus* are of the *Metacarabus* type. Betz (1992) shows that they also contribute to dispersal: in its 3rd instar, a larva could move up to 32.1 m within 25 days. The larvae of *C. auronitens* are of the *Neocarabus* type. During a long-term study in the Westphalian Lowlands (Germany) they were only rarely caught in pitfall traps. But the year of 1990 was an exception: numerous larvae were found in the pitfall traps (in this year, the young beetles were significantly smaller than those of the previous year (Althoff *et al.*, 1992). These examples show that larval behaviour is not simply linked to morphological characters, as suggested in the first papers about *Carabus* larvae.

Due to the (assumed) high vulnerability of the larval (and other pre-imaginal) stages (Lövei & Sunderland, 1996), length of development is an important ecological factor. Data concerning larval development in the laboratory are given by Sturani (1962). At 18°C, the period of development ranges from 30 (*C. arvensis*) to 80 days (*C. solieri*). In general, it is difficult to study larval development in the natural habitat, because egg deposition occurs asynchronically (often over a period of several weeks). The three instars therefore show a strong temporal overlap. The sparse field data available suggest that the same periods of development are found under natural conditions. In a Westphalian woodland, *C. auronitens* completes its larval development in 4-6 weeks (summer larvae; Althoff *et al.*, 1992; Weber, *pers. comm.*). Grüm (1984) mentioned a period of development of 80-100 days. Species with winter larvae may need more time (cf. the data from van der Drift, 1958; Rijnsdorp, 1980; Betz, 1992), but they are able to show locomotory activity at surprisingly low temperatures: in a woodland near Marburg (Germany) appreciable catches of the winter-active *C. problematicus* larvae in pitfall traps were obtained at mean daily temperatures of little over 3°C (Betz, 1992).

Many *Carabus* larvae are specialised snail-feeders (e.g. Cavazzuti, 1989; Luff, 1993). The larvae of some species show morphological features, which could be interpreted as an adaptation to a particular prey (comparable to the imagines, see section 6.5). An example may be *C. cychroides* (a species specialised in eating *Helicigona glacialis*) with its toothed terebra[3] and retinaculum[4], and small forebody (Casale *et al.*, 1982, 1998; Arndt, 1985). Similar toothed inner sides of the mandibles and relatively small heads are found in the larvae of Cychrini and Licinini, both categorised as specialised snail-feeders in larval instars as well as in imagines (Arndt, 1991a; Luff, 1993). Detailed analyses of hunting and eating behaviour of larvae are still missing for the genus *Carabus*. But with all probability, the larvae of some species do not live exclusively on snails, because snails are extremely rare or absent in some habitats (e.g. *Sphagnum* bogs: *C. nitens* and *C. clatratus*; swamp peat forests: *C. violaceus*; *own observ.*).

The mean growth ratios (head width of L2/head width of L1 and head width of L3/head width of L2, respectively) are small for *Carabus* larvae (from 1.21 to 1.38), compared with other holometabolous insects. This is perhaps a consequence of the large egg size and the few larval stages (Huk & Kühne, 1999). The fully-grown larvae had only about 15 % of the dry weight of the mature imago (Grüm, 1975a). The weight differences between newly hatched and mature individuals result from rapid feeding by the tenerals. Grüm (1975b) and Lövei & Sunderland (1996) assumed that highest mortality in the *Carabus* life cycle occur during larval stages. For other ground beetles (e.g. *Nebria brevicollis*;

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[2] Parental care encompasses any form of parental behaviour that appears likely to increase the fitness of a parent's offspring (Clutton-Brock, 1991).

[3] Distal, long incisive edge of the mandible.

[4] Basal part on the inner side of the mandible.

Nelemans, 1987a, b; 1988) it was shown that the growth of larvae is largely dependent on food supply. Moreover, *Carabus* larvae do not seem able to starve for long periods. Larval mortality is about 47 % in *C. clatratus* after a period of only 7 days without food (Huk, 1998). The starvation capacity of newly hatched *C. violaceus* larvae ranges from 9 to 15 days at 10°C (Luff, 1994).

Little is still known about the biology and ecology of *Carabus* larvae. One important reason for this seems to be that rearing is very difficult in many species. Surprisingly, rearing is rather more successful in some stenotopic species than in a lot of eurytopic ones (cf. Mossakowski, 1971; Hůrka, 1972; Huk & Kühne, 1999; 2000). Another reason may be the low capture rates in pitfall traps because of the locomotory activity of larvae in the natural habitat.

6.3.6. Pupae and tenerals

Pupation occurs in a hollow in the ground and lasts from four to 20 days (at 18°C; Sturani, 1962). The exarate adecticous pupae of many species are described by Sturani (1962) and Casale *et al.* (1982). The newly emerged beetle is white with dark appendages (incl. mandibles), and after one to a few days the characteristic colour has usually developed (Kern, 1921; Sturani, 1962; Huk, 1998). The tenerals of some species may remain in the pupal hollow (e.g. *C. auratus*; Scherney, 1957). However, in most cases they leave the hollow and show obligatorily feeding behaviour (at least for a short time) (e.g. *C. auronitens*: Althoff *et al.*, 1992). The latter is also true for a lot of species assumed (by some authors) to stay in the pupal hollow for a longer period after moulting (e.g. *C. clatratus*: Huk, 1998; *C. nodulosus*, *own observ.*). The endocuticle (inner layer of the exoskeleton) is formed over a number of days. In *C. auronitens*, the mean postecdysial development of the exoskeleton takes 20 to more than 30 days. If the tenerals starve, mortality is very high (e.g. 80 % after a starving period of 10 days) (Klenner, 1989). These data demonstrate the necessity of a teneral activity shortly after emergence for this species.

6.3.7. Rearing

The rearing of *Carabus* species has a long tradition in carabidology. Starting about a century ago, Zang (1901), and subsequently Verhoeff (1917), von Lengerken (1921) and other biologists, reared many species with the aim of obtaining all the developmental stages and also for systematic purposes (see above). In addition to eco-physiological investigations, taxonomic and phylogenetic problems have also been an additional important focus in breeding programmes. In one case (*C. olympiae*), a great breading program was done to release the beetles into nature (cf. section 9.4).

Following Hůrka (1996), laboratory rearing can be carried out in containers with a layer of the substrate in which the species live or of sifted garden soil, a few cm in depth. Because cannibalism is a common phenomenon within the genus *Carabus*, it is best to separate the eggs individually into Petri dishes (about 10 cm in diameter) with the substrate just described. Appropriate light conditions (see section 6.4 for discussion of the control of gonad development by the photoperiod) and temperature (between 15 and 20°C) and a moist substrate to provide air humidity are prerequisites for successful breeding. Larvae and adults of many *Carabus* species accept mealworms (larvae of *Tenebrio molitor*), earthworms and gastropods. They also feed on scrapes of raw meat, but sometimes the mandibles and other mouthparts become clogged up with fat and then there is a strong rise in the mortality rate. The same may happen after intensive consumption of ripe fruit, which are very attractive for many *Carabus* adults. In most rearing experiments, larval mortality is very high (cf. the values given by Hůrka, 1972 and Huk & Kühne, 1999). The best and most adequate food is probably the natural prey (e.g. earthworms for *C. auratus* and snails for *Procerus*, *Iniopachys* and *Platycarabus* species: Cavazzuti, 1989; *pers. observ.*). The best breeding results can be obtained in outdoor terraria (cf. Sturani, 1962; Hůrka, 1996). A short but nonetheless very helpful overview dealing with different aspects of rearing ground beetles is given by Hůrka (1996).

6.4. ACTIVITY

6.4.1. Daily rhythms

Daily rhythm of *Carabus* species has been studied in many field investigations using pitfall traps (incl. time sorting traps: e.g. Skuhravý, 1956; Lauterbach, 1964; Grüm, 1966; Novák, 1971, 1972, 1973; Schiller & Weber, 1975; Grimm & Jans, 1984) and in laboratory investigations using actographs (e.g. Greenslade, 1963; Kirchner, 1964; Weber, 1965a, 1966a, 1966b, 1968a, 1983; Lamprecht & Weber, 1971, 1973; Neudecker, 1971; Balkenohl & Weber, 1981; Meyer-Peters, 1988, 1993a, b). An important review was published by Thiele & Weber (1968). From the 24 species analysed, 16 were strictly night-active and only four species showed relatively high day activity (over 45 % of activity during the day); the others occupied an intermediate position. The patterns of daily activity depended considerably on individual and seasonal features. For example *C. cancellatus* is a night-active species, but during its reproductive period, diurnal activity also occurs (Weber, 1966a). Within the same population of *C. auratus*, individuals are predominantly diurnal, nocturnal or intermediately active (Thiele & Weber, 1968). Moreover, geographic location significantly influences activity patterns. *Carabus glabratus* and *C. violaceus* populations in Central Europe are predominantly night-active, but in northern Scandinavia, the same species are also active during the day (Thiele & Weber, 1968; Neudecker, 1971).

For the Japanese species *C. yaconicus*, Yamashita & Kanehisa (1979) revealed a complete change in the main activity period from diurnality to nocturnality. A similar change in activity patterns is described by Meyer-Peters (1993a) for *C. auronitens* under natural light-dark (LD) cycles. During the reproductive period in spring, the beetles are mainly nocturnally active, whereas in summer (shortly before aestivation), activity peaks turn into diurnality within one day. No geographic differences could be detected in 285 beetles from 13 populations ranging from southern France to northern Central Europe.

Within the genus *Carabus*, daily rhythm is controlled by an 'internal clock' (Kirchner, 1964; Weber, 1968a)[5]. Under constant conditions (especially with respect to light) meaning that 'Zeitgebers' are missing (that is without external time impulse), many beetles show a free-running activity with a periodicity deviating significantly from 24 h. With the dark-active *C. problematicus*, the free-running activity shows a periodicity of less than 24 hrs. In actographs with an LD 12/12 (12 h light and 12 h darkness), a period of 'preactivity' could be found before the onset of darkness, in which the beetles got 'ready' to start their locomotory activity. This may be interpreted as a mechanism of 'endogenous preparation'. Immediately after the signal 'light off', they could be very active (e.g. Weber, 1983). This phenomenon, but not the 'preactivity', is in agreement with field observations on this and other nocturnal *Carabus* species, which show the highest activity during the first hours of the night (e.g. *C. auronitens*, but not *C. nemoralis*; Hockmann *et al.*, 1992; *C. problematicus* and *C. glabratus*; *own observ.*).

Synchronisation potential and its variability exhibit an extreme plasticity in the endogenous periodicity. After phase reversal of the 'Zeitgeber' some members of the genus *Carabus* are able to resynchronise after very few periods (e.g. *C. problematicus* at 75-250 lux: 1-2 periods, Weber 1966b). Many *Carabus* specimens can follow short 'Zeitgeber' periods (e.g. LD 8/8 for *C. cancellatus*; Lamprecht & Weber, 1971), but other specimens of the same species do not seem to be influenced by the 'Zeitgeber' and are active for a period deviating from 24 h. In numerous other animals it is not possible to synchronise the daily rhythm by such short 'Zeitgeber' periods.

6.4.2. Annual rhythm

Larsson (1939) was the first to describe different annual rhythms of ground beetles, which correspond with reproduction and development. Larsson (1939), Thiele (1977) and Paarmann (1979) recognised 5 types[6]: (1) 'Autumn breeders' which exhibit a peak of activity of imagines during summer and/or autumn, during which period the imagines reproduce; larval development occurs during winter. (2) 'Spring breeders with autumn activity' lay eggs in spring and early summer, larvae appear in summer and the tenerals are active in autumn. (3) 'Spring breeders without autumn activity' have the same reproductive activity as type 2, but the tenerals are not active during autumn.[7] Additionally, there are species with a (4) flexible reproduction period (e.g. *Abax parallelepipedus*, see Thiele, 1977) and (5) ground beetles that require more than one year to develop (e.g. *Cicindela* species). Under cold conditions (in high mountains and in northern Europe) some *Carabus* species exhibit the latter type ('biennial development cycle', e.g. *C. glabratus*, *C. violaceus*, *C. coriaceus*; Houston, 1981; Refseth, 1984; Lindroth, 1985). Differences in the annual activity of conspecific populations living at low and high altitudes are interpreted as their adaptation to the diverging environmental conditions (e.g. *C. creutzeri*: Brandmayr & Zetto-Brandmayr, 1979; *C. problematicus*: Sparks *et al.*, 1995; see also Sota, 1994).

Especially in subregions of Central Europe, which experience mild winters (e.g. near the Atlantic or the North Sea), some ground beetles reproduce preferentially during winter (e.g. *Bembidion nigricorne*, *Amara infima*, *Bradycellus* and *Trichocellus* species; den Boer & den Boer-Daanje, 1990). In the northern half of Europe, no *Carabus* species is known with such a reproduction period. The 'earliest' *Carabus* species in this region is *C. nemoralis*, which commences its activity period and oogenesis in February/March (Kern, 1912). But in southern Europe, some species may be considered 'winter breeders' (e.g. *C. dufourii* in the lowlands of Andalusia, Cardenas & Hidalgo, 2000; *own observ.*, *C. alysidotus* in lower altitudes near Rome: Casale *et al.*, 1982, and *C. morbillosus*: Casale *et al.*, 1982). Further studies with ovary dissections and of larvae are necessary.

In a more recent paper dealing with the analysis of reproduction and developmental periodicity of ground beetles in the province of Drenthe (the Netherlands), den Boer & den Boer-Daanje (1990) recommend a distinction between only two groups: (1) species with summer larvae and (2) species with winter larvae. The former group corresponds to the 'spring breeders' and the latter one to the 'autumn breeders' of Larssons scheme. However, the terminology of den Boer & den Boer-Daanje (1990) seems to be more accurate because numerous studies have demonstrated that *Carabus* imagines are able to reproduce several times, while some species have a different seasonal activity of first-year and older adults. Schjøtz-Christensen was the first to prove the iteroparity of ground beetles by

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[5] In members of the genus *Carabus*, the 'master clock' is not localised in the centre of the brain, the protocerebrum, but in the lobus opticus (as in cockroaches and some other insects) (Balkenohl & Weber, 1981).

[6] This scheme also seems to be valid for the Mediterranean region (cf. Cárdenas, 1994).

[7] It does not seem to be absolutely clear whether the latter 2 reproductive types really differ from each other, since a lot of spring breeders have tenerals which are active for only a very short time (see section 6.2). These specimens can easily be overlooked.

dissecting their ovaries[8] (Schjøtz-Christensen, 1965) and by mark-recapture experiments (Schjøtz-Christensen, 1968). Further investigations on the genus *Carabus* with at least one of the two methods have now been described (e.g. Althoff *et al.*, 1992; Storre *et al.*, 1996; Baumgartner *et al.*, 1997; Assmann & Janssen, 1999; section 6.2). In each *Carabus* species studied, a life span of more than one year was demonstrated, at least for some individuals. It can therefore be speculated that iteroparity is a special feature of the genus *Carabus* (for the longevity of other carabid species, see for example Rusdea, 1994).

The control of gonad development and hence the annual rhythm of ground beetles by the photoperiod was studied intensively by Thiele and co-workers (review: Thiele, 1977; see also: Ferenz, 1977, 1986). With a spring breeder (e.g. *Pterostichus nigrita*), previtellogenesis (euplasmatic growth of oocytes) is determined by short-day conditions (e.g. LD 8/16), which occur during autumn, when the young beetles of many species are active. Long-day conditions, which occur during spring and early summer, after this phase initiate the vitellogenesis and hence the oogenesis (see also section 6.2). If a young female is first exposed to long-day conditions, neither previtellogenesis nor vitellogenesis is initiated, meaning that the sequence of short- and long-day conditions is decisive for the maturation of ovaries. Similar reproductive controls by the photoperiod were found in other ground beetles (spring and autumn breeders) and can also be assumed for *Carabus* species, although it has not been proved by experiments. This gap in our knowledge is at least partly due to the problems of rearing many species of this genus.

Sometimes a certain species is characterised by several authors as a spring breeder (with summer larvae) and by others as an autumn breeder with winter larvae. An example of such a diverging classification is *C. auronitens*. Following Hůrka (1972), this species shows larval development during winter in Czechia, whereas in the Westphalian lowlands it is a true spring breeder with summer larvae (Althoff *et al.*, 1992). In montane altitudes of the Westphalian Sauerland, larvae also hibernate beside imagines (Hemmer & Terlutter, 1987). In a translocation experiment in the Westphalian lowlands, Schwöppe *et al.* (1998) examined the population biology of *C. auronitens* populations from this montane altitude under lowland conditions. In spite of the environmental conditions, which differ from those in their region of origin, the individuals (in the parental and offspring generation) showed a seasonality characteristic of montane populations (especially the later ending of the spring season). This indicates that the differences in annual activity are at least partly genetically controlled (i.e. by different alleles) and that they are the consequence of an evolutionary process. Additionally, environmental modifications may occur.

6.4.3. Locomotory activity and orientation

Most ground beetles are known to be rapid runners with slender legs, which led to the German name 'Laufkäfer' (literally translated as: 'running beetles'). Some members of the genus *Carabus* are particularly fast runners: the maximum speed recorded by Mossakowski & Stier (1983) in the laboratory was 25 cm/s for *C. problematicus* (*C. coriaceus* was the slowest of ten species studied: maximum speed: 7.7 cm/s)[9]. As with most other insects, running with six legs occurs by a tripod of the foreleg and hindleg on one side and the midleg of the opposite side, whilst the opposite legs are moved forwards. The centre of gravity during running always lies within this tripod (Gullan & Cranston, 1994).

But the legs and coxae are functionally not only adapted to running, but also to pushing (as with many other terrestrial Adephaga). Evans (1977) detected on the forelegs of *C. problematicus* four major features, which are modifications to strengthen leg articulations (reduced trochantin, sternal coxal articulation, lateral femoral flanges, and tarsal feathering system). The midleg is similar, but the coxo-sternal articulation is less well defined and the feathering mechanism is lacking (due to diverging orientation of the leg). The hindleg can deliver a powerful forward thrust to the body and a vertical thrust with its femoral reductor (rotator) muscle in the trochanter. Both functions enable *Carabus* species to penetrate horizontal crevices in litter by wedge pushing (Evans 1986).

Forsythe (1981, 1983) and Evans (1986) arranged carabid beetles into three groups based on leg structure: group I has evolved better running ability but poorer pushing ability; group III is characterised by strong pushing potential and slow running speed; group II shows intermediate characters. The genus *Carabus* (and *Calosoma* and *Cychrus*) cannot be integrated without inconsistency (Evans, 1986): They are slower runners but stronger pushers than one would expect from their leg morphology. A possible explanation may lie in the relative sizes and insertions of the leg muscles.

Baars (1979) was the first to describe movement patterns of ground beetles in their natural habitat. Using radioactively labelled *Poecilus versicolor* and *Calathus melanocephalus* specimens, he detected periods of directed movement with large distances covered per day and alternating periods of random walk with small distances covered per day in random directions. These two differing patterns of movement were also described for members

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[8] Female ground beetles, which have already laid eggs, can be recognised after dissection by their corpora lutea, which appear as a yellow to brown coloration at the base of the ovarioles. These originate from degenerating follicle cells which are not reabsorbed in carabids and which can be recognised for a long time (Schjøtz-Christensen, 1965; Krehan, 1970; Storre *et al.*, 1996; see also section 6.2).

[9] Although reaching a rather high actual speed, *Carabus* species are moderate runners in relation to their large body size.

of the genus *Carabus* using harmonic radar[10] (Hockmann *et al.*, 1989, 1992; Kennedy, 1994; Niehues *et al.*, 1996; Riecken & Raths, 1996; Assmann, 1998; Huk, 1998). The obvious ability to keep moving in a constant direction is also demonstrated by capture-recapture experiments with individually marked beetles in circular enclosures (Hockmann *et al.*, 1989, 1992). The specimens were caught in pitfall traps on the inner side of the enclosure fence, and were released again in the centre of the enclosure. Recaptures of single individuals deviate from a random distribution, i.e. they are able to keep moving in a constant direction and also to reorientate if disturbed by handling and releasing. Directed movement can contribute considerably to the power of dispersal. The speediest specimens analysed covered the following distances: *C. auronitens* 40.4 m per night (Hockmann *et al.*, 1989); *C. coriaceus* 51.25 m per 12 h (Riecken & Raths, 1996); *C. problematicus* 132 m per night (Assmann, 1998); *C. nemoralis* 200 m per night (Kennedy, 1994). The physiological basis of the ability to keep moving in a constant direction is still unknown (cf. Hockmann *et al.*, 1992 for a discussion about orientation based on the magnetic field).

Outside the preferred habitat, woodland-inhabiting *Carabus* species in particular, use silhouettes on the horizon for orientation (*C. problematicus*: Neumann, 1971; *C. auronitens*: Niehues *et al.*, 1996). Some ground beetles at least use olfactory parameters to find their habitats (e.g. *Bembidion obtusidens* orients on the volatile metabolic methyl esters of palmitic and oleic acid from filamentous blue-green algae *Oscillatoria* spec.: Evans, 1982). A similar basis for orientation in *Carabus* species is possible.

For some beetles, tree trunk activity is documented (e.g. *C. irregularis*: Martius, 1986; *C. auronitens*: Hockmann *et al.*, 1989; see also Chapter 5). All species with climbing behaviour have long legs and a slender body (e.g. *C. intricatus* and members of the subgenus *Chrysocarabus*). Beetles have been observed on tree trunks during feeding on several occasions (e.g. *C. auronitens* feeding on caterpillars and snails; Hockmann *et al.*, 1989; *Procerus* spp. feeding on *Helix* spp.: Cavazzuti, 1989; *C. irregularis* feeding on shell-bearing snails of the family Clausiliidae, *own observ.*). This type of behaviour can also be observed in species inhabiting subalpine and alpine grasslands and edges of snow fields above the timber-line: *C. auriculatus* and *C. depressus* are able to climb on vertical rock faces (*own observ.*). *Carabus menetriesi* is able to climb on blades of grass (Nüssler, 1969).

6.5. ABIOTIC FACTORS

6.5.1. Climatic factors, temperature, humidity, and light

An experimental analysis of the importance of abiotic factors on ground beetles was commenced in the 1930s and 1940s in some excellent Scandinavian studies (Bro Larsen, 1936; Krogerus, 1932, 1948, 1960; Lindroth, 1949), followed by Central European carabidologists (e.g. Schmidt, 1955, 1956; Weber, 1965b; Thiele and co-workers, see Thiele, 1977). In recent decades, studies on their natural habitats have been emphasised.

In a gradient apparatus, woodland-inhabiting *Carabus* species generally prefer darker, more humid and lower temperature conditions than species that inhabit arable land (Thiele, 1964b; Weber, 1965b). These differences may be of importance for habitat selection (Thiele, 1977; see also Evans, 1983). In field experiments, a significant correlation between running activity and temperature could be demonstrated for several species. Such a result does not seem to be particularly surprising for a poikilothermic animal. More remarkable is the measure of correlation found: Althoff *et al.* (1992) was able to demonstrate that running activity (measured as number caught in pitfall traps) of *C. auronitens* depends strongly on air temperature during the first half of the night (correlation coefficients often exceed 0.9) and that temperature reaction changes during the reproductive period. Although, in a temperature gradient apparatus this species behaves as a more hygrophilous species (Weber, 1965b), no correlation with air humidity could be detected in the study area near Münster (Westphalia) (Althoff *et al.*, 1992). In this relatively wet woodland, the humidity in the litter may be sufficient during the whole activity period. In a beech forest in Luxembourg, Nève (1994) detected that the higher the mean daily humidity, the more active *C. problematicus* and *C. auronitens* were (and the higher the temperature, the higher the catch rates).

The transpiration rate in *Carabus* species does not linearly increase with temperature, but shows a 'plateau' within a certain narrow range (Schmidt, 1956). This is interpreted as an active ability to regulate transpiration. The 'preferred temperature' of a given species could be determined by the optimal transpiration rate, the determination of which is very important for members of this genus, due to the increase of transpiration rate with decreasing water content. The relation between oxygen consumption and temperature is weak (Schmidt, 1955/56), which means that they do not follow the van't Hoff's rule (reaction rate/temperature rule).

Some species (imagines and larvae) are found in extremely wet habitats, and may even hunt in water (*C. variolosus*, *C. nodulosus*, *C. galicianus*, *C. clatratus*, *C. alysidotus*, and *C. melancholicus*; cf. Chapter 5; Sturani, 1962; 1963). Other *Carabus* species (e.g. *C. granulatus*; *own observ.*) can take refuge in water and are able to swim.

Fuellhaas (1997) demonstrated with individually marked specimens in an enclosure that *C. granulatus* is able to survive a long-term inundation of about 6 months during the winter! During autumn, when inundation begins, beetles can be found swimming on the surface of the

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[10] For a detailed description of the method, see Mascanzoni & Wallin (1986), Hockmann *et al.* (1989) and Lövei *et al.* (1997).

water. Beetles may retire during the long inundation period into crevices with 'air bubbles', which may occur within the peat. But it is not impossible that beetles are able to live in anaerobic conditions like other ground beetles (e.g. *Pelophila borealis*, which can survive undamaged for 127 days at a temperature of 0 °C in nearly oxygen-free conditions; Conradi-Larsen & Sømme, 1973a, b).

Carabus species hibernate in small hollows in rotten wood, underneath mosses and in the ground. It is not certain whether the beetles are exposed to temperatures below 0 °C, because the substrate layers above them may provide effective isolation. For a brief review on freezing tolerance of ground beetles see Thiele (1977) (experiments on *Carabus* species are still lacking).

6.5.2. Chemical factors

Above the importance of chemical factors (mainly of the soil) as requirements of the ground beetle's habitats controversy exists. Krogerus (1960) was the first to demonstrate that pH-values could be recognised by carabids: Inhabitants of *Sphagnum* bogs, such as *Agonum ericeti* and *A. munsteri*, prefer acid regions (up to pH 3.3) in a pH-gradient apparatus (Krogerus, 1960; Paje & Mossakowski, 1984). Lindroth (1949) investigated some so-called 'limestone species' of Carabidae, which are restricted in Fennoscandia to open land on a soil rich in $CaCO_3$. He did not find any evidence that the beetles (mainly from the genus *Harpalus*) were able to perceive the Ca^{2+} content of the ground. Most of the species he tested are not restricted over their whole distribution area to limestone. This is in contrast to some *Carabus* species: for example, *C. irregularis* and *C. auriculatus* seem to be restricted to habitats with a neutral or alkaline soil pH (Weber, 1966c; Franzen, 1995; *own observ.*). Their habitat selection shows possible links to their preferred prey, shell-bearing snails (cf. Casale *et al.*, 1998; Assmann *et al.*, 2000), which occur in higher densities on soils with a high limestone content. *Carabus menetriesi* is a species found mostly on *Sphagnum*-rich bogs; a similar preference for acid regions as described above for the two *Agonum* species is possible. Preference experiments with pH-gradient apparatus are still lacking for those *Carabus* species.

6.5.3. Structural parameters of the habitat

Many important structural parameters of the natural habitat derive from vegetation (e.g. trees with rotten logs and leaves, which result in the litter). As described above, these structures are used (at least partly) by *Carabus* species. A negative influence seems to be given by dense vegetation (mainly grasses), which could hinder locomotory activity. Kennedy (1994) showed by radar tracing that *C. nemoralis* is seven to 19 times more active in arable habitats than in set-aside and semi-natural habitats, both showing a greater inhibition due to dense vegetation ('Raumwiderstand' in the sense of Heydemann, 1957). Vegetation is especially dense on fallow land after several years. *Carabus* species may be completely absent from such areas in north-west Germany (*own observ.*), possibly due to the unfavourable habitat structure.

Holdhaus (1911, 1954) was the first to recognise the importance of a phenomenon he called 'petrophily': Some species live exclusively on bedrock. Although his concept was strongly criticised, Lindroth (1949) and numerous other carabidologists now have accepted it. Many years later, a realistic explanation for petrophily was given by Brandmayr (1983: 165): Petrophilous ground beetles are 'particularly influenced by the morphologic and microclimatic properties of lithosols and climaphytomorphic soils developing on bedrocks: the highly reduced inundation risk, and a soil habitat of high pore space, with constant moisture and rich of suitable microhabitats'. Many montane to alpine distributed *Carabus* species can be regarded as petrophilous (e.g. *C. creutzeri*, *C. caelatus*, *C. ghilianii*, but not *C. sylvestris* which also lives in montane peat bogs; Brandmayr, 1983; *own observ.*).

6.6. BIOTIC FACTORS

6.6.1. Diet

Carabus species are polyphagous and consume nearly every kind of prey of adequate size. In most cases, earthworms, snails and caterpillars are recorded (e.g. von Lengerken, 1921; see also Chapter 5). The beetles can also be found feeding on carrion, and in the laboratory they accept many types of meat (incl. mince). All members of the genus show an extra-intestinal digestion (or predigestion), first described for this taxon by Jordan (1910). Von Lengerken (1921) was the first scientist to detect this method of feeding in *Carabus* larval instars. In most cases, the prey is held by the mandibles, partly cut up, and digestive fluid is regurgitated into the incisions to dissolve the tissues. The liquid resulting from the proteolysis is then ingested. *Carabus problematicus* ejected 30 ml midgut juices within the first 30 secs of exposure to meat (Metzenauer, 1981). *Carabus* specimens can feed continuously for several hours. The weight increase from food intake of a single 'meal' is up to about 30 % of their own body mass (*C. auratus*, von Lengerken, 1921; *C. glabratus*, *own observ.*). Scherney (1957a) recorded a much greater daily food consumption of more than 1.3 times their own body weight.

Vegetarian food is also consumed. In the natural habitat, at least some *Carabus* species are attracted to ripe and overripe fruits (e.g. *C. auratus* and *C. cristoforii* to strawberries, bananas, etc.; von Lengerken, 1921; *own observ.*)[11]. From laboratory experiments, Goldschmidt & Toft (1997) described that *C. nemoralis* and *C. convexus* consumed *Capsella bursa-pastoris*, *Poa annua* and leaves of wheat. Fungi are also accepted (e.g. by *C. auratus*, von Lengerken, 1921).

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[11] After excessive intake of fruits, the mortality of beetles may be increased (*own observ.*).

Cannibalism can occur under artificial conditions (laboratory, pitfall traps), particularly if there are tenerals or beetles, which have eaten so much that the intersegmental membranes of the abdomen, are visible. The possible role of cannibalism (presumed for larvae of some other ground beetles, e.g. *Pterostichus oblongopunctatus*, cf. section 6.5) in both larval instars and imagines is still unknown for *Carabus* species. Lindroth (1949) supposed exclusive predation of *C. hortensis* by *C. nemoralis* as a special form of a predator-prey-relationship: *C. nemoralis* imagines are active in spring, its reproductive period, and may hunt the larvae of *C. hortensis*, which is an autumn breeder with larvae in winter and spring.

In contrast to many laboratory and field observations, exact data on qualitative and quantitative composition of food in the natural habitat are sparse. Dissection of the gut does not provide any further information – in contrast to other ground beetles without extra-intestinal digestion (Hengeveld, 1980). Analyses of esterases from the crop content and from possible prey species after a separation by electrophoreses give an insight into food composition. Prüser & Mossakowski (1990) detected a similar prey spectrum for syntopically living populations of *C. lineatus* and *C. nemoralis* using isoelectric focusing of the esterases (*Oniscus* spec., Araneae, and a large amount of *Arion ater*). In a field study combined with esterase electrophoresis in Carinthia, *C. violaceus* was found to feed mainly on the slug *Arion lusitanicus* (Paill, 2000). Using the serological method, Lukasiewicz (1996) detected that earthworms and tipulid larvae were consumed by *C. granulatus*. Further information about the food spectrum of *Carabus* species is given by Oertel (1924), Delkeskamp (1930), Jung (1940), Loreau (1986), and Hockmann *et al.* (1989).

Actograph experiments with natural LD cycles carried out by Meyer-Peters (1993b) revealed that daily locomotory activity in *C. auronitens* is affected by food supply. Feeding leads to a reduced duration of daily activity for a period of up to four days. The feeding-dependent reduction of activity is paralleled by the temporarily reduced activity of trypsin- and chymotrypsin-like enzymes, which is at a maximum in starving animals (Vaje *et al.*, 1984).

Some macromorphological differentiations within the genus *Carabus* are often interpreted in the light of diverging and specialised modes of nutrition (e.g. Krumbiegel, 1936; 1960; Casale *et al.,* 1982; Thiele, 1977). The two most spectacular types are perhaps the (1) 'cychrisation' and (2) 'macrocephalisation', both supposedly related to different snail-hunting strategies. Species with a slender forebody simply enter the shell through the aperture and catch the gastropod body with their forceps-like, sharp mandibles ('cychrisation', e.g. *C. cychroides*, *C. intricatus*: Fig. 6.10). The body shape of some other *Carabus* species is characterised by a head that tends to be enlarged, sometimes to an enormous size and disproportionate to the other parts of the body ('macrocephalisation', e.g. *C. auriculatus*). In some species of this type, short and powerful mandibles occur. The morphology of these members resembles that of *Licinus* specimens whose asymmetrical mandibles enable them to break shells efficiently (Brandmayr & Zetto Brandmayr, 1986). The mandible form of some large-headed species differs from that of a typical *Carabus*: in *C. irregularis* they are strong, broad, and asymmetric (the outer margin of the left mandible is angulated, with a short tooth before the apex: Casale *et al.*, 1998) and its terebral and retinacular teeth are reduced (Fig. 6.10). In north-west Germany, the beetles are able to crush a number of different gastropod shells (from the helicid *Trichia hispida* to the enid *Ena montana* and different clausiliids). As described for *Licinus* species, conical shells are perforated behind the (mostly) strong aperture (*own observ.*). Due to the smaller and longer mandibles with an asymmetric terebral region, *C. pyrenaeus* and *C. auriculatus* seem to be less adapted (Fig. 6.10), nevertheless successful predators of shell-bearing snails, as indicated by a high number of crushed shells in the natural habitat and in the laboratory (Assmann *et al.*, 2000; *own observ.*). The beetles attack the gastropod shells in a similar way as the *Licinus* species (beginning from the aperture). The well-developed terebra could indicate that the mandibles are not only used to crush shells but also to hold on to prey. Whether the enlargement of the head is important for the mode of nutrition in some *Carabus* species or not is still unclear. Many populations of *C. macrocephalus*, a species with a disproportionately enormous head size, reach high densities in habitats, which are nearly free of shell-bearing gastropods (e.g. Bosque de Iraty, Sierra de Ancares, Murrielles: *own observ.*). Therefore the term 'licinisation' (cf. also Casale *et al.*, 1998) seems to be more appropriate for shell-breaking ground beetles than 'macrocephalisation'. In any case, some *Carabus* species with 'normal' mandibles (Figs 6.10, 6.11) are able to break shells, as described for *C. coriaceus* by Sturani (1962).

6.6.2. Interspecific competition

Interspecific competition can be defined as a negative, i.e. detrimental, interaction between organisms of different species caused by their need for a common resource (Calow, 1998). Niemelä (1993) reviewed 32 papers dealing with this topic, which is very controversial in carabidology. Half of the papers reported that interspecific competition was in operation or was responsible for apparent resource partitioning. However, many authors, while emphasising the role of competition, could not dismiss alternative explanations. Only a few papers deal with interspecific competition in *Carabus* assemblages (e.g. two North American species: Lenski 1982a, b, 1984; north-west German woodland inhabiting species: Günther & Assmann, 2000). Based on the current literature, it is not possible to decide if or to what extent competition occurs in natural *Carabus* assem-

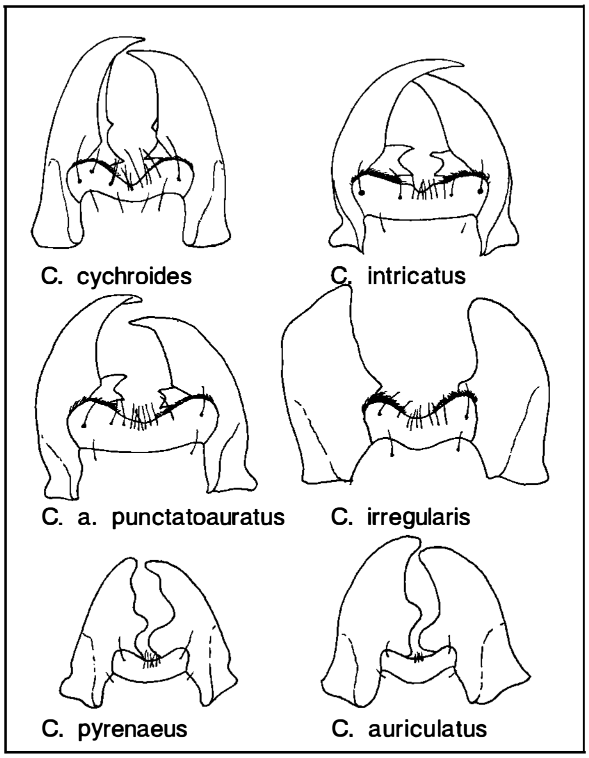

Fig. 6.10. Mandibles of *Carabus* species.

blages. Further studies have been undertaken, as emphasised by Niemelä (1993): (1) Population-biological parameters should be determined in sym- and allopatric conditions of the potential competitors. The observational and distributional data should be supplemented by experimental work in the field (e.g. enclosures). (2) Further attention should be paid to the possible role of larval competition. (3) Natural and human-induced introductions and invasions should be used to study effects on the composition and structure of assemblages. (4) Phylogenetic relationships in combination with present-day ecology may give further insight into the patterns of community organisation and may help to test if competition has occurred in the past.

6.6.3. Parasites and Parasitoids [12]

Several parasites and parasitoids are known to occur on members of the genus *Carabus* from field studies and rearing in laboratories. A brief overview follows:

Fungi imperfecti – Moniliales: Sturani (1962) detected an infection of *Carabus* larvae with *Botrytis bassiana* in the laboratory and Thiele (1977) assumed that *Metarrhizium anisopliae*, which was found frequently on *Pterostichus oblongopunctatus* and *Pt. quadrifoveolatus*, can also infect members of the genus *Carabus*. Nothing is known about the occurrence of these fungi on *Carabus* spp. in

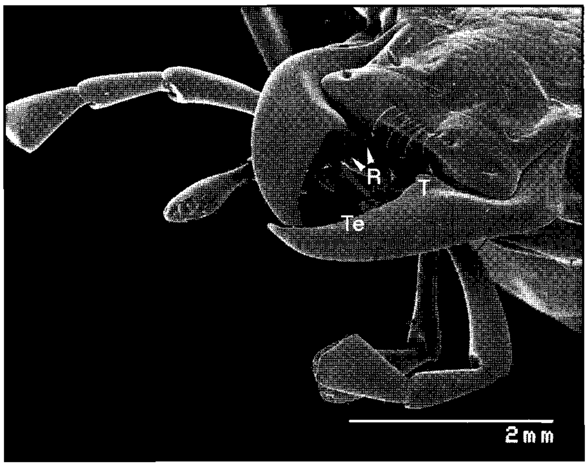

Fig. 6.11. Mandibles, *C. auronitens punctatoauratus*, male. Te: terebra; T: terebral tooth; R: retinacular teeth (photo: J. Lange & T. Assmann).

their natural habitat; the parasite species mentioned above are not restricted to ground beetles.

Fungi – Ascomycetes – Leotianae – Clavicipitales: *Cordyceps* (= *Cordiceps*) *militaris* and *Torrubia cinerea* were found by Sturani (1962) on both the larvae and imagines of the genus *Carabus* (also own observations on *C. auronitens punctatoauratus* and *C. splendens*). These non-specific parasites develop conspicuous fruiting bodies, some centimetres in length.

Fungi – Ascomycetes – Laboulbeniales: This is perhaps the most characteristic parasitic group living predominantly on beetles and is apparently completely absent from *Carabus* species. But as an interesting form of hyperparasitism, the mite genus *Canestrinia* (e.g. *C. carabicola*, which lives on *C. morbillosus*, see below) can be infected by *Dimeromyces falcatus* (Samsinak, 1971).

'Monocellular Eucaryota' – Alveolata – Gregarinea: Gregarinea are the only protozoans known to live as parasites in members of the genus *Carabus*. Geus (1969) lists three Gregarinea genera (six species: *Ancyrophora gracilis*, *A. stelliformis*, *Actinocephalus digitatus*, *A. permagnus*, *A. puisseguri*, *Monocystis legeri*) for imagines and *Cometoides wellmeri* for a larva, which is not determined to the species level. One *Carabus* species can be infected by at least three Gregarinea species. Further records are given by Delkeskamp (1930), Sturani (1962) and Puisségur (1972). Within a few days, infection with ripe spores leads to mature cysts (mostly in the body cavity). The number of these cysts, which look like (small) 'white tennis balls', can be enormous in a single *Carabus* specimen (up to 220 cysts in *C. nemoralis*: Delkeskamp; up to 100-150 cysts in *C. auronitens punctatoauratus* and *C. auronitens auronitens – own observ.*). In 10 out of 33 *C. auronitens* populations and in 18 out of 29

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[12] The systematics and nomenclature of the higher taxa follows Daly *et al.* (1998), Ehrendorfer (1999), Hausmann & Hülsmann (1996), Lorenzen (1996a,b), Westheide & Rieger (1996), and Weygolt (1996).

C. auronitens punctatoauratus populations studied for electrophoreses (Assmann *et al.*, 1994; Assmann & Weber, 1997), Gregarinea were detected during dissection of the beetles. The infection rate of some populations exceeds 41 % (*C. auronitens* population near the Mont Lozère in the Cevennes), as revealed by dissection of pitfall catches (killing and preserving agent after Renner (1980): 40 % ethanol, 20 % acetic acid, 10 % glycerol, 30 % water: *own observ.*). The consequences for the fitness of the infected beetles are still unclear. Sturani (1962) and Thiele (1977) assumed that death or at least a strong reduction in fertility could be one effect. It is still unclear whether this occurs in the natural habitat; in some *C. auronitens punctatoauratus* females with more than 50 mature cysts, ripe eggs were found in the ovaries. Further studies are urgently needed to estimate population biological consequences of these parasites.

Nemathelminthes – Nematoda – Secernentea: Burgess (1911, cited after Thiele, 1977) recorded rhabditids in *Carabus monilis*. An undetermined nematode (perhaps a Secernentea) was found on *C. auronitens* from the Montagne Noire held in the laboratory. The ectoparasites were found on intersegmental membranes of the thorax and the abdomen (especially of the tergites) where they swam in hemolymph, which leaked from the membranes. Within a few days of diagnosis, the infected beetles died.

Nemathelminthes – Nematomorpha – Gordioida: The Nematomorpha show juvenile parasitism, and develop in the body cavity of arthropods. The often 10-50 cm long and only 1-3 mm thin adults copulate (in the form of a 'Gordian knot') and reproduce outside their hosts. One of the most conspicuous characters of the life cycle of Gordioida is that freshwater species infect mainly or exclusively terrestrial hosts like ground beetles and grasshoppers (Schmidt-Rhaesa, 1997). The method of infecting ground beetles is still unknown. The hooks and stylets of the larvae may possibly enable them to penetrate the outer surface (as described for snails). But infection through the intestinal tract may be the rule for arthropods (via snails as food) (Schmidt-Rhaesa, 1997). *Gordius* spec. was reported by von Lengerken (1924) and Sturani (1962) from *Carabus* imagines[13]. Further records with respect to ground beetles are given by Schmidt-Rhaesa (1995), but no definite infection of a *Carabus* specimen was detected. An excellent photograph of a *Gordionus* spec. specimen leaving a *C. coriaceus*, is given by Lorenzen (1996: 711).

Acari – Anactinotrichida (Parasitiformes) – Gamasida: *Parasitus* spec. is often found on *Carabus* species, both in the laboratory and in the field (Thiele 1977). However, interactions between the mites and the beetles are not a form of parasitism, but rather of phoresia, which also is assumed for the deutonymphs of Uropodidae. They have also often been found on the exoskeleton of *Carabus* species (*own observ.*).

Acari – Actinotrichida (Acariformes) – Tarsonemini: Perhaps the most spectacular parasites living on ground beetles are mites of the family Podapolipidae. The members of this taxon are restricted to insects and two genera parasitize only on ground beetles. Two species of the genus *Dorsipes* are exclusively found on *C. granulatus* (Regenfuß, 1968). Synhospital podapolipids show a diverging occupation of niches (e.g. the *Eutarsopolipus* species on *Poecilus cupreus*: *E. abdominalis* lives on the intersegmental membranes of the abdominal tergites, *E. thoracis* on those of the thorax, and *E. squamarum* on the squamae of the elytra). Perhaps due to the low numbers of records (only 5 and 8 specimens of *Dorsipes carabi* and *D. dorsipes*, respectively, on 256 *C. granulatus* individuals) no data on niche occupation are given by Regenfuß (1968). *Eutarsopolipus* species move to another host exclusively during copulation. A similar change of host can also be assumed for the *Dorsipes* species and may explain the strong host specifity. A pair of stylets to drill through the cuticle enables the podapolipids to ingest the hemolymph of the beetle. The number of pairs of legs (usually four in Acari) is reduced to three pairs in the females of the genus *Dorsipes*. The 4th pair of legs is dorsally located in males. In other genera the number of legs is further reduced (up to one pair of legs in females). There is strong evidence that the podapolipids living on carabids are not regularly distributed in Central Europe: Regenfuß (1968) did not find them on beetles collected by Thiele near Cologne (North Rhine-Westphalia) and by Heydemann near Kiel (Schleswig-Holstein), but he did find them on those collected by himself in Franconia.

Acari – Actinotrichida (Acariformes) – Acaridida: The genera and species of the Acaridida, which are restricted to members of the genus *Carabus*, were dealt within a monograph by Samsinak (1971). 29 species from 6 genera (*Canestria*, *Mesophotia*, *Procericola*, *Dicanestrinia*, *Neophotia*, *Photia*) were recorded on about 170 *Carabus* species. Some mites were only found on one species or a pair of sister species (e.g. *Neophotia jureceki* Samsinak, 1971 on *C. pyrenaeus*; *Dicanestrinia knobi* Samsinak, 1971 on *C. nodulosus* and *C. variolosus*). These parasites live in the subelytral space and sometimes occur in great numbers (up to several hundreds or a thousand on a single beetle, see Sturani, 1962, Thiele, 1977, *own observ.*). Although Samsinak (1971) studied about 2,000 beetles, our knowledge of the geographic distribution of the mites (especially in relation to their hosts) is poor. Some species are perhaps restricted to the southern parts of the distribution areas of their host(s) (e.g. *Canestrinia occidentalis* on *C. auronitens*). Further investigations (also on the mites' method of nutrition) may provide a better insight into population history and biology of *Carabus*.

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[13] Rivard (1964, cited after Thiele 1977) suspects that some of these reports are due to confusion with large mermithids.

Hymenoptera – Proctotrupoidea: Proctotrupids are internal parasitoids of coleopterous larvae. In many species the wings are reduced in one sex. According to Scherney (1957a) and Weidemann (1965), one or more *Phaenoserphus* species develop on *Carabus* larvae, but the species (mainly *Ph. viator*) is not restricted to this ground beetle genus.

Diptera – Tachinidae: Tachinids are internal parasitoids, which develop in adults or the larvae of insects. Most species are polyphagous and are not specialised on one host. *Viviana cinerea*, *Freraea denudata*, *F. gagathaea*, and *Frontia austera* have been recorded for several *Carabus* species (Sturani, 1962; Lindroth, 1949; for a table, see Thiele, 1977).

6.6.4. Predators and defence mechanisms

Carabus species are predated by numerous Insectivores (hedgehogs, shrews, moles), bats, rodents, birds, and amphibians (Thiele, 1977). None of these are specialised in ground beetles, although they can be (at least for some periods) the main prey (e.g. for white storks; Bauer & Glutz von Blotzheim, 1966). The variety of prey of some spiders (Araneae) comprises members of the genus *Carabus,* too. Especially species of the genus *Gnaphosa* (maximum body length of more than 20 cm) hunt these beetles. Trautner (1994a) discovered numerous remains of *C. convexus* and *C. granulatus* in the retreats (spiders' hiding places) under stones (*Gnaphosa lucifuga*). In the Pyrenees and north-west Spain, a gnaphosid spider, which occurs in subalpine altitudes, is able to overpower large *Carabus* species (e.g. *C. macrocephalus*, *own observ.*). A remarkable decrease in the population density of the beetles is described from the environments of ant nests (Kolbe, 1968, 1969). This seems to be (at least partly) caused by direct predation by the Formicidae.

Carabus species are able to defend themselves by using chemicals. The pygidial glands in the distal part of the abdomen contain cytotoxins (unsaturated acids, mainly methacrylic acid, and 5 % tiglinic acid = trans-2-methyl-2-butenic acid) (Schildknecht *et al.*, 1968), which polymerises after spraying. By exerting a strong muscular contraction of the abdomen and pointing the tip of the abdomen towards the antagonist, the beetles eject their secretions in a fine jet, directing their discharge through the mobile orifice. The spray is very unpleasant, and it acts as an irritant to the mucous membranes, eyes and skin of entomologists (and other humans).

During handling, some *Carabus* specimens regurgitate crop contents (which can be used for food analyses). It is not known whether this defence behaviour occurs under natural conditions.

Stridulation is discussed as a possible defence mechanism by several authors. For most *Carabus* species, this method of sound production is unknown, but *C. irregularis* is able to stridulate (under stress) by rubbing the rough surface of the 5th and 6th abdominal tergite on bristles of the inner surface of the elytra (Bauer, 1975).

6.7. POPULATION BIOLOGY

6.7.1. Population ecology

Fluctuations of population size

The amplitude of population fluctuations in ground beetles, which can exceed more than the 10 square, were studied intensively by den Boer and co-workers (e.g. 1981, 1990; den Boer & van Dijk, 1994), but members of the genus *Carabus* were rare in their investigation area, in the province of Drenthe (Netherlands), and the decrease or increase of the heathland species seemed to be (at least partly) caused by changes in habitat quality (cf. Chapter 9).

In several *Carabus* species of a Westphalian woodland on limestone ground (Melico-Fagetum), Giers-Tiedtke *et al.* (1998) observed over an investigation period of five years, largely synchronous fluctuations of the numbers of individuals trapped. The catch rate varied from year to year with a maximum factor of about 5 (*C. auronitens*, *C. purpurascens*). Asynchronous differences from year to year were found by Grüm (1986) for *Carabus* species in Polish pine stands (Vaccinio uliginosi-Pinetum and V. myrtilli-Pinetum). The most extreme change in the catch rate was found in *C. arvensis*, which exceeded a factor ten within four years, over an investigation period of 9 years. But in general, the extent of fluctuation was perhaps smaller in members of the genus *Carabus*. During an investigation period of 16 years, the number of active *C. auronitens* individuals within an enclosure of 0.2 hectares in the spring season varied between 252 and 576 (Giers-Tiedtke *et al.*, 1998; Althoff *et al.*, 1992).

Age structure

An important parameter affecting low fluctuations of the population size is the iteroparity of all *Carabus* populations, which were studied with regard to this topic (section 6.3). A detailed analysis of the age structure of the well-studied Westphalian *C. auronitens* enclosure population is given by Baumgartner *et al.* (1997). The probability of surviving from autumn until the spring season was about 75% in this spring breeder; survival probability from the 1st to the 2nd spring season was about 65%; for the following years (2nd to 3rd, 3rd to 4th, and 4th to 5th) the probability decreased from about 60% to about 40%. Iteroparity of a *Carabus* population may be interpreted as a strategy of 'spreading of risk' in time (den Boer, 1968): If in some years the (climatic) conditions are adverse to the extent that reproduction does not occur or is strongly reduced, the overall population size will only change slightly and the chance of extinction is reduced. In the above-mentioned *C. auronitens* population, the number of beetles active in autumn was very low in 1987, but their abundance in the following spring only decreased from 403 to 271 individuals.

Power of dispersal

Patterns of locomotory (epigeic) activity have already been presented in this chapter (section 6.4). Dimorphic alae (with a predominance of macropterous individuals) have only been recorded in 2 species (*C. granulatus*, *C. clatratus*: Lindroth, 1949). In Fennoscandia, which was (re)colonised by these beetles after the last glacial period, the frequency of full-winged specimens is not higher than in Central Europe. Therefore, there is no support for the assumption that flight ability contributes to the overall power of dispersal of these species. Eggs and larvae of the genus *Carabus* seem to be very sensitive to artificial or adverse climatic conditions, therefore these stages are supposed to contribute only slightly or not at all to dispersal by chance introduction. The locomotory mobility of the larvae is generally low compared with that of imagines. The locomotory behaviour of the imagines seems to be the main factor of the power of dispersal.

Records in woodlands of different age indicate that some species colonise new habitats more frequently than others (e.g. Terrel-Nield, 1990; Assmann, 1999). This may be a consequence of different powers of dispersal as well as of diverging habitat quality. The locomotory behaviour of two species in north-west Germany (*C. glabratus* and *C. problematicus*) correspond very well with the assumption that differences in activity patterns may be one reason (or one of several reasons) for different distribution patterns in a certain area (Assmann & Günther, 2000). Dispersal does not only depend on the behaviour of a given species, but also on landscape parameters (e.g. availability of habitat corridors, arrangement of habitats).

A great power of dispersal must be postulated for postglacial colonists, which spread from southern European refugia to Central Europe and perhaps northwards to Scandinavia. One such species is doubtlessly *C. hortensis*. There is strong evidence that this species is still in the process of extending its range. In Baden-Württemberg, this species was known only from the environs of the city of Ulm during the 1920s (von der Trappen, 1929). The recent western periphery of the distribution is situated near the cities Heilbronn and Sigmaringen (at a distance of more than 60 km from Ulm (Trautner, 1992)). On the other hand, no changes in the established borderline east of the river Weser in north-west German lowlands have been found (cf. Gersdorf & Kuntze, 1957; *own observ.*).

The colonisation history of *C. auratus* in north-eastern Europe is well documented. In the middle of the last century, the species reached Mecklenburg-Vorpommern and is now widespread in Poland (Gersdorf, 1937; Burakowski, *et al.,* 1973; Arndt, 1989). *Carabus* species, which live close to habitats under strong human influences (e.g. fields or gardens), can easily be transported, which may contribute to their power of dispersal: The recent immigrants *C. granulatus*, *C. nemoralis*, and *C. auratus* arrived in North America with ballast trade from Europe in ships (Lindroth, 1957). These three species established populations in North America (Lindroth, 1961-69). The populations of *C. morbillosus* in southern France, Central Italy and eastern Spain are probably introduced in a similar way by humans (Casale *et al.*, 1982; Zaballos & Jeanne, 1994).

The power of dispersal seems to be much lower in many other *Carabus* species. This assumption is supported by the often small distribution ranges and the strong differentiation of the populations (see below). *Carabus nemoralis*, *C. auratus*, *C. granulatus*, and *C. hortensis*, which exhibit a great power of dispersal, show only slight morphological differentiation between conspecific populations.

The colonisation process of *Carabus* species is still only poorly understood. More information is needed to improve our knowledge of the power of dispersal (patterns of locomotory activity or the possibility of transfer by chance ('stowaway')) and also of demographic parameters and, if a population is initiated by a few individuals (or one fertilised female), of the ability of the offspring to find mating partners (aggregation behaviour) (Andrewartha & Birch, 1954; Niehues *et al.*, 1996).

6.7.2. Differentiation and population history

Morphometric differentiation

Only in a few animal taxa the extent of differentiation among conspecific populations is as great as in *Carabus* species. Many names have been proposed for subspecies of the genus *Carabus* and three hierarchically ordered categories below the subspecies level (natio, morpha, and aberratio: Breuning, 1932-39: 5) have been regularly used, although treated very differently by different authors (e.g. Breuning, 1932-39; Deuve, 1994; Forel & Leplat, 1995; Forel & Leplat, 1998; Brezina, 1999). Some species are supposed to have more than 40 subspecies (e.g. *C. cancellatus*: Deuve, 1994).

Morphometric analyses of conspecific populations were initiated in the 1930s (e.g. Zarapkin, 1934; Krumbiegel, 1936; Rensch, 1943) and continued with modern statistical methods (incl. multivariate approaches) over the last decades of the last century (e.g. Lindroth, 1968; Mossakowski, 1971; Gries *et al.*, 1973; Bonadona, 1973; Mossakowski & Weber, 1972, 1976; Terlutter, 1991; Assmann & Schnauder, 1998; Assmann *et al.*, 2000).

An important result of these studies is that conspecific populations, which are strongly differentiated at the morphometric level, occur particularly in south European mountains. Sometimes only two characters are needed to separate the members of the two populations (significance level: $p < 0.05$, Fig. 6.12: Terlutter, 1991; see also Bonadona, 1973, and Mossakowski & Weber, 1976). Such great differences are exclusively known from the potential glacial refugia (see below). Therefore it can be assumed,

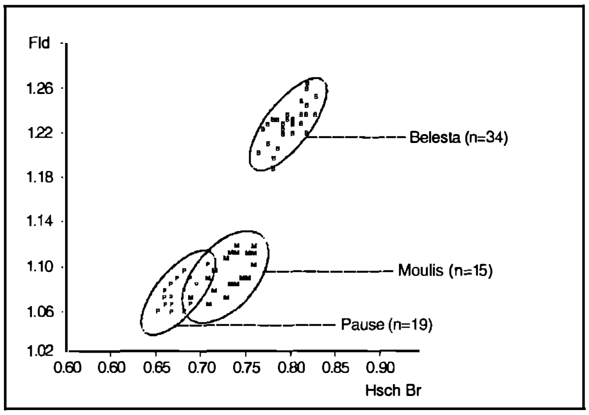

Fig. 6.12. Divariate comparison of three *C. auronitens punctatoauratus* populations using 95% ellipses for the characters pronotal width (abscissa) and elytral lenght (ordinate)(after Terlutter, 1991).

that most of the divergence between these populations originated during a process of long-lasting separation.

Carabus problematicus is perhaps the only species with a strong morphometric differentiation in northern Europe. Lindroth (1968) studied the Scandinavian subspecies and found clear differences.

It was surprising that populations, which are separated for only a few decades or centuries, show significant morphometrical differentiation: *C. arvensis* in drained heather moors in Schleswig-Holstein (Mossakowski, 1971) and *C. auronitens* in fragmented forests in Westphalia (Gries *et al.*, 1973; Terlutter, 1991). For both species no correlation between differentiation and habitat quality could be found. Significant differences are also obtained among local populations of *C. auronitens punctatoauratus* in one mountain range (Massif de Larize, Pyrenees) (Terlutter, 1991). No geographical dispersal barriers were recognisable between the sampling sites. Thus one can suppose that this region is inhabited by one large population or several local populations with apparently unrestrained gene flow.

Usually, both genetic and environmental factors add (perhaps in similar amounts) to morphometric variance. The number of loci involved in some selection experiments on single morphometric characters in mice and *Drosophila* (e.g. bristle numbers on the prothorax) is in the range 30-100 (Maynard-Smith, 1998). For the genus *Carabus*, there are available very little data concerning these topics. Crossbreeding experiments between and within some species have been carried out and showed that a given character can segregate in a normal Mendelian manner (e.g. a recessive allele determines dark elytra in *C. auronitens*: Puisségur, 1964), but the amount of heritability[14] of any quantitative trait (except elytral colour) is completely unknown.

In most cases, the described morphometric variance of many characters seems to be selectively neutral (e.g. the striae on the elytra). But in two species specialised in eating shell-bearing snails, there are indications that morphometric divergence is caused by natural selection: (1) Boettger (1921) described a congruence between the forebody shape of North African populations of *C. morbillosus* and the occurrence of dents at the aperture margin of the shell of the preferred snail: 'cychrisation' occurs in regions with snails showing a confined aperture. (2) *C. pyrenaeus* attacks mainly two allopatric and endemic helicids (*Arianta xatarti*, a species with more fragile shells, in the eastern Pyrenees, and *Pyrenaearia carascalensis*, a species with more massive shells, in the central and western Pyrenees). The differentiations of the mandible shape (mainly in the retinacular region) can be interpreted in the light of an adaptation to prey (Assmann *et al.*, 2000).

Karyotypic differentiation[15]

In contrast to some other ground beetle genera (cf. Serrano, 1981; Nettmann, 1986), chromosome numbers do not vary between members of the genus *Carabus*. All 23 species studied by Weber (1966d) had 26 autosomes and 2 heterosomes (2n), males were heterogametic (XY-type). In contrast to the uniformity of the karyotype, intraspecific differentiation of homologous chromosomes was frequently found. One pair of autosomes was relatively long and consisted of a euchromatic and a heterochromatic arm (Weber, 1967; 1968b). The latter one varied in length between individuals. The mean heterochromatin content of the chromosome is similar in *C. auronitens* populations from Westphalia and southern France (Mossakowski & Weber, 1972).

Differentiation at the level of single loci

An increasing number of papers deal with the differentiation of single loci, mostly to get a better insight in the phylogeny of the subgenera and species within the genus *Carabus* (e.g. Braun, 1988; Su *et al.*, 1996a,b; Prüser, 1996; Casale *et al.*, 1998). For a better understanding of evolution within this taxon, it is also necessary to know to what extent differentiation occurs below the species level.

A striking phenomenon often found is that local populations inhabiting a homogenous region show significant differentiations[16], which seem to be caused by genetic drift (allozyme surveys; *C. auronitens punctatoauratus*: Assmann, 1990; Assmann & Weber, 1997; cf. section 'Morphometric differentiation'; *C. granulatus*: Reimann, 1996; *C. arvensis*

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[14] Heritability is a population-dependent parameter, which measures how much of the observed phenotypic variation in a quantitative character is influenced by genetic variation (Calow, 1998: 339).

[15] For a discussion of fluctuating asymmetry, see section 9.4.

[16] The significant deficit of heterozygotes in the samples can also be explained by the assumption of genetic differentiation at a very local scale (Wahlund effect, Assmann & Weber, 1997).

in the nature reserve 'Lüneburger Heide': *own observ.*). The amount of differentiation is different from species to species (e.g. low in *C. glabratus*: Assmann & Günther, 2000).

The values of differentiation between populations of *C. solieri* inhabiting separated mountain ranges are probably the highest ever found in an insect species. Rasplus *et al.* (2000) used an average mutational rate for microsatellite DNA to determine the divergence time of the two main lineages of this species (subspecies *bonnetianus* and *solieri*). They assumed that the two subspecies might have originated from two glacial refuges separated by the Younger Dryas glaciation event. Large genetic differences were also found in populations of *C. auronitens* in southern France (Montagne Noire and neighbouring mountains, Cevennes and parts of the Massif Central, environs of Rodez) (Assmann *et al.*, 1994; Reimann *et al.*, 2002).

The patterns of genetic divergence of both *C. auronitens* (*s.str.*) and *C. auronitens punctatoauratus* are only partly in agreement with subspecies or morphometric classifications (cf. Terlutter, 1991; Assmann & Weber, 1997). The same is true for *C. solieri*. The studied populations of the 'subspecies' *curtii* share 89.9% of their microsatellite DNA alleles with surrounding populations and their position in phenograms is intermediate (Rasplus *et al.*, 2000). The microsatellite data support a hybrid origin of these populations. But the subspecies *solieri* and *bonnetianus* are clearly genetically differentiated. Thus within the genus *Carabus*, character congruence as well as incongruence between genetic and morphometric data can be found.

Character congruence is simple to explain. Morphological and single locus peculiarities may both be selected by region-specific environmental factors. However, also in the case of neutral polymorphism, congruence of a more or less marked degree could arise if populations, which have evolved adaptive morphological peculiarities, experience episodes of genetic drift (bottlenecks) by which the frequencies of alleles are changed. Character incongruence could have been evolved by drift as well as by selection. If the latter one is acting, it seems more probable that morphometric parameters (e.g. body length or body proportions) are affected.

Some ground beetles (incl. *Carabus* species) in the landscape of Central Europe show none or only slight genetic differences between conspecific populations (e.g. *C. nemoralis*: Butterweck, 1997; *Abax ater*: Desender *et al.*, 1999). In contrast to this, at least one species living in habitats, which are stable over a long period, is characterised by a strong genetic differentiation (*C. glabratus*: Assmann & Günther, 2000; cf. section 9.4). It is difficult to compare the results, because (1) the geographic scales of the investigation areas are different and (2) many population-biological parameters influencing genetic differentiation are only poorly known (e.g. power of dispersal, fluctuations of population size, dispersion of the individuals).

The average number of alleles per polymorphic enzyme locus ranges from 2.6 to 6.5 (Easteal, 1988). Many enzyme loci studied in *Carabus* populations are within this range. But the glucose phosphate isomerase (GPI) and an esterase (EST-X) locus (of which the enzymes are localised within the fat body and musculature) exceed this number in a few species (up to more than 15 alleles: Assmann *et al.*, 1994; Mossakowski *et al.*, 1995; Reimann, 1996), whereas in others, no genetic variation can be detected.[17] Comparable allozyme numbers are only found in very few other insect species (e.g. 13 and 14 allozymes in *Drosophila pseudoobscura* and *D. melanogaster*, respectively: Coyne *et al.*, 1978; Keith, 1983). The reasons for the strikingly diverging allele numbers are still unknown. That the postglacial history of the species is the main reason for low variability should be excluded (*C. granulatus* colonised Central Europe with all probability after the last glacial period and shows much genetic variability at enzyme coding loci: Reimann, 1996; *own observ.* at eight further enzymes). Selection should also be taken into account for the enzyme GPI (cf. Riddoch, 1993; Mitton, 1997).

Glacial fauna and postglacial history

During the last glacial period, the landscapes in Europe were quite different from nowadays: Scandinavia was nearly completely covered by an enormous ice sheet. In Central Europe, tundra (rich in *Artemisia* and Chenopodiaceae) dominated the permafrost and remnants of woodlands survived only in southern Europe (not only in the most southern parts as Andalusia or Calabria, but also in southern France and northern Spain and Italy).[18] In spite of many studies (Coope, 1977; Elias, 1994), the ground beetle fauna of this period is only incompletely known, because (1) most depositions analysed are located in the northern half of Europe and (2) the chance of conservation is very small for inhabitants of some habitats (e.g. of well drained grounds in mountainous altitudes: petrophilous species; cf. section 6.4), which results in their complete absence in all species lists.

Nevertheless the following scenario can be given (Coope, 1977, Elias, 1994): A cold-adapted fauna lived during the last ice age in Western and Central Europe. *Amara alpina* and *Diacheila polita*, which are now distributed from central or north-east Scandinavia eastwards, and *Cryobius* species were abundant ground beetles in some habitats. The latter genus is actually not only distributed in north-east Asia and northern America, but also in high

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[17] GPI: 13 allozymes in *C. auronitens punctatoauratus* (Assmann, 1990; Assmann & Weber, 1997), 15 allozymes in *C. auronitens* (Assmann *et al.*, 1994), more than 15 allozymes in *C. granulatus* (Mossakowski *et al.*, 1995; Reimann, 1996), more than 11 allozymes in *C. violaceus* (Mossakowski *et al.*, 1995; *own observ.*), EST-X: 14 allozymes in *C. auronitens punctatoauratus* (Assmann & Weber, 1997).

[18] For a more detailed description, see for example Birks & Line (1993) and Lang (1994).

montane zones of Central Europe (Molenda, 1996). Our knowledge of the *Carabus* fauna in the past is poor, but *C. maeander*, a species now living in north-east Asia and North America, was found several times in European deposits from the last glacial period (Lindroth, 1970).

For this period, refugia in southern (and eastern) Europe must be postulated for species adapted to warmer climatic conditions and/or woodlands (so-called 'gross refugia', Lindroth, 1970). The northern limit of these refugia ('massifs de refuge') is zoologically clearly indicated as the northern boundary of endogean and hypogean anophthalmic beetles ('Holdhaus borderline', Fig. 6.13: Holdhaus, 1954; Assmann, 1995). In the postglacial period, the (re)colonisation process of many species starts from these refugia. A second main type of glacial refugia may have been within the limits of the continuous northern ice-cap and consisted of relatively small ice-free regions ('nunataks', 'coastal refugia'; Lindroth, 1970). The 'tabula rasa' hypothesis alternatively postulates that no species survived in north European refugia (Dahl, 1989).

The importance of the glacial period with its great northern ice-cap is also illustrated by a multivariate analysis of local faunas of the genus *Carabus* over the Russian Plain (Penev, 1996). Among 17 parameters, the distance from Valdai (=Würm) glaciation border shows the greatest Spearman's rank correlation on the first axis of a detrended correspondence analysis. For the Russian Plain (as for Central and western Europe), both postglacial (re)colonisation and survival during the last glacial period are postulated for members of the genus *Carabus*.

Morphometric characters for some species indicated that populations from the massif de refuge are more variable than from regions colonised in postglacial period (Rensch, 1958; Terlutter, 1991). In an allozyme survey, the genetic consequences of both their persistence in glacial refugia and the postglacial expansion are studied in *C. auronitens*, a species living either in alpine areas or on permafrost ground (Assmann *et al.*, 1994; Assmann, 1995; Reimann *et al.*, 2002). Thus it seems that survival during glacial periods, north of the Holdhaus borderline was not possible. South of this boundary, *C. auronitens* had three or four refugia as revealed by strong genetic differences. North of this boundary, the genetic differentiation and variability decreased significantly, but not very strongly. Some genetic variability is still found at the north-western border of their distribution (Westphalia) and the supposed population from where (re)colonisation started shows only poor variability at the studied loci (which means that not very much variability could be lost). The other refugial populations did not contribute (or to a low extent) to the genetic variability of the postglacial colonised populations.[19] The hypothesis of allele elimination during postglacial expansion was first suggested by Reinig in 1938. He developed his hypothesis after studying morphological variation in different species. Further hypotheses and theoretical aspects are given by Hewitt (1996). On a genetic basis, this hypothesis was first verified by Highton & Webster (1976) for the North American salamander *Plethodon cinereus*.

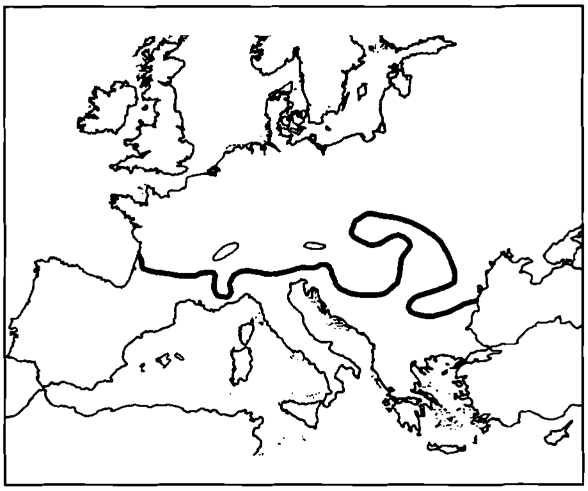

Fig. 6.13. The 'Holdhaus borderline' (after data from Holdhaus, 1954; Bonadona, 1971; Casale, 1988).

Other genetic studies of several *Carabus* species in southern European mountains give reason to assume, that a long-lasting persistence of those populations in 'massifs de refuge' are the driving forces for great variability and differentiation (e.g. Mossakowski & Braun, 1993; Assmann & Weber, 1997; Rasplus *et al.*, 2000). The different rates of divergence of *Carabus* species in Central Europe can be interpreted by different assumptions: diverging power of dispersal, persistence of some cold-tolerant species in Central Europe, or secondary contact of previously separated populations (Mossakowski *et al.*, 1995).

North European refugia for some ground beetle species during the last glacial period are postulated by Lindroth (1970). His assumption is supported by the finding of morphometric differences between the Scandinavian population ranges of *C. problematicus* (Lindroth, 1968). Genetic analyses are necessary for a better understanding of the history of this (and other north European) ground beetles. For some plant species, the hypothesis of a north European refuge should be rejected (e.g. Gabrielsen *et al.*, 1997; Frantzke, 1999). An Icelandic refugium during the Wisconsin glaciation gives best explanation for the geographic differentiation of the rock ptarmigan (*Lagopus mutus*) (sequence variation in the mitochondrial control region, in a nuclear intron (Gapdh), and in an internal transcribed spacer (ITS 1) (Holder *et al.*, 1999)).

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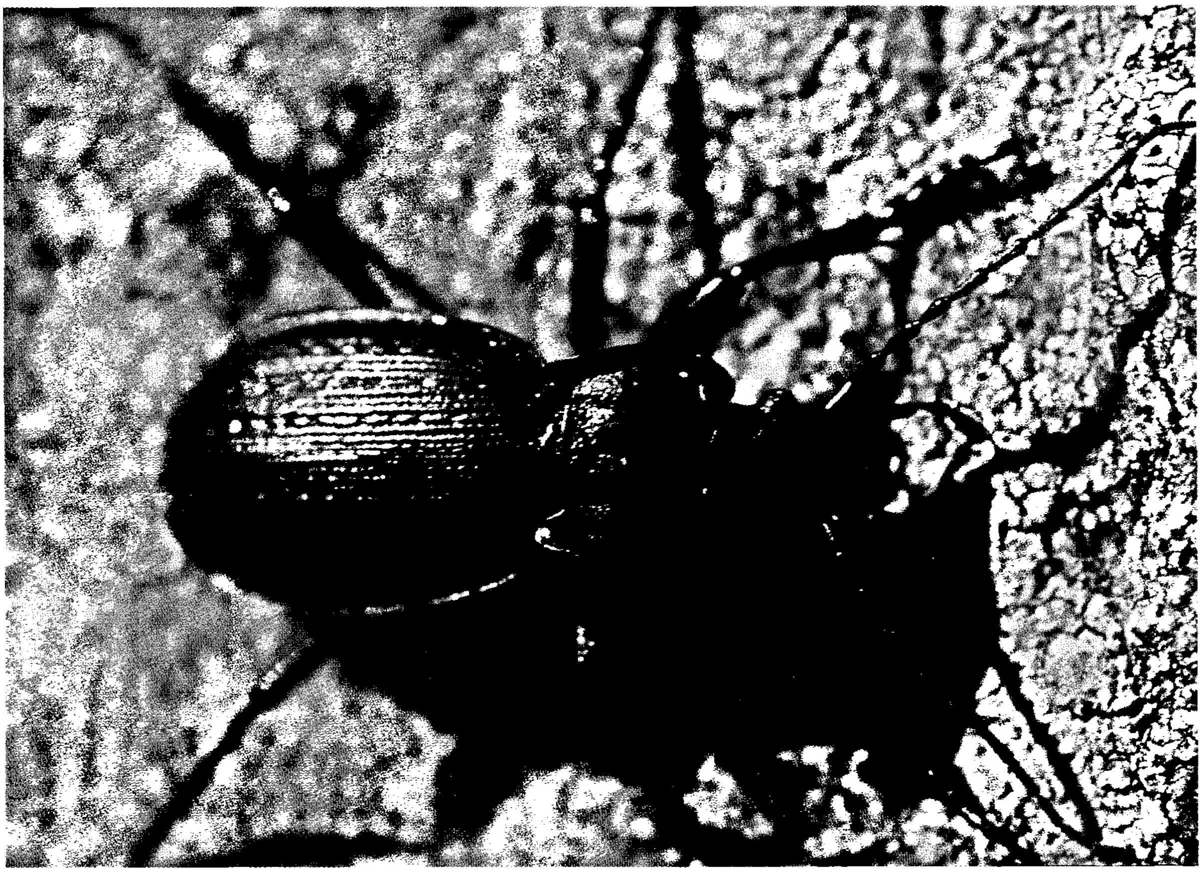
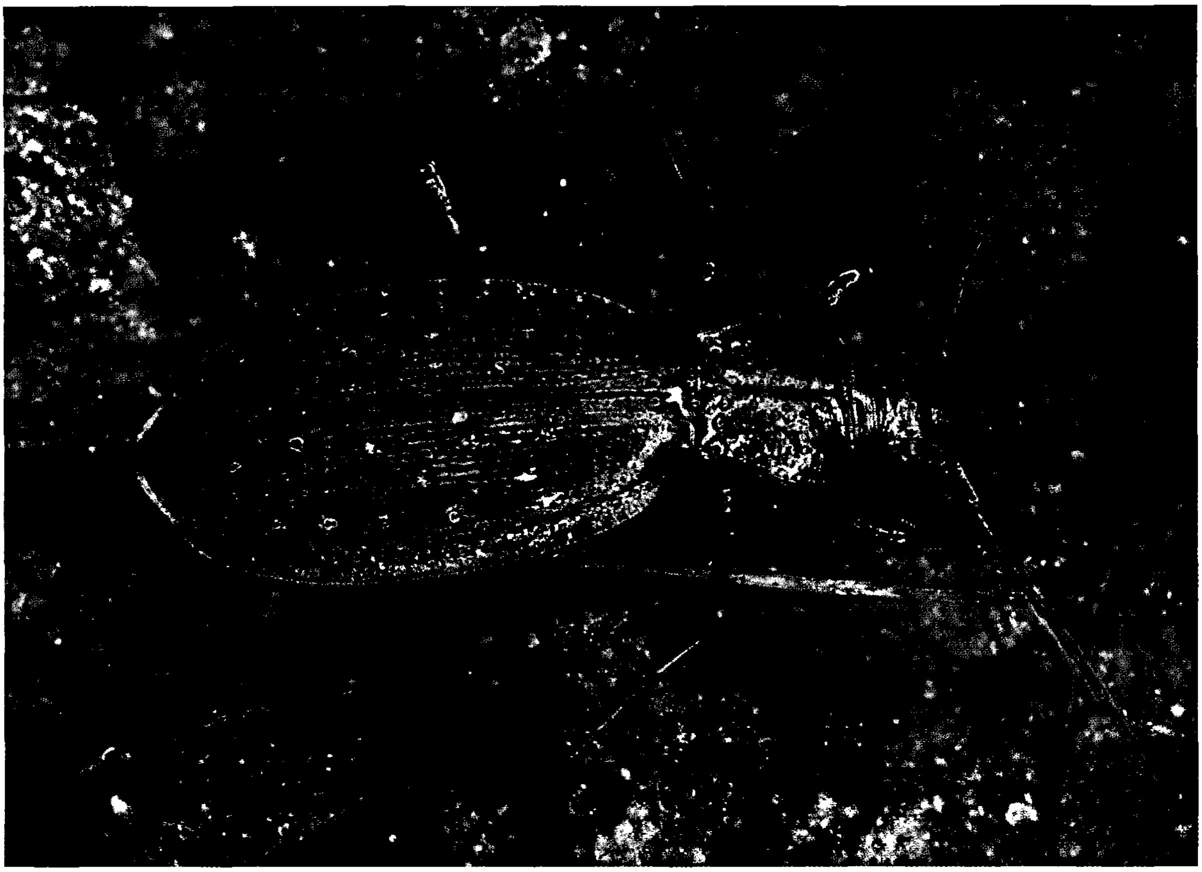
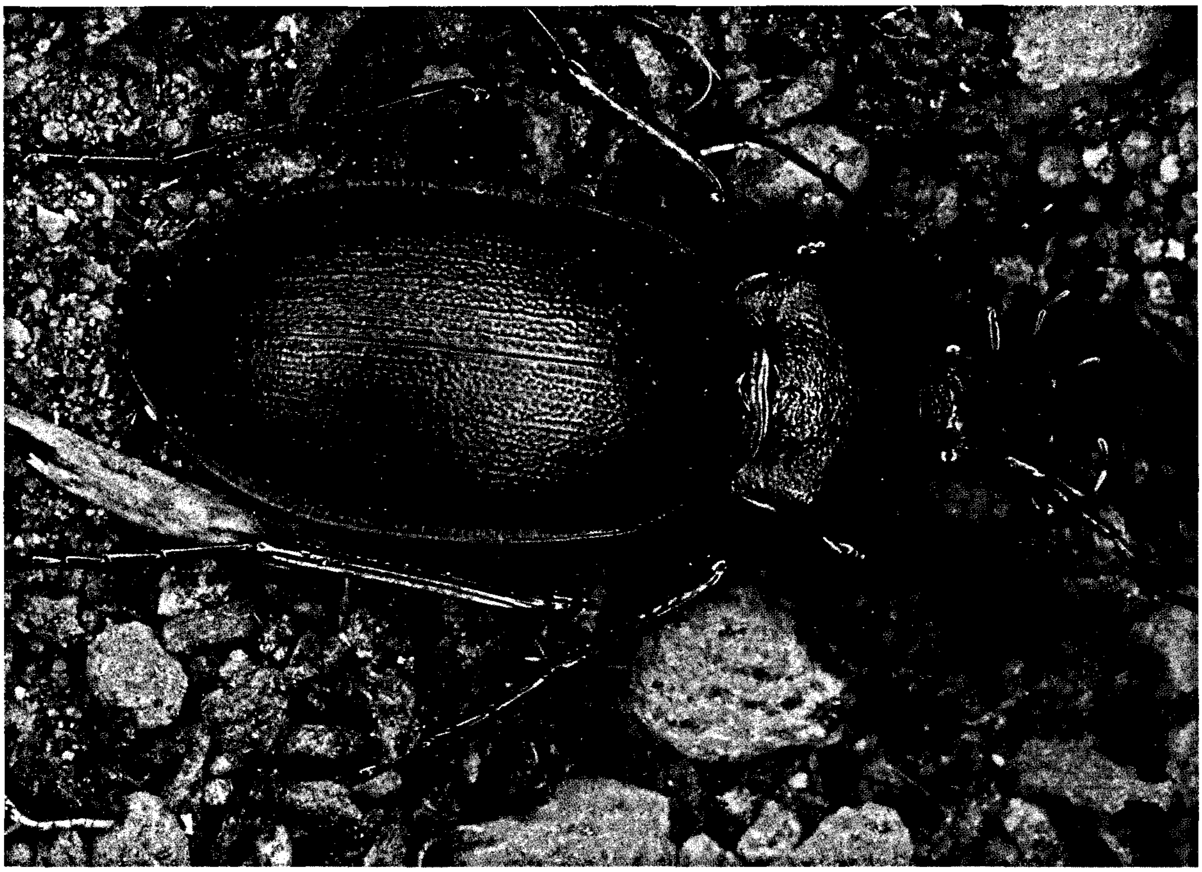
[19] For populations from the Vosges and the Black Forest additional refugia must be postulated because of the occurrence of additional geographic variants not found in the Cevennes or in central and northern France.



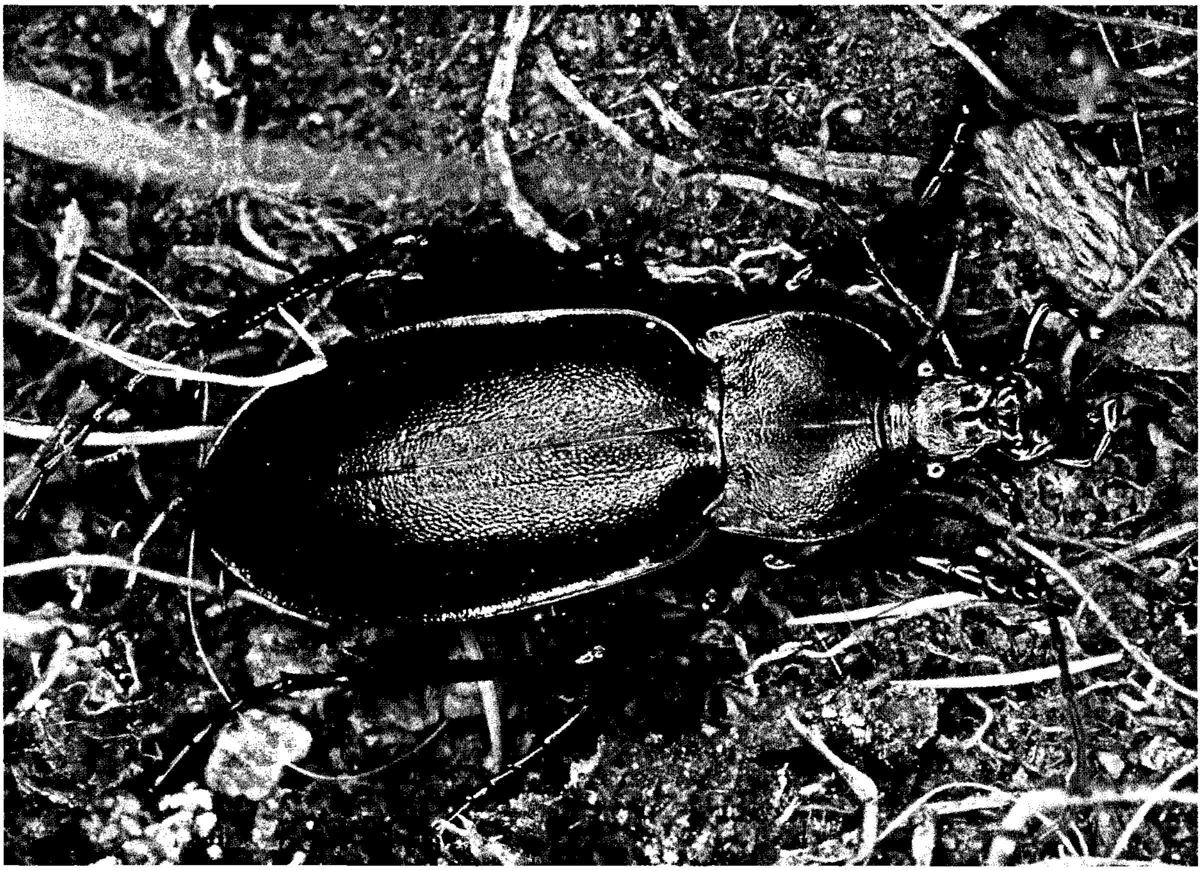
C. problematicus inflatus Kraatz
Italy,
Maritime Alps
(C. Lombarda).
Photo by
A. Vigna Taglianti.



C. depressus
Bonelli
Italy, Cottian Alps
(C. Finestre).
Photo by
A. Vigna Taglianti.



C. violaceus picenus
A.& G.B.Villa
Italy, Latium (Rome).
Photo by A. Vigna Taglianti.



C. germarii fiorii
Born
Italy, Cottian Alps (Sambuco).
Photo by A. Vigna Taglianti.

Hybrids and hybrid zones

Natural (cross-species) hybrids and those resulting from cross-breeding experiments in the laboratory have been known for the genus *Carabus* for a long time (e.g. Breuning, 1932-39; Puissegur, 1964; Allemand & Malausa, 1984; Deuve, 1994). In some (rare) cases, natural hybrids occur between species, which are not closely related to each other (e.g. *C.* (*Chrysocarabus*) *auronitens punctatoauratus* × *C.* (*Iniopachys*) *pyrenaeus*: Deuve, 1997a), but in most cases hybrids have been found from inter-breeding of species of the same subgenus (e.g. *C. glabratus* × *C. hortensis*, frequency of about 0.1% in the nature reserve 'Lüneburger Heide': Günther, *pers. comm.*; Assmann, *pers. observ.*). In syntopic populations of *Chrysocarabus* species, the number of natural hybrids is high. In woodlands of the Plateau de Sault (eastern Pyrenees), it can exhibit frequencies of about 1% of the total catch of *C. punctatoauratus* and *C. splendens* individuals. In some years, the proportion of hybrids between *C. splendens* and *C. lineatus* exceeds 40 % in the Val d'Hayra. Large differences exist in the relative numbers of hybrids between the populations; at other sites, the proportion is much smaller (Mossakowski *et al.*, 1986, 1990). Roschen & Mossakowski (1986) showed that both species diverged with respect to habitat selection under natural conditions and to behaviour in the laboratory (daily locomotory behaviour and reactions to temperature and humidity).

The excessive natural hybridisation within the subgenus *Chrysocarabus* may enable horizontal gene flow, a possible explanation of the common mtDNA haplotypes found within some species of this subgenus (see also Chapter 7). Puissegur (1964) pointed out that cross-species-hybrids showed reduced fertility. But his results were based on only a few individuals and a few cross-breeding experiments. Additionally, Allemand & Malausa (1984) and Assmann (1995) pointed out, that in polytypic species (e.g. *C. auronitens punctatoauratus*) cross-breeding experiments between individuals from different regions were necessary for a correct interpretation of cross-breeding incompatibility.

Hybrid zones between species or subspecies, which can be defined as 'narrow zones where genetically differentiated populations meet, mate and produce hybrids' (Calow, 1998: 347) are not evolved among members of the subgenus *Chrysocarabus*. Hybrids occur in the whole sympatric range of the species and are not restricted to a zone, where allopatric forms meet each other. However, hybrid zones have evolved in *Carabus* species. An example from two *Ohomopterus* species is discussed in section 6.2. A further example is the contact zone between *C. violaceus* and *C. purpurascens* in northwest Germany (Assmann & Schnauder, 1998). Within this zone, populations are characterised by intermediate values of two morphometric characters (the end of the aedeagus and elytron sculpture). The width of the hybrid zone is at least 40 km (as revealed by the two characters). An allozyme survey of this contact zone revealed a similar gradient (Schnauder, *in prep.*; *own observ.*). Differences in the width of clinal changes cannot be interpreted as evidence for the duration of contact, if gene flow and selection within the hybrid zone are unknown (Hewitt, 1988). Many hybrid zones (not only in Europe) originated during the postglacial period, when populations, which were separated in different refugia, met each other during their subsequent expansion (Harrison, 1990).

Chapter 7 Phylogeny

E. Arndt, M. Brückner, M. Marciniak, D. Mossakowski & F. Prüser

7.1. INTRODUCTION

About 800 species in 114 subgenera are joined in the genus *Carabus* (*s.l.*) (Březina, 1999; see also Chapter 8). The majority of these species occur in the Palaearctic region, only 11 species are native in the Nearctic region (Bousquet & Larochelle, 1993). Despite the rather well-known taxonomy of the group and several taxonomic approaches to divide the genus into subgroups, few efforts have been made to analyse the whole genus based on cladistic methods. Moreover, the proposed groups were mainly established on the evaluation of a single complex of characters.

Bengtsson (1927) and Lapouge (1929-32) both divided the genus *Carabus* into three groups based on larval characters (Tab. 7.1). Lapouge (1929-32) named these groups after the characteristic shape of the nasale: *Carabi serrilabres* with a nasale of four small, partially reduced teeth, *Carabi quadricuspides* with a nasale of four distinct teeth, and *Carabi rostrilabres* with a rostrum-like nasale (Figs. 7.1-7.5). Bengtsson (1927) interpreted the characters of the *Carabi serrilabres* as most primitive, the characters of the *Carabi rostrilabres* as most advanced and the *Carabi quadricuspides* as an intermediate group, and hence called the three groups *Archeocarabi*, *Neocarabi* and *Metacarabi*, respectively. In principle, it is possible to place all *Carabus* species into these three groups (Raynaud, 1975-76; Makarov, 1992, Turin *et al.*, 1993). Exceptions may be *Hygrocarabus* Thomson, *Ctenocarabus* Thomson, and *Rhabdotocarabus* Seidlitz, which seem to combine characters of different groups. However, gradual transitions between the typical differences in the shape of the nasale are found in some species, especially in first instar larvae. Therefore, convergent development of these structures cannot be excluded.

In his monograph of the genus *Carabus*, Breuning (1932-37) divided the genus into two subgeneric groups. He proposed the *Carabi brevimandibulares* and the *Carabi longimandibulares* mainly based on the shape of the adult mandible. Both groups correspond with the larval groups established by Bengtsson (1927) and Lapouge (1929-32) (Tab. 7.1). The *Carabi brevimandibulares* include the *Archeo-* and *Metacarabi*, and the *Carabi longimandibulares* correspond with the *Neocarabi*. Breuning's classification contradicts the larval type groups only in some cases where larvae were unknown at that time.

More recently, a completely different classification of the genus based on the structures of the internal sac of the male aedeagus was presented by Ishikawa (1973, 1978, 1979). As already described by Meurgue & Ledoux (1966) and Sturani (1967), the internal sac (endophallus) shows a variety of lobes, sclerotized areas and spines. Ishikawa (1973, 1978, 1979) divided the genus *Carabus* into three main groups ('subdivisions') each containing several genera. Deuve (1991, revised edition 1994) adapted Ishikawa's classification maintaining the generic state of *Carabus* (*s.l.*) and proposed five subgeneric groups (*Spinulati*, *Digitulati*, *Lipastromorphi*, *Archicarabomorphi*, *Lobifera*, Tab. 7.2). Deuve's classification contained the first complete list of subgeneric taxa after the monograph of Breuning (1932-37) and provided an important alternative approach to those based on larval characters. This author, in fact, drew attention to the general agreement of the classification based on endophallic characters with that based on larval characters. The only exception (Deuve, 1994: 55) is the position of *Cyclocarabus* Reitter, a subgenus with a *Neocarabi*-type larva inside the *Lipastromorphi* group. However, this view is not necessarily correct because we now recognise several incompatibilities of both systems (compare representatives in Tab. 7.2)

Recently, Imura (1996) in a discussion of Deuve's classification, mentioned that some of the subgeneric groups did not have equivalent taxonomic rank and that the *Lobifera* 'contains too many subgenera that seem more or less randomly enumerated...'. In conclusion, Imura (1996) proposed a new classification with 8 subgeneric groups which were based mainly on Deuve's system. This classification was improved by Imura *et al.* (1998) using molecular data partially supported by genital characters. Imura *et al.* (1998) separated a ninth subgeneric group, splitting the *Lepidospinulati* from the *Spinulati* (Tab. 7.3). This classification was adopted in a complete catalogue of species and subgeneric taxa by Březina (1999).

All the papers mentioned above had one aim: the presentation of a classification. However Deuve (1994, p. 55) stated with good reason: 'Demeurant les 'Archeocarabi', les 'Metacarabi' et les 'Lobifera', qui sont probablement paraphylétique ou polyphylétique.'

Table 7.1. Classification of *Carabus* (*s.l.*) based on characters of the larva. The corresponding names of Reitter (1896) are given in parenthesis.

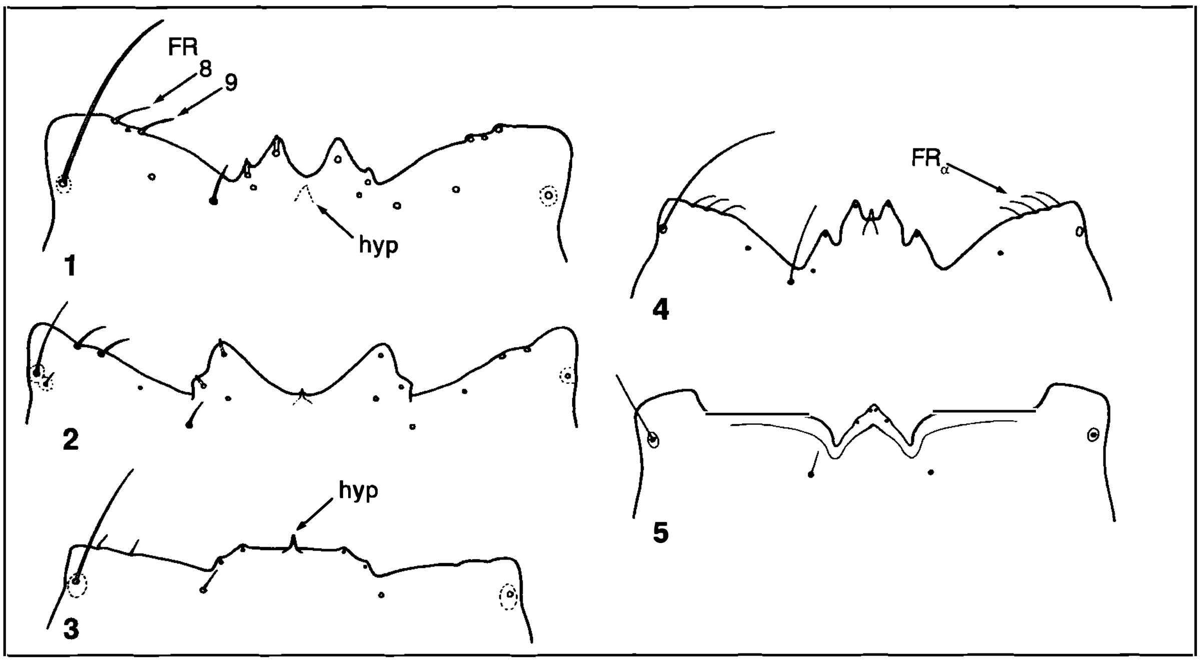
Bengtsson (1927)	Lapouge (1929-1932)	Breuning (1932-1937)
Archeocarabus*	Carabi serrilabres	Carabi brevimandibulares (Carabogenici Reitter)
Metacarabus*	Carabi quadricuspides (Multistriati Reitter)	Carabi brevimandibulares (Multistriati Reitter)
Neocarabus*	Carabi rostrilabres	Carabi longimandibulares

* Following Deuve (1994: 52) we use Archeocarabi, Metacarabi, and Neocarabi in the text instead of Bengtsson's terms.

Table 7.2. Classification of the genus *Carabus* based on endophallic characters compared with the classification based on larval characters.

Ishikawa (1978)	Deuve (1994)	**Representatives of larval groups**
Spinulati	Spinulati	Archeocarabi: *Apotomopterus*, *Limnocarabus*, *Euleptocarabus*
Carabogenici		
Carabus	Digitulati	Archeocarabi: e.g. *Eucarabus*, *Carabus* (*s.str.*) Metacarabi: *Nesaeocarabus*, *Eurycarabus*
Lipaster	Lipastromorphi	Archeocarabi: e.g. *Morphocarabus* Neocarabi: *Cyclocarabus*, *Lipaster*
Ischnocarabus	Archicarabomorphi	Archeocarabi: e.g. *Archicarabus*
Multistriati*	Lobifera	Archeocarabi: e.g. *Tachypus auratus* Metacarabi (excluding *Eurycarabus*, *Nesaeocarabus*) Neocarabi (excluding *Cyclocarabus*, *Lipaster*)

* Sensu Ishikawa (1978) and Deuve (1991), nec sensu Reitter (1896) and Deuve (1994).



Figs. 7.1.-7.5. Nasale and adnasale of first instar larvae. 7.1. *Carminaria denticolle*, 7.2. *Tachypus auratus*, 7.3. *Archicarabus nemoralis*, 7.4. *Oreocarabus glabratus*, 7.5. *Procrustes coriaceus* (hyp – hypodon).

Table 7.3. Classification of the genus *Carabus* by Imura (1996), modified by Imura *et al.* (1998) compared with classification by Deuve (1994). Imura's classification was accepted by Březina (1999).

Imura, 1996; Imura et al., 1998	**Deuve, 1994**	**Representatives of subgenera**
Lepidospinulati	Spinulati partim	*Limnocarabus, Euleptocarabus*
Digitulati[+]	Digitulati partim	*Carabus, Eucarabus, Ohomopterus, but Eurycarabus + Nesaeocarabus excluded*
Lipastromorphi	Lipastromorphi	*Morphocarabus*
Archicarabomorphi	Archicarabomorphi	*Archicarabus, Ischnocarabus*
Spinulati[+]	Spinulati partim	*Apotomopterus*
Crenolimbi	Lobifera partim	*Hemicarabus, Homoeocarabus*
Latitarsi	Digitulati partim, Lobifera partim	*Tomocarabus, Pachystus, Eurycarabus, Nesaeocarabus,* *Tachypus, Mesocarabus, Oreocarabus, Meganebrius*
Arcifera	Lobifera partim	*Platycarabus, Chaetocarabus, Hygrocarabus, Heterocarabus*
Procrustimorphi	Lobifera partim	*Iniopachys, Tribax, Cathoplius, Coptolabrus, Damaster, Megodontus, Procerus, Macrothorax, Chrysocarabus, Procrustes, Lamprostus*

[+] Digitulati, Spinulati in a new, restricted sense.

Our approach is to re-analyse the subgeneric relationships of the genus *Carabus* using cladistic methods. We try to improve the monophyly of the genus and various proposed subgroups and discuss the reconstruction of intrageneric relationships within the genus *Carabus*. For this purpose, we analysed both larval and endophallic characters and combined them in a single data matrix including new larval characters like the complex chaetotaxy. Additionally, we used mitochondrial DNA sequences for further information. The DNA data were combined from our own analysis and recently published sequences of Japanese and European *Carabus* species (Su *et al.*, 1996a,b,c). Although the mitochondrial protein genes were shown to be unsuitable at this taxonomic level (Su *et al.*, 1996a; Prüser, 1996), we received some additional and important information concerning the morphological data analysis. Morphological characters of adults like those used by Breuning (1932-37) were not taken into consideration because of their high level of homoplasy and their comparatively low value for a phylogenetic classification of adults. Both, morphological as well as molecular data were analysed by searching for the most parsimonious trees. Furthermore, we discuss our results in comparison to different earlier classifications of the genus and other phylogenetic approaches.

In contrast to other chapters of the present book, it is impossible to restrict our analysis and discussion to European taxa. A phylogenetic examination of the genus must include all available taxa. In this paper, we generally use subgeneric names for single taxa, but for the genus as a whole we use '*Carabus* (*s.l.*)' or mark *Carabus* with the label genus. The subgeneric taxa are named and listed after Casale & Kryzhanovsky (this volume). Non-European taxa which are not included in Casale & Kryzhanovsky are listed after Březina (1999).

Larval examination, study of the internal sac of male genitalia, the molecular analysis of the DNA, and even the phylogenetic analysis of all these data require a number of special preparation techniques and evaluation methods. For those readers who are interested in these techniques, a detailed description of methods as well as a list of examined material is added as an appendix to this chapter.

7.2. RESULTS

7.2.1. Analysis of morphological data

Eleven characters of the male endophallus and 29 larval, morphological characters were examined (Tab. 7.6; appendix). The character state matrix (Tab. 7.7, appendix) was analysed by searching for the most parsimonious trees with the computer program PAUP (Swofford, 1998). The analysis was performed under different conditions but we present results only without character weighting.

Twenty-nine trees were found with a score of 152 steps using character states and character types as indicated in Tab. 7.6 (14 characters of type ordered, two user-defined, remaining unordered). The matching results of these trees are shown as a strict consensus tree in Fig. 7.16. The trees were rooted by using three calosomine genera as outgroups. Although there is only moderate resolution, there are some *Archeocarabi* species separated basally and also from each other: both *Tachypus* Weber species and *Limnocarabus* Géhin. *Hygrocarabus* splits also basally. The remaining *Metacarabi* and *Neocarabi* form clades, the relationships of the subgenera of which are only partly resolved. The *Neocarabi* clade includes *Chaetocarabus* Thomson and *Platycarabus* Morawitz, *Archiplectes* Gottwald and

Microplectes Reitter, *Sphodristocarabus* Géhin together with *Lamprostus* Motschulsky and *Coptolabrus* Solier, *Cathoplius* Thomson and *Iniopachys* Solier, as well as the unresolved subgenera *Megodontus* Solier, *Chrysocarabus* Thomson, *Macrothorax* Desmarest, and *Procrustes* Bonelli. The remaining *Archeocarabi* do not form a clade in this analysis.

The results presented in Fig. 7.16 were evaluated by means of the decay index. It is defined as the number of additional steps required to collapse a particular branch in the strict consensus tree (Bremer, 1994). The decay index is very low in the morphological tree presented.

7.2.2. Analysis of molecular data

Molecular data were obtained from the DNA sequences of the mitochondrial NADH-dehydrogenase subunit 5 gene (ND 5) of 32 species representing 21 *Carabus* subgenera and two Calosomina as an outgroup. The analysis of the unweighted mitochondrial DNA sequences resulted in two most parsimonious trees with tree lengths of 1615 steps. The resulting strict consensus tree shows little resolution in the basal relationships (Fig. 7.17). Well supported clades with bootstrap values ≥ 90% and/or higher decay indices were found for *Platycarabus* species + *Chaetocarabus* which were separated from the remaining *Neocarabi*, for most of the species of subgenera which include more than one species like *Limnocarabus* and *Tachypus*, for *Hemicarabus* Géhin + *Homoeocarabus* Reitter, *Eucarabus* + *Carabus* (*s.str.*), *Eurycarabus* Géhin + *Nesaeocarabus* Bedel, *Coptolabrus*/*Acoptolabrus* Morawitz + *Damaster* Kollar, and *Megodontus* + *Procrustes*. All these acceptable values are found in the terminal branches.

The molecular data were also analysed using a weight of two, five and ten, respectively, for all changes except the transitions at third codon positions. The results are very similar to those shown in Fig. 7.17. The same clades as found in the earlier analysis were supported by bootstrap values of at least 50 percent. Because the number of subgenera available for the molecular analysis is much lower than that of our morphological examination (see Appendix, material), both analyses cannot be compared directly. Therefore, the results of the molecular analysis should be regarded as useful addition to the morphological examination.

7.3. DISCUSSION

7.3.1. Comparison of examined genital and larval characters

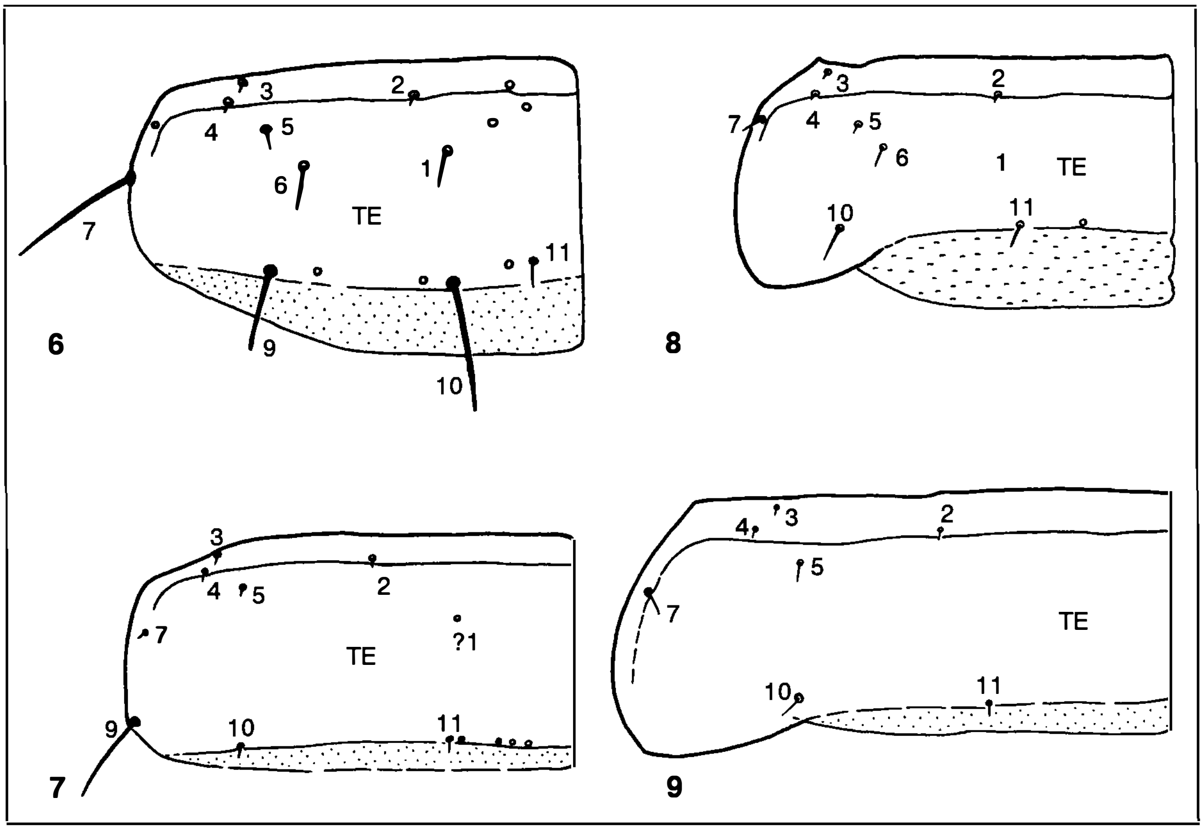
One of the character complexes used for classification of the genus *Carabus* is the structure of the inflated internal sac (endophallus) of the aedeagus. The ligulum (= ligula auct., following Deuve, 1994), lacinia, digitulus and pigmented fields are more or less sclerotized structures of variable shape and position, ostium lobes, praeputial pad, and aggonoporius are membranous structures of the internals sac (Figs. 7.11-15 and Tab. 7.6, characters 30-37). Both sclerotized and membraneous structures are highly conserved in *Carabus* species and were used by Ishikawa (1973, 1979) and Deuve (1994) for the classification of the genus *Carabus*.

However, it is very difficult to homologise the structures between different groups as a detailed analysis shows. Moreover, most of the mentioned structures are lacking in *Calosoma* (*s.l.*) (Fig. 7.10) which represents the plesiomorphic states of most characters in Carabini (*Calosoma* (*s.l.*) and *Carabus* (*s.l.*)). Even the determination of structures which are homologous to the tongue-shaped ligulum basal to the endophallus in *Calosoma* is not evident in *Carabus* (see Sturani, 1967). Consequently, the plesiomorphic character states and direction of transformations of several characters of the internal sac in *Carabus* are unclear. This is an important disadvantage in the phylogenetic interpretation of these characters.

In contrast, the homologisation, the plesiomorphic state, and even the transformation series of characters of different *Carabus* groups are obvious for most larval characters. We also have found all these characters in the outgroups. Previously, the shape of nasale and adnasale, mandible, abdominal tergites and urogomphi of *Carabus* larvae have been used in phylogenetic discussions (Bengtsson, 1927, Lapouge, 1929-32; Hůrka, 1971a). First attempts to use the larval chaetotaxy are made by Makarov (in Turin *et al.*, 1993).

The pattern of larval setae (chaetotaxy) gives us a useful set of characters for phylogenetic analysis. Bousquet & Goulet (1984) and Bousquet (1985) described the hypothesized ground plan of chaetotaxy in first instar larvae of Carabidae and the most important differences of the chaetotaxy between the first instar and later instars. First instar larvae of the vast majority of taxa of Carabidae show a defined ground plan pattern of setae and pores, whereas the later instars usually have a varying number of additional ('secondary') setae on nearly all sclerites, especially on tergites, sternites and urogomphi. However, larvae of *Carabus* (*s.l.*) and *Calosoma* (*s.l.*) differ distinctly from the described ground plan. On the one hand, larvae of *Carabus* (*s.l.*) have a reduced setal pattern. On the other hand, second and third instar larvae of *Carabus* (*s.l.*) do not have regular secondary setae except on the ventral side of the tarsi.

One complex of setae found to be useful for phylogenetic investigations is that of abdominal tergites. The chaetotaxy of abdominal tergites I-VIII with only 11 setae in the basic pattern (Bousquet & Goulet, 1984) is highly variable in *Carabus* (*s.l.*) and nearly independent from the shape of tergites and the different expansion of the posterolateral angles (lobes). The tergal setae TE$_{6,7,9,10}$ (Figs. 7.6-9) appear in a variable pattern that allows to draw phylogenetic conclusions. The homologisation of the setae is possible using the outgroup for comparison and comparing the position of homologous setae on the pronotum and metanotum (see Arndt, 1993, p.12). For instance, seta TE$_7$ on abdominal tergites is duplicated in *Eupachys* Chaudoir, *Coptolabrus* and *Damaster* like the homologous setae ME$_9$ on the mesonotum and metanotum.



Figs. 7.6.-7.9. Abdominal tergite I, left half of first instar larvae. 7.6. *Carminaria denticolle*, 7.7. *Tachypus auratus*, 7.8. *Hemicarabus nitens*, 7.9. *Chrysocarabus auronitens*.

Seta TE_9 (erroneously coded as TE_7 in Arndt *et al.*, 1994 and Prüser & Arndt, 1995) shows a unique irregularity. It is a 'primary' seta sensu Bousquet & Goulet (1984), that is to say a ground plan seta for all larval instars. Seven species of different phylogenetic lineages were found, however, which have the apomorphic state (seta TE_9 reduced) in the first instar, but the plesiomorphic state (seta TE_9 present) in higher instars (Tab. 7.4). For these species, TE_9 became a 'secondary' setae sensu Bousquet & Goulet (1984), that is a ground plan seta in the later instars which is lacking in the first instar.

The setae FRa of certain representatives of *Metacarabi* (Fig. 7.4, compare Tab. 7.5, 7.6 and 7.7, character 4.1) and setae on antennomere II (*Neocarabi*) are autapomorphic structures in addition to the basic pattern.

Most larval characters were found to be suitable for phylogenetic analysis. Exceptions are the variable characters of the larval nasale and presence or absence of certain setae (Tab. 7.6 and 7.7, characters 8, 10, 15, 19) which show a high degree of homoplasy.

7.3.2. Phylogenetic results

7.3.2.1. Monophyly of the genus *Carabus* Linné

The genus *Carabus* (in the widest sense) represents a monophyletic group, which is supported by the following autapomorphies in the larval morphology. The setae PA_4, PA_6, ME_2, and TE_1 (Tab. 7.6, characters 5, 6, 12, 16) are lacking in all examined *Carabus* larvae. These setae are present in the outgroup. The presence of these setae represents the ground plan state not only of Carabini, but also of Carabidae. The reduction of these setae in *Carabus* species is a derived state and regarded as autapomorphic for the genus.

The shape of the endophallus supports the monophyly of *Carabus* (*s.l.*). The endophallus of *Calosoma* (outgroup) is simple with a large ligulum (Fig. 7.10). Ostium lobes, ppd-lobes, digitulus and pigmented fields are absent in the outgroup. All *Carabus* species however show a complex structure of the endophallus. The presence of ostium lobes, ppd-lobes and/or a small ligulum are autapomorphies of *Carabus* (*s.l.*).

Table 7.4. Species with different states of character 18 (Tab. 7.6) in different larval instars: 0 - seta TE$_9$ present; 1- pore-like; 2 - completely reduced. Only species which were available in first AND second instar are listed.

Species	Instar I	Instars II, III	Species	Instar I	Instars II, III
Morphocarabus monilis	2	0	*Homoeocarabus maeander*	2	0
Morphocarabus scheidleri	2	0	*Platycarabus depressus*	1	0
Eucarabus ulrichii	2	0	*Platycarabus fabricii*	2	0
Tachypus cancellatus	2	0			

7.3.2.2. Discussion of the monophyly of subgroups

Basal split-off

A lot of supraspecific taxa were proposed in the past based on various character sets. However, the basal split-offs in the phylogeny of *Carabus* (*s.l.*) were not analysed with cladistic methods.

In our analyses, *Tachypus auratus* Linné is the sistergroup of the remaining taxa of *Carabus* (*s.l.*) (Fig. 7.16). This is supported by several characters. Setae PA$_4$ and PA$_8$ are completely reduced in all *Carabus* larvae except *Tachypus auratus*. They are present in the outgroup and in other larval Carabidae which is the plesiomorphic state. *T. auratus* has pore-like setae PA$_4$ and PA$_8$ which could be the basic condition in *Carabus* (*s.l.*). The complete absence of both setae in all *Carabus* species except *T. auratus* is a synapomorphy of these taxa. Furthermore, *T. auratus* has a nasale with four teeth in the larval stage, exactly as found in the outgroup, which is regarded as plesiomorphic (Figs. 7.1, 7.2). A similar shape of nasale is only found in the subgenera combined as *Metacarabi* (see below). Larvae of *Metacarabi*, however, have sharper nasale teeth placed close to each other (Fig. 7.4). All other *Carabus* larvae have a derived nasale shape (Tab. 7.6, character 26).

The basal position of *Tachypus auratus* and the proposed sistergroup relationship to the other *Carabus* taxa is supported by several additional larval characters (e.g. presence of two ground plan setae on adnasale, three ground plan setae on ventral side of head, the presence of abdominal setae TE$_7$, TE$_9$, absence of setae on first maxillary and labial palpomeres (Tab. 7.6, characters 2, 3, 7, 18, 20, 22, 23), and the stout abdominal tergites). *T. auratus* shows the plesiomorphic state in all of these characters. The basal position of *T. auratus* is also confirmed by the characters of endophallus. The presence of a simple ligulum, simple ppd-lobes and ostium lobes, as well as the absence of a digitulus, a lacinia and pigmented fields (Fig. 7.13) are plesiomorphic characters for *Carabus*. Molecular data also imply a basal position of *Tachypus cancellatus* together with *T. auratus* (Fig. 7.17). Larval characters of *T. cancellatus* show a transition form between *T. auratus* and other basal *Carabus* taxa. Therefore *T. cancellatus* does not group together with *auratus* in Fig. 7.16 when all morphological data are analysed together.

Eucarabus cristoforii Spence – which is also regarded as member of *Tachypus* by Březina (1999; *Autocarabus* of Deuve, 1994 and Turin *et al.*, 1993) – has the apomorphic character states and should be excluded from *Tachypus* as Casale & Kryzhanovsky propose (this volume).

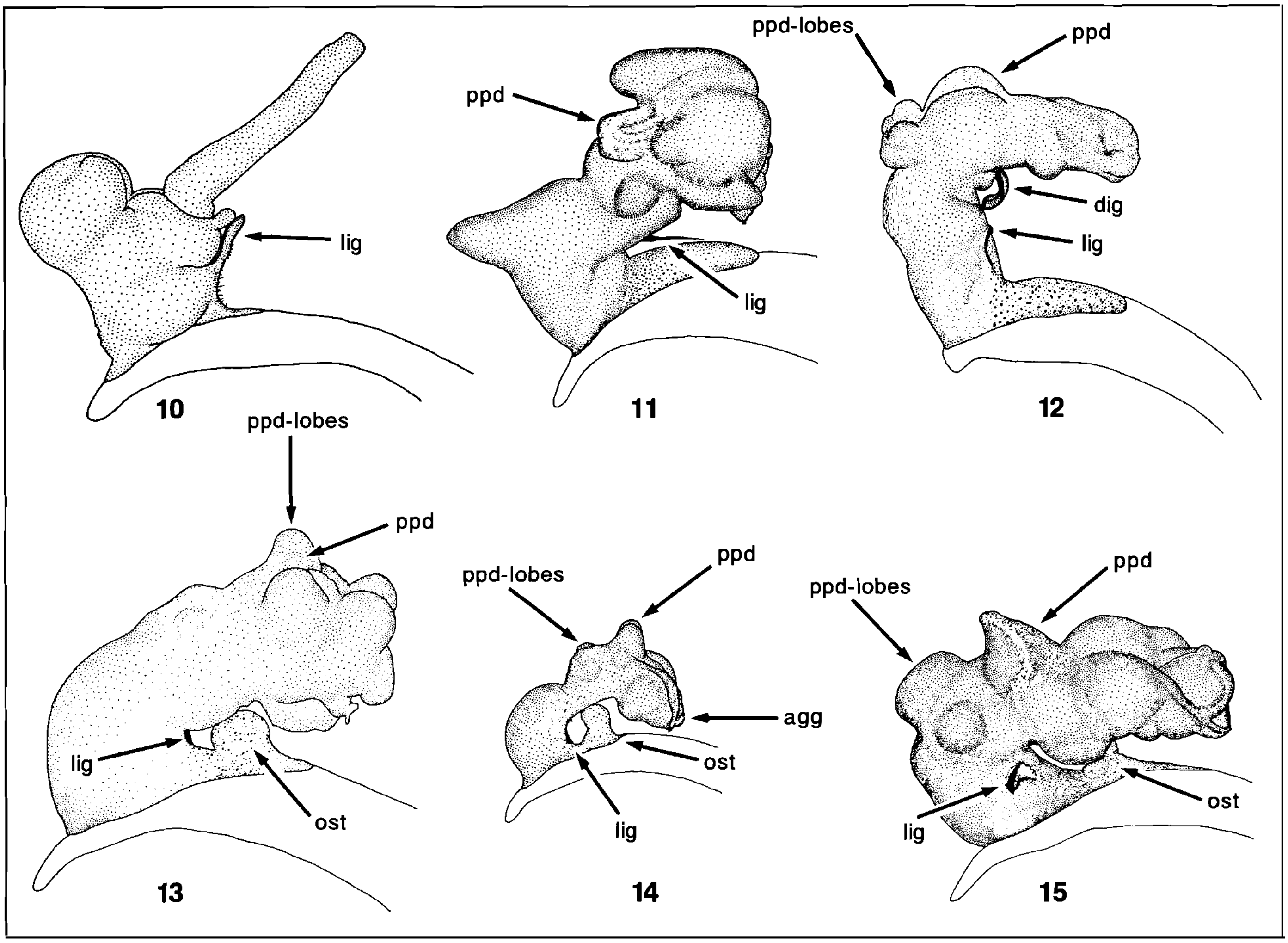
Metacarabi

Representatives of the *Metacarabi* (sensu Bengtsson, 1927 = Quadricuspides Lapouge, 1929, see Tabs. 7.1 and 7.5) show a high number of plesiomorphic character states in the adult and in the larval stage. The monophyly of this group (*Hygrocarabus* excluded) is implied by the parsimony analysis of the morphological data (Fig. 7.16), but with weak statistical support (decay index). The nasale consists of four teeth which is a ground plan character (Arndt, 1993), the characteristic narrow position of these teeth and the strongly sloped adnasale region ('butterfly-shape', Fig. 7.4) could be regarded as an autapomorphy. The arrangement of nasale teeth is not narrow and the adnasale region has a different shape in the outgroup and in other *Carabus* larvae (e.g. subgenera *Tachypus*, *Carabus* (*s.str.*), *Eucarabus*, and *Neocarabi*). Turin *et al.* (1993) mentioned a terebral tooth on the mandible as further autapomorphic character. However, this tooth is indistinct or lacking in several species.

In the analysis of molecular data (Fig. 7.17), the *Metacarabi* are split and its species are grouped together with species of various other subgenera. However, most of these arrangements are not supported by significant bootstrap values (compare section 3.3).

A close relationship of *Aulonocarabus* + *Leptocarabus* is found by Su *et al.* (1996a) using molecular data, that of *Nesaeocarabus* + *Eurycarabus* is supported in the present analysis of molecular data by a bootstrap value of 73% and a decay index of +5.

A monophyly of *Metacarabi* and proposed relationships of various subgenera contradict the results of Deuve (1994), who listed the subgenera of *Metacarabi* in two different groups, each combined with other taxa. Deuve (1994) placed most of the subgenera of *Metacarabi* together with *Neocarabi* and *Tachypus* in the *Lobifera*. The Lobifera are exclusively characterised by endophallic characters. Ostium lobes and a ppd are present in *Lobifera*, whereas the endophallic ligulum is reduced. However, these characters are probably



Figs. 7.10.-7.15. Male aedeagus with inflated endophallus. 7.10. *Calosoma sycophanata*, 7.11. *Limnocarabus clatratus*, 7.12. *Nesaeocarabus coarctatus*, 7.13. *Tachypus auratus*, 7.14. *Hemicarabus nitens*, 7.15. *Chaetocarabus intricatus* (agg – aggonoporus, dig – digitulus, lig – ligulum, ost – ostium lobe).

ground plan characters of *Carabus* (*s.l.*). Deuve (1994: 55) already regarded the Lobifera as para- or polyphyletic. Furthermore, he included *Eurycarabus* and *Nesaeocarabus* (as part of *Carabus* (*s.str.*)) in the *Digitulati*. We did not find any evidence for a close relationship of *Nesaeocarabus* + *Eurycarabus* with *Carabus* (*s.str.*)

Neocarabi

The *Neocarabi* (sensu Bengtsson, 1927; = Rostrilabres Lapouge, 1929 = Carabi longimandibulares Breuning, 1932-37; see Tab. 7.1) probably represents a large monophyletic unit only weakly supported by morphological data (Fig. 7.16). There are several autapomorphic characters in the larval stage. The nasale is rostrum-shaped in all Neocarabi (Fig. 7.5, Tabs. 7.6 and 7.7, character 26.2) and the single nasale teeth are fused. The nasale consists of four teeth in other *Carabus* (*s.l.*) larvae and the outgroup, which is the plesiomorphic state of the Carabini and the Carabidae (Arndt, 1993). The setae FR$_8$ and FR$_9$ on the anterior margin of the nasale are reduced, pore-like, or lacking. In the outgroup and all other species examined with the exception of *Morphocarabus monilis* Fabricius, both setae are present which is the plesiomorphic state of *Carabus* (*s.l.*) and a ground plan character of Carabidae. The pore-like setae in *M. monilis* are almost certainly due to convergent reduction. One seta is present in *Iniopachys auriculatus* Putzeys which seems to be homologous to FR$_9$.

The antennomere II has at least one seta (Tabs. 7.6 and 7.7, character 21.1) in all taxa except the subgenera *Chaetocarabus* and *Cathoplius*. Setae on antennomere II are lacking in other *Carabus* larvae and in the outgroup, which is the plesiomorphic state. A secondary reduction is supposed in *Cathoplius*, whereas *Chaetocarabus* could show the plesiomorphic state because of its basal position (see below).

The anterior margin of adnasale is S-shaped in all taxa except *Chaetocarabus* and *Platycarabus*, which is a synapo-

Table 7.5. Distribution of larval character states in the subgenera of the Metacarabi group. 'Other Metacarabi' combines *Mesocarabus*, *Tomocarabus*, and *Oreocarabus* (Character states correspond to Tab. 7.6: FRa=character 4; ME_1=11; TE_9=18; LAI=22; MXI=23).

Subgenus/characters	FRa	ME_1	TE_9	LAI	MXI
Hemicarabus nitens	0	0	0	0	0
H. serratus	1	2	1	0	0
Homoeocarabus	0	0	0	0	0
Eurycarabus	0	2	1	1	0
Nesaecarabus	0	2	1	0	0
Pachycarabus	0	2	1	1	0
Orinocarabus	0	2	1	1	0
Orinocarabus linnaei	1	2	1	0	0
Leptocarabus	0	2	1	1	0
Meganebrius	1	2	1	1	0
Ulocarabus	1	2	1	1	0
Leptocarabus	1	2	1	1	0
Oreocarabus glabratus	1	0	1	1	0
Other Metacarabi	1	2	1	1	1

morphy of the *Neocarabi* excluding *Chaetocarabus* and *Platycarabus* (Fig. 7.5, Tab. 7.6 and 7.7, character 27:1). The adnasale region is straight in *Chaetocarabus* and *Platycarabus*, and straight or slightly rounded in all other taxa and the outgroup.

The *Neocarabi* in a strict sense (without *Chaetocarabus* and *Platycarabus*) include all taxa examined from *Cathoplius* to *Macrothorax* (see appendix, list of material). Furthermore they contain the subgenera *Plesius* Semenov, *Pseudotribax* Kraatz, *Alipaster* Reitter, *Cratocarabus* Reitter, *Cratocephalus* Kirschner, *Cratocechenus* Reitter, *Cratophyrtus* Reitter, *Pantophyrtus* Thieme, *Cechenotribax* Semenov & Znoiko, *Deroplectes* Reitter *Pachycranion* Solier, and *Goniocarabus* Géhin from which larval material was not available or larvae were not included in the analysis. All other subgenera listed as 'Procrustimorphi' by Březina (1999) most probably belong to the *Neocarabi*, but this cannot be proven due to a lack of knowledge of larval characters and absence of molecular data.

Cyclocarabus was included in the *Neocarabi* by Makarov (1992), but Deuve (1994) indicated that the position of *Cyclocarabus* is questionable, because all *Neocarabi* are included in his *Lobifera* group, *Cyclocarabus,* however, was included in his *Lipastromorphi* group.

Within *Neocarabi* (*s.str.*) two monophyletic groups are proposed based on larval characters alone. The first monophylum is composed of *Macrothorax*, *Procrustes* and *Megodontus*. Representatives of these subgenera have a divided setal field gMX on stipes. A large group of setae is on the dorsal side and a row of setae lies on the mesal margin. This is interpreted as an apomorphic character state and regarded as synapomorphy of the three mentioned taxa. All other *Carabus* (*s.l.*) and larvae of the outgroup have a single large setal group gMX on the stipes.

The second monophyletic group within the *Neocarabi* (*s.str.*) shows duplicated or multiplied setae TE_7 and ME_9, which is regarded as synapomorphy of these taxa. One seta TE_7 and one ME_9 is present in the outgroup and – if not reduced – in the other *Carabus* larvae which represents the ground plan state (see Arndt & Makarov, Chapter 4 of this volume, and Figs. 7.4, 7.6). The group with multiplied tergal setae contains *Eupachys*, *Damaster* and *Coptolabrus* (in part). Endophalli of these taxa were not examined and the taxa are therefore not included in Fig. 7.16. Both proposed monophyletic groups of *Neocarabi* are also supported (weakly: *Megodontus* and *Procrustes*; very good: *Damaster* and *Coptolabrus*) by molecular data as far as the included taxa were examined (Fig. 7.17). The endophallic structure is not distinctly differentiated between examined *Neocarabi* taxa and therefore does not contradict these monophyla.

We did not find apomorphic characters which support a close relationship of *Chrysocarabus* + *Macrothorax* + *Lamprostus* + *Megodontus*, and a group including the rest of the 'specialised' *Neocarabi* respectively as proposed by Turin *et* *al.* (1993). On the other hand, Turin *et al.* (1993), did not give characters on which these groups were based.

Relationship of *Chaetocarabus, Platycarabus* and *Hygrocarabus*

Chaetocarabus and *Platycarabus* appear as a terminal branch of *Neocarabi* in the morphological analysis (Fig. 7.16). Both groups are lacking the S-like adnasale region of the larvae, *Chaetocarabus* additionally lacks the setae on antennomere II of the larvae. Endophallic characters support a relationship between both subgenera and *Hygrocarabus* (Ishikawa, 1984, Casale *et al.*, 1998). All three taxa show a strongly enlarged ligulum with free, tooth-shaped apex. Ishikawa (1984) also placed *Heterocarabus* Morawitz, which was not available for our study, in this group. On the other hand, Deuve (1994) and Casale & Kryzhanovsky (Chapter 3 of this volume) regarded *Ctenocarabus* Thomson (incl. *Rhabdotocarabus*) as closely related with *Hygrocarabus*. *Hygrocarabus* was mentioned as a transition form between *Neocarabi* and *Metacarabi* by Hůrka (1971a) and as closely related to *Neocarabi* by Makarov (1992) and Turin *et al.* (1993).

The larvae of *Hygrocarabus* and *Ctenocarabus* have the 'general appearance' of a *Neocarabi* larva (e.g. wide tergites and long urogomphi), but lack the mentioned autapomorphies of that group. Rather they could be a derived group of *Metacarabi*, because of their typical metacarabi-like shape of nasale. Furthermore, at least some specimens of *C. melancholicus* Fabricius have duplicated frontal setae FRa as known for certain *Metacarabi* only and the seta TE_9 is present (absent in *H. variolosus*). *Ctenocarabus* therefore could represent the plesiomorphic state of both characters for the mentioned taxa.

Ctenocarabus was not included in our morphological analysis because of incomplete larval data. *Hygrocarabus* represents a basal branch of *Carabus* excluding *Tachypus* and *Limnocarabus* in our morphological analysis (Fig. 7.16). The molecular data confirm the close relationship of *Chaetocarabus* and *Platycarabus* by high bootstrap values and decay index, but whether they give evidence for a closer relationship of both taxa with *Hygrocarabus* nor evidence for the relationship between *Hygrocarabus* and *Ctenocarabus* (*Heterocarabus* was not examined).

Spinulati

The subgenera *Apotomopterus* Hope, *Euleptocarabus* Nakane and *Limnocarabus* are placed together by Deuve (1991, 1994) under the name 'Spinulati'. A probable autapomorphic character of the *Spinulati* is the spine-like prolongation of the endophallic ligulum. The ligulum is a very small sclerotised spot in other *Carabus* (*s.l.*), which represents the ground plan character of the genus.

A strong relationship at least of *Euleptocarabus* and *Limnocarabus* is also proposed by Su *et al.* (1996a) based on molecular data. Imura *et al.* (1998) separated both subgenera from *Apotomopterus* and named this new taxon *Lepidospinulati*.

Larvae are only known from *Limnocarabus*, the single taxon of *Spinulati* included in our analysis. It represents a basal split off as shown in Fig. 7.16.

Digitulati (partim)

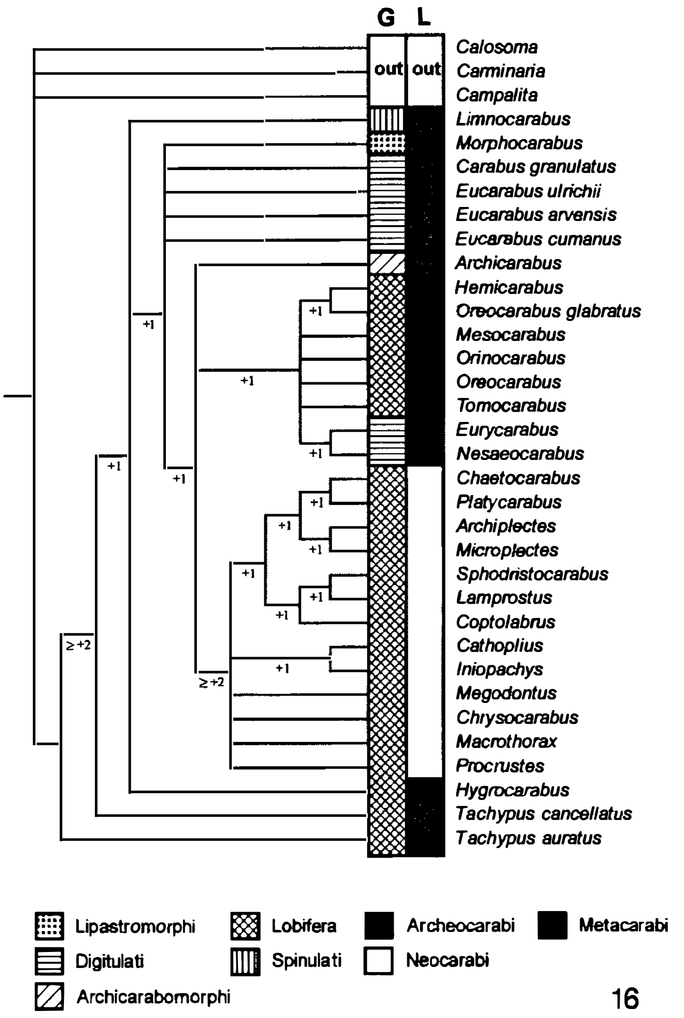
The monophyly of *Digitulati* is neither supported by morphological nor by molecular data analysed in this study. The group *Digitulati* (Deuve, 1994) is based on a symmetrical single sclerite (digitulus, Fig. 7.12) which is situated distally on the ligulum of the endophallus. Deuve regarded this as a synapomorphic character of all taxa included in the *Digitulati*. This sclerite is variable in shape and size. Nothing is known about the evolutionary origin of the digitulus. The interpretation of the digitulus as synapomorphy contradicts several other characters of the mentioned taxa. Whether the analysis of the morphological data (Fig. 7.16) nor the molecular analysis (Fig. 7.17, see also Prüser, 1996) support the monophyly of the Digitulati is unclear. Moreover, Deuve (1994) placed the *Nesaeocarabus* species in the subgenus *Carabus* (*s.str.*) but maintained the subgenus *Eurycarabus*. The molecular analysis clearly supports the monophyly of *Eurycarabus* + *Nesaeocarabus* instead of a group *Carabus* (*s.str.*) + *Nesaeocarabus* (Prüser *et al.* 2000). The latter two taxa are clustered on completely different branches analogous to the distribution of their larval characters.

Therefore, we assume a convergent evolution of the digitulus in *Eurycarabus* + *Nesaeocarabus* on one side, and *Carabus* (*s.str.*) + *Ohomopterus* (incl. *Isiocarabus*?) on the other side. Other characters of the endophallus of *Digitulati* like the absence of an ostium lobe and the presence of a moderately sclerified lacinia are also found in several other taxa. The *Digitulati* excluding *Eurycarabus* and *Nesaeocarabus* may form a monophyletic group, because of the characters of the endophallus. The molecular analysis of Su *et al.* (1996a) does not support a sister group relationship of *Carabus* (*s.str.*) and *Ohomopterus* but does also not exclude it. The larval characters of *Ohomopterus* do not contradict either (only one larva of *Ohomopterus* is known, Kurosa, 1959). The larva of *Isiocarabus* is unknown.

The subgenus name *Nesaeocarabus* should be maintained for species from the Canary Islands which is supported by zoogeographic data arguments. The larvae of *Eurycarabus* and *Nesaeocarabus* are distinguished only by a few characters (Tabs. 7.6 and 7.7, characters 8, 22, 26, compare Prüser *et al.* 2000).

Archeocarabi

The subgenera combined as *Archeocarabi* (Bengtsson, 1927) were regarded as related by Lapouge (1929-32), Hůrka (1971a), Turin *et al.* (1993), and Makarov & Atamuradov (1994) based on larval characters. No information was given, however, concerning which larval characters of the *Archeocarabi* are synapomorphies. Representatives are for instance *Carabus* (*s.str.*), *Eucarabus*, *Morphocarabus*, *Trachycarabus* Géhin, *Mimocarabus* Géhin, *Cryptocarabus* Reitter, *Ophiocarabus* Reitter, and *Archi-*



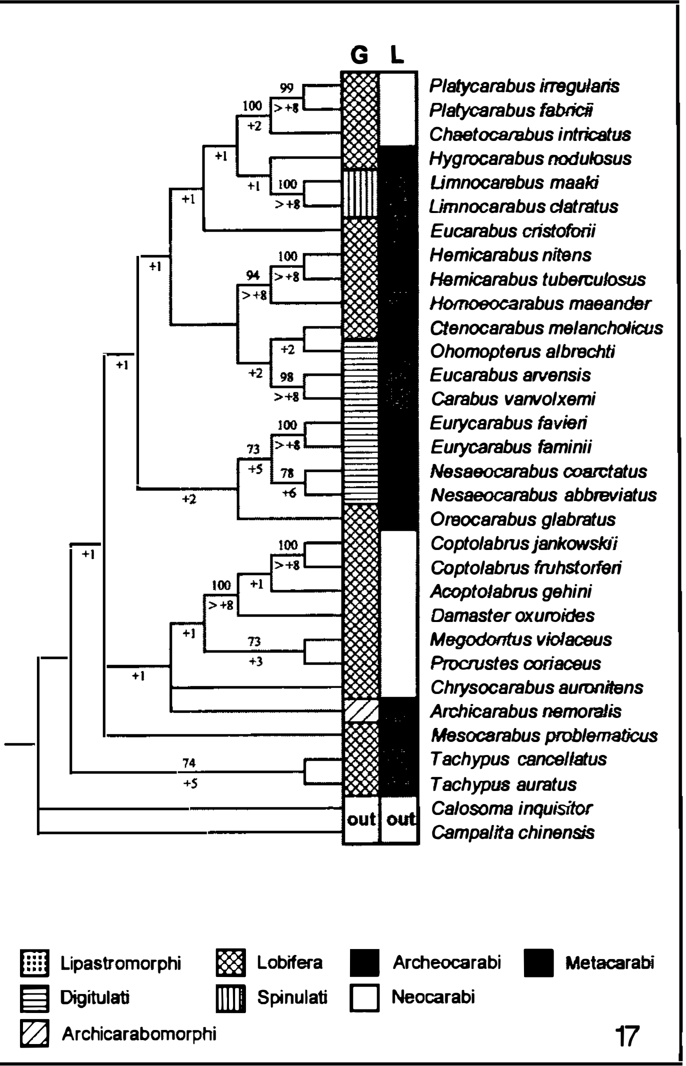


Fig. 7.16. Cladogram of *Carabus* taxa based on morphological characters using the computer program PAUP: Strict consensus tree of 29 MPT's of 152 step length. Only taxa with complete data sets (larval + genital characters, compare appendix, Tab. 7.7) are included in this analysis. Characters were used unweighted; 14 characters ordered, 2 user definded, remaining unordered. G: subgenus groups based on male genital characters (cf. Deuve, 1994); L: subgenus groups based on larval characters (Bengtsson, 1927); out: outgroup; numbers: decay index.

Fig. 7.17. Cladogram of *Carabus* taxa based on molecular data. Consensus tree of 2 MPT, tree length: 1615 steps, data unweighted.

carabus. Our examination (see Figs. 7.16, 7.17) clearly contradicts a monophylum of all taxa included in the *Archeocarabi*. Rather, the *Archeocarabi* sensu Bengtsson (1927) also contain *Tachypus* and *Limnocarabus* which are likely to have been split off basally as previously suggested and therefore doubtless represent a polyphyletic group.

Lipastromorphi and Archicarabomorphi

Two further groups, the *Lipastromorphi* and *Archicarabomorphi*, were established by Deuve (1991, 1994). Both groups are based on endophallic characters. The *Lipastromorphi* are characterized by reduction of the digitulus to a pigmented field and a simple shape of ppd, the usually presence of the lacinia and the absence of an ostium lobe of endophallus. The *Archicarabomorphi* are characterized by a paraligular fold. Other endophallic characters of *Archicarabomorphi* are ground plan character states (absence of ostium lobe and digitulus). However, the homology and the transformation series of these characters are unclear. Both groups combine taxa from different groups established by Bengtsson (1927), Lapouge (1929), and Hůrka (1971a).

The *Archicarabomorphi* (Deuve, 1994) contain *Archicarabus* (*Archeocarabi* sensu Bengtsson, *l.c.*) and the subgenus *Ischnocarabus* Kraatz which was listed in the *Metacarabi* series by Breuning (1932-37).

In addition to the subgenera *Mimocarabus*, *Morphocarabus*, *Ophiocarabus*, and *Cryptocarabus* (Archeocarabi) the *Lipastromorphi* (Deuve, 1994) include *Lipaster* Motschulsky, which was listed in the *Neocarabi* group by Breuning (1932-37) and Kryzhanovsky *et al.* (1995) as well as *Cyclocarabus* (*Neocarabi* according to Makarov, 1992). Larval material and molecular data of the questionable groups *Ischnocarabus*, *Lipaster*, and *Cyclocarabus* were not available for our studies. Therefore, we cannot prove or disprove the monophyly of Deuve's groups *Archicarabomorphi* and *Lipastromorphi*.

7.3.3. Phylogenetic relationships inferred from molecular data

There may arise several problems when interpreting molecular data. In general, the analysis of molecular data results in a tree reflecting the history of the genes under study, called a gene tree. Therefore, discussions must take into account the assumption that the evolution of the genes represents the evolution of species. Changes in the base composition of the DNA are not complex, therefore, an evaluation of the support for the branches of a tree is necessary. Only such branches should be discussed which are supported by acceptable values calculated by methods like bootstrap analysis or decay index.

In order to demonstrate the acceptable phylogenetic information of our tree given in Fig. 7.17 we present the same tree in which all branches were collapsed that are not supported by bootstrap values higher than 70% (Fig. 7.18). This resulting tree indicates that only very few subgenera of the genus *Carabus* are grouped together and that the basic divisions of *Carabus* are totally unresolved. Well supported groups are (see also Tab. 7.3): the *Arcifera* with *Chaetocarabus* and *Platycarabus*; the *Crenolimbi* with *Hemicarabus* and *Homoeocarabus*; *Eucarabus* and *Carabus* within the *Digitulati*, but not the *Digitulati* as a whole; within the *Procrustimorphi* only the subgenera *Coptolabrus* + *Damaster* and *Procrustes* + *Megodontus*, but not at all the Procrustimorphi as a whole. Additionally, we found a sister group relationship in our analysis between *Eurycarabus* + *Nesaeocarabus* (compare Prüser *et al.* 2000).

A similar result is obtained when other mitochondrial genes were used or the same gene was analysed by another analytical strategy. Prüser (1996) analysed the ND 1 gene of *Carabus* species and got a very low resolution of the basic linages; Su *et al.* (1996a,b,c) and Imura *et al.* (1998) published phylogenetic trees which are based on ND 5 sequence data, analysed using a distance method (Neighbor Joining). The relationships of all subgroups within the genus *Carabus* proposed by Su *et al.* (1996a,b,c) and Imura *et al.* (1998) are not well supported, with exception of the *Lepidospinulati* (Tab. 7.3) and the groups above. So, the *Spinulati* sensu Deuve, the *Procrustimorphi*, the *Digitulati* and the *Latitarsi* do not form acceptable groups in any analysis of the ND 1 or ND 5 gene. Mitochondrial DNA sequences have evolved relatively fast, therefore the basal splits within the genus *Carabus* are probably too old to be resolved by this kind of data.

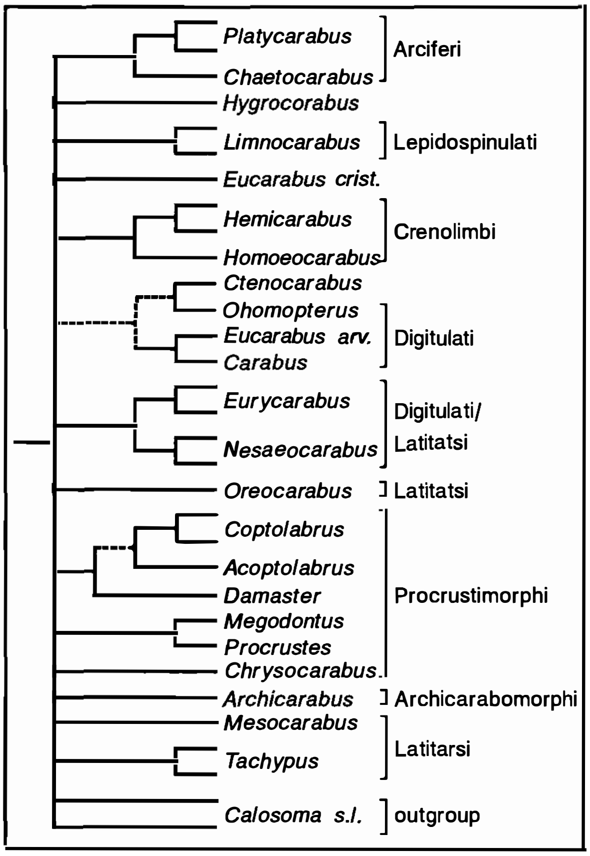


Fig. 7.18. Transformed consensus tree of molecular data (ND 5). The original tree of Figure 17 was reduced to those nodes which were supported by acceptable bootstrap values (³ 70 %).

7.4. CONCLUSION – A TENTATIVE PHYLOGENETIC HYPOTHESIS FOR THE GENUS *CARABUS* (*S.L.*)

The evaluation of multiple characters does neither support the simple concept of three larval groupings (Bengtsson, 1927; Lapouge, 1929-32; Turin *et al.*, 1993), nor five supraspecific taxa based on characters of the endophallus (Ishikawa, 1978; Deuve, 1994), nor the eight or nine taxa based on molecular data (Imura, 1996; Imura *et al.*, 1998). Several groups of all recent classifications are not monophyletic. The phylogenetic analysis based on cladistic methods implies a much more differentiated relationship between species and subgroups.

Doubtlessly, *Carabus* (*s.l.*) is monophyletic and *Calosoma* (in the widest sense) is its sistergroup. This is supported by larval and genital characters and by molecular data (compare Prüser & Mossakowski, 1999).

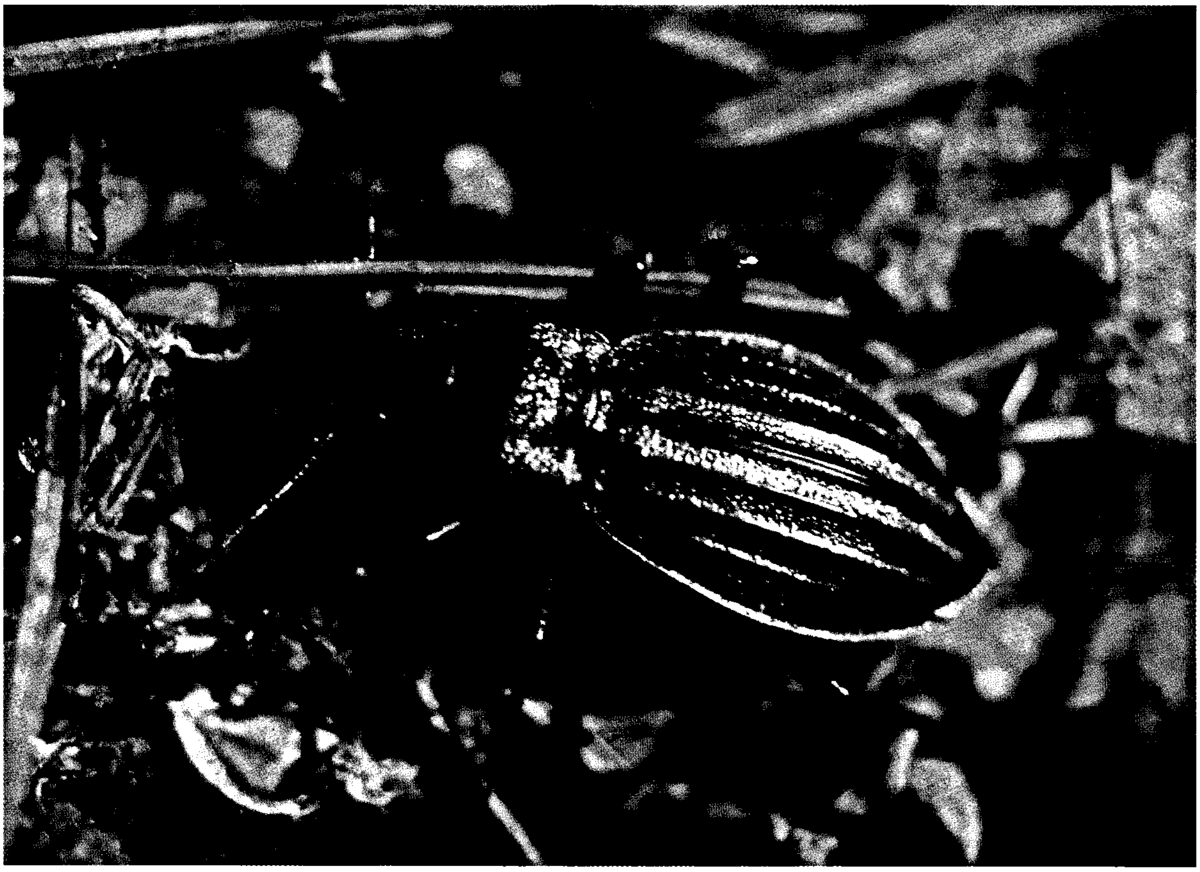
The first split-offs at the basis of *Carabus* (*s.l.*) are the subgenera *Tachypus* (in part), *Limnocarabus*, and *Hygrocarabus*. Then several taxa of *Archeocarabi* form a paraphylum. The two large groups *Metacarabi* (excl. *Hygrocarabus*) and *Neocarabi* are possibly monophyletic.

The *Neocarabi* sensu Bengtsson (1927) probably evolved most recently and represents the largest monophylum in the genus today (Fig. 7.16). Only one representative of this Palaearctic group (*C. vietinghoffi*) reached North-America and only in the most North-Western part, whereas several representatives of other groups occur in Canada and the USA. *Chaetocarabus* + *Platycarabus* may be the first branch of this group and the sister group of the *Neocarabi* (*s.str.*) (= *Procrustimorphi* sensu Imura, 1996; Březina, 1999).

A branching of basal groups like *Tachypus* or *Limnocarabus* as proposed here is not reflected in any published classification of *Carabus* (*s.l.*) However, the recently published classification of Imura (1996) and the checklist built upon it by Březina (1999) come closest to our ideas. However, they must be evaluated by new data because of missing support by molecular data and the relatively poor support given by morphological data in the case of the basal branches.

Acknowledgements

The examination, especially that of larvae, of such a large number of taxa was only possible through the kind support by several colleagues. We thank all colleagues who sent us larval material as gift or loan, especially C. Jeanne (Bordeaux), L. LeSage (Centre for Land & Biological Recources Research, Ottawa), J.-C. Malausa (Centre de recherches d'antibes, Valbonne), G. R. Noonan (Milwaukee Public Museum), J. Schmidt (Rostock) and D. W. Wrase (Berlin). R. G. Beutel (Jena) and J. P. Clapp improved the MS and gave many helpful comments. E. Arndt thanks B. Březina (Prague) for sending of literature and discussion of taxonomic details.



C. ***auronitens***
Fabricius
Poland, Rogow Forest (near Koluszki, province of Lodz).
Photo by J. Sklodowski.

C. nemoralis
O.F. Müller
Poland, Człuchowska Forest (Puszcza Człuchowska).
Photo by
J. Skłodowski.

C. granulatus interstitialis
Duftschmid
Italy, Latium (Central Apennine).
Photo by
A. Vigna Taglianti.

APPENDIX

Material examined

The study is based on the examination of the following *Carabus* subgenera and species (L1, L2, L3 refers to the larval instars I, II, and III; 'male' refers to the male aedeagus and endophallus; 'ND5' refers to the DNA sequences of the mitochondrial NADH-dehydrogenase subunit 5. For sequences which were taken from the GenBank Sequence Data Base also the reference and the accession number are given):

- *C. (Limnocarabus) clatratus* Linné (L1, male, ND5), *C. (L.) maaki* Morawitz (ND5: Su *et al.*, 1996a-D50358).
- *C. (Morphocarabus) monilis* Fabricius (L1, L2, L3, male), *C. (M.) scheidleri* Panzer (L1, L2, L3), *C. (M.) chamissonis* Fischer von Waldheim (L1, L2, L3), *C. (M). aeruginosus* Fischer von Waldheim (male), *C. (M.) hummeli* Fischer von Waldheim (male), *C. (M.) venustus* Morawitz (male).
- *C. (Trachycarabus) sibiricus* Fischer von Waldheim (L2, L3).
- *C. (Carabus) granulatus* Linné (L1, L2, L3, male), *C. (C.) vanvolxemi* Putzeys (ND5: Su *et al.*, 1996a-D50345).
- *C. (Eucarabus) ulrichii* Germar (L1, L2, L3, male), *C. (E.) arvensis* Herbst (L2, L3, male, ND5: Su *et al*, 1996c-D86203), *C. (E.) cumanus* Fischer von Waldheim (L1, L2, male), *C. (E.) cristoforii* Spence (ND5).
- *C. (Ohomopterus) albrechti* Morawitz (ND5: Su *et al.*, 1996a: D50359).
- *C. (Tachypus (=Autocarabus)) auratus* Linné (L1, L2, L3, male, ND5: Su *et al.*, 1996c-D86204), *C. (T.) cancellatus* Illiger (L1, L2, L3, male, ND5),.
- *C. (Cryptocarabus) subparallelus* Ballion (male).
- *C. (Ophiocarabus) striatulus* Géhin (male), *C. (O.) successor* Reitter (male).
- *C. (Lipaster) stjernvalli* Mannerheim (male).
- *C. (Archicarabus) nemoralis* Müller (L1, L2, L3, male, ND5: Su *et al.*, 1996c-D86209), *C. (A.) montivagus* Palliard (L1, L2, L3, male).
- *C. (Apotomopterus) songshanicus* Kleinfeld (male).
- *C. (Hemicarabus) nitens* Linné (L2, L3, male, ND5), *C. (H.) serratus* Say (L1), *C. (H.) tuberculosus* Dejean (ND5: Su *et al.*, 1996a-D50353).
- *C. (Homoeocarabus) maeander* Fischer von Waldheim (L1, L2, ND5: Su *et al.*, 1996a-D50354)
- *C. (Diocarabus) beybienkoi* Kryzhanovsky (male).
- *C. (Aulonocarabus) canaliculatus* Adams (male).
- *C. (Mesocarabus) problematicus* Herbst (L1, L2, L3, male, ND5: Su *et al.*, 1996c-D86210), *C. (M.) dufourii* Dejean (male).
- *C. (Orinocarabus) linnaei* Panzer (L1, L2, L3), *C. (O.) silvestris* Panzer (L1, L2), *C. (O.) alpestris* Sturm (L2, L3), *C. (O.) carinthiacus* Sturm (L3, male).
- *C. (Oreocarabus) hortensis* Linné (L1, L2, L3, male), *C. (O.) glabratus* Paykull (L1, L2, L3, male, ND5: Su *et al.*, 1996c-D86207), *C. (O.) preslii* Dejean (L2, L3), *C. (O.) taedus* Fabricius (male).
- *C. (Tomocarabus) convexus* Fabricius (L1, L2, L3, male).
- *C. (Ulocarabus) theanus* Reitter (L2).
- *C. (Eurycarabus) favieri* Fairmaire (L1, L2, ND5), *C. (E.) faminii* Dejean (male, ND5).
- *C. (Nesaeocarabus) coarctatus* Brullé (L3, male, ND5), *C. (N.) abbreviatus* Brullé (male, ND5).
- *C. (Pachystus) graecus* Dejean (male).
- *C. (Pachycarabus) koenigi* Ganglbauer (L1, L2, L3), *C. (P.) imitator* Reitter (male), *C. (P.) roseri* Faldermann (male).
- *C. (Leptocarabus) seishinensis* Lapouge (male), *C. (L.) yokoae* Deuve (L1, L2, L3).
- *C. (Meganebrius) quinlani* Mandl (L1, L2, L3).
- *C. (Rhabdotocarabus) melancholicus* Fabricius (male, ND5).
- *C. (Hygrocarabus) variolosus* Fabricius (L1, L2, L3, male), *C. (H.) nodulosus* Creutzer (L1, L2, L3, ND5)
- *C. (Chaetocarabus) intricatus* Linné (L1, L3, male, ND5: Su *et al.*, 1996c-D86208), *C. (C.) arcadicus* Gistl (male).
- *C. (Platycarabus) fabricii* Panzer (L1, L2, ND5), *C. (P.) depressus* Bonelli (L1, L2, male), *C. (P.) creutzeri* Fabricius (L2), *C. (P.) irregularis* Fabricius (L1, L2, L3, male, ND5).
- *C. (Cathoplius) asperatus* Dejean (L1, L2, male), *C. (C.) stenocephalus* Lucas (L1).
- *C. (Cechenochilus) ?boeberi* Adams (L3).
- *C. (Tribax) steveni* Ménetries (male), *C. (T). apschuanus* Rost (male).
- *C. (Archiplectes) reitteri* Retowski (L1), *C. (A.) starckianus* Ganglbauer (male), *C. (A.) prometheus* Reitter (male).
- *C. (Microplectes) argonautorum* Semenov (L1, L2), *C. (M.) convallium* Starck (male).
- *C. (Sphodristocarabus) adamsi* Adams (L1, L2), *C. (S.) macrogonus* Chaudoir (male).
- *C. (Megodontus) violaceus* Linné (L1, L2, L3, male, ND5: Su *et al.*, 1996c-D86211), *C. (M.) croaticus* Dejean (male).
- *C. (Iniopachys) auriculatus* Putzeys (L1), *C. (I.) pyrenaeus* Serville (male).
- *C. (Chrysocarabus) olympiae* Sella (L3, male), *C. (C.) solieri* Dejean (male), *C. (C.) lineatus* Dejean (L2, male), *C. (C.) splendens* Olivier (L2, L3, male), hybrid *C. (C.) splendens* × *lineatus* (L3), *C. (C.) auronitens* Fabricius (L1, L2, L3, male, ND5: Su *et al.*, 1996c-D86205), *C. (C.) hispanus* Fabricius (male), *C. (C.) rutilans* Dejean (male), hybrid *C. (C.) rutilans* × *hispanus* (L3).
- *C. (Macrothorax) rugosus* Fabricius (L1, L2, L3), *C. (M.) morbillosus* Fabricius (L1, L2, L3, male).
- *C. (Lamprostus) torosus* Frivaldsky (=*spinolae* Cristofori & Jan) (L3), *C. (L.)* cf. *calleyi* Fischer von Waldheim (L1), *C. (L.) nordmanni* Chaudoir (male), *C. (L.) erenleriensis* Schweiger (male).
- *C. (Procrustes) coriaceus* Linné (L1, L2, L3, male, ND5: Su *et al.*, 1996c-D86206), *C. (P.) anatolicus* Chaudoir (male), *C. (P.) banoni* Dejean (male), *C. (P.) chevrolati* Cristofori & Jan (male).
- *C. (Procerus) scabrosus* Olivier (L2).
- *C. (Eotribax) eous* Morawitz (L2, L3).
- *C. (Cratocechenus) akini* Morawitz (male).

C. (Pseudocranion) taibaishanicus Deuve (L3).
C. (Eupachys) glyptopterus Fischer von Waldheim (L3).
C. (Coptolabrus) jankowskii Oberthür (L1, L2, male, ND5), *C. (C.) formosa* Semenov (L1), *C. (C.) smaragdinus* Fischer von Waldheim (L1), *C. (C.) fruhstorferi* Roeschke (ND5: Su *et al.*, 1996a-D50346).
C. (Acoptolabrus) gehini Fairmaire (ND5: Su *et al.*, 1996b-D50429).
C. (Damaster) blabtoides Kolbe (L2), *C. (D.) oxuroides* Schaum (ND5: Su *et al.*, 1996b-D5042).
Calosoma inquisitor (Linné) (L1, L2, L3, male, ND5: Su *et al.*, 1996a-D50342), *Carminaria denticolle* Gebler (L1, L2, L3), *Campalita auropunctatum* Herbst (L1, L2, L3) and *C. chinensis* Kirby (ND5: Su *et al.*, 1996a D50343) were examined for outgroup comparison. *Ceroglossus chilensis* Eschscholtz (L1, L2, L3, male) was examined additionally.

Methods

Morphological examination of larval characters

All larvae were preserved in 70% ethanol. Some specimens (first instar) of each species were cleared in 10% KOH for 12 hours, transferred into a series of three water baths for two hours each to wash out potassium hydroxide, then transferred in an ethanol/xylol series and finally mounted in Canada balsam on a microscope slide. This procedure allowed for ready examination under a phase contrast microscope at a magnification up to 400x and a detailed study of the cleared head capsule and pronotum.

Terms used to describe larval morphology follow Lawrence (1991). The specific notation of setae of Carabini are adapted from Bousquet & Goulet (1984); see Figs. 7.6-7.9 for the actually used exact chaetotaxy codes of abdominal tergites; see also Arndt & Makarov, this volume.

Preparation of male genitalia

After extraction of the genital apparatus, the genital plate, genital wall, muscular fibres, and the parameres were removed. Afterwards an injection needle (0,50 X 23 mm/ 0,60 X 25 mm) was inserted in the penis exactly at the opening of the ductus ejaculatorius and the endophallus was inflated with warm water. The cannula was removed after complete unfolding of the endophallus and a second cannula was connected with the base of aedeagus using an instant glue. Next, Berlese's mixture (60g gelantine ,100ml glycerine, 20g ZnSO4, 200g distilled water), which was heated in a water bath, was injected into the endophallus. The aedeagus with the completely inflated endophallus was transfered afterwards into an ice bath to accelerate the solidification of the Berlese's mixture. It is not only possible to inflate the endophallus of fresh animals but in many cases also of dried specimens. Nevertheless, such material needs a pretreatment with KOH for successful preparation.

Molecular techniques

Total DNA was isolated from thorax muscle of frozen adult specimens using phenol-chloroform extraction as described in Prüser, 1996. Amplification of the mitochondrial NADH-Dehydrogenase subunit 5 gene (ND5) was performed by PCR using the primers from Su *et al.* (1996a). Conditions for the PCR include a denaturation step at 96°C for 5 min., 5 cycles 96°C for 90 sec., 46°C for 90 sec., 68°C for 90 sec., 28 cycles 96°C for 90 sec., 50°C for 90 sec., 68°C for 90 sec., followed by a terminal extension step of 3 min at 68°C. For PCR the PCR Master Kit (Boehringer, Mannheim, Germany) or the Taq PCR Master Mix Kit (QIAGEN, Hilden, Germany) were used.

The PCR-products were purified using the Qiaex gel extraction kit (QIAGEN, Hilden, Germany), after separation of the fragments by electrophoresis in a 1,5 % agarose gel. The DNA sequencing was done on an ABI 737 stretch automatic sequencer using the Prism Ready Reaction DyeDeoxy Terminator Cycle Sequencing Kit (Perkin Elmer) or the Thermo Sequenase Dye Terminator Cycle Sequencing Kit (Amersham).

In addition to the PCR primers internal sequence primers were used (Düring & Brückner, 2000). Conditions for Cycle-sequencing are: 96°C for 2 min. and 25 cycles 96°C for 30 sec., 50°C for 15 sec., 60°C for 4 min. For the primers 850 and 850r an annealing temperature of 44°C instead of 50°C was used.

The DNA sequences determined for this study are available from the EMBL Sequence Data Base under the accession numbers: AF231687- AF231690, AF231692-AF231694, AF231698- AF231703.

Methods of phylogenetic analysis

All morphological characters were coded in the way that lower numbers indicate the presumptive plesiomorphic state of the higher numbers (0 = plesiomorphic, 1 = apomorphic but 1 = plesiomorphic with regard to 2 = apomorphic). Nevertheless, characters were treated as indicated in Tab. 7.6 (partly unordered, two user defined and 14 ordered) and in a seperate search as unordered.

The ND5 DNA-sequences were aligned using the multiple sequence alignment program Clustalw (Thompson *et al.*, 1994). In addition to the sequences determined for this study, we included several sequences from Su *et al.* (1996a,b,c) as stored in the GenBank Sequence Data Base.

Morphological and molecular data were analysed using the maximum parsimony method. The computer analysis of morphological characters contained only taxa with complete (larval and male aedeagus) data sets. Analyses were conducted with test version 4.0b2 of PAUP (Swofford, 1998), using the heuristic search option. The search parameters were: addition of sequence random with 10 replicates and using the TBR (tree bisection and reconnection) as well as the NNI (nearest-neighbor interchange) branch swapping option as implemented in PAUP. Multiple MPTs were summarised by their strict consensus trees. Branch support is indicated for the molecular data by bootstrap percentage values. These values were calculated with PAUP using the heuristic search option with 1000 replicates. In addition, the decay index, defined as the number of extra steps required to collapse the branches in the strict consensus tree (Bremer, 1994), is given for both analyses. These values were determined using PAUP's heuristic search, retaining also suboptimal trees of increasing length.

Data

Table 7.6. Examined morphological characters. Characters 1-29 concern to larval morphology, characters 30-37 to the male endophallus (For characters 7-15, 29 see also Figs. in Arndt & Makarov, this volume). Ordered: 0 « 1« 2; unordered: 0 « 1, 2 « 0, « 1 « 2.

No.	Character and character states
1	Seta FR$_1$ of frontale. 0 - seta present; 1 - seta lacking.
2	Seta FR$_8$ in adnasale region (Figs. 7.1-7.5). Ordered0 - seta present (Figs 7.1-7.3); 1 - seta reduced, pore-like; 2- seta lacking (Fig. 7.5).
3	Seta FR$_9$ in adnasale region (Figs 7.1-7.5). Ordered0 - seta present (Figs. 7.1-7.3); 1 - seta reduced, pore-like; 2 - seta lacking (Fig. 7.5).
4	Additional setae in adnasale region (Figs. 7.1-7.4). 0 - additional setae lacking (Figs. 7.1-7.3); 1 - one or more additional seta FRa present beside setae FR$_{8/9}$ (Fig. 7.4).
5	Seta PA$_4$ of parietale. Ordered0 - seta present; 1 - seta reduced, pore-like; 2 - seta lacking.
6	Seta PA$_6$ of parietale. Ordered0 - seta present; 1 - seta reduced, pore-like; 2 - seta lacking.
7	Setae of ventral side of head capsule, posterior of level of stemmata (setae PA$_{15/16/17}$ of plesiomorphic pattern sensu Bousquet & Goulet, 1984). Ordered0 - three long setae present; 1- two long setae present; 2 - one long seta present only.
8	Seta PR$_8$ of pronotum. Ordered0 - seta present; 1 seta reduced, pore-like; 2 - seta lacking.
9	Seta PR$_{10}$ of pronotum. Ordered0 - seta present; 1 seta reduced, pore-like; 2 - seta lacking.
10	Seta PR$_{14}$ of pronotum. Ordered0 - seta present; 1 seta reduced, pore-like; 2 - seta lacking.
11	Seta ME$_1$ of meso- and metanotum. Ordered0 - seta present; 1 seta reduced, pore-like; 2 - seta lacking.
12	Seta ME$_2$ of meso- and metanotum. Ordered0 - seta present; 1 seta reduced, pore-like; 2 - seta lacking.
13	Seta ME$_8$ of meso- and metanotum. 0 - seta present; 1- seta lacking.
14	Seta ME$_9$ of meso- and metanotum. user defined: : 3 « 0 « 1 « 20 - seta present; 1 seta reduced, pore-like; 2 - seta lacking; 3 - seta dublicated, more than one seta present.
15	Seta ME$_{14}$ of meso- and metanotum. Ordered0 - seta present; 1 seta reduced, pore-like; 2 - seta lacking.
16	Seta TE$_1$ on abdominal tergites I-VII (Figs. 7.6-7.9). Ordered0 - seta present (Fig. 7.6); 1 seta reduced, pore-like (Fig. 7.7); 2 - seta lacking (Figs. 7.8, 7.9).
17	Seta TE$_6$ on abdominal tergites I-VII (Figs. 7.6-7.9). Ordered0 - seta present (Fig. 7.6, 7.8); 1 seta reduced, pore-like; 2 - seta lacking (Figs. 7.7, 7.9).
18	Seta TE$_9$ on abdominal tergites I-VII (Figs. 7.6-7.9). 0 - seta present (Figs. 7.6, 7.7); 1 – seta lacking (Figs. 7.8, 7.9).
19	Seta TE$_{11}$ on abdominal tergites I-VII (Figs. 7.6-7.9). 0 - seta present (Figs. 7.6-7.9); 1 – seta reduced, pore-like.
20	Seta TE$_7$ on abdominal tergites I-VII (Figs. 7.6-7.9). user defined: 1 « 0 « 20 - seta present (Figs. 7.6-7.9); 1 – seta lacking; 2 - seta duplicated, more than one seta present.

No.	Character and character states
21	Setae on antennomere II. 0 - setae lacking; 1 - one or more setae present apically.
22	Dorsoapical setae on labial palpomere I. 0 - setae lacking; 1 - one or more setae present.
23	Dorsoapical setae on maxillary palpomere I. 0 - setae lacking dorsoapically, only seta MX10 present ventrally; 1 - one or more setae dorsoapically present.
24	Setal group gMX on inner side of stipes. 0 - setae equally distributed, arranged in one group; 1 - setal group divided in two parts, a row of setae on inner margin of stipes and a group of equally distributed setae dorsally.
25	Tarsus of first instar larva. 0 - tarsus without bristles mesoventrally; 1 - tarsus with bristles mesoventrally.
26	Shape of nasale (Figs. 7.1-7.5). Ordered0 - nasale with four distinct and sharp teeth (Figs. 7.1, 7.2, 7.4) ; 1 - nasale wide, teeth stout, reduced (Fig. 7.3); 2 - nasale rostrum-like rounded, teeth lacking (fused) (Fig. 7.5).
27	Shape of adnasale region (Figs. 7.1-7.5). 0 - adnasale region straight or convex rounded (Figs. 7.1-7.4); 1 - adnasale distinctly S-like sloped (Fig. 7.5).
28	Hypodon (Figs. 7.1-7.5). 0 - hypodon (= strong tooth on ventral side of nasale) present (Figs. 7.1-7.4); 1 - hypodon lacking(cf. Fig. 7.5).
29	Sclerotized hump in ocellar region. 0 - parietale without distinct hump in ocellar region; 1 - sclerotized hump mesally of stemmata present.
30	Ostium lobe (Figs. 7.13-7.15).0 – absent; 1 – present, simple; . 2 – wing-shaped; 3 – divided medially.; 4 – moved laterally to the left side
31	Ligulum (Figs. 7.10-7.15).0 - present, large, arched medially; 1 – spine-shaped ("spinula"); 2- tooth-shaped, arched laterally.
32	Praeputial pad lobes (ppd-lobes) (Figs. 7.12-7.15).0 – absent; 1 – two lobes present.
33	Digitulus (Fig. 7.12).0 – absent; 1 – present.
34	Pigmented field (cf. Deuve, 1994: p. 37 and Fig. 7.22, p. 24).0 – absent; 1- present.
35	Lacinia (cf. Deuve, 1994: p. 37 and Fig. 7.22, p. 24).0 – absent; 1 – present.
36	Aggonoporius (Fig. 7.14).0 – simple shape; 1 – distinct elongated.
37	Praeputial pad (ppd) (Figs. 7.11-7.15).0 – ppd without vault, at most with weakly sclerotized field; 1 – ppd distinct vaulted with simple divided sack.

Tab. 7.7. Distribution of character states in *Carabus* larvae (characters 1-29) and structure of endophallus (characters 30-37). Only subgenera and species with complete data (larval and male aedeagus) were included in the computer analysis.

Taxa	**Characters**																																				
										1	1	1	1	1	1	1	1	1	1	2	2	2	2	2	2	2	2	2	2	3	3	3	3	3	3	3	3
	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7
outgroup																																					
Calosoma	1	0	0	0	2	0	0	0	1	2	0	1	0	0	1	1	1	0	1	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	-	-
Carminaria	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	?	?	?	?	?	?
Campalita	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	1	0	0	0	0	0	1	0	0	0	0	?	?	?	?	?	?	?	?
Carabus taxa with complete data sets (included in the computer analysis)																																					
Limnocarabus	1	0	0	0	2	2	1	2	2	2	0	2	0	2	2	2	2	0	0	1	0	0	0	0	1	1	0	0	0	0	1	1	1	0	0	0	0
Morphocarabus	1	1	1	0	2	2	2	2	2	2	2	2	1	0	1	2	2	1	0	1	0	1	0	0	0	1	0	0	0	0	3	0	0	1	01	0	0
Carabus granulatus	1	0	0	0	2	2	1	2	2	2	2	2	1	0	2	2	2	1	0	1	0	1	1	0	1	1	0	0	0	0	3	0	1	0	0	0	0
Eucarabus ulrichii	1	0	01	0	2	2	2	2	2	2	2	2	1	0	2	2	2	1	0	1	0	1	1	0	0	1	0	0	0	0	3	0	1	0	0	0	0
Eucarabus arvensis	1	0	0	0	2	2	2	2	0	2	1	2	1	0	1	1	2	0	0	0	0	1	1	0	0	1	0	0	0	0	3	0	1	0	0	0	0
Eucarabus cumanus	1	0	0	0	2	2	1	2	2	2	2	2	1	1	2	2	2	1	0	1	0	1	1	0	0	1	0	0	0	0	3	0	1	0	?	0	0
Tachypus cancellatus	1	0	0	0	2	2	1	1	2	1	1	2	0	2	1	1	2	1	0	1	0	0	0	0	1	1	0	0	0	1	3	1	0	0	0	0	0
Tachypus auratus	1	0	0	0	1	1	0	1	2	1	1	2	1	0	1	1	2	0	0	0	0	0	0	0	1	0	0	0	0	2	3	1	0	0	0	0	0
Archicarabus	1	0	0	0	2	2	0	2	2	2	2	2	01	0	2	2	2	1	0	0	0	1	1	0	0	1	0	0	0	0	3	1	0	0	0	0	0
Hemicarabus	1	0	0	01	2	2	1	2	2	2	0	2	0	0	2	2	0	01	0	0	0	0	0	0	0	0	0	0	0	2	0	1	0	0	0	0	0
Mesocarabus	1	0	0	1	2	2	1	2	2	2	2	2	0	0	2	2	0	1	0	0	0	1	1	0	0	0	0	0	0	3	3	1	0	0	0	0	0
Orinocarabus spp.	1	0	0	0	2	2	1	02	2	2	2	2	0	0	2	2	0	1	0	0	0	1	0	0	0	0	0	0	0	23	3	1	0	0	0	0	1
Oreocarabus spp.	1	0	0	1	2	2	1	2	2	2	2	2	0	0	2	1	0	1	1	0	0	1	1	0	0	0	0	0	0	1	3	1	0	0	0	0	0
Oreocarabus glabratus	1	0	0	1	2	2	1	0	2	2	0	2	0	0	2	1	0	1	0	0	0	1	0	0	0	0	0	0	0	1	3	1	0	0	0	0	0
Tomocarabus	1	0	0	1	2	2	1	2	2	2	2	2	1	0	2	2	2	1	1	0	0	1	1	0	0	0	0	0	0	1	3	1	0	0	0	0	0
Eurycarabus	1	0	0	0	2	2	1	2	2	2	2	2	0	0	2	2	0	1	0	0	0	1	0	0	0	0	0	0	0	0	3	1	1	0	0	0	0
Nesaeocarabus	1	0	0	0	2	2	1	01	2	2	2	2	01	0	2	02	0	1	0	0	0	0	0	0	?	0	0	0	0	0	3	1	1	0	0	0	0
Hygrocarabus	1	0	0	0	2	2	0	2	2	2	1	2	1	2	1	2	2	1	0	1	0	0	0	0	0	0	0	0	0	3	2	2	-	0	0	0	0
Chaetocarabus	1	2	2	0	2	2	0	2	2	2	2	2	1	0	?	2	2	0	0	1	0	1	0	0	1	2	0	0	0	1	2	?	0	0	0	0	0
Platycarabus	1	2	2	0	2	2	0	2	2	2	2	2	01	0	2	2	2	1	0	1	1	1	1	0	1	2	0	0	0	1	2	1	0	0	0	0	0
Cathoplius	1	1	1	0	2	2	1	2	2	1	0	2	0	0	1	1	2	0	0	0	0	1	1	0	1	2	1	0	0	3	3	1	0	0	0	0	0
Archiplectes	1	2	2	0	2	2	0	2	2	2	2	2	1	2	2	2	2	1	0	1	1	1	1	0	0	2	1	0	0	3	3	1	0	0	0	1	0
Microplectes	1	2	2	0	2	2	0	2	2	2	2	2	1	0	2	2	2	1	0	01	1	1	1	0	0	2	1	0	0	3	3	1	0	0	0	0	0
Sphodristocarabus	1	2	2	0	2	2	1	2	2	2	2	2	1	0	2	2	2	1	0	0	1	1	1	0	?	2	1	1	1	3	3	1	0	0	0	0	0
Megodontus violaceus	1	2	2	0	2	2	0	0	2	2	1	1	0	0	1	2	2	1	0	0	1	1	1	1	1	2	1	0	1	0	3	1	0	0	0	0	0
Iniopachys	1	0	1	0	2	2	1	2	2	2	0	2	0	0	1	2	2	1	0	0	1	1	1	0	1	2	1	0	0	1	3	1	0	0	0	0	0

Taxa	Characters																																				
										1	1	1	1	1	1	1	1	1	1	2	2	2	2	2	2	2	2	2	2	3	3	3	3	3	3	3	3
	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7
Chrysocarabus	1	1	1	0	2	2	0	2	2	2	2	2	0	0	2	2	2	1	0	0	1	1	1	0	1	2	1	0	1	3	3	1	0	0	0	0	0
Macrothorax	1	2	2	0	2	2	1	2	2	2	1	2	1	0	1	2	2	1	0	0	1	1	1	1	1	2	1	1	0	3	3	1	0	0	0	0	0
Lamprostus	1	2	2	0	2	2	1	2	2	2	2	2	0	0	2	2	2	1	0	0	1	1	0	0	1	2	0	1	1	4	3	1	0	0	0	0	0
Procrustes	1	2	2	0	2	2	0	2	2	2	2	2	0	2	2	2	2	1	0	0	1	1	1	1	1	2	1	0	0	2	3	1	0	0	0	0	0
Coptolabrus	1	2	2	0	2	2	1	2	2	2	2	2	1	3	2	2	2	1	0	2	1	1	1	0	?	2	1	0	1	3	3	1	0	0	0	0	0
Carabus taxa with larval or endophallic data sets (not included in PAUP analysis)																																					
Trachycarabus	1	0	0	0	2	2	1	2	2	2	0	2	1	0	2	2	2	0	0	0	0	1	1	0	?	1	0	0	0	?	?	?	?	?	?	?	?
Cryptocarabus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	3	0	0	0	0	0	0
Ohiocarabus striatulus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	3	0	0	0	1	0	0
Ohiocarabus successor	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	3	0	0	0	0	0	0
Lipaster	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	3	0	0	1	?	0	0
Apotomopterus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	1	1	0	0	0	0	0
Homoeocarabus maeander	1	0	0	0	2	2	1	1	2	2	0	2	0	0	2	1	2	0	0	1	0	0	0	0	?	0	0	0	1	?	?	?	?	?	?	?	?
Diocarabus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	3	1	0	0	0	0	0
Aulonocarabus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	3	3	1	0	0	0	0	0
Orinocarabus linnaei	1	0	0	1	2	2	1	02	2	2	2	2	0	0	2	2	0	1	0	0	0	1	0	0	0	0	0	0	0	?	?	?	?	?	?	?	?
Ulocarabus	1	0	0	1	2	2	1	2	2	2	2	2	0	0	2	1	0	1	0	0	0	1	0	0	0	0	0	0	0	?	?	?	?	?	?	?	?
Pachystus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	2	3	1	0	0	0	0	0
Pachycarabus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	2	3	1	0	0	0	0	0
Leptocarabus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	3	3	1	0	0	0	0	0
Meganebrius	1	0	0	1	2	2	0	2	2	2	2	2	1	0	2	2	2	1	0	0	0	1	0	0	?	0	0	0	0	?	?	?	?	?	?	?	?
Ctenocarabus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	3	3	1	0	0	0	0	0
Cechenochilus	1	2	2	0	2	2	0	2	2	2	2	2	1	2	2	2	2	1	0	1	1	1	1	0	0	2	1	0	0	?	?	?	?	?	?	?	?
Tribax	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	3	3	1	0	0	0	0	0
Procerus	1	2	2	0	2	2	1	2	2	2	2	2	1	3	2	2	2	0	0	2	1	1	1	0	?	2	1	0	1	?	?	?	?	?	?	?	?
Cratocechenus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	3	3	1	0	0	0	0	0
Pseudocranion	1	2	2	0	2	2	1	2	2	2	1	2	1	0	1	2	2	1	0	0	1	1	0	0	?	2	1	0	1	?	?	?	?	?	?	?	?
Eupachys	1	0	0	0	2	0	1	2	2	0	1	2	0	3	0	0	0	1	0	2	1	1	0	0	?	2	1	-	0	?	?	?	?	?	?	?	?
Damaster	1	2	2	0	2	2	1	2	2	2	2	2	1	3	2	2	2	1	0	2	1	1	1	0	?	2	1	0	1	?	?	?	?	?	?	?	

Chapter **8** Biogeography

L. Penev, A. Casale & H. Turin

8.1. INTRODUCTION

The present shapes and sizes of geographical ranges of living organisms are a result of a complex and long-term sum of events, the origin of which is derived from both historical (paleogeographic and paleoclimatic) and ecological (recent) factors. The corollary of this statement is that biogeography, as a science, provides explanatory hypotheses about the origin and significance of these geographical ranges. It is a difficult discipline, in which the procedures and information of expert taxonomists, biologists, geologists and ecologists became complementary and indispensable to each other. Relationships among taxonomy, phylogeny and biogeography, derive from the fact that the geographical distribution of any taxon is changing, in agreement with the evolution of the taxon itself; therefore, the study of such distribution coincides with the study of spatial (geographical) effects of the evolution of the investigated taxon, and biogeography is the spatial transcription of evolution (Vigna Taglianti & Forestiero, 1994). Thus, although it is clear now that information about the geographical range of a taxon is not accessory but fundamental to the evolution of the taxon, it was not very clear to the taxonomists and students of biological evolution of preceding centuries: most specimens – including those of *Carabus* – collected in the XVIIIth and XIXth centuries, were provided with very vague indications of locality ('Siberia', 'Graecia', 'Asia Minor'). Only in the later decades of the XXth century, botanists and zoologists provided consistently a set of data associated with any collected specimen: exact locality, altitude, date of collecting, and often ecological information on environment. Furthermore, in the last decade, geographical coordinates became easily available through use of the Global Positioning System (GPS).

In spite of being a science of high reputation, biogeography receives endless criticism from the viewpoint of the modern reductionism that plagues the scientific endeavour. Accumulating in itself facts and methods from various natural sciences – systematics, floristics and faunistics, phylogeny, paleontology, geography, historical geology, climatology etc. – biogeography allows approaches which are regarded as 'old-fashioned' or 'speculative' by biologists understanding the scientific method only in terms of either proposing and confirming or rejecting statistical hypotheses. On the other hand, no other discipline in organismic biology, demands so much and so varied knowledge to attempt to explain the extremely diverse and complicated patterns of distribution of plants, animals and their communities. Therefore, we use here some 'old' but well-proved methods in analysing the recent distribution of organisms, taking into account facts and data obtained by modern methods of molecular systematics and phylogeny.

Mayr (1976), analysing the concept of fauna, very effectively stressed some major questions that zoogeographers meet in their work. He stated that the validity of any zoogeographical reconstruction is based on three different categories of information: (1) relative ages of taxa that make up the investigated fauna; (2) knowledge of dispersal power of any taxon present in that fauna; and (3) geographical distribution of taxa geographically and phylogenetically close to those present in the investigated fauna. These statements, allow us to understand that not all taxa present the same opportunities for biogeographical inferences: in fact, objectively, times of evolution and dispersal power are different in different taxa; and, subjectively, our knowledge of many groups of organisms is too sparse, so that such groups are not reliable at present for phylogenetic and biogeographical reconstructions.

In spite of these facts, different biogeographers – such as students of other scientific branches – have adopted divergent points of view, based respectively on intrinsic (dispersal) or extrinsic (vicariance) factors that are peculiar to every species, or to a phyletic lineage as a whole. This is not the place to debate all questions about the origin of the extant biota and of their present geographical distributions, on which biologists, biogeographers, ecologists, and carabidologists interested in biogeography, have expended so much energy. As recently stated (Casale & Vigna Taglianti, 1999, among others), concerning carabids (but not only carabids), an attentive critical review of some general, older publications (Jeannel, 1942; Darlington, 1957), and of some more recent, basic contributions (see, among others, Darlington, 1979; Erwin, 1979; Noonan, 1979) should be instructive. From these, the conflicting approaches become evident between dispersalists (more attentive to dynamic, recent factors), and historical biogeographers (more influ-

◀ ***C. gigas*** Heer. Italy. Friuli. Val Cornappo. Photo by A. Vigna Taglianti.

enced by paleogeographical aspects). We note that some of the leaders in biogeography of the XXth century have been carabidologists. For instance, Darlington, Franz, Holdhaus, Jeannel, Lindroth and Kryzhanovskij, among others, have been partisans of different points of view; but each of them, using carabids, showed that several lines of evidence, and not only one, are available to help understand the present patterns of distribution of species, or higher taxa.

The genus *Carabus*, as a monophyletic unit, and a rather well-known animal group from all scientific points of view, is excellent for biogeographical analysis. Most biogeographical studies of *Carabus* published so far can hardly be separated from the biogeographical aspects of carabids as a whole (for a review, see Noonan, 1979). Several classical works in zoogeography from the last century use *Carabus* species as one of the best models for ecological or historical explanation of biogeographical hypotheses (i.e. Holdhaus & Lindroth, 1939; Lindroth, 1945 and others). Nevertheless, some studies focused on the genus *Carabus* or certain species of it to resolve biogeographical questions.

Any biogeographical work on this genus would hardly be possible without the outstanding monograph of Breuning (1932-37), where the geographical ranges of many *Carabus* species were mapped for the first time. Also remarkable was the pioneer work of Kryzhanovskij (1953) on the genus *Carabus* of Central Asia, in which he published his ideas on the origin and evolution of the highly diverse fauna of that region, developed afterwards in his outstanding monograph 'Composition and origin of the terrestrial fauna of Central Asia (based chiefly on materials on beetles)' (Kryzhanovskij, 1965b). Other remarkable zoogeographers, the Austrian coleopterologists, Herbert Franz (Franz, 1943, 1970, 1971) and Karl Mandl (Mandl, 1955, 1956, 1958, 1965, 1967, 1984), used *Carabus* for the same purposes but in a completely different region, the Alps and Central Europe.

Numerous papers treat the geographical distribution of *Carabus* at local or regional scale, as a distinct object of study (i.e. Buresch and Kantardzhieva, 1928; Van Dyke, 1945; Panin, 1955; Lagar, 1965; Heinz & Korge, 1967; Drovenik, 1972; Arndt, 1989; Turin *et al.*, 1993; Penev & Turin, 1994; Penev, 1996; Deuve, 1997b, and others).

The last three decades have been marked by an increased interest in the distribution and postglacial history of *Carabus*, studied with modern methods of genetics and/or phylogenetic systematics, most of them originating from the 'Bremen' and 'Münster' schools: i.e. *Chrysocarabus* (Mossakowski, 1979; Mossakowski *et al.*, 1986; Mossakowski & Braun, 1993; Düring *et al.*, 2000); *Nesaeocarabus* (Prüser *et al.*, 2000); *C. irregularis* (Weber, 1966c); *C. glabratus* (Assmann & Günther, 2000); *C. punctatoauratus* and *C. auronitens* (Assmann, 1994, 1995); *C. auronitens* (Assmann & Janssen, 1999; Reimann *et al.*, 2002); general *Platycarabus* (Casale *et al.*, 1998); and general (Assmann, 1994, 1999); see also Chapters 6 and 7 in this volume.

Nevertheless, in spite of the extreme popularity of *Carabus* among coleopterists, biogeographers, and collectors, a general 'biogeographical picture' of the genus has not been published so far, neither at World nor at European scale. According to De Lattin's division of zoogeography into *descriptive* and *causal* (De Lattin, 1967), a biogeographical analysis should start with a detailed description of the patterns of the recent distribution of taxa, from which some hypotheses and explanations about centers of their origin and dispersal may be derived and tested afterward. Therefore, we begin our analysis by outlining the present-day patterns of both the World and European distribution of the genus.

8.2. WORLD DISTRIBUTION OF *CARABUS*

8.2.1. The general range and its limits

The genus *Carabus* is an example of a typical Holarctic taxon, ranging through the northern and temperate regions of Europe, Asia and North America, and in the south following almost perfectly the southern borders of the Holarctic (Kryzhanovskij, 1983) (Fig. 8.1). Moreover, though its habitat and climatic preferences are generally temperate, the genus covers most landscape zones and altitudinal belts of the Holarctic Realm, except the driest deserts. This extensive range makes *Carabus* an excellent candidate for analyses of biogeographical patterns and processes in the Holarctic Realm.

The northern border of the geographical range of *Carabus* coincides with the northern limits of the tundra; no records are known from the Arctic deserts yet. The species composition of the northernmost faunal assemblages of *Carabus* in the Palaearctic Region changes gradually in a western-eastern direction. The only *Carabus* species present in Iceland (ca. 65°N) is *C. problematicus,* ssp. *islandicus* (Lindroth, 1968). Among the species ranging farthest to the north in Fennoscandia are *C. problematicus, C. violaceus* and *C. glabratus.* All three species live in Fennoscandia north of 70°N, and the first two reach the northernmost continental part, the island Nordkapp (71°N) (Lindroth, 1945). Eastward, on the Russian Kola Peninsula, the species composition remains almost the same, enriched however by the presence of *C. nitens*, whose northernmost limits are at 70°N.

Farther to the east, the *Carabus* fauna of the northern regions of European Russia and Ural Mountains is characterised by the occurrence of five species: *C. truncaticollis,* rather common in Bol'shezemelskaya tundra in the eastern region of European Russia (ca. 68-69°N); *C. glabratus* (Kovda, Kanin Peninsula and upper stream of Adzyva River, both last localities north of the Northern Polar Circle at a latitude of about 68°N); *C. ermaki* (Naryan Mar at the lower stream of Pechora River, ca. 67.5°N); *C. henningi* (lower stream of Pechora River and upper stream of Adzyva River, ca. 67-68°N); and *C. canaliculatus* (upper stream of Adzyva

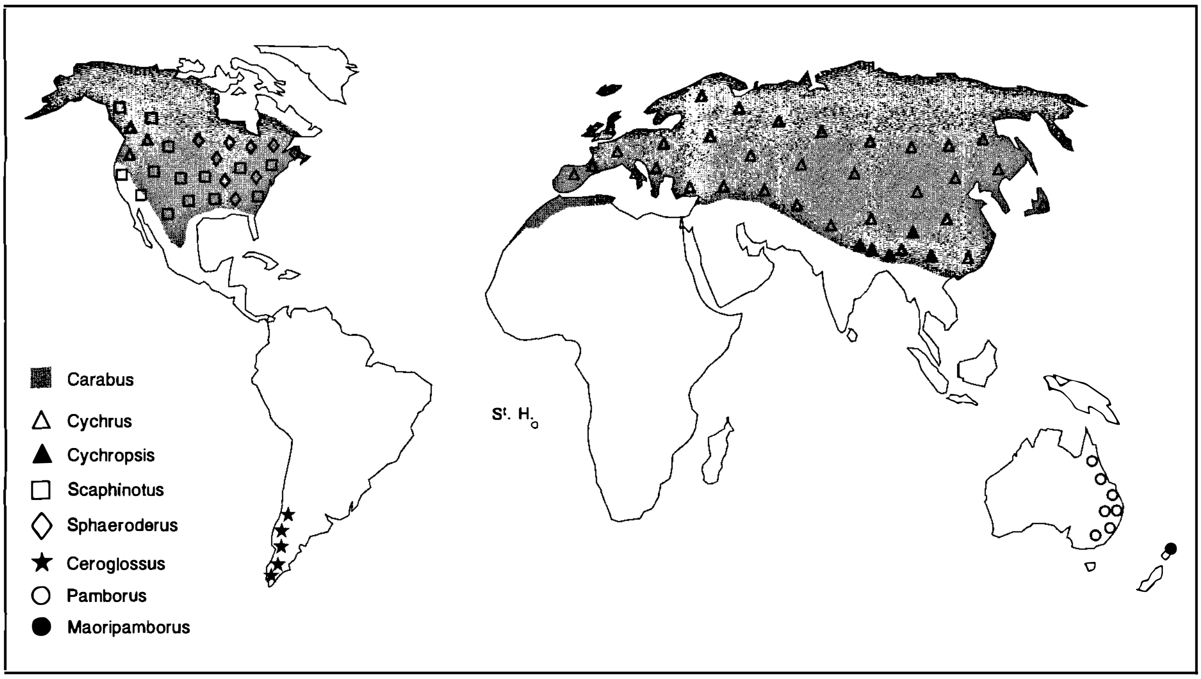


Fig. 8.1. General distribution of the 'carabite' genera (i.e. Carabini, Cychrini, Ceroglossini, Pamborini), excluding *Calosoma s. latissimo* (after Prüser & Mossakowski, 1998, with corrections of Mossakowski, *in litt.*).

River, ca. 68°N) (ZIN). Similar to its geographical range in Fennoscandia, *C. nitens* approaches the northern limits of the above mentioned species and reaches the Arctic Circle but not as far to the north. The latitudes around 67-68°N seem to be a northern limit also to *C. odoratus, C. hummeli, C. henningi* and *C. aeruginosus.*

Compared to Fennoscandia, the *Carabus* fauna of the north of European Russia is enriched by several Siberian species, but at the same time impoverished with respect to European species: two species common in Northern Fennoscandia (*C. problematicus* and *C. violaceus*) are absent from the northern territories eastward of Kola Peninsula, probably due to the increase of continentality and severity of the climate.

Siberia is relatively rich in *Carabus* species (Shilenkov, 1994, see also Tab. 8.1), however, most of them occur in the middle and southern temperate regions. *Carabus truncaticollis* ranges farthest north and is known from several localities in the tundra zone, to the coasts of the Arctic Ocean. On the northernmost continental territory, Taymyr Peninsula, *C. truncaticollis* lives in the environs of Dikson (73°N) and Amu-tarida River on NE Taymyr (probably beyond 75°N) (ZIN). A significant number of species ranges in Siberia approximate the latitudes of 68-70°N: for instance, *C. aeruginosus* (Obskaya Guba, Dudinka at lower Enissei River, Tazov Peninsula); *C. canaliculatus* (Timanskaya tundra, Bilibino nr Chukotka); *C. ermaki* (Dudinka, Norilsk); *C. henningi* (Dudinka, Khadytayakha, Nosok (71°N) and *C. vietinghoffi* (Khatanga) (ZIN). *Carabus hummeli, C. regalis* and *C. odoratus* are also known from several localities in the Polar Ural (66-68°N) (Salekhard, Khadytayakha, Neroika, Labythangi etc.) (ZIN; Korobeinikov, 1990; Andreeva et Eremin, 1991).

In comparison to the Palaearctic Region, the northern regions of Canada and Alaska have fewer *Carabus* species. The northern limit of the range of the genus on the American continent seems to be formed by three species, namely: *C. vietinghoffi* (Siberia, Arctic and Subarctic America from western Alaska eastward to Bathurst Inlet, Northwest Territories); *C. truncaticollis* (Siberia, western regions of North America from Aklavik (68°N), Northwest Territories to some islands (St. Paul and St. George) in the Bering Sea; and *C. chamissonis* Fisch. (Canada and Alaska, however it ranges farther to the south in comparison to the first two species) (Breuning, 1932-1937; Ball, 1960).

The southern limits of the genus in North America are formed by the southern subgenus *Tanaocarabus* Reitt., represented by four species, two of them occurring in the Mexican Sierra Madre (*C. forreri* Bates and *C. hendrichsi* Bolivar, Rotger, and Coronado-Luz) extending in this way the range of the genus to approximately 17-18°N).

In the western part of the Eastern Hemisphere, the southernmost localities of the genus are in the Canary Islands (ca. 28°N), from where three species of the endemic subgenus *Nesaeocarabus* Bedel are known: *C. abbreviatus* Brullé (Tenerife), *C. coarctatus* Brullé (Gran Canaria) and *C. faustus* Brullé (Tenerife) (Machado, 1992). Approximately at the same latitude is also the southern limit of the range in North Africa. Of the seven species known from that region, penetrating farthest to the south is *C. asperatus* Dej., known from Southwestern Morocco (Sidi-Ifni and Tan-Tan, 28-29°N). The northwestern Mediterranean coast of Africa (Algeria, Tunis) is characterised by the presence mostly of *C. faminii* Dej. and of two species of the subgenus *Macrothorax* Desm. (*C. morbillosus* F. and *C. rugosus* F.). The southern limits of the genus in Africa are also marked by the strikingly isolated *C. (Relictocarabus) meurguesianus* Ledoux described recently from the Higher Atlas Mountains.

Eastward, the southern range boundary passes along ca. 35°N through the Greek islands of Crete (*C. banoni*), Cyprus (*C. trojanus* and *C. anatolicus* Chaud.), and Karpathos (*C. trojanus oertzeni*).

The Near East is also characterised by many endemic species occurring at the southernmost range limits of the genus (see Casale & Vigna Taglianti, 2000). These are some species of the subgenera *Lamprostus, Procrustes* and *Procerus*. Probably the southernmost localities in that region are of *C. (Procrustes) impressus* Klug, known to the south from the Negev region in Israel and Petra in West Jordan (30-31°N). *Carabus (Lamprostus) hemprichi* Dej. and *C. (Procerus) syriacus* Collar do not range south of 31°N and are known from Turkey, Syria and Lebanon south to Northern Israel. The only *Carabus* species mentioned from Egypt (El Arish, NE Egypt) are *C. impressus* and *C. hemprichi* (Alfieri, 1976); both records, however, were questioned by Březina (1999).

The Middle East (Iran, Afghanistan, Pakistan) hosts also several endemic *Carabus* species, although the fauna becomes significantly less diverse in comparison to the adjacent regions of Caucasus and Central Asia. South of the Caspian Sea, several species penetrate into Northern Iran or are endemic to that region. For instance, *C. maurus* Reitt. known from the Caucasus and Turkey, extends farther to the south and reaches Shiraz (29.38°N). Eastward, groups of species, mainly of the subgenera *Imaibus* Bates and *Meganebrius* Kraatz occupy Afghanistan, Nepal, Northern India and Northern Pakistan. The southernmost representatives of these groups seem to be *C. boysi* Tatum and *C. caschmirensis* Redtb., known from Kashmir and Northern India, south to Uttar Pradesh (27-28°N). From the environs of Darjeeling (27°N) in West Bengal, India, *C. indicus* Fairm. has been recorded.

The southernmost localities of the genus are far beyond the limit of the Palaearctic Region, in the Oriental Indochinese Peninsula. Five species of the mainly Chinese subgenus *Apotomopterus* Hope, are described from the Indochinese Peninsula: *C. birmanus* Andrewes (known from Mogok in Burma (23°N)); *C. fallettiellus* Deuve and *C. kouichii* Imura et Mizusawa (described from Cao Bang, 200 km N of Hanoi (ca. 22.50°N)); *C. vitalisi* Lap., the only known species of *Carabus*, from Northern Laos (Xien Khouang, 19.21°N); and *C. vogtae* Beheim & Breuning in Northern Thailand (Chiang Mai, 18.48°N, probably the southernmost locality of the genus in the Old World).

In conclusion, the northern limits of distribution of genus *Carabus* follow approximately the latitude of 70°N, with the northernmost known locality around 75°N (Amutarida River on Taymyr Peninsula). The southern limits are between 27° and 31°N in the western and central regions of the Palaearctic Region, and are shifted to the south (18-19°N) in Nearctic Mexico and Oriental Indochinese Peninsula. Obviously, such a shift may be due to the presence of desert climates south of 29-30°N in the southwestern and central regions of the Palaearctic Region.

8.2.2. Patterns of diversity and specificity

According to the last world checklist of Březina (1999), the genus *Carabus* consists of 115 subgenera and 803 valid species. We avoid here some highly disputable questions of validity or taxonomic status of certain subgenera and/or species and base our analysis mostly on Březina's checklist as being the latest comprehensive summary of *status quo*. The changes in Březina's checklist concern some subspecies recognised as valid species in the present book. By incorporating those changes the number of species becomes 829.

To reveal a general world scale pattern of distribution of *Carabus* diversity, the range of the genus has been divided into 19 major geographic regions. The respective numbers of species and subgenera, numbers of endemic species/subgenera, and some simple statistics are shown in Table 8.1.

As may be seen from Table 8.1, the diversity of *Carabus* at both species and subgeneric level is the highest in China with its 326 species (93.9 % endemic), which is nearly 40 % of the world fauna (see also Deuve, 1997b). Another remarkable speciation center is Central Asia hosting 117 species (14 % of the world fauna, 95.7 % endemic). The European continent has more species (132) than Central Asia, however, the level of endemism is lower (67.2 %). Caucasus and Anatolia are also marked by high diversity and specificity of *Carabus* with 81 species (66.7 % endemic) and 61 species (49.2 % endemic), respectively.

Hence, the major geographical regions within the genus range may be divided approximately in five groups: very high diversity (above 300 species) – China; high diversity (60-140 species) – Europe, Central Asia, Caucasus and Anatolia; medium diversity (25-45 species) – all regions of Siberia, Far East, Korea, Japan, and Middle East, low diversity (10-25 species) – Near East, Mongolia, Nepal, North America; and very low diversity (less than 10 species) – Canary islands, North Africa, India, Indochinese Peninsula.

Generally, the regions of the northern and temperate zones of the Palaearctic Region (Northern, Central and Eastern Europe, Siberia, northern regions of the Far East) have a relatively equally distributed species richness from west to east, ranging on average from 29 to 40 species per region. The

Table 8.1. Diversity and specificity of the fauna of *Carabus* across major regions.

Abbr	Region	No sp	No sg	End sp	End sg	%End sp	%End sg	%Sp	%Sg	Sp/Sg
EU	Europe as a whole	132	31	88	7	67.2	22.6	15.8	26.7	4.2
CA	Caucasus	81	22	54	5	66.7	22.7	9.8	19.0	3.7
AM	Asia Minor (Anatolia)	61	19	30	2	49.2	10.5	7.4	16.4	3.2
NE	Near East (Syria, Lebanon, Israel)	11	5	4	0	36.4	0.0	1.3	4.3	2.2
WS	West Siberia	39	16	8	1	20.5	6.3	4.7	13.8	2.4
CS	Central Siberia	36	15	3	0	8.3	0.0	4.3	12.9	2.4
ES	East Siberia	25	13	2	0	8.0	0.0	3.0	11.2	1.9
FE	Russian Far East	30	15	1	0	3.3	0.0	3.6	12.9	2.0
JP	Japan	30	12	21	3	70.0	25.0	3.6	10.3	2.5
KO	Korea	42	12	19	0	45.2	0.0	5.1	10.3	3.5
CH	China	326	41	306	27	93.9	65.9	39.3	35.3	8.0
MO	Mongolia	17	8	0	0	0.0	0.0	2.1	6.9	2.1
ME	Middle East (Iraq, Iran, Afghanistan, N. Pakistan)	37	9	29	1	78.4	11.1	4.5	7.8	4.1
CE	Central Asia (former Soviet republics)	117	23	112	18	95.7	78.3	14.1	19.8	5.1
IN	India	5	3	2	0	40.0	0.0	0.6	2.6	1.7
NP	Nepal	22	3	20	0	90.9	0.0	2.7	2.6	7.3
VI	Indochinese Peninsula	5	1	5	0	100.0	0.0	0.6	0.9	5.0
US	USA and Canada[1]	11	7	7	2	63.6	28.6	1.1	6.0	1.3
MX	Mexico	2	1	2	0	100.0	0.0	0.2	0.9	2.0

Abbreviations: **EU** – Europe; **CA** – Caucasus; **AM** – Asia Minor (Anatolia or Asiatic Turkey); **NE** – Near East (Syria, Lebanon, Israel); **WS** – West Siberia (between the Urals and river Enissei); **CS** – Central Siberia (between the rivers Enissei and Lena); **ES** – East Siberia (NE of Lena River including Chukotka and Kamchatka); **FE** – Russian Far East (Russian provinces of Khabarovsk, Vladivostok and Sakhalin south to the Chinese border; **JP** – Japan; **KO** – Korea; **CH** – China; **MO** – Mongolia; **ME** – Middle East (Iraq, Iran, Afghanistan, Northern Pakistan, Kashmir); **CE** – Central Asia (former Soviet Central-Asian republics); **IN** – India; **NP** – Nepal; **VI** – Indochinese Peninsula (Vietnam, Thailand, Laos); **US** – USA and Canada; **MX** – Mexico.

No sp – number of species; **No sg** – number of subgenera; **End sp** – number of endemic species; **End sg** – number of endemic subgenera; **%End sp** – percentage of the endemic species; **%End sg** – percentage of the endemic subgenera; **%Sp** – percentage of the species of a region per the total of the world fauna; **%Sg** – percentage of the subgenera of a region per the total of the world fauna; **Sp/Sg** – number of species/number of subgenera ratio (based on Březina, 1999 and the present volume).

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[1] Of the 15 Nearctic Carabus species, only one (*C. hendrichsi*) is not in the United States – that is, 14 species are in the USA and Canada. Of these, three species (*granulatus, nemoralis, auratus*) are introduced, and if these are excluded from the total, we are left with 11 native species. *C. forreri* has most of its range in the Mexican Sierra Madre Occidental, but it enters the USA by way of the Southern Arizona mountains (Ball, *in litt.*).

diversity and specificity of the fauna demonstrate a rather clear trend from north to south, having the highest point in the so called Alpi-Himalayan mountain system, that is, the montane regions ranging along the southern border of the Palaearctic Region (Alps, Balkans, Anatolia, Caucasus, mountains of Central Asia, Middle East, Nepal and China). To the south of these regions, the semidesert and desert climates cause a significant loss in diversity of *Carabus*, becoming finally zero in the driest parts of deserts.

The diversity of subgenera confirms in general the above mentioned patterns, that is, the regions rich in species are characterised by high numbers of subgenera as well. The ranking of the regions based on their subgeneric diversity is similar to the above, discussed with respect to the species richness. Some interesting patterns are shown by the ratio between number of species and number of subgenera (Table 8.1), which can be taken, as a simple measure of the intensity of the speciation process. The rationale of this measure is that in regions with active speciation process few subgenera evolve *in situ* into considerable number of species; hence, the species/subgenera ratio in these regions should be higher. A value of the ratio of 3.0 and higher is characteristic for most montane regions in southern and southeastern regions of the Palaearctic Region – China, Nepal, Central Asia, Indochinese Peninsula, Korea, Caucasus, and Anatolia. At the same time, the northern and temperate Palaearctic areas have values around and below 2.5.

The level of endemism is another measure confirming some conclusions made above. Many of the southernmost marginal regions have 100 % endemic species, although this percentage is based on occurrence of very few species of 1-2 subgenera (Canary Islands, Indochinese Peninsula). Mexico may also be included there, although one of two Mexican species is known only from Mexico (*C. hendrichsi*); the other (*C. forreri*) is known also from southern Arizona (Ball, *in litt.*)

Again, regions like China, Central Asia, Europe (in fact its southern part and the Alps), Caucasus and Central Asia are characterised by high endemism of species and subgenera. China and Central Asia have remarkably higher numbers of endemic subgenera, 27 (65.9 %) and 18 (18.3 %), respectively, in comparison to any other region. This fact suggests the long history of the speciation processes in isolated and relatively stable conditions in these regions.

Thus, taking into consideration all three criteria described above, namely *diversity*, *specificity* (endemism) and *intensity of speciation*, analysed at both species and subgeneric level, the most important centers of speciation and diversity of *Carabus* are China and Central Asia, followed by Caucasus, Anatolia and Southern Europe.

Remarkably, most of the species and subgenera occur in one region only (Tab. 8.2 and 8.3). So, in both calculations, 83 % of all species are endemics (considering the regions as defined here) and 54% of the subgenera are. In other words, the percentage of endemics in *Carabus* per region is extremely high. However, this can be caused partly by the definition of relatively large areas for China and Central Asia. Inevitably, the bigger an area, the more endemics, but splitting, for instance China, into smaller regions, would not change the pattern significantly, because most species have been described as very local endemics, anyway.

The extremely high number of endemics within the *Carabus* fauna as a whole, reinforces the importance of local speciation processes in this genus and suggests that *Carabus* meets all known criteria to be determined as a group in active speciation, at present. The presence of secondary speciation centers along the entire range of mountain areas in the Southern Palaearctic Region is one more piece of evidence for a long and constant intensive diversification of the different lineages of the genus (see also section 8.5.). If one has to explain in few words why the *Carabus* fauna is so diverse through Europe, the only answer could be: a high level of local allopatric speciation processes within most of the European subgenera. The distribution maps of some subgenera (*Archicarabus, Eucarabus, Megodontus, Morphocar-*

Table 8.2. Patterns of distribution of species richness of *Carabus* presented as number of species occurring in one region only (R01) (= endemic), two regions (R02) etc.

	R01	R02	R03	R04	R05	R06	R07	R08	R09	R10	Tot
No	689	68	40	14	7	2	4	2	1	2	829
%	83.1	8.2	4.8	1.7	0.8	0.2	0.5	0.2	0.1	0.2	100

Table 8.3. Patterns of distribution of subgeneric richness of *Carabus* presented as number of subgenera occurring in one region only (R01), two regions (R02) etc. (all recognised subgenera according to Březina 1999).

	R01	R02	R03	R04	R05	R06	R07	R08	R09	R10	R11	R12	R13	Tot
No	63	11	12	8	3	3	2	4	3	1	2	3	1	116
%	54.2	9.5	10.3	6.9	2.6	2.6	1.7	3.4	2.6	0.9	1.7	2.6	0.9	100

abus and others), clearly illustrate almost no overlap among the species ranges within each subgenus (see maps in Chapter 5. *Species Accounts*). For some subgenera, the range of only one (or very few) species covers or touches the ranges of the others. The role of local speciation processes and vicariance are discussed in more detail in section 8.5.5.

8.3. PRESENT-DAY DISTRIBUTION OF *CARABUS* IN EUROPE

8.3.1. Species composition, diversity and regional distribution

In summary, the *Carabus* fauna of Europe consists at present of 132 species belonging to 31 subgenera representing nearly 16 % and 27 % of the world fauna, respectively (see Tab. 8.1). Besides, most of the European species are polytypic and very polymorphic.

Compared to the total, large surface area (10.520.000 km^2), the species richness of *Carabus* in Europe is relatively low, in spite of a high percentage of endemics, 132 species recorded so far, a figure that markedly contrasts with the 320 to 400 species known so far from China, according to the opinions of different authors (Deuve, 1997b; Březina, 1999, see also Tab. 8.1), which has a comparable surface (9.327.600 km^2), and with the some 60 to 80 species known so far for the much smaller (750.000 km^2 about) Asia Minor (Casale & Vigna Taglianti, 1999, see also Tab. 8.1). The diversity of the genus, however, appears to be very high, if compared with other larger regions, for instance with the 15 species present in North America, three of which have been introduced by man (Ball, 1960; Bousquet & Larochelle, 1993, see also Tab. 8.1).

Eighty-eight species and seven subgenera are endemic to Europe, that is, 67.2 % and 22.6 % respectively of all species and subgenera recorded from Europe (Tab. 8.1.). In this respect, Europe is a region of rather diverse and specific *Carabus* fauna and is comparable at least in some points with such regions as Central Asia, Caucasus and Anatolia (Tab. 8.1, see also Fig. 8.1).

This preliminary datum, in spite of its limits, is important because it confirms two facts. First, the Euro-Mediterranean area has been a marginal, but important centre of intensive diversification for a typically Angarian lineage, such as the genus *Carabus*. Second, the diversity of the Mediterranean biota cannot be explained in ecological, dynamic terms only, or as an overlap of recent faunas in a transition zone among Europe, Asia and Africa. It must be explained as a combination mostly of paleogeographic, geodynamic and paleoclimatic factors, with subsequent clado-vicariance events (Balletto & Casale, 1991).

In order to analyse some regional specifics in the distribution and species composition of *Carabus*, Europe was divided into 11 sub-regions, which correspond to the geographical regionalisation of Europe according to Gerasimov (1964) (Fig. 8.2).

Among the European regions, the highest diversity is recorded from Western and Central Europe (WC) with the Alps (58 species), followed by the Balkan Peninsula (BA – 44 species), Eastern Europe (RU – 42 species) and Pannonian-Carpathian region (PC – 37 species). Maximum diversity of European *Carabus* is in the middle part of the continent and roughly coincides with the zone of predominance of the mesophilous broad-leafed forests. Species richness significantly decreases in both southern and northern directions. The (sub-)Mediterranean and northern regions of Europe have markedly less diverse *Carabus* faunas.

At the same time, the specificity of the fauna, estimated as a percentage of endemic species, is highest in the three southern peninsulas of Europe, with the Iberian Peninsula characterised by the most distinct *Carabus* fauna: 16 of the 28 species recorded (57.1 %) are strictly endemic to that region; besides, it hosts also one endemic subgenus. The percentages of endemics in the Apennine and Balkan peninsulas are comparable to each other (approximately 20 %). The high percentage of endemic species in Western and Central Europe (27.6 %) is mainly due to presence the many Alpine endemics.

The species/subgenera ratio varies around 2 for most of the European regions and is close to 1 in the northern regions.

A specific feature of *Carabus* is the presence of endemic species in almost all regions of Europe with exception of the northernmost territories (Iceland, British Isles and Fennoscandia), a phenomenon which could hardly be stated for many other groups of plants or animals. Even the territories of Eastern Europe occupied by plains have specific faunas of *Carabus* including their own endemic species. The intensity of local speciation processes starting ***in situ*** from the Miocene Epoch and existing to the present time is more than obvious in this genus and is traceable in different lineages evolving in different regions in different historical periods (see sections 8.5 and 8.6).

The faunal connections of Europe with the adjacent regions are characterised as follows:

(1) The 'influence' of Siberian elements on the fauna of Europe is stronger than of European elements on the Siberian fauna. Thirteen Siberian species penetrate into Europe from the east. At the same time most European species decline in abundance and distribution toward some eastern major historical barriers such as the Dnieper and Volga rivers and the Ural Mountain Range. The commonness between the European and Siberian faunas is based mostly on both Siberian and widely distributed Euro-Siberian species.

(2) The faunal connections with the southern regions demonstrate the opposite trend, that is, more European species have penetrated into the Caucasus, Anatolia and North Africa, than the reverse: of 12 species common to Europe and the Caucasus, only three can be regarded as species of purely Caucasian origin. Common to Europe and Anatolia are 13 species, 4 of which are termed

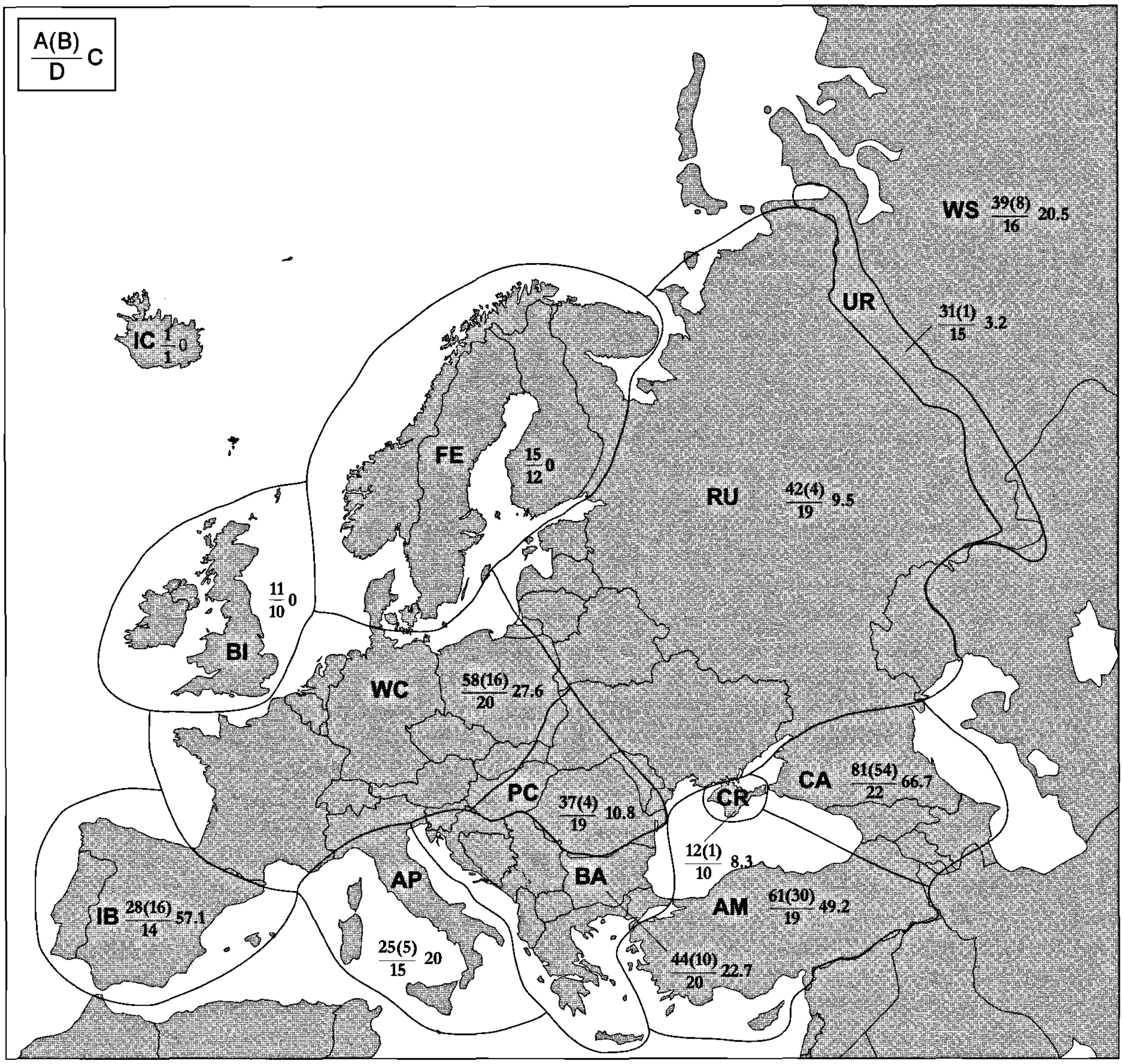


Fig. 8.2. Patterns of variation in species and subgeneric richness across European subregions (division of Europe into natural subregions, according to Gerasimov, 1964) (compare Tab. 8.4).

Abbreviations: **IC** –Iceland; **FE** – Fennoscandia (including Kola Peninsula and Russian Karelia, southern boundary coincides with the gulfs of Dvina and Onega, and with the southern shores of the lakes Ladoga and Onega); **WC** – Western and Central Europe (France, north of Garona River, Benelux, Alps, Germany, Switzerland, Italy north of Po River, Austria, Czech and Slovac republics, Poland); **PC** – Pannonian-Carpathian Region (Hungary, Romania, Northern Serbia, Ukrainian Carpathians); **RU** – East European (Russian) Plain – Byelorussia, Estonia, Lithuania and Latvia, Ukraine except for the Carpathians, all the European part of Russia southwards to the Kumo-Manych Basin (north of the line Rostov-Kizlyar Bey)); **UR** – The Ural Mountains; **WS** – West Siberia; **CR** – Crimean Peninsula; **BA** - Balkan Peninsula, nothern boundary along the rivers Danube, Sava and Izontso, including Northeast Italy (Triest region); **AP** – Apennine Peninsula (south of Po River, including Corsica, Sardinia and Sicily); **IB** – Iberian Peninsula (Spain, Portugal and France south of Garona River); **CA** – Caucasus; **AM** – Asia Minor (Anatolia).

The numbers within the regions refers to the letters on the sample as follows: **A** – number of species, **B** – number of endemic species, **C** – percentage of endemic species per region, **D** – number of subgenera.

Table 8.4. Patterns of diversity and specifity of the *Carabus* fauna across subregions within Europe.

Abbr	Subregion	No sp	No sg	End sp	End sg	%End sp	%End sg	%Sp	%Sg	Sp/Sg
IC	Iceland	1	1	0	0	0.0	0.0	0.8	3.2	1.0
BI	British Isles	11	10	0	0	0.0	0.0	8.4	16.1	1.1
FE	Fennoscandia	15	12	0	0	0.0	0.0	11.5	16.1	1.2
WC	Western and Central Europe	58	20	16	0	27.6	0.0	44.3	41.9	2.9
PC	Pannonian-Carpathians	37	19	4	0	10.8	0.0	28.2	16.1	1.9
RU	Eastern Europe	42	19	4	0	9.5	0.0	32.1	32.3	2.2
UR	Urals	31	15	1	0	3.2	0.0	23.7	35.5	2.1
CR	Crimea	12	10	1	0	8.3	0.0	9.2	9.7	1.2
BA	Balkan Peninsula	44	20	10	0	22.7	0.0	33.6	32.3	2.2
AP	Apennine Peninsula (Alps excl.)	25	15	5	0	20.0	0.0	19.1	22.6	1.6
IB	Iberian Peninsula	28	14	16	1	57.1	11.1	21.4	29.0	2.0

No sp – number of species; **No sg** – number of subgenera; **End sp** – number of endemic species; **End sg** – number of endemic subgenera; **%End sp** – percentage of endemic species per region; **%End sg** – percentage of endemic subgenera per region; **%Sp** – percentage of the number of species per the total of the whole European fauna; **%Sg** – percentage of the number of subgenera per the total of the whole European fauna; **Sp/Sg** – number of species/number of subgenera ratio (compare Fig. 8.2).

Anatolian. Of 4 species common to Both North Africa and Europe, only one species is mainly North African.

According to a concept developed in Russian phytogeography (Krasnov, 1888, cited by Lavrenko, 1938), regional floras are classified into three major groups: 'relict', 'orthoselective'; and 'migratory'. Relict floras have persisted *in situ* since the Tertiary Period, e.g., those of the Colchis or western Caucasus. Orthoselective floras consist mostly of autochthonous elements and have developed under the impact of one-way oriented, principally climatic, changes, for an extended period of time, i.e., the flora of Central Asia. The migratory floras are normally characterised by different 'chronological layers' in their composition, and consist of species of different origin and age of evolution.

Krasnov's concept seems to be applicable in zoogeography as well. In his terms, the *Carabus* fauna of the Iberian Peninsula is closer to being 'relict', in the sense that its distinctiveness is markedly higher than the distinctiveness of any other European region. The faunas of the Apennine and Balkan peninsulas, as well as Alps and Carpathians are 'orthoselective' to a certain extent, because local speciation processes there are obvious and have led to several specific features. At the same time, those faunas, especially Alpine and Carpathian, are enriched by numerous species which seem to have migrated from the north during the Pleistocene Epoch. The faunas of Northern Europe and of the Russian Plain are 'migratory', as they consist mainly of widely distributed species, or such of Siberian origin.

In conclusion, Krasnov's concept helps us to understand the high complexity of European fauna of *Carabus*. Within the territory of one continent, we have good examples of regional faunas of rather different history leading to different present-day biogeographical pictures.

The history of European *Carabus* is discussed in section 8.6. We note here only some 'classical' biogeographical phenomena, excellently illustrated by the European species of *Carabus*: isolation and distinctiveness (i.e. Iberian fauna); between-region faunal exchange during different historical epochs, i.e. European-Nearctic, European-Siberian, European-Anatolian etc.; immigration and remarkable consequent allopatric speciation *in situ*, demonstrated by many *Carabus* lineages in different parts of Europe; and complete devastation of the fauna and consequent colonisation and re-colonisation from various sources during the Pleistocene Epoch.

8.3.2. Taxonomic structure

The taxonomic structure is understood here as proportions of the different subgenera (Fig. 8.3A) or suprasubgeneric groups (Fig. 8.3B) in each subregional fauna of Europe. The taxonomic structure of the whole fauna of Europe is presented in Fig. 8.3. The division into suprasubgeneric groups is taken according to Turin *et al.* (1993, see also legend to Fig 8.3).

The European fauna is dominated by three main suprasubgeneric groups, *Multistriati-B*, *Multistriati-A* and *Digitulati+Lipastromorphi*, according to the classification accepted

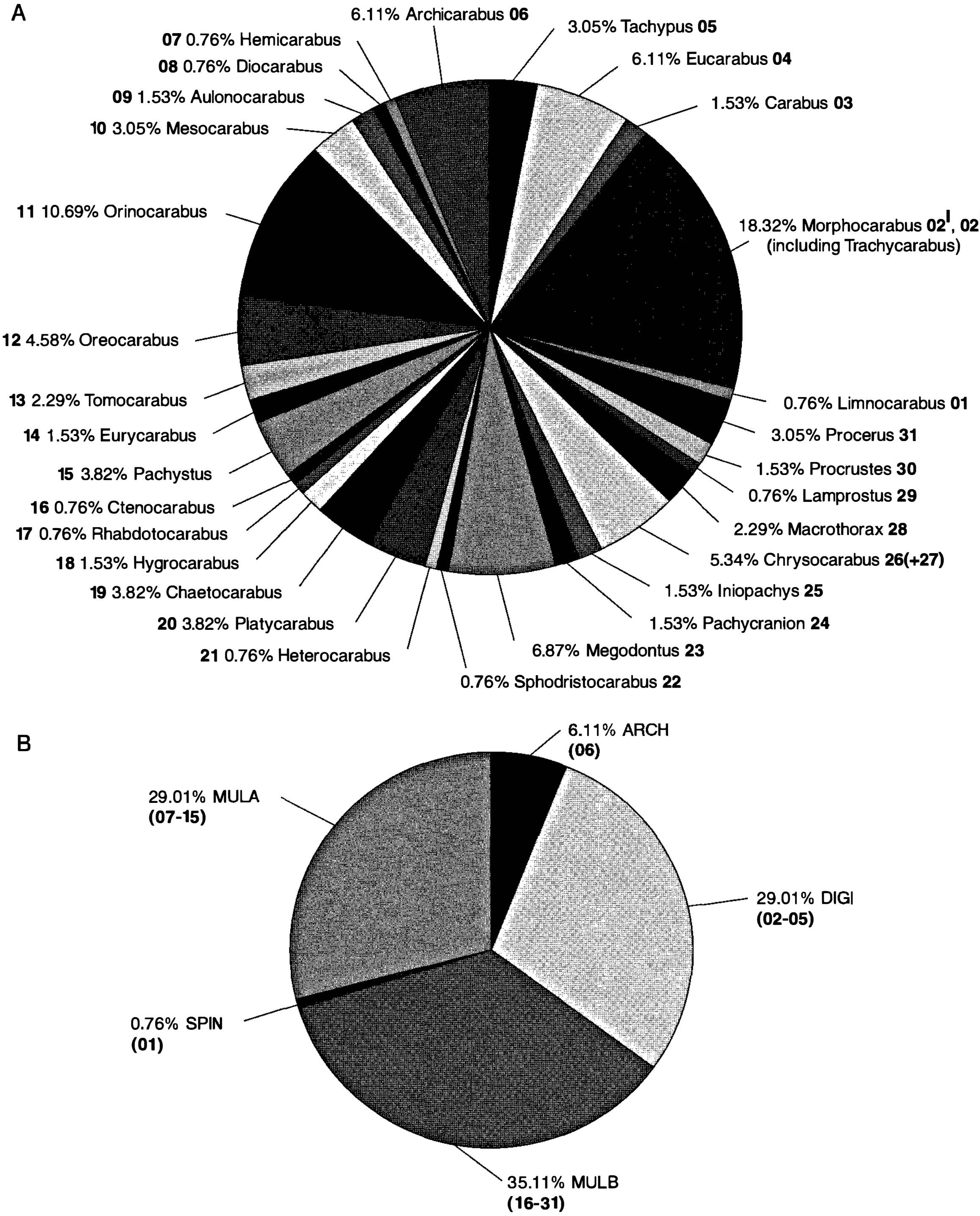
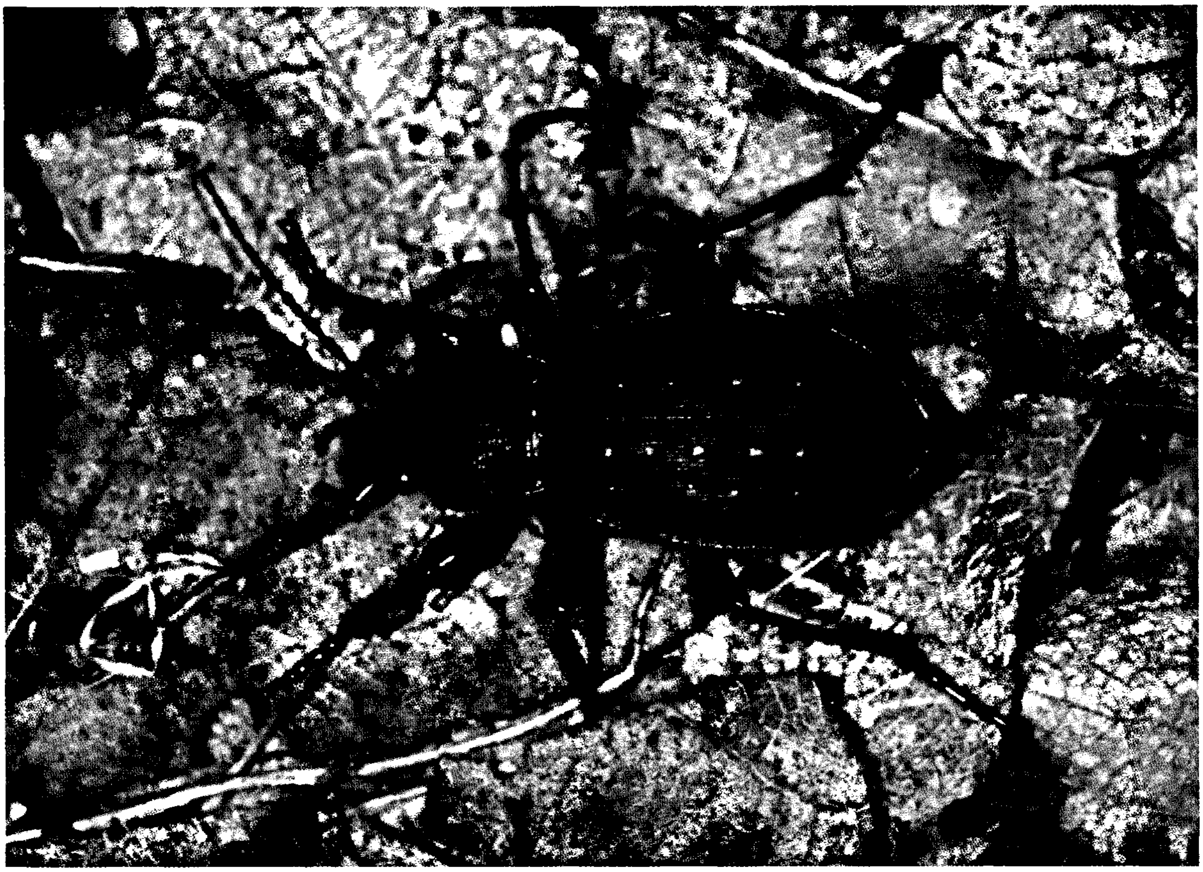


Fig. 8.3. Taxonomic structure of European fauna of Carabus presented as proportions of the number of species of each subgenus (A) or each suprasubgeneric groups (B). Numbers in bold refer to the respective numbers of subgenera in Chapter 2 and 5.

Abbreviations: The compositions of suprasubgeneric groups are as follows: **SPIN** – Spinulati (subgenus *Limnocarabus*); **DIGI** – Digitulati & Lipastromorphi (*Morphocarabus, Carabus s.str., Eucarabus, Tachypus*); **ARCH** – Archicarabomorphi (*Archicarabus*); **MULA** – Multistriati-A (*Hemicarabus, Diocarabus, Aulonocarabus, Mesocarabus, Orinocarabus, Oreocarabus, Tomocarabus, Eurycarabus, Pachystus*); **MULB** – Multistriati-B (*Ctenocarabus, Rhabdotocarabus, Hygrocarabus, Chaetocarabus, Platycarabus, Heterocarabus, Sphodristocarabus, Megodontus, Pachycranion, Iniopachys, Chrysocarabus, Chrysotribax, Macrothorax, Lamprostus, Procrustes, Procerus*) (see also Turin *et al.*, 1993 and Chapter 7. *Phylogeny*).

C. *hispanus*
Fabricius
Forêt de Saou,
France.
Photo by
A. Casale &
G. Delitala.

C. *auratus*
Linnaeus
The Netherlands.
Photo by
Th. Heijerman.



C. hortensis
Linnaeus
Lüneburger Heide,
Germany.
Photo by
J.-H. Stücke &
Th. Assamann

C. planatus
Chaudoir
Sicily.
Photo by
P. Brandmayr &
A. Casale

in Turin *et al.*, 1993. The prevalence of the three groups in the European fauna is caused as a rule by high species richness of few subgenera within each group, for instance *Morphocarabus* (24 species, 18.3% of the European fauna) within *Digitulati+Lipastromorphi*, *Orinocarabus* (20 species, 10.7%) within *Multistriati-A*, *Megodontus* (9 species, 6.9%) and *Chrysocarabus* (7 species, 5.3%) within *Multistriati-B*.

The taxonomic structure varies among subregions in a way which suggests some historical and phylogenetic implications for the origin and formation of the European *Carabus* fauna. The northern and eastern regions of Europe (British Isles, Fennoscandia, Russian Plain, Ural) are dominated by Digitulati+Lipastromorphi with Multistriati-B in the second position (Tab. 8.5.).

The Western and Central European fauna is characterised by prevalence of *Multistriati-A* with *Multistriati-B* in second position. The intermediate position of the Pannonian-Carpathian fauna between the Central and East European is also reflected by its taxonomic structure, which is dominated by *Digitulati+Lipastromorphi* but on the same time is characterised by a high proportion of *Multistriati-B*. The peninsulas of Southern Europe have also distinctive taxonomic structure dominated by *Multistriati-B* and *Multistriati-A* in second position (in the Balkans – *Digitulati+Lipastromorphi* in second position). Thus, we conclude that three types of faunas are present in Europe with regard to relative numerical presence of the main suprasubgeneric groups:

(1) North and East European Boreal – *Digitulati+Lipastromorphi*, *Multistriati-A*, *Multistriati-B*
(2) Central European Nemoral (connected to the zone of broad-leafed forests) – *Multistriati-A*, *Multistriati-B*, *Digitulati+Lipastromorphi*
(3) South European Nemoral & Submediterranean – *Multistriati-B*, *Multistriati-A*, *Digitulati+Lipastromorphi*

The dendrogram (Fig. 8.4) yields an idea about the similarity between regions with regard to their taxonomic structure. Three main clusters are at 0.8 similarity level: (1) North and East European, including Pannonian-Carpathian region, (2) South and Central European and (3) Iceland (a fauna consisiting of one species only).

The similarity in taxonomic structure among regions suggests two major historical types of fauna existing presently in Europe: (1), Euro-Siberian, prevailing in Northern and Eastern Europe; and (2), Euro-Mediterranean occurring in Central and Southern Europe. The Euro-Siberian

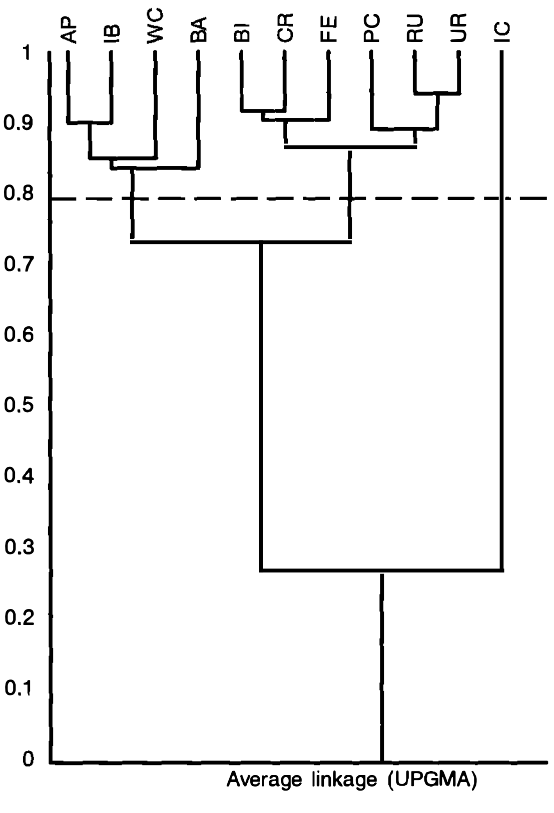


Fig. 8.4. Similarity in taxonomic structure among the European subregions, calculated on the basis of relative abundances of the three suprasubgeneric groups in each region (numerical form **b** of Czekanoswki-Dice-Sørensen's index, Pesenko, 1982; Baev & Penev, 1995).
For the abbreviations of the subregions see Tab. 8.4.

Table. 8.5. Taxonomic structure of the European subregions based on the proportion of each suprasubgeneric group in the regional fauna.

	IC	BI	FE	WC	PC	RU	UR	CR	BA	AP	IB
Spinulati	0.0	9.1	6.7	1.7	2.7	2.4	3.2	8.3	2.3	4.0	0.0
Digitulati+Lipastromorphi	0.0	**45.5**	**40.0**	24.1	**40.5**	**47.6**	**41.9**	**41.7**	27.3	16.0	21.4
Archicarabomorphi	0.0	9.1	6.7	6.9	5.4	2.4	3.2	8.3	6.8	16.0	10.7
Multistriati-A	**100.0**	27.3	33.3	**36.2**	24.3	28.6	32.2	25.0	20.4	28.0	28.6
Multistriati-B	0.0	9.1	13.3	31.0	27.0	19.0	19.4	16.7	**43.2**	**36.0**	**39.3**

For the abbreviations of the subregions see Table 8.4.

faunas are assumed to consist of younger forms with a greater ecological amplitude, which colonised the territories of Northern and Eastern Europe during Interglacial stadia, primarily from Siberia, and secondarily, from the refugia in the Central and South European mountains.

The Euro-Mediterranean fauna consists of phylogenetically older taxa, some of which persisted in Southern Europe from the time of the Miocene Epoch (Josifov, 1981; see also section 8.5 for details). Within the Euro-Mediterranean type of fauna, two main groups are delimited: one, of Central European elements connected to the zone of broad-leafed mesophilous forests; and another, of Southern-European elements, connected to the zone of broad-leafed xerophilous forests and Mediterranean vegetation of Southern Europe.

The results presented above suggest that analyses of taxonomic structure, understood as proportions of taxa of higher rank, requires mostly explanation based on events that happened in the more or less remote past, in contrast to explanations resulting from analyses at species level, which are based on temporally more proximate circumstances (Chernov, 1975). Thus, prevalence of one or another phyletic group or proportions of major groups within a certain regional fauna reflects mainly the history of the region, whereas species compositions are affected principally by present-day ecological and climatic conditions. In other words, to understand regional faunas, both taxonomic structure and local species compositions must be taken into account. Therefore, we consider taxonomic structure as a useful method applicable in both descriptive and historical biogeography.

8.3.3. Chorology

A chorological classification of the ranges of a certain group of organisms may be derived in different ways and therefore is criticised by various authors as highly subjective. On the other hand, each range classification should meet the requirements set by the aims of the respective study. Any classification could be used if its method and basic principles are clearly defined and consistent from the very start of the particular study.

In the present work, we have chosen an hierarchical, multilevel approach to the chorological classification of the European *Carabus* species in order to achieve two main goals: (1) to properly describe each species' range by classifying it into one of the predefined types of distribution or 'Range characteristics' (after Penev & Alekseev, 1996), and (2) to group the range characteristics into larger 'chorotypes' (sensu Vigna Taglianti *et al.*, 1993 and Vigna Taglianti *et al.*, 1999, with some changes), that is, groupings of species with presumably common distribution centre. Finally, each 'chorotype' may be placed in one of the major 'faunal types', such as European, Siberian, or Mediterranean. Following De Lattin's (1967) rules for *descriptive* and *causal* stages of zoogeographical studies, 'range characteristics' may be regarded as purely descriptive characteristics of species ranges made on the basis of their present-day distribution. 'Chorotypes' are intermediate between descriptive and causal interpretation. They implicate a description of the main area where a species range is situated, but at the same time, the grouping of several species into one 'chorotype' assumes a common centre and reasons of such distribution, what De Lattin called 'Verbreitungszentrum'. Finally, the 'fauna types' reflect the major centres of origin and subsequent evolution of the Palaearctic fauna and therefore are classified as mainly causal characteristics.

The chorological categories are explained in Chapter 5 and in the legend to Appendix 8.1. The chorological characteristics of each species are shown in Chapter 5 and listed in comprehensive form also in Appendix 8.1 and Table 8.6.

Table 8.6. The chorotypes of the European Carabus and species belonging to each chorotype (for explanations of the abbreviations see Appendix 8.1).

CHOROTYPES	**SPECIES** (Note: *antipai* is omitted: see *Checklist*)	**NUMBER**
ASE	*clatratus, granulatus*	2
SIB	*aeruginosus, henningi, hummeli, odoratus, regalis, sibiricus, zherichini, loschnikovii, canaliculatus, truncaticollis, cribellatus, ermaki, schoenherri*	13
SIE	*arvensis, cancellatus, nitens, bessarabicus, convexus, aurolimbatus*	6
NAF	*faminii*	1
WME	*morbillosus*	1
EME	*graecus*	1
CAUC	*varians, exaratus, septemcarinatus*	3
CAUC-CRIM	*bosphoranus, gyllenhali, perrini*	3
ANAT	*wiedemanni, marietti, torosus, sommeri*	4

CHOROTYPES	**SPECIES** (Note: *antipai* is omitted: see *Checklist*)	**NUMBER**
POCA	*scabrosus*	1
EUR	*monilis, nemoralis, problematicus, glabratus, hortensis, intricatus, irregularis, violaceus, coriaceus*	9
CEU	*ulrichii, auratus, nodulosus, auronitens*	4
EEU	*estreicheri, menetriesi, stscheglowi, marginalis*	4
EEU-CARP	*comptus, hampei, kollari, rothi, zawadzkii, rybinskii, obsoletus, planicollis*	8
EEU-PANN	*scheidleri, variolosus*	2
EEU-SEEU	*scabriusculus, hungaricus*	2
EEU-SWRU	*besseri, excellens, errans*	3
EEU-CRUS	*haeres*	1
EEU-URAL	*karpinskii*	1
WEU-PYRE	*cristoforii, pseudomonticola, pyrenaeus, splendens, rutilans*	5
WEU-IBER	*lusitanicus, melancholicus, rugosus*	3
WEU-IBEN	*deyrollei, steuartii, macrocephalus, amplipennis, auriculatus, lineatus*	6
WEU-IBEC	*guadarramus, ghilianii, galicianus*	3
WEU-IBES	*dufourii*	1
SEU-ALAP	*italicus*	1
SEU-ALPW	*vagans, monticola, cenisius, concolor, fairmairei, heteromorphus, latreilleanus, putzeysianus, cychroides, olympiae, solieri*	11
SEU-ALPC	*adamellicola, castanopterus, lepontinus*	3
SEU-ALPE	*alpestris, bertolinii, carinthiacus, creutzeri*	4
SEU-ALPI	*depressus, germarii*	2
SEU-ALCA	*linnaei, sylvestris, fabricii*	3
SEU-APPE	*rossii, lefebvrei*	2
SEU-APDI	*preslii, cavernosus*	2
SEU-CADI	*catenulatus, parreyssii, caelatus, croaticus*	4
SEU-DIBA	*gigas, versicolor*	2
SEU-CABA	*montivagus*	1
SEU-TYRR	*alysidotus*	1
SEU-SACO	*genei*	1
SEU-SICI	*planatus*	1
SEU-CRET	*trojanus, banoni*	2
SEU-GRNC	*arcadicus*	1
SEU-THES	*krueperi*	1
SEU-PELO	*merlini, duponchelii*	2
SEU-FRAS	*hispanus*	1
	TOTAL	**132**

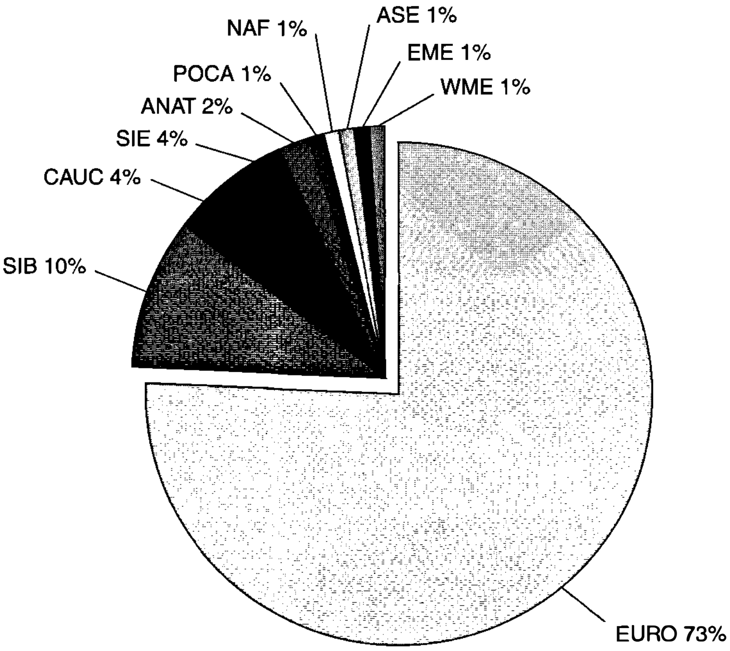


Fig. 8.5. Chorological structure of the European Carabus fauna (for explanations of the abbreviations see Appendix 8.1; for the chorotypes included in 'EURO' see Fig. 8.6).

Generally, the chorological structure of the European fauna is characterised as rather diverse with regard to its composition of different chorotypes (Figs. 8.5, 8.6). The most important basic features of it can be summarized as follows:

1. The total number of species belonging to the European fauna element *sensu latissimo* is 97, which represents 73 % of all European fauna. The main conclusion of this figure could be that the bulk of the European *Carabus* fauna is probably autochthonous and evolved *in situ* in different parts of Europe. The migratory (allochtonous) component in the European fauna comprises in first line 13 species of obviously Siberian origin and distribution (10 % of the European fauna) which penetrate to the northeastern regions of European Russia, and can be regarded as Pleistocene immigrants (i.e., several *Morphocarabus* species). Second, the European fauna is enriched also by few species of Anatolian origin, such as *C. marietti, C. wiedemanni, C. torosus,* and *C. sommeri*. Third, the ranges of some Caucasian species extend to the southernmost territories of the Russian Plain (i.e., *C. perrini, C. exaratus,* and *C. varians*).
2. In general, Caucasus and Anatolia contributed little to the colonization of Europe. Despite a very rich assemblage of *Carabus* species, both territories owing to reasons outlined in section 8.5 (see also Golovatch, 1984; Penev & Alekseev, 1996; Casale & Vigna Taglianti, 1999) have mostly gained European species but shared to a far lesser extent 'their own' species.
3. The European fauna is dominated by elements with more or less restricted distributions in different parts of Europe, i.e. Central European (4 species), East European (21 species), West European (18 species), and South European (45 species) (Fig. 8.6).
4. A more analytical examination of the geographical patterns of species peculiar to Europe stresses a high percentage (46 %) of taxa endemic either to the entire Southern Europe, or to one region of it. However, the percentages of Central, Western, and Eastern European elements, respectively, or of species widely distributed through Central Europe, are high, and confirm the ecological constraints of an insect group most of whose members are adapted to mesophilous forest, mountains, or wet habitats.
5. With 53 *Carabus* species (a few less than half of the total number of European species), the position of Italy in the Mediterranean area appears favoured. Located between Central Europe to the north, and North Africa to the south, this country houses a fauna much enriched by Middle European, Balkan and Maghrebian elements, and with a high percentage of endemics in the Alps, Apennines, and in two major islands (Sardinia and Sicily).
6. In the transitional zone between Central and Eastern Europe, the Alpine chain is very rich in species of *Carabus*: 42 species, with different origins and chorotypes, are present, and often overlapped. Maximum diversity is in the Western Alps (Casale & Vigna Taglianti, 1992).
7. In other mountain areas of Western and Southern Europe, such as the Cantabrian chain, Pyrenees, the

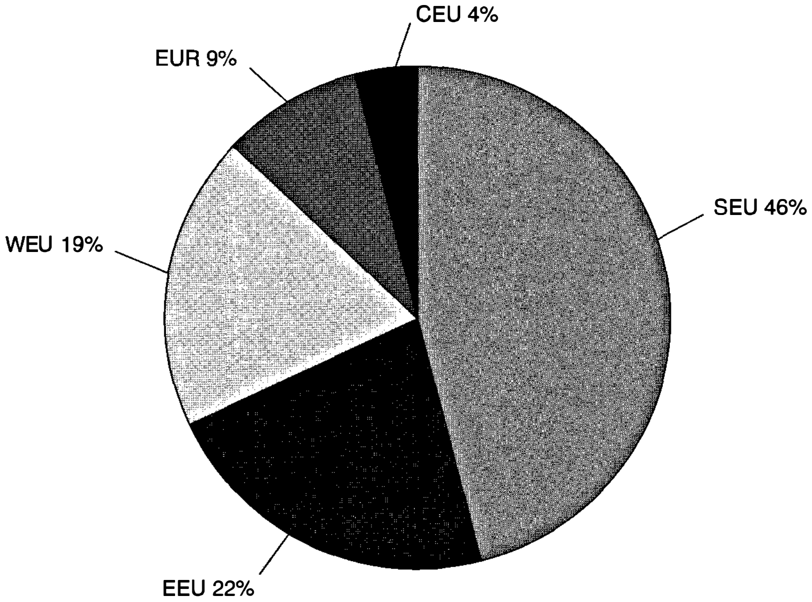


Fig. 8.6. Percentages of chorotypes within the species of European distribution type (for abbreviations of chorotypes, see Appendix 8.1).

Dinaric and Balkan areas, several endemic taxa are also present .

8. The purely Mediterranean faunal elements *sensu stricto* are represented by few species, only (7 species, 5.3 %). Very few species are endemic to the major Mediterranean islands, i.e., *C. genei* to Corsica and Sardinia; *C. planatus* to Sicily; and *C. banoni* to Crete.
9. The endemism in European *Carabus*, however, does not seem to be connected to montane areas alone. Eastern Europe, for instance, with its huge plain territory, extending from the Carpathians to the Urals, hosts also a remarkable number of species, endemic or subendemic to it (see also section 8.3.4).
10. The proportion of widely distributed species is always low in *Carabus*, at least lower than has been observed in many other insect groups. Relatively few species in the European fauna are nearly Pan-Palaearctic or Holarctic in distribution (5 species) and their proportion in the whole list does not exceed 4%.
11. Within the European regions, the Central European chorotype is present in large number of species in Western and Central Europe, the Pannonian-Carpathian region, and also in the Balkan and Apennine peninsulas. The northern European faunas (British Isles, Fennoscandia) are characterised by a large proportion of widely distributed Siberian, Euro-Siberian and some North and Central European species. The East European regions of Russian Plain, Crimea and Ural Mountains have also a distinctive chorological structure, characterised by the presence of East European, Siberian and also some Central European faunal elements.
12. Finally, the most isolated position of the Iberian Peninsula is reinforced by the chorological structure of its fauna as well, characterised not only by a high percentage of Southwest European species (in fact endemic to the Iberian Peninsula) but also by presence of some Mediterranean and Central European faunal elements.

8.3.4. Zoogeographical division of Europe based on the *Carabus* fauna

Attempts are numerous to establish a clear criterion for dividing the Globe in phyto- or zoogeographical regions and there are also several schemes of such divisions. They are not discussed here, nor do we aim to prove or reject a particular zoogeographical division of Europe on the basis of the data for *Carabus*. Every zoogeographical division cannot and should not be extrapolated to a generalisation extended beyond the limits of the particular taxonomic groups and the questions of the particular study. Doubtless, the coincidence of zoogeographical patterns recognized for different taxonomic groups is the best evidence for the existence of common centres of origin and dispersal of organisms of particular distribution types.

It is also evident, that a meaningful zoogeographical division can not be produced on the basis of a single criterion. For instance, taking into account the level of endemism, one would not be able to outline the zoogeographical regions which lack endemics, but are characterised by other remarkable features of their faunas. The same holds, when only range complexes (isochores) are used as a basis for zoogeographical division, because such an approach may lead to underestimation of some important patterns of specificity of the regional faunas. Therefore, we use here a combination of criteria for a division of Europe into zoogeographical regions:

1. More or less uniform species composition within a region
2. Dissimilarity in species compositions between regions
3. Level of specificity of the fauna (endemism)
4. Presence of bunches of range boundaries (isochores)
5. Characteristic species' absences

The similarity between the *Carabus* faunas of the European subregions has been discussed already in this chapter on the basis of several different criteria, such as taxonomic and chorological structure, presence of endemics etc. In Fig. 8.7 (A & B) the subregional faunas of Europe have been grouped according to their similarity of species compositions calculated with two indices, one of them taking into account the species absences (both '1' and '0' values in Appendix 8.1.), and the other one considering only the species presences (only '1' values in Appendix 8.1). Both dendrograms clearly demonstrate, the marked similarity between the faunas of: (a), Fennoscandia and British Isles; (b), Russian Plain and Ural Mountains with Crimea being related to them; (c), Western and Central Europe and Pannonian-Carpathian region with Balkan Peninsula being close to them; and (d), the isolated position of the Apennine and especially the Iberian peninsulas.

The dendrogram B, which includes species absences in the calculation, seems even more meaningful, probably because the *Carabus* faunas are so well studied that an absence of a species is unlikely to be explained by insufficient sampling or other kinds of artefacts, that is, absence of a species is as informative as its presence. Therefore, we consider the pattern revealed by dendrogram 8.7(B) at approximately 0.7 similarity level as a good basis for a zoogeographical division of Europe.

On the basis of the criteria listed above as well as some patterns of similarity/dissimilarity in the taxonomic and chorological structure of the *Carabus* faunas, we propose the following division of the European continent into zoogeographical regions (Fig. 8.8):

(1) North European subregion (N) – Iceland, the British Isles and Fennoscandia.

Characterised by fauna of low diversity (15 species), predominance of *Digitulati*+*Lipastromorphi*, prevalence

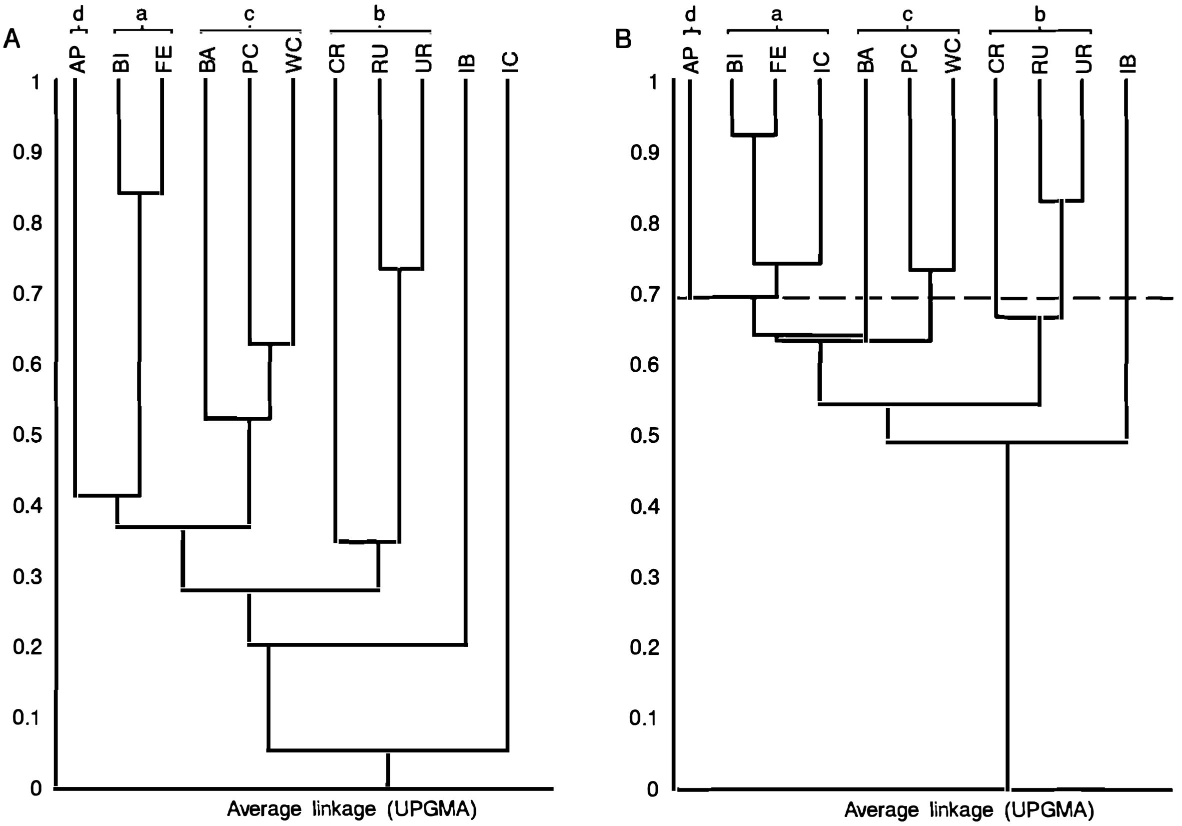


Fig. 8.7. Similarity in species compositions between the European subregions.
A – calculated with exclusion of species absences (index of Czekanowski–Dice–Sørensen) (Baev & Penev, 1995).
B – calculated with inclusion of species absences (index of Sokal–Sneath (2)) (Baev & Penev, 1995).
For the abbreviations of the subregions see Tab. 8.4 or Fig. 8.2. For the groups of clusters indicated under 'a', 'b', 'c' and 'd' see text.

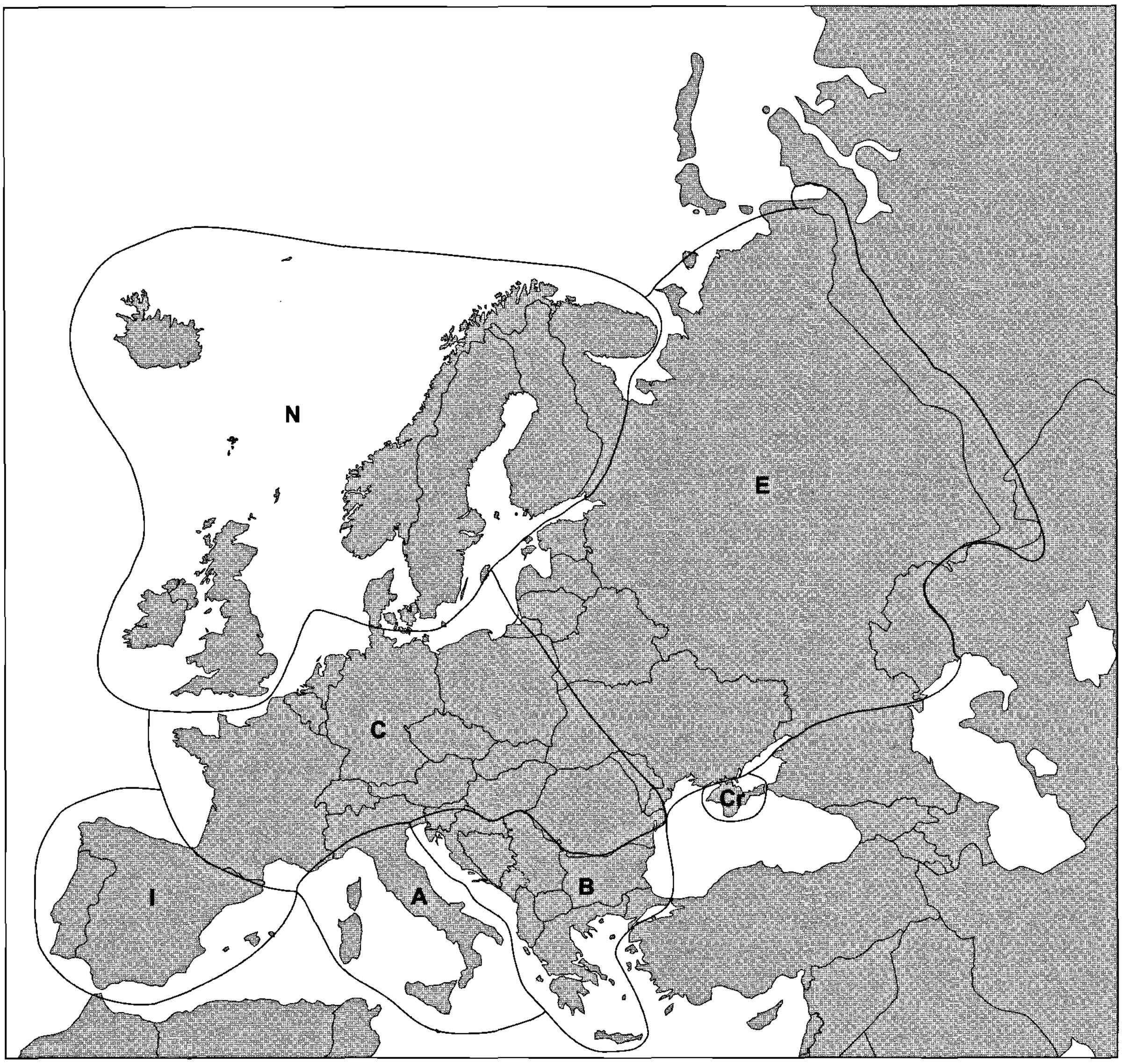


Fig. 8.8. Zoogeographical division of Europe based on the *Carabus* fauna.
N – North European subregion (Iceland, the British Isles and Fennoscandia); **C** – Central European subregion (Western and Central Europe, Pannonian-Carpathian area); **E** – East European subregion (Russian Plain and Ural); **Cr** – Crimean subregion; **B** – Balkan subregion; **A** – Apennine subregion; **I** – Iberian subregion.

of widely distributed and North European species. No endemic species. Characteristic absences are in first place several Siberian species (mainly *Morphocarabus* and *Diocarabus*) which occur in the northern regions of the Russian Plain but do not reach Fennoscandia. Remarkably absent is also *C. menetriesi*, widely distributed in the adjacent areas of Eastern Europe but absent from Fennoscandia. A characteristic element of the fauna is also *C. problematicus*, the only species known from Iceland and distributed from Fennoscandia along the coasts reaching to the east the Russian part of Fennoscandia (Kola Peninsula).

(2) **Central European subregion (C)** – Western and Central Europe, Pannonian-Carpathian area.
This seems to be the most complicated zoogeographical unit, consisting however of two main faunal elements, the Euro-Siberian boreal and Central European nemoral (=connected to the broad-leafed forests). Besides, a remarkable number of species endemic to the Alps (mainly *Orinocarabus* and *Platycarabus*), as well also some Carpathian endemics contribute to the specificity of the fauna. Generally, Central Europe together with the Carpathian Mountains and the Alps host most, more than 50 %, of the European fauna. Twenty species and the subgenus *Orinocarabus* are endemic

for the subregion. Species indicative for the Central European subregion are for instance *C. obsoletus, C. ulrichii, C. linnaei, C. sylvestris C. variolosus, C. nodulosus, C. fabricii, C. auronitens*, as well as some other locally distributed endemics. Faunal connections extend to all surrounding regions. The fauna of Northern Europe can be regarded for instance as a kind of impoverished version of the Central European fauna. From the east, several Eastern European species range to the Carpathians and Central Europe (*C. scabriusculus, C. menetriesi, C. marginalis*). Connections to the Iberian and Apennine peninsulas are marked mostly by several Central European species which reach the northernmost territories of Spain or Italy (see below). Several species penetrate into Central Europe from the Balkans (*C. montivagus, C. gigas*) or in contrast, from Central Europe to the Balkans (*C. scheidleri, C. ulrichii, C. nodulosus, C. irregularis*). Characteristic absences are mainly Eastern European species ranging to the West to Ukrainian Carpathians (several *Morphocarabus*), as well as some Southern European species occurring in the northern areas of Southern Europe, but absent from Central Europe

Further, the Central European subregion is divided into three provinces:

2.1. West and Central European province
Characteristic species are the so-called Atlanto-Mediterranean elements, such as *C. auratus, C. problematicus* (more widely distributed than the previous species), *C. violaceus purpurascens*. Species typical for Central Europe *sensu stricto* are *C. irregularis*, *C. nodulosus,* and *C. auronitens.*

2.2. Alpine province
Rich in local endemics, mostly of the subgenera *Orinocarabus, Platycarabus, Archicarabus* and some others. There are species common to the Alps and the Apennines (*C. italicus*) or to the Alps and western Balkans (*C. catenulatus, C. carinthiacus, C. caelatus, C. gigas,* and others).

2.3. Pannonian-Carpathian province
The fauna is transitional between the Eastern, Central- and Southeastern European faunas. Relatively rich (37 species), 4 of which are endemics. Faunal connections are present to Eastern Europe (*C. hungaricus*), Balkans (*C. scheidleri, C. montivagus, C. gigas,*) and the Alps (*C. fabricii*). Species indicative for this province are *C. obsoletus, C. hampei, C. kollari* and *C. linnaei.*

(3) East European subregion (E) – Russian Plain and Urals.
Characterised by 'northern' type of fauna with prevalence of *Digitulati+ Lipastromorphi*, and especially with remarkable richness of subgenus *Morphocarabus*, 8 species of which are endemic or subendemic for the subregion. The faunas of the territories to the east of Volga River and especially the northeastern part of European Russia and Polar Ural are enriched with several Siberian species, such as *C. truncaticollis, C. ermaki, C. henningi, C. hummeli, C. aeruginosus, C. odoratus* and others. The endemic and subendemic species are distributed mainly in the forest-steppe and steppe zones in the middle part of the Russian Plain (*C. besseri, C. errans, C. haeres, C. excellens*). Only one endemic species is located in the easternmost part, that is *C. karpinskii* (Southern Ural). Characteristic absences are several Central European species connected to the zone of the Central European nemoral (broad-leafed) forests which do not extend to the east of the eastern slopes of the Carpathians, Transcarpathia or Poland (*C. auronitens, C. problematicus, C. auratus, C. ulrichii, C. scheidleri*). In west-eastern direction, three main range boundaries generally follow river valleys of Dnieper and Volga (Penev, 1989; Esjunin *et al*, 1993; Penev & Turin, 1994). According to these boundaries, three provinces are delimited:

3.1. West-Russian province (Byelorussia, Baltic States, West and Central Ukraine to the east to Dnieper River) – a province of low specificity, characterised by presence of Central European species which generally extend to the east to the rivers Dnieper or Severski Donets (*C. intricatus, C. ulrichii*). Subendemic for the province are *C. besseri* and, to a certain extent, also *C. excellens.* At the same time, eastern species do not exceed Dnieper to the west (*C. stscheglowi, C. haeres* and more or less *C. errans*).

3.2. Central-Russian province (Middle Russia between the rivers Dnieper and Volga) – a province which is remarkable by hosting several endemic and subendemic *Morphocarabus* species, such as *C. errans, C. haeres, C. campestris* (in the south).

3.3. East Russian-Uralian province (eastwards of Volga, including Urals) – a province characterised by reduction of the Central European fauna elements, such as *C. coriaceus, C. violaceus*, but enriched with several Siberian species.

(4) Crimean subregion (Cr)
Characterised by impoverished fauna (12 species), of East European type, marked by presence of some Pontic and Caucasian species. The dominant taxa are *Digitulati+Lipastromorphi.* The northern part of the peninsula is covered by steppe-like habitats and in faunal composition does not differ from the South-Russian and Ukrainian steppes (*C. bessarabicus, C. campestris. C. hungaricus*). The mountain part of the peninsula (Crimean Yaila) is distinguished by specific fauna, most characteristic elements of which are the endemic *C. gyllenhali* and the Circum-pontic *C. scabrosus tauricus.*

Several remarkable absences help to characterize the Crimean fauna, most interesting of which are species widely distributed in the neighbouring regions of Ukraine and Central Russia but absent from Crimea (*C. convexus, C. coriaceus*), while other species of similar distribution type are present there (*C. granulatus, C. cancellatus*).

(5) Balkan subregion (B)

One of richest European faunas comprising 44 species, 20 % of them endemic, belonging mainly to the subgenera *Chaetocarabus* (*C. arcadicus, C. kruepeni, C. merlini*), *Megodontus* (*C. caelatus, C. croaticus*) and *Procerus* (*C. duponchelii, C. sommeri, C. banoni*). No endemic subgenera; *Multistriati-B* prevail, followed by half as many representatives of *Digitulati+Lipastromorphi* and *Multistriati-A*. A very diverse fauna in biogeographical respect, with its own autochthonous elements as well as migrants from the adjacent regions, such as Anatolia (*C. wiedemanni, C. graecus, C. marietti*), some Pontic species (*C. scabrosus, C. torosus*), species common to Apennines and Balkans (*C. preslii, C. cavernosus*) or especially Balkans and Pannonian-Carpathian region (*C. scheidleri, C. catenulatus, C. nodulosus, C. irregularis, C. germarii*). Northern species are present in the Balkan fauna, as well (*C. violaceus* and *C. hortensis*). Characteristic absences from the Balkan fauna are few, probably the only remarkable ones are *C. glabratus* and *C. nemoralis*, species widely distributed in Europe and penetrating nearly to the borders of the Balkan peninsula, but absent from it.

(6) Apennine subregion (A)

With regard to specificity of its fauna, the Apennine peninsula (regarded here as the territory south of Po River) can be characterised as intermediate. Twenty-five species are known to occur here, 5 (20 %) of them are endemics, there is also one subgenus common to North Africa, Sardinia, Corsica and Sicily (*Eurycarabus*). Connections with the Balkan peninsula are discussed above, there are also several species or sister groups common to the Apennines and the Alps (mainly from the subgenera *Archicarabus, Eucarabus, Oreocarabus*). Subendemic to the Apennine Peninsula ranging in northern direction to the Alps are, for instance, *C. italicus* and *C. rossii*. Absences from the Apennine peninsula are impressive, such as the subgenus *Orinocarabus,* widely distributed in the Alps, or the Southeast European-Anatolian subgenus *Procerus.* Also several Central-European or Paneuropean species, despite their more or less wide distribution in the Alps (such as *C. arvensis, C. nemoralis, C. hortensis, C. irregularis, C. intricatus*), do not reach the Apennine peninsula from the north; a few others (*C. cancellatus, C. glabratus, C. problematicus*) only reach the north-central part of the peninsula).

(7) Iberian subregion (I)

Not species-rich, however doubtless the most specific and isolated fauna of Europe with 57% of its 28 species endemic to the subregion. Subgenus *Iniopachys* is endemic to the Iberian Peninsula. The bulk of the fauna is autochthonous, developed into mostly locally distributed endemics. Faunal connections with the adjacent subregions are mostly species penetrating slightly into the northernmost parts of the peninsula, i.e., *C. problematicus, C. auronitens, C. violaceus purpurascens* (West and Central Europe), and *C. splendens* (France). The connections to the adjacent Mediterranean regions are not as many as one may suspect; three examples are *C. melancholicus, C. rugosus* (North Africa) and *C. morbillosus* (West Mediterranean region).

Few widely distributed European species penetrate only the northern areas of the Iberian peninsula (*C. cancellatus, C. granulatus, C. nemoralis*). Many Paneuropean species are absent from the region (i.e., *C. coriaceus*); besides, also some widely distributed subgenera do not occur there (i.e., *Limnocarabus, Morphocarabus, Tomocarabus*).

8.4. LOCALITY-BASED BIOGEOGRAPHY OF *CARABUS*

8.4.1. Outline of the 'local fauna' concept: an anastomosis between zoogeography and ecology

The classical methods of zoogeography use a number of criteria, such as species ranges, groups of species range limits ('isochores'), chorological types, level of endemism and some other features, to determine the distinctiveness of each regional fauna, and hence, to explain its origin and position within the zoogeographical division of the Globe. However, operating with regional faunas, many covering large regions up to continents, one has to become reconciled with the only possibility to look for explanations among factors acting at large scale, such as macroclimate or historical development of the particular area.

To change the focus of biogeography from large to local scale is the concept of 'local floras, faunas or biotas'. The idea of 'local fauna' originated from the concept of the 'concrete flora' developed by the Russian botanist A. Tolmachev (1931). The history and the basic principles of the concept are discussed in several papers (Yurtsev, 1975; Shelyag-Sosonko, 1980; Chernov, 1975, 1984; Penev & Turin, 1994; Penev, 1996, 1997). The main idea is that each list of species, whether of plants or animals, or both, occurring in all habitats around a geographical location can be regarded as a 'sample' representative of the flora, or fauna, or both, existing in the respective geographical region. The weakest point of the concept is how the area of each local flora/fauna is determined. For practical reasons it was proposed to use the area of a circle of radius 5-6 km, i.e. ca. 100 km^2 (Yurtsev, 1975). The rationale of the concept is described as follows: each species population exists locally and its presence at the respective location is determined by both local ecological and regional historical reasons. Hence, each 'local fauna' is an extraction of the regional species pool whose existence at a site is determined by the local habitat conditions and biotic interactions. Generally, the 'local flora/fauna' concept is a juncture between ecology and biogeography and allows quite a new approach in studying biogeographical phenomena (Penev, 1999).

8.4.2. The dataset: local faunas of European *Carabus*

The concept of 'local fauna' was used in biogeography of *Carabus* within the Russian Plain (Penev & Turin, 1994; Penev, 1996). To test the idea at the European scale, and keeping in mind that the local fauna concept requires as many localities as possible for analyses, pitfall data and inventories were sought to establish a dataset including a vast number of sites across Europe. However, it soon appeared that the existing data were less available than expected and also more or less concentrated in certain parts of Europe, mainly in its central and western regions. Data from some faunistic inventories substituted for data from pitfall trapping, with more or less the same shortcoming. Therefore, we realised that we could collect a suitable set only with the help of a number of carabidologists throughout the territory. Ideally, we should have a dataset of some hundreds of 'local faunas' from lowlands, hills and mountains, from coastal and inland localities equally spaced throughout Europe. Possibly, in a well coordinated international project such a set could be built within a few years, but from some countries neither data nor carabidologists who could provide reliable information could be found.

Our main goal was that the data should cover the whole territory and as many species as possible, including local endemics. Of course, as could be expected from the chorological analysis, variation and diversity are not equally distributed, and we should need more transects in the Mediterranean area than in the boreal parts. So, in fact, we could obtain sufficient data from the regions for which we need less and the other way around for the more complex fauna of the Mediterranean parts of Europe. Therefore, we choose a slightly different approach, using ecological transects instead of the ideal data. We obtained 100 sites in Europe, with real or hypothetical samples that included a maximum of habitat variation, thus providing a typical picture of the *Carabus* fauna in that area. They should describe a fauna situation that is not unrealistic, but not necessarily actually recorded either in one site or in one year. These transects were compiled from long-term ecological investigations, or from inventories in combination with catalogues, local maps, but most of them in combination with data from pitfall trapping in the same area. Most transects have relatively short distances; varying from a few hundred meters to a maximum of 25 km. Some long-distance transects (e.g. for W. Germany, C. Italy (Apennines) and S. Italy (Calabria), were split into two or more units. We believe that most of these transects are useful 'local faunas' suitable for the kind of eco-biogeographical analysis offered in this chapter. The map in Appendix 8.2 shows that, although the sites seem to be well-spread, for some areas, especially in Northern Sweden, Northern Finland, and Northern Russia, data are insufficient. However, the *Carabus* fauna is rather small in those areas, and the variation from locality to locality is slight.

The dataset of 100 local faunas is spread over Europe (Appendix 8.2, see also Fig. 8.9). Each local fauna is illustrated as lists of species occurring in habitats along local gradients (Appendix 8.2). This allowed not only some statistical analyses, but also gave a rather informative picture of the distribution of each species or species assemblages in various parts of Europe. Besides, from such a set of illustrations one obtains a clear idea about habitat preferences or habitat changes of a certain species across the territory of its range. Nearly 75 % of the local gradients are based on pitfall data or personal observations from sampling by hand, from a certain field locality. Most of the remaining are hypothetical transects, compiled from realistic data from the respective region, but for many samples gathered from several sources. Some transects were constructed from published data.

Altogether, the transects cover about 100 species, that is more than 75% of the European list. Although we miss especially a number of local endemics (mainly of the Alps, the Carpathians and some islands), we consider this dataset to be suitable for our goals, that is to carry out a biogeographical analysis on the basis of local samples, taken from a range of habitats existing around a geographical location, hence representative for the respective regional faunas.

Although the habitat types in a gradient may differ considerably in different parts of the territory, we classified them into 10 main groups. From Table 8.7 one can see how often these main groups are present in all transects together and how many records in the database (taken over all species and all transects) come from these habitat types.

In Europe, the *Carabus* fauna in general is particularly prominent in the different types of forests which comprise about 36% of the sites, generating 53% of the records (single species occurrences in a certain site) in the database. The other 47% of the records are rather evenly distributed over the other biotope groups.

In the dataset, for each site the highest, lowest and average altitude was added to the environmental variables. From this we learned that in about 75% of the transects, lowlands (up to 50 m) were investigated, and in 71% hills (50-500 m) were present. About 52% of the transects covered the montane belt (500-2000 m) and in 31% they reached the alpine zone (above 2000 m).

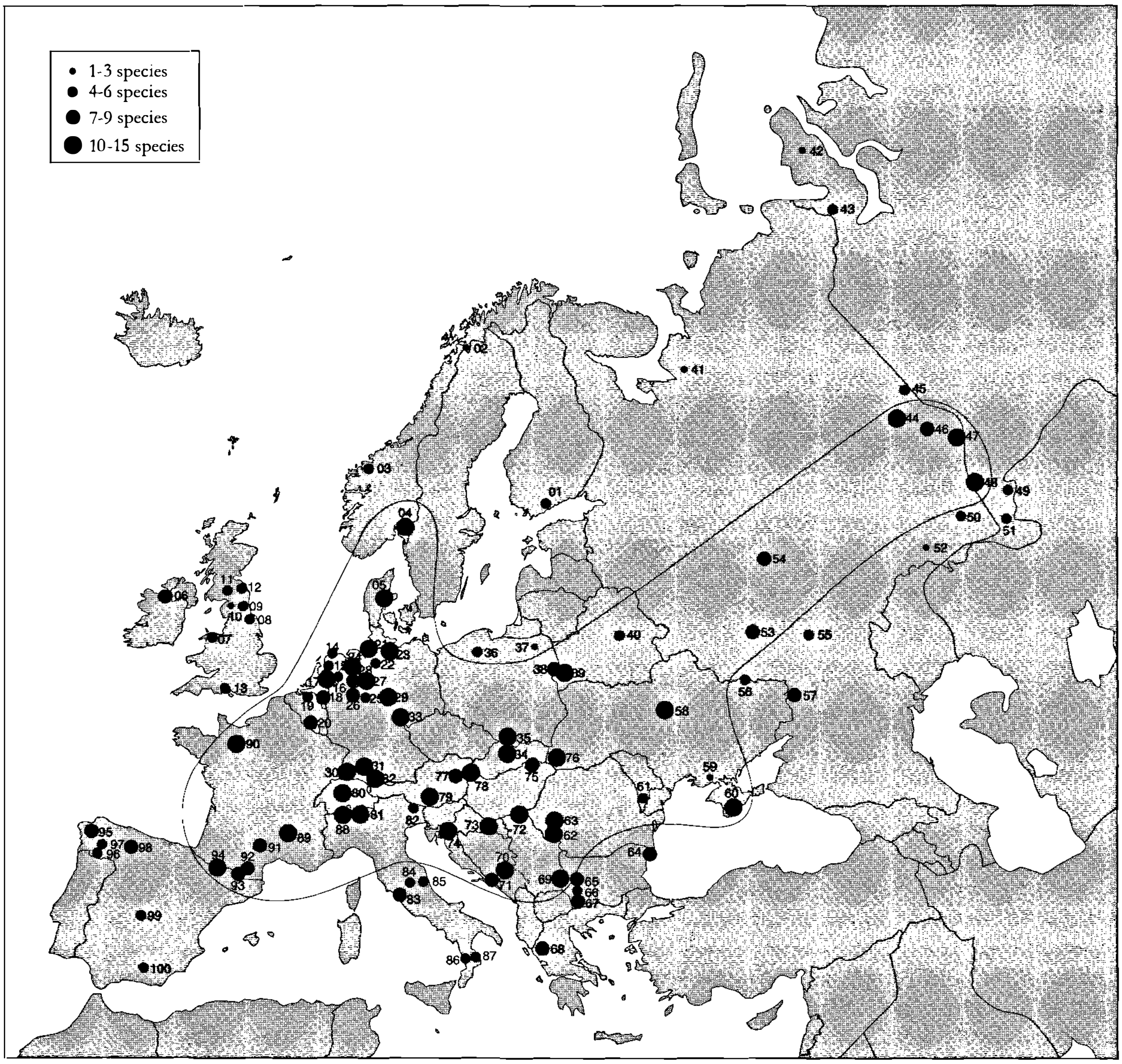


Fig. 8.9. Variation in local species diversity across Europe.
Numbers on the map refer to those of the respective sites on the map in Appendix 8.2. The line delimits areas with the highest local diversity of *Carabus.*

8.4.3. Variation in local species diversity

The local diversity of *Carabus* is mapped in Fig 8.9. and generally confirms the pattern already observed on the basis of regional faunas (section 3.1.). In spite of some variation in richness of local faunas, caused by local habitat conditions, number of habitats, area size etc., the local diversity shows a clear trend to be connected to the zone of mesophilous broad-leafed forests in the middle part of all Europe, where most localities are characterised by occurrence of 7 to 15 species.

The territories covered by the last two glaciations (Northern Europe and the northern part of the Russian Plain), seem to have not only impoverished regional faunas, but also a remarkable lower local diversity of *Carabus,* consisting of 2-5 species per locality. Another delimiting factor of primary importance for *Carabus* seems to be humidity. Despite the presence of different kinds of water basins and woodlands in several sites, situated in the southernmost regions of Europe (Mediterranean Basin and steppes of the Russian Plain), the local *Carabus* faunas there are always much less diverse than those of the neighbouring regions with a moderate climate (forest-steppe regions of Russia and the mountain regions of Southern Europe).

Local diversity decreases eastward from the Carpathian Mountains and western Ukraine to the central regions of Russia. The ranges of several species do not extend to the east of the above mentioned regions, though in *Carabus,*

Table 8.7. Distribution of the habitat types ('sampled' sites) within the dataset of local faunas.

	Biotope group	Representation	Records
1	Open water, wetlands, shores, bogs, moors	68 (13.8%)	203 (10.2%)
2	Open grasslands, extensive, limestone	75 (15.3%)	187 (9.2%)
3	Scrub, dwarf scrub, heath	53 (10.8%)	151 (7.5%)
4	Small-leafed forests	20 (4.2%)	15 (0.7%)
5	Mixed and deciduous forests	88 (17.9%)	841 (41.5%)
6	Coniferous forests	68 (13.8%)	222 (10.9%)
7	Clear cuttings, forest pastures, forest edges	25 (5.2%)	74 (3.7%)
8	Alpine and subalpine biotopes	27 (5.5%)	114 (5.6%)
9	Steppes and semi deserts	11 (2.2%)	57 (2.7%)
10	Agricultural, ruderal, urban, intensive	57 (11.0%)	162 (8.0%)

in contrast to many other groups (i.e. Penev, 1989; Esjunin *et al.*, 1993; Golovatch, 1992), the impoverishment of western species is rather well compensated by the appearance of several Siberian species or local endemics, derivations of Siberian lineages (i.e. *Morphocarabus*). Further to the east, the diversity on the western slopes of the Urals seems to increase again. This pattern coincides with the existing belief about the almost complete devastating of the biota of central European Russia during the last two glaciations, especially due to the maximum phase of last, Upper Valdai (=Würm) glaciation, ca. 20,000 years ago (Grichuk, 1989; Esjunin *et al.*, 1993). The biota connected to the broad-leafed forests recolonised the Plain from two main sources, the Carpathians and Uralian refuges and from secondary remnant refuges in the south of the Russian Plain. This phenomenon could be a possible explanation for the higher diversity of *Carabus* in Transcarpathian and Cisuralian areas.

8.4.4. Types of species distribution across habitat and space

The species-by-site matrix of all 100 local faunas yielded some interpretable phenomena in the distribution of different species. About 15 % of all species occur in more than 20 sites and are considered as species which are more or less widely distributed in certain subregions of Europe or through the whole continent (Tab. 8.8). All other species are present in less than 15 sites and about the half of the species on the list are recorded from 1-2 sites.

As some bias would certainly be caused by the uneven distribution of the number of local faunas across regions, we concentrate mostly on the types of distribution of the most common species.

For the classification of species based on their distribution among the 100 sites a divisive clustering procedure performed by Two-way Indicator Species Analysis (TWINSPAN) (Hill, 1979a) was used. The resulting matrix, the so called 'Petri table' or 'Petri matrix' gives a good overall impression about the geographical distribution and commonness of each species.

TWINSPAN classifies the species into 'end groups' which reflect the main chorological types of species' ranges, based however in this case only on their within-European distribution. The following main groups, ranked approximately according to their consecutive separations by TWINSPAN, are outlined among the European Carabus species:

(1) Iberian species – several representatives of the subgenera *Oreocarabus, Ctenocarabus, Mesocarabus* and some others.

(2) Boreal Siberian species, from the easternmost regions of European Russia, the Urals and the adjacent regions of Siberia – i.e., *C. henningi, C. odoratus, C. loschnikovii, C. aeruginosus, C. canaliculatus, C. truncaticollis* and others.

(3) European polyzonal species widely distributed from north to south in virtually all regions of Europe, except for the southernmost areas, however rare or absent in the easternmost regions of Europe – *C. violaceus, C. nemoralis.*

(4) Paneuropean polyzonal species widely distributed from north to south in virtually all regions of the continent and adjacent territories – *C. granulatus, C. clatratus.*

(5) European boreal species widely distributed in Northern, Western and Central Europe, some of them ranging in the east to central Russia and/or Ural – *C. problematicus, C. glabratus, C. arvensis, C. nitens.*

(6) European species, connected to the zone of broadleafed forests, widely distributed in the middle and south-

Table 8.8. A list of species, most widely distributed in Europe.

Species	Number of presences in the 100 local faunas
Species widely distributed in most parts of Europe	
C. granulatus	63
C. convexus	59
C. violaceus	57
C. coriaceus	49
C. cancellatus	48
C. nemoralis	46
Species widely distributed in certain regions of Europe	
C. problematicus	39
C. glabratus	38
C. arvensis	36
C. intricatus	28
C. auronitens	25
C. hortensis	25
C. clatratus	24
C. nitens	20

ern zones of Europe, however rare or absent from the northernmost regions – *C. cancellatus, C. convexus, C. coriaceus, C. hortensis.*

(7) Southeast European species, occurring on the Balkans, Pannonia and Carpathians, some of them also in southwestern parts of European Russia and/or Italy – *C. montivagus, C. gigas, C. ulrichii* (also in Central Europe), *C. scabriusculus, C. cavernosus.* Several species endemic to the Apennine peninsula, the Carpathians and/or the Balkans could also be included here.

(8) Central European species, connected to the zone of broad-leafed forests, widely distributed in Western and Central Europe – *C. auronitens, C. auratus, C. monilis, C. irregularis,* as well some endemics with restricted distribution within the region.

(9) Eastern European forest-steppe species with main distribution in the middle regions of the Russian Plain – mainly *Morphocarabus* and *Trachycarabus* (*C. haeres, C. errans, C. estreicheri, C. excellens*), however also *C. stscheglowi, C. marginalis, C. bessarabicus* and some others.

In short, the TWINSPAN classification of local faunas reinforced again the conclusion already made on the basis of analysis of regional faunas and their taxonomic and zoogeographical structure: two main types of *Carabus* faunas dominate nowadays in Europe: *Euro-Siberian Boreal* and *Euro-Mediterranean* (see section 8.3). Besides, it appeared that the use of local faunas may lead to an unprejudiced and rather detailed classification of the species' distributions, based not only on the general area of distribution of each species, but also on the frequency of occurence of each species in local faunas throughout its range. For instance, many species usually termed as 'widely distributed in Europe and Siberia' and classified into chorotypes like 'Palaearctic' or 'Euro-Siberian', have in fact rather different distributions within those territories. Such differences are detected by TWINSPAN, thus allowing a more precise classification of species ranges, based on both their geographical and present-day ecological (latitudinal and longitudinal) characteristics.

8.4.5. Geographical variation in local species compositions

To evaluate similarity and hierarchical classification of the species' compositions the same TWINSPAN procedure described in the previous section has been used. All 100 local faunas have been clustered consequently yielding in this way the main trends in similarity/dissimilarity between faunas. The results of classification are represented in Fig. 8.10 and can be described as follows:

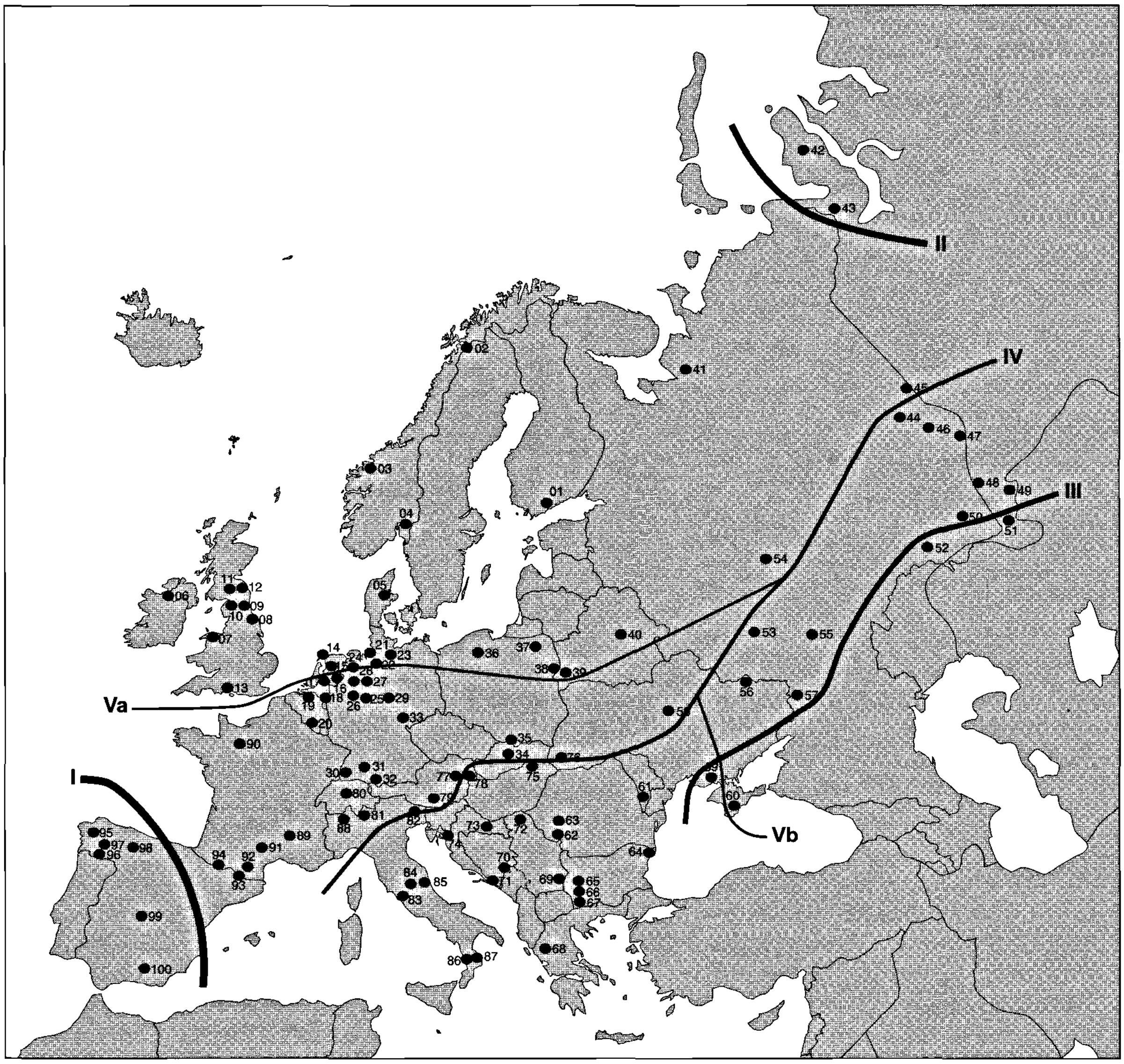


Fig. 8.10. A map illustrating the divisive subsequent (I to V) classification of the 100 local faunas yielded by TWINSPAN (see explanations in the text).

1. The first TWINSPAN division distinguished clearly all Iberian faunas consisting of a good number of endemic species, such as *C. amplipennis, C. melancholicus, C. steuartii, C. deyrollei, C. guadarramus, C. ghilianii* and some others. Interestingly, in all six Iberian local faunas, only two non-endemic species are represented by two records each, namely *C. nemoralis* and *C. violaceus*. Thus, even at local level, the Iberian faunas seem to have most distinguished species composition in Europe, which is reinforced by the generally very distinct species pool of the whole Iberian Peninsula. Inside the group of Iberian faunas, those from Galicia are further distinguished from those from Central and South Spain.
2. The next, second, division separates two high-latitude faunas from the adjacent regions of Siberia (Yamal Peninsula) composed almost entirely by East European-Siberian species (*C. henningi, C. odoratus, C. truncaticollis*).
3. The third division separates three faunas of the southernmost steppe zone of European Russia, namely Askania Nova Nature Reserve and two sites in the Orenburg province. All three faunas are poor in species (3-4 species) but very characteristic, dominated by typical steppe inhabitants like *C. bessarabicus, C. hungaricus,* and *C. cribellatus*, however at the same time including also one widely distributed species (*C. clatratus*).
4. After subtracting the most specific faunas, such as the Iberian, Siberian and those of southern steppes, the rest of sites are further separated into two major groups which could be named as *Southeastern – Eastern European* (33 sites situated in Italy, Balkan Peninsula, some

sites in Hungary and Lower Austria, and several sites in the middle and southern parts of the Russian Plain) and *Northern – Central European* (56 sites located on British Isles, Northern and Central Europe including as well some sites in the Alps, Arkhangelsk region in Northern Russia and Baseg Mountain, a high-altitude site in the Middle Urals). The *Southeastern – Eastern European* group is marked by TWINSPAN by the presence of the indicator species *C. convexus* and some preferential species distributed only or mostly in those regions. Besides numerous species endemic to Italy, Balkans or the Russian Plain, which will not be listed here, as preferentials for the region *C. estreicheri, C. gigas, C. montivagus, C. stscheglowi, C. ulrichii* are outlined. The opposite group of *Northern – Central European* sites is characterised by the indicator species *C. problematicus, C. nemoralis,* and *C. arvensis* and the preferentials *C. auratus, C. auronitens, C. glabratus,* and *C. nitens.* The group of species classified as non-preferentials, that is without clear preferences to neither of the two regions, is composed by well-known, more or less widely distributed species, such as *C. cancellatus, C. clatratus, C. coriaceus, C. granulatus, C. hortensis* and *C. violaceus.*

5. Further, the *Northern – Central European* local faunas are divided into groups which could be named as (1) *Northern European* (26 sites situated on the British Isles, in Fennoscandia, also most sites in the Netherlands, Northern Germany, Poland and Byelorussia) and (2) *Central European* including 30 sites, among them most locations of Germany, France, Northern Italy, Switzerland, Slovakia eastwards ending to Dnieper River (Kanev Nature Reserve). Indicator species of the *Northern European* faunas is *C. nitens*, and for the *Central European* faunas are *C. auratus, C. auronitens, C. convexus, C. monilis, C. coriaceus*, and *C. intricatus.* Species irrelevant regarding their distribution in both regions appear to be *C. arvensis, C. cancellatus, C. glabratus, C. granulatus, C. hortensis, C. nemoralis, C. problematicus,* and *C. violaceus.*
6. The *Southeastern – Eastern European* faunas are separated in groups which can be outlined as *Southeastern European* (22 sites, including all locations on the Balkans, in Romania, Southern Moldova, Hungary, Lower Austria (Leithagebirge) and Italy with exception of a site in the highest Northwest (Piemonte). Indicator and preferential species of this group of sites are *C. intricatus, C. coriaceus, C. montivagus, C. gigas, C. ulrichii, C. cavernosus, C. scabriusculus.* The opposite, *Eastern European* (*Russian*) group consists of sites situated on the Russian Plain eastwards of Dnieper ranging to the Ural Mts. The indicator and preferential species for the Russian Plain are *C. estreicheri, C. stscheglowi, C. haeres, C. marginalis, C. schoenherri.* As non-preferentials, that is species more or less equally present in both regions appear *C. cancellatus, C. convexus,* and *C. granulatus.*
7. Further divisions of the groups are of less interest to the aims of the present analysis. We note, however some remarkable features, for instance that at the last, sixth level of division, the *Northern European* faunas are not divided in a way which implies a meaningful explanation. Obviously, within the regional species pool of Northern Europe, species compositions are affected by local or by purely stochastic factors rather than zonal or geographical reasons. Within the *Central European* group of faunas, the last division indicates some specifics of the sites in Southern France characterized by presence of species like *C. cristoforii, C. pyrenaeus* and *C. splendens*, and at the same time absence in those 4 sites of some widely distributed species like *C. glabratus, C. arvensis, C. coriaceus*, and *C. hortensis.* As one may expect, the Southeastern European faunas, are divided into Apennine and Balkan faunas, each characterised by its own set of endemic and subendemic species. It is remarkable that the site Prescudin in Northeastern Italy (Friuli Venezia-Giulia) is grouped together with the Balkan sites, a fact probably reflecting the natural geographical division between the Balkan and Apennine peninsulas which passes along the river Isonzo in Friuli Venezia-Giulia. The rest of the Apennine sites (5) are marked by some absences of common European species, such as *C. cancellatus, C. glabratus, C. hortensis* and *C. intricatus.*
8. TWINSPAN analyses indicate some conclusions of a more general character. Obviously, the distribution of *Carabus,* known as a genus rich of endemic and subendemic species even in regions where endemics in other groups are absent (i.e. Russian Plain), is largely affected by historical processes, which at European scale seem to prevail over the present-day ecological factors. The consequent divisive splitting of the local faunas marked some major groups of faunas, whose distinctiveness could hardly be explained by ecological factors. These groups, let us call them faunal types, are to be distinguished as follows:

(1) The most distinctive fauna appears to be the *Iberian,* characterised by the highest proportion of endemics and absence of many widely distributed European species, present in almost all of the other European subregions.
(2) Two other main faunal types can be outlined within the European continent: (a) *Euroboreocentral* dominating over Western, Central and Northern Europe and (b) *Eurorientomeridional*, consisting of the faunas of the Southeastern Europe (Pannonian-Carpathian region, Apennine and Balkan Peninsulas) and central and southern parts of European Russia.

The present classification into major faunal types, produced from an analysis of local faunas, fully confirms our earlier conclusion (see section 8.3.1.) about the relict character of the fauna of the Iberian Peninsula, the migratory character of the faunas of Northern and Central Europe, consisting of mainly phylogenetically younger, European and Euro-Siberian elements, and the more distinct and ancient character of the South European faunas, consisting of both Mediterranean and Euro-Mediterranean elements *sensu lattissimo* and migrants from the north. Penev (1996) showed that the first DCA ordination axis of Eastern European *Carabus* faunas correlates significantly with the distance from the front border of the last Valdai (= Würm) glaciation. The present analysis leads to similar conclusions. The grouping of local faunas into Northern and Central European on one side, and Southeastern European and South Russian on the other side, follows roughly the line separating territories covered by an ice cap during the last glaciation period. This line called in Western and Central Europe a 'Holdhaus line', is illustrated in section 6.6.2 of Chapter 6. The situation in Eastern Europe seems to be similar and a kind of 'prolongation' of this line passes through the middle regions of European Russia, separating in this way the boreal and subboreal faunas dominating in the northern and central regions of the Russian Plain and the faunas, connected to forest-steppe and steppe zones of European Russia.

Obviously, though one may call the local habitat gradients analysed here as purely ecological constructions, the variation in their species composition over geographical space implies explanations which could be of primary interest to historical zoogeography as well (see section 8.5).

8.4.6. Gradient analysis

The dataset of 100 local faunas may be considered a representation of the European *Carabus* fauna. However, Europe is very diverse in climatic and historical conditions, local habitat characteristics and above all, covers a territory ranging over several thousands of kilometers both latitudinally and longitudinally. The possible explanation of the patterns of spatial variation in local faunas cannot be simple and may be due to an unpredictable number of factors.

Let us imagine how many influences are to be encountered on the possible presence of a species at a site, starting from the past and ending with the present-day regional and local conditions. Assuming also some biotic interactions influencing the presence of a species at a site, makes the patterns even more complicated.

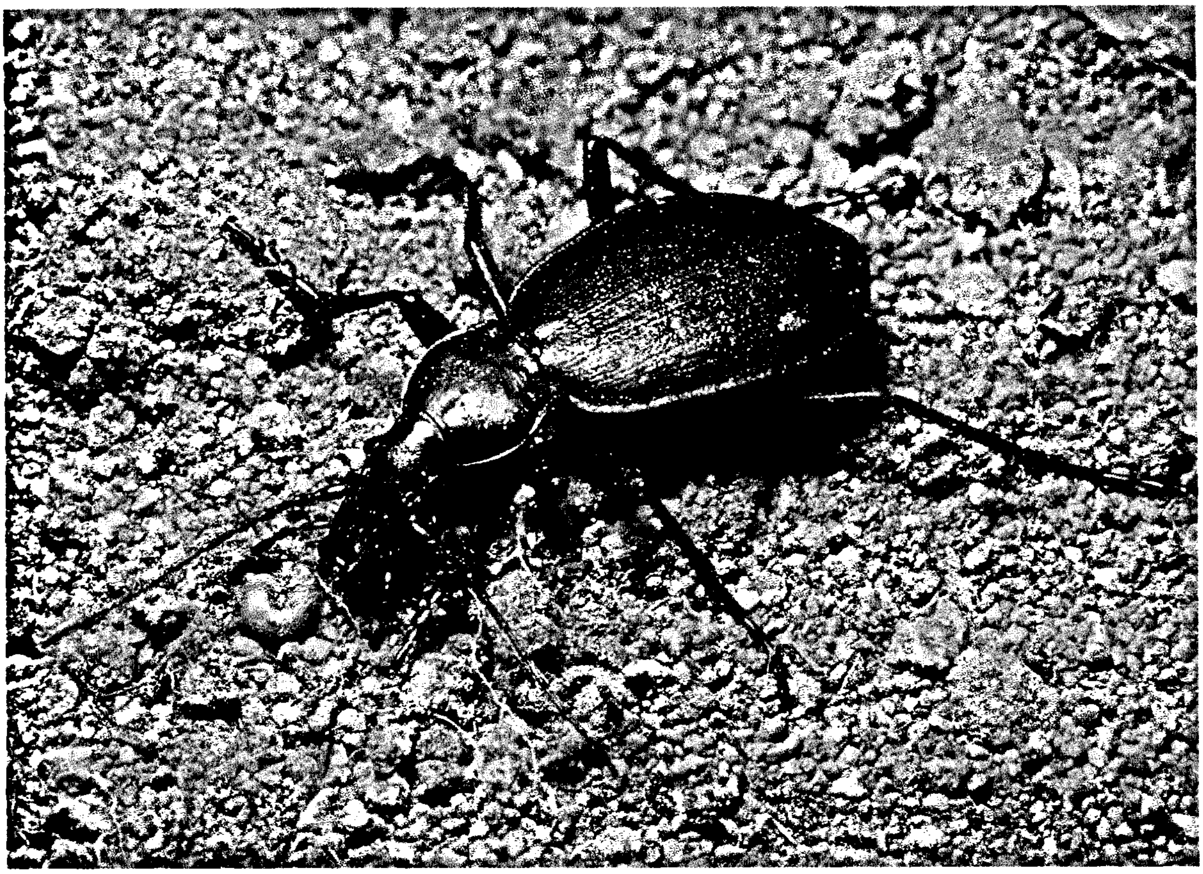
An attempt was made to reveal at least some main trends in spatial variation in local faunas of *Carabus* over the whole European continent by using a gradient analysis performed by the DCA (Detrended Correspondence Analysis) technique of CANOCO (Ter Braak, 1988). The DCA analysis was performed at several stages with consecutive exclusion of faunas which largely differed in species compositions and in this way affected the overall pattern of variation. Several environmental factors encountered at each location were tested with respect to their correlation with the main ordination axes. The rationale of such tests lies in the logic of the gradient analysis presuming that those factors which show the highest correlation with an ordination axis have possibly the highest explanatory value for the underlying trend in variation of the faunas along the same axis (Ter Braak & Prentice, 1988; Ter Braak, 1988). The following environmental factors have been encountered at each site and were tested with the DCA technique:

(1) Presence of (a) water reservoirs (rivers, lakes, shores swamps); (b) open grassland; (c) shrubs; (d) birch and poplar forests; (e) deciduous and mixed forests; (f) coniferous forests; (g) clear cuttings and open areas; (h) subalpine and alpine biotopes; (i) steppes and semi-deserts; (j) agricultural, ruderal, intensively exploited land.
(2) Presence of (a) lowlands; (b) hills; (c) mountains; (d) high mountains (alpine).
(3) Geographical longitude
(4) Geographical latitude
(5) Habitat diversity measured as number of habitats at a site
(6) Altitude range of a site

The first DCA ordination (eigenvalue 0.917) (Fig. 8.11) was much affected by the isolated position of the Iberian faunas. The second axis (eigenvalue 0.525) clearly demonstrated a gradient from faunas of the purely boreal type (both sides T-42 and T-43 situated in the Yamal Peninsula in the polar region of West Siberia and T-45, a high-altitude site in the Middle Urals) to the faunas of 'southernmost' type, located in the southern regions of the Russian steppes and Crimea.

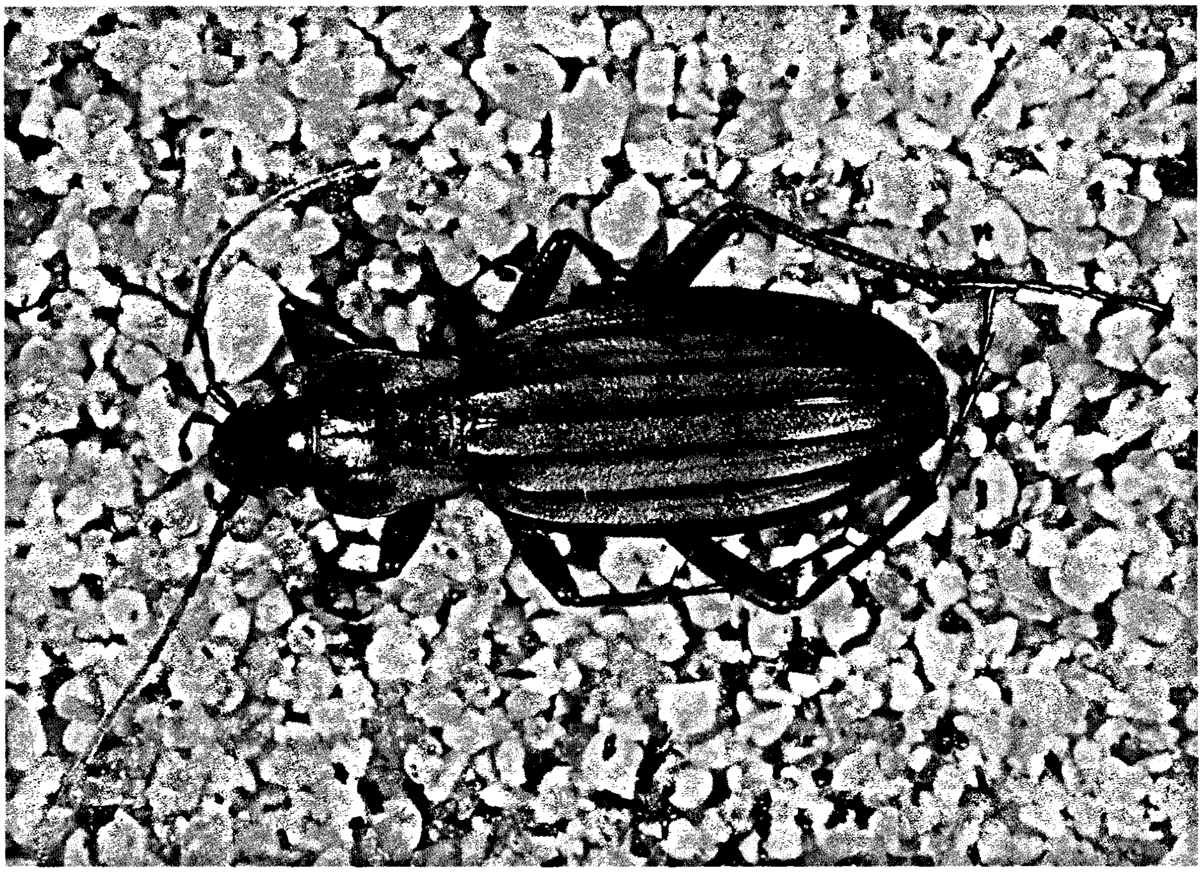
Thus, the first axis can be called a 'regional historical' gradient caused by the distinctiveness of the Iberian fauna. The second axis is of a more complex character and indicates a trend in variation in species composition from faunas situated in Southern Russia and Southeastern Europe to the boreal and subboreal faunas of the Urals Mts. The variety in local species compositions in Eastern Europe is great when comparing northern and southern faunas due to the marked zonation of the Russian Plain (Penev & Turin, 1994), and this pattern strongly influences the second axis, termed as a more or less 'zonal' gradient. The present pattern confirms an earlier conclusion made by Penev (1996) on the basis of study of local faunas of Eastern European *Carabus*. Doubtless, both axes are markedly affected by the species composition of the 'outsiders', i.e. Iberian, Siberian and South Russian steppe sites.

In the next step of the analysis (Fig. 8.12), the 6 Iberian sites have been omitted from the analysis. The DCA scattergram reinforced the isolated position of the Siberian



C. cychroides
Baudi di Selve
Piemonte,
Val Chisone.
Cotte delle Finestre.
Italy.
Photo by
A. Casale &
G. Delitala.

C. intricatus
Linnaeus
Italy,
Maritime Alps
(M. Vaccia).
Photo by
A. Vigna Taglianti.



C. galicianus Gory
Spain, Sierra de Invernadeiro, prov Orense (Galicia). Photo by J. Serrano.

C. nitens Linnaeus
Lüneburger Heide, Germany. Photo by P. Rasch & Th. Assamann.

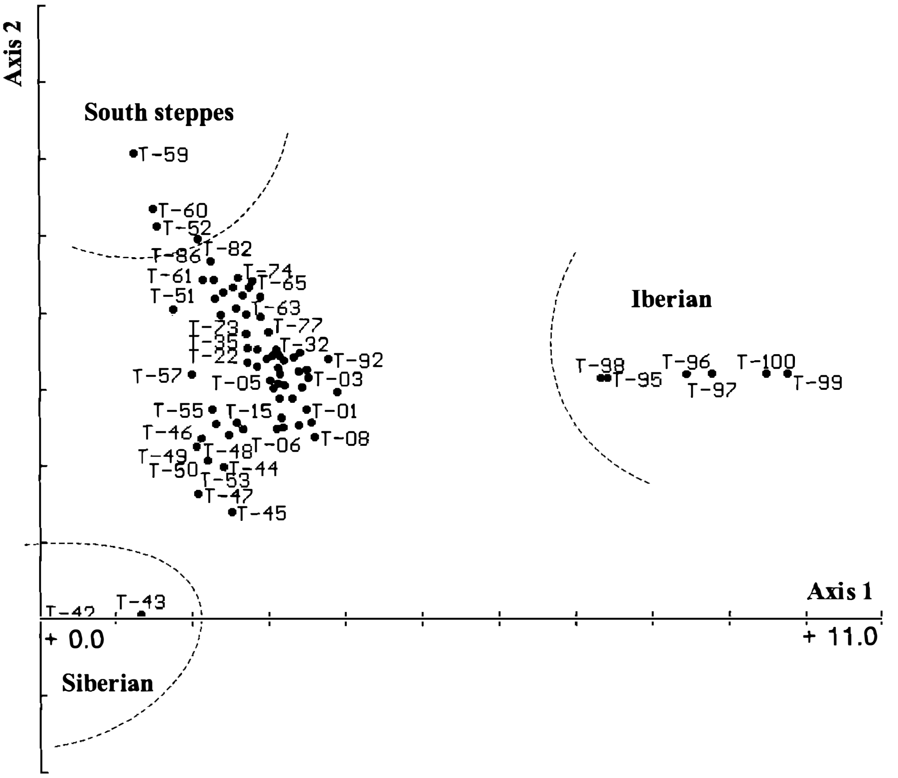


Fig. 8.11. DCA ordination of all 100 local faunas.
Numbers of local faunas refer to those in Appendix 8.2 (explanation: see text).

faunas, which dominated the first axis (eigenvalue 0.711) forming again the above described gradient from the boreal and subboreal faunas of the Urals to those of Southeastern Europe. The second DCA axis (eigenvalue 0.490) isolated the faunas of southern steppes and indicated some similarity of the local faunas of Southeastern Europe and Southern Russia as opposed to the faunas of Northern and Central Europe (see section. 8.4.5).

After elimination of the outliers from both the Iberian Peninsula and Siberia (Fig. 8.13), the patterns in variation seem to be less affected by outstanding species compositions and some general 'types of faunas' delimited. Besides, it seems that the ranking of faunas on the axes follow some general trends directed from south to north and from west to east. For instance, the first axis is termed 'longitudinal' and trends from Eastern European to Western and North European faunas. In the intermediate position between both ends, the Central and Southeastern European faunas are grouped. Besides, the first axis clearly demonstrates the very significant role of the Dnieper Valley as a zoogeographical barrier, a phenomenon established previously on the basis of many other groups of plants and animals (see Golovatch, 1984; Penev, 1989; Esjunin *et al*, 1993; Penev & Turin, 1994, see also section 8.3.4).

The second axis starts from the sites situated in Italy and the Balkans and extends through sites in southern regions of Central Europe (Slovakia, Hungary, Austria, South Poland) to the faunas of Northern Europe. The three high-altitude sites (T-92-94) situated in the French Pyrenees are classified in the 'northern' group, due to presence of some boreal and Paneuropean species, such as *C. cancellatus, C. nemoralis, C. problematicus, C. convexus* and *C. violaceus*.

The third DCA axis (Fig. 8.14) has also a meaningful explanation, showing the separation between the Balkan and Apennine faunas.

The subsequent ordinations included also testing of the correlations between a set of environmental variables, listed above. The set of environmental variables reflects only the present-day ecological conditions and the geographical position of the sites. None of the analyses showed a significant correlation of the ordination axes to any of the environmental variables. We are only able to draw some general conclusions on the basis of the highest values of the species-environment correlation axes. At all stages of the analyses, the highest values of correlation were shown by the longitude; that is the main trend in variation in species composition seems to be somewhat stronger in longitudinal than in latitudinal direction. Also relatively higher values were revealed for the presence of deciduous and mixed forests, a fact generally correlated on the European continent to longitude. Another set of factors of relatively high-

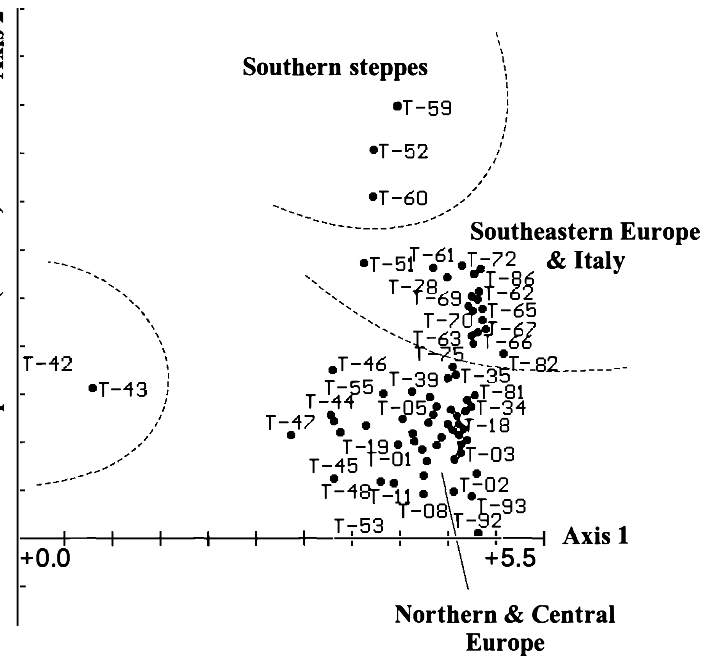


Fig. 8.12. DCA ordination of 94 local faunas (the sites of the Iberian Peninsula are excluded from the analysis). Numbers of the local faunas refer to those in Appendix 8.2 (explanation: see text).

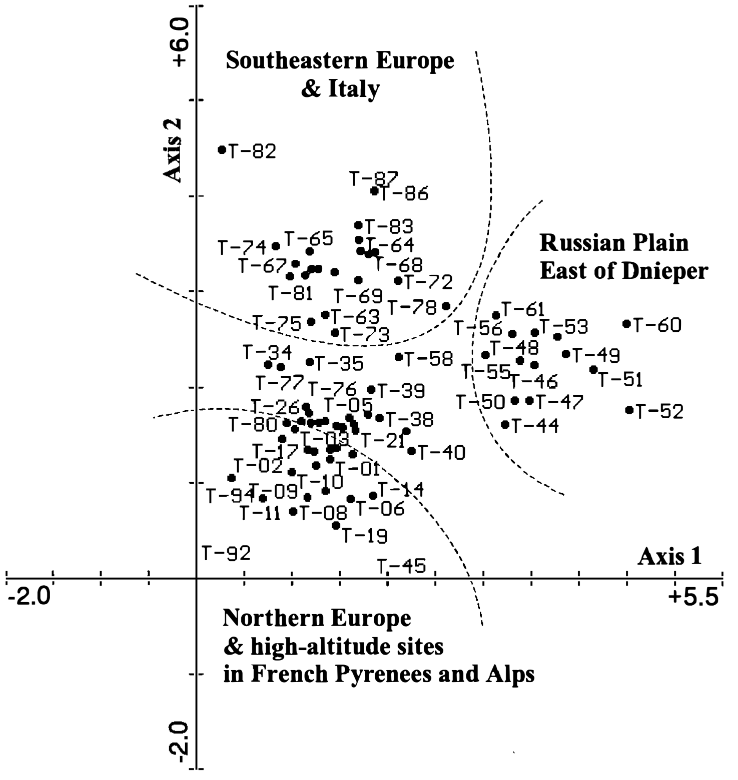


Fig. 8.13. DCA ordination of 92 local faunas (the sites of the Iberian Peninsula and Urals are excluded from the analysis). Numbers of the local faunas refer to those in Appendix 8.2 (explanation: see text).

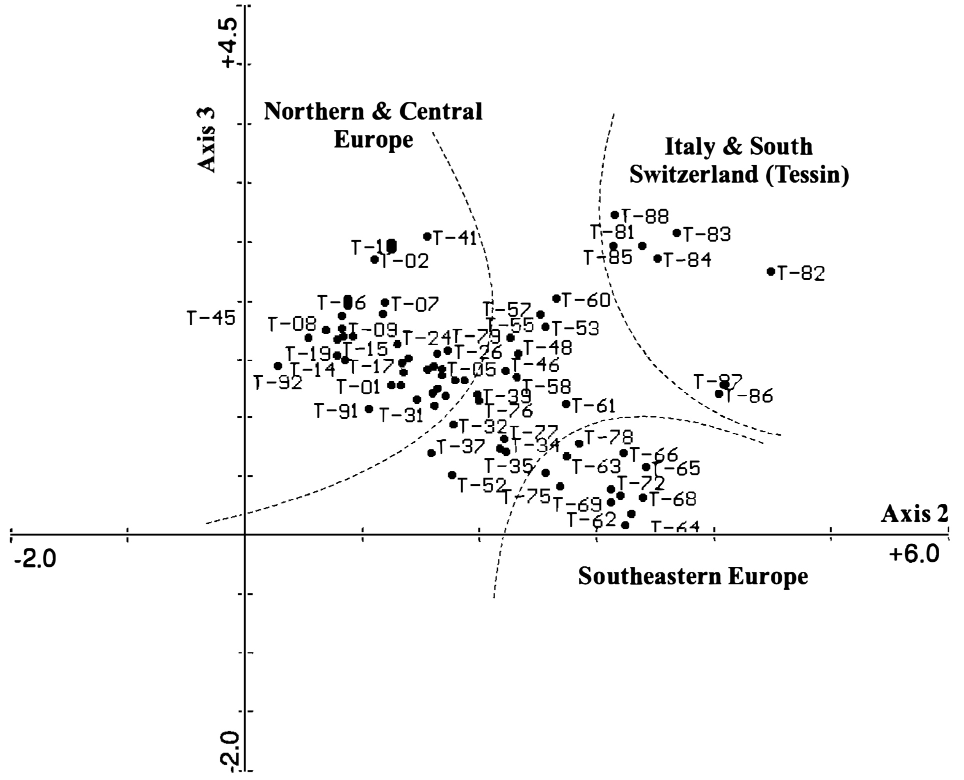


Fig. 8.14. DCA ordination of 92 local faunas (the sites of the Iberian Peninsula and Urals are excluded from the analysis), Axes 2 and 3.

Numbers of the local faunas refer to those in Appendix 8.2 (explanation: see text).

er values of correlation in comparison to those of the other variables seems to be the presence of mountains and alpine habitats, a factor clearly affecting local faunas towards their 'borealisation'.

Generally speaking, the ordination results suggest a complicated explanation of the variation at continental scale and therefore need special comments:

(1) Absence of any correlation between axes suggests two possible explanations, i.e. (*i*) most significant factors have not been encountered, and (*ii*) a high complexity of the patterns of variation at a so large, continental scale, which does not allow a single factor to be used for explanation of the general trends.
(2) Obviously, the key factor affecting variation at continental scale can be identified as 'historical'. It is difficult, if not impossible, to formalize such a factor to be used in statistical procedures, however it is quite clear that the isolated position of the Iberian Peninsula and its very distinct fauna affects the strongest trend in variation at the European scale.
(3) The more general impression from the ordination results reinforces the conclusions made from the TWINSPAN classification, i.e. the main reason for the faunal changes across space at the European scale are regional differences caused by historical processes, especially isolation, consequent allopatric speciation *in situ* and postglacial colonisation. The main faunal types of *Carabus*, identified with different methods in the previous sections of this chapter, namely the Iberian, North-Central European, Southeastern European and Eastern European have been confirmed by the ordination of local faunas as well. The presence of these faunal types, revealed by an unambiguous analysis of 100 local species compositions, reinforced the theory of De Lattin (1967) about the main distribution centers of the European biota from refugia during the glaciation periods.
(4) Another key factor seems to be macroclimate. After eliminating the most distinct faunas from the analysis, one can imply clear trends of variation following the present-day natural zonation.
(5) The local habitat conditions do not seem to affect much the variation at larger geographical scale, or at least their effect cannot be identified easily with statistical methods at such a scale. The regional differences caused mostly by historical processes, followed by the impact of macroclimate on the present-day distribution of the biota, determine the composition of each regional fauna, from which local habitat conditions and possible biotic interactions 'filter' the local species assemblages and faunas.

(6) The present analysis showed once more again, that local faunas can successfully be used for answering biogeographical questions. Being the only realistic connection between large-scale and local patterns and processes, local faunas offer us the unique opportunity to approach the old complicated question 'Why and how faunal compositions differ across space?' from the opposite side, that is, from the viewpoint that each local fauna represents an unprejudiced local reflection of the regional faunal composition and structure.

8.5. BIOGEOGRAPHICAL INSIGHTS INTO THE PHYLOGENY AND FAUNOGENESIS OF *CARABUS*

8.5.1. Classification, phylogeny, and historical biogeography: an unfinished story

An opinion, currently accepted in biogeographical practice, evident in Jeannel's writings that were published during the middle years of the preceding century, and formalized in more recent contributions (Wiley, 1981), is that to be reliable, any biogeographical hypothesis about a taxon must be based on a sound taxonomic revision, classification, and phylogenetic analysis of the taxon itself. Furthermore, the reconstructed phylogeny should be derived from the study of all species that belong to a homogeneous lineage, at the global scale (Casale, 1988). This kind of work could also provide and test area cladograms in a well defined area.

However, in spite of the fact that biogeographers have available today many and different principles, methods, approaches and techniques (Aa. Vv., 1981; Crisci, 2001), many of which are accessible in computerized programmes (cladistic analysis; absolute and relative dating of fossil remains; careful paleogeographic, paleoclimatic and paleoenvironmental reconstructions of scenarios in the remote past; and molecular data), the goal of reconstructing both evolutionary pathways and origins of distribution is not easy to reach. Reconstructing the phylogeny of Caraboidea is a work-in-progress (Ball *et al.*, 1998), and origins, relationships, and distributions in different continents of the extant tribes and subtribes of the 'supertribe Carabitae' (Carabini including the genus *Carabus*, only), Calosomatini (including Haplothoracina), Cychrini, Pamborini and Ceroglossini), re-examined recently with the support of molecular data, are subjects of friendly dispute. Such dispute is derived from different phylogenetic and biogeographic hypotheses (Erwin, 1979; Prüser & Mossakowski, 1998; see also Chapter 7. *Phylogeny*).

Similarly, general agreement has yet to be reached about the evolutionary history of the genus *Carabus*, with the only consensus so far available, being that the genus is monophyletic, with a Holarctic distribution at present and with *Calosoma* (*sensu latissimo*, i.e., Calosomatini of authors) as adelphotaxon. In all other aspects, the studies on *Carabus* are characterised by different approaches to morphological evidence, imaginal and pre-imaginal external features, structures of male genitalia, and molecular data, different classifications and phylogenetic reconstructions (see, for a review, Chapters 3. *Key to the adults*, and 7. *Phylogeny*). In spite of such uncertainty, and in the light of what is known about chorological and ecological aspects of the taxa included in *Carabus*, and about geological and climatic history, we offer some thoughts about the geographical history of the European species of *Carabus*.

8.5.2. The scene: Europe and its evolution from the Permian Period to the present

Europe, the western appendage of the Euro-Asian continent, is not a biogeographic unit in the sense that its boundaries (north-eastern (Urals), southeastern (Caucasus, Bosporus), and western (Gibraltar strait)) are not insuperable biogeographical barriers. Only some parts of Europe are biogeographical units: Mediterranean islands or peninsulas, for instance, or mountain chains, such as the Alps, Carpathians, and Pyrenees.

In the last several millenia, the boundaries between the different states of Europe have been dictated by political factors and not by geological or biological considerations. Thus Europe is defined by convention, and this fact does not make it easy to treat the geographical history of the European segment of a Holarctic taxon, such as the genus *Carabus*.

The present shape of Europe is the result of a very long and complex process as reflected by evidence derived from geology, and study of paleogeography and paleoclimate. During the opening of the Neotethys Sea, and the drifting of the Cimmerian continents since the Early Permian, Apulia (with the autochthonous Ionian units from Dinarides, Hellenides and Taurides), represented the western end of the Cimmerian continent. In the Triassic Period, 180 mybp, the Alboran, Adriatic and the Irano-Anatolian plates were parts of Gondwanaland, and became parts of the southern coast of the Tethyan Sea, and hence of southern Europe, with their migrations. In the Eocene Epoch, the formation of the Atlantic basin interrupted connections between Europe and North America. From Late Cretaceous time (70 mybp) to the Miocene Epoch (15 mybp), further continental drifting of the African plate northward, closed the Tethyan Sea, between Gondwanaland and Laurasia, and formed the Palaeo-Mediterranean basin (Barron *et al.*, 1981; Smith *et al.*, 1981; Torsvik & Smethurst, 1994). Large continental fragments or microplates (corresponding, in the opinions of different authors, to parts of present Greece, Central Anatolia, Central Iran and Afghanistan) were drifting, which favoured exchanges and immigrations – at least for the surfaces which were above sea level – of floras and faunas.

However, geologists have not achieved a general consensus about sizes, features and limits of these continental sub-units that contributed to the formation of Southern Europe, North-Africa and the Near East. Rage (1995), for instance, illustrates a series of fully separated fragments in late Cretaceous time (from West to East, respectively: Kabylies, the Calabro-Sicilian massif, Alboran, Apulia, and the Dinaro-Hellenic, Anatolian and Iranian plates), that partially fused and increased in size later, in Mid Eocene time. Some authors hypothesize that, in the Mesozoic Era, three contiguous subcontinents were present north of the African plate: Apulia, Rhodopes and Anatolia. Conversely, in the opinions of Dercourt *et al.* (1986), in the East Mesozoic Tethys, between the African plate and Eurasia, an extensive Greek-Anatolian continent was present, which coincides with the South Aegean continent illustrated in the classic paper of Furon (1950).

We believe that ancestors of the present *Carabus* lineages were already present in this remote past, at least in the Angarian area: in fact, highly evolved, harpaloid carabids are known from Late Cretaceous deposits of Russia (Ponomarenko, 1977). Such lineages must have evolved after the generally more primitive carabite lineage had become established. Nonetheless, the occurrence in Europe of *Carabus* species in the Mesozoic Era (*Carabus winkleri* Weyenberg, 1869, described from Upper Jurassic deposits of Germany), is rightly questioned by Deuve (1994).

Therefore, the most informative paleogeographic and paleoclimatic events must be sought in the Cenozoic Era, to hypothesize the origin and present composition of the *Carabus* fauna of Europe.

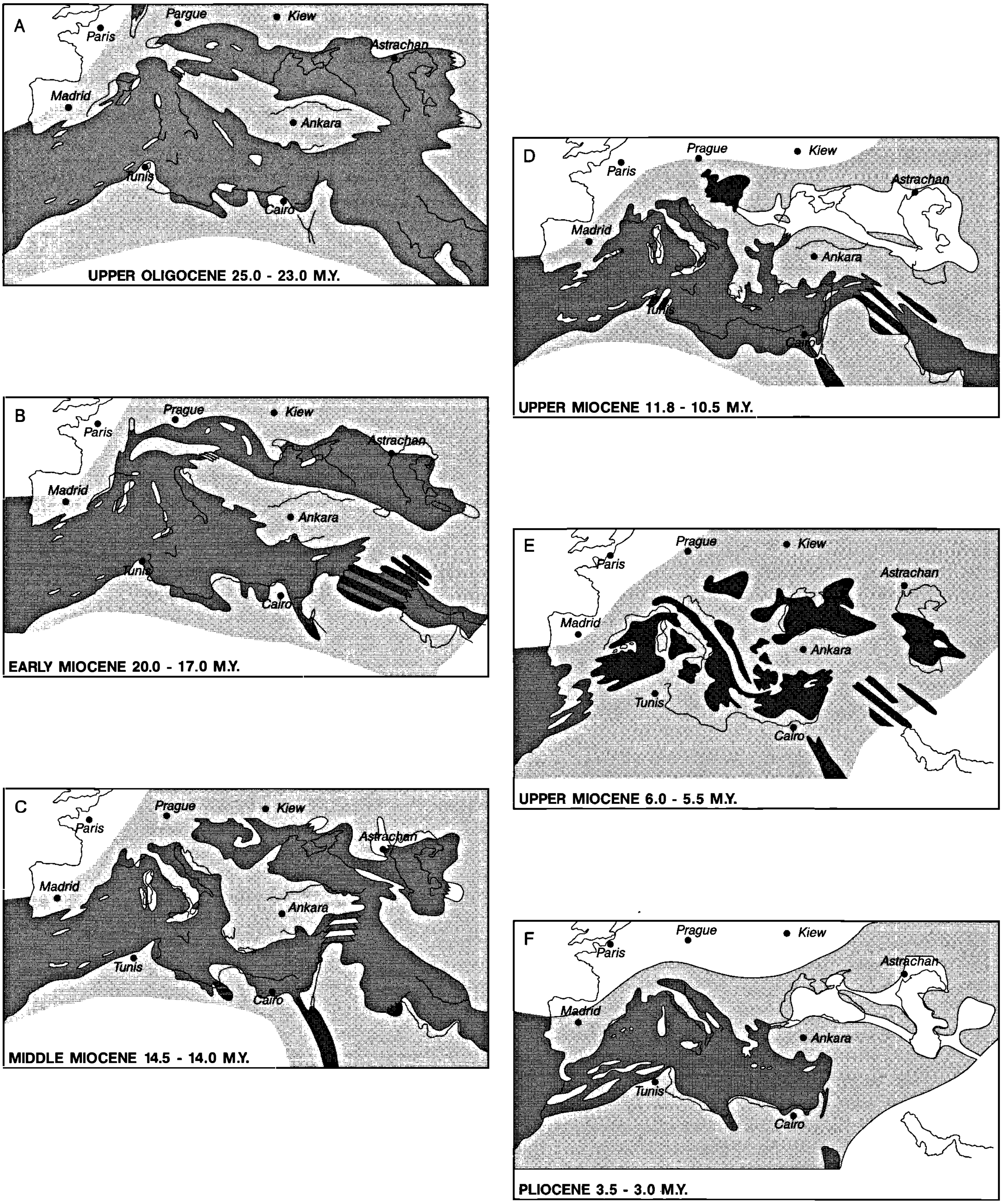
The geological evolution of the Euro-Mediterranean area in the period since 25 mybp to 3.0 mybp, in which the main events of the recent geographic, floristic and faunistic evolution of Europe happened, is extensively documented (Fig. 8.15, see, among others, Rögl & Steininger, 1983; Robertson *et al.*, 1991). Additionally, several deposits have furnished fossil wood and pollen of different plant species, which made possible the reconstruction of both paleoclimate and palaeovegetation in the area since the Miocene Epoch to the Present. In particular, from 15 mybp to 3.2 mybp – when the pollen data show in South-eastern France the appearance of plant species more tolerant to summer drought – a markedly subtropical, wet forest existed in the Mediterranean area and in most of Europe (see, among others, Grangeon, 1958; Biondi *et al.*, 1985; Suc, 1984).

Despite this generally held view, however, the evolution of both climate and vegetation has been much more complex in the Euro-Mediterranean area: for instance, until 20 mybp, the coasts of the Tethys Sea were characterized by a hot, arid climate, with steppe or semidesert vegetation (the 'Ancient Mediterranean' described by Popov, 1927; Kryzhanovskij, 1965b; and Pravdin & Mishenko, 1980). Pollen evidence described by Bertoldi *et al.* (1989), from Calabria and Sicily, show there the presence of Mediterranean vegetation as early as 3.8 mybp, moister and less seasonal conditions at 3.2 mybp, and again arid conditions 2.4 mybp, at the time of the onset of Northern hemisphere glaciation, when the Po valley hosted montane vegetation (Estabrook, 2001).

It is important to stress, that the impressive Cenozoic orogenic phases, which gave to Europe the main orographic features present today, were of considerable importance for the evolution of floras and faunas in the area. This led to both the formation and modification of massifs and valleys, and climatic modifications which are important for isolation and speciation processes and distribution patterns.

Some main phases can be summarized as follows:

1. In the Eocene Epoch, the formation of the Atlantic basin interrupted faunal exchange between Europe and North America. In the Oligocene Epoch, the closing of the Ural sea made possible important migrations of organisms from Asia (Angarian area) to Northern Europe (Baltic area), and vice versa. During the time interval 25.0-23.0 mybp, the Balkan-Anatolian region became a markedly insular area inside the Tethyan Sea. In that period, part of central Europe (Armorica) was connected with south-western Europe (Tyrrenian area), and the latter was fully isolated from the Alpine chain. Furthermore, from 25 mybp to Upper Miocene time, movements of microplates in the western Paleo-Mediterranean area of northern (Corso-Sardinian, Baleares) and southern (Kabylies, and parts of southern Italy and Sicily), strikingly modified the shape of the basin, and contributed to the origin of the present biota.
2. Since early Miocene time (23 mybp), an almost uninterrupted montane (Alpidic) chain, from the Baetic chain to the Balkans, was available for colonization by carabids derived from both Angarian and Gondwanaland lineages (Dewey *et al.*, 1973; Casale & Vigna Taglianti, 1992). Subsequently, from 20.0 to 19.0 mybp, important land connections of the Dinaric-Balkan area with Anatolia and central-western Asia became possible. At the end of early Miocene time, 17.0 mybp, all territories of the trans-Tethyan area were definitively connected with Eurasia (Dewey *et al.*, 1973). However, a new isolation of the eastern side of the Balkan-Anatolian area happened in Middle Miocene time (16.5 – 15.8 mybp). Subsequently, at about 15 mybp, interruption of connections between the Mediterranean and the Black Seas produced an inner sea, which extended from Southeastern Europe to the Aral Lake (Paratethys). The Caucasian area, on the contrary, has been characterized by more prolonged insularity or peninsularity, since early in the Cretaceous Period, in Middle and during Upper Miocene time, and in Pliocene time, again. Isolation characterized also the Alpine chain, at least until Middle Miocene time. Such isolation or semi-isolation is probably the cause of the peculiar, autoch-



A UPPER OLIGOCENE 25.0 - 23.0 M.Y.

B EARLY MIOCENE 20.0 - 17.0 M.Y.

C MIDDLE MIOCENE 14.5 - 14.0 M.Y.

D UPPER MIOCENE 11.8 - 10.5 M.Y.

E UPPER MIOCENE 6.0 - 5.5 M.Y.

F PLIOCENE 3.5 - 3.0 M.Y.

Fig 8.15. (A – F) – Palaeogeographic evolution of Euro-Mediterranean area (after Casale & Vigna Taglianti, 1999; redrawn from Rögl & Steininger, 1983).

thonous, very rich insect (*Carabus* included) faunas of these montane regions. In the meantime, between 8 and 5 mybp, new orogenic phases and the formation of the Apennine chain gave to the Italian peninsula the main features of its present shape.

3. In Upper Miocene time (6.0-5.3 mybp), the Messinian Mediterranean salinity crisis (Hsu *et al.*, 1977) made possible extensive land connections among Europe, North Africa and Asia Minor. In this period, however, the Mediterranean Basin was reflooded several times from the east (Hsu, 1983); narrow connections of the Mediterranean basin with both Paratethys and the Indian Ocean became possible.
4. By 5.3 mybp, opening of the Gibraltar Straits, with extensive transgressive phases and the formation of the present Mediterranean Sea, gave to the southern coasts of Europe the main features of their modern shape.
5. The Plio-Pleistocene climatic deterioration remodelled profoundly both the geographic and orographic features of Europe, leaving glacial evidence, and modified greatly both the landscape and the biotic scenario. Since the end of the Pliocene to the Quaternary Epoch, at least seven changes of sea level are known, some reaching 120 m in difference in the Mediterranean basin (Azzaroli, 1983; Pirazzoli, 1991): important land connections between continental coasts and Mediterranean islands became possible during the glacial peaks, with successions of forest, tundra and steppe vegetation in northern and central Europe, and Mediterranean flora along the southern coasts. The Aegean Sea, with its present shape, is a recent basin; furthermore, during the Last Glacial, and until 7500 years BP, the Dardanelles and Bosporus straits, separating today Europe from Asia Minor, were transformed into land or river valleys, available for migration of plants and animals, and the Black and the Marmara Sea were occupied by lakes in a state of desalination.

Only a few traces of the evolution of the genus *Carabus* are visible in this ancient European landscape and these are described below.

8.5.3. The early Carabini in Europe

Fossil remains of insects are rare and usually preserved inadequately and scattered in time and space. Therefore, they are scarcely useful for phylogenetic reconstructions. However, they may be highly informative about past faunal associations and – associated with paleofloristic data – about the paleoecologic and paleoclimatic conditions present in a region.

Species of Calosomatini and Carabini, belonging to the recent genera *Calosoma* and *Carabus*, were present in Europe at least in early Cenozoic time. On the contrary, as specified above, the occurrence of *Carabus* species in Europe in the Jurassic Period is doubtful. Most fossil Mio-Pliocene remains, attributed to the genus *Carabus*, have to be attributed to the genus *Calosoma* (Lapouge, 1929-1932; Casale *et al.*, 1982), and present morphological features similar, or identical, to those of extant species living in Europe.

The most ancient representative of the genus *Carabus* in Europe, reported so far, is *C. billieti* Mortillet, 1850, from the Oligocene Epoch of France. This fact, however, requires confirmation.

Very informative fossils of *Carabus* species living in the European paleo-continent have been described and illustrated by Deuve (1998b), from the diatomite deposits of the Massif Central (France). The high quality of their state of preservation, both in elytral sculpture and colour, allowed Deuve to furnish an extensive description of these remains. One of these belongs to an extinct species, *Carabus neli* Deuve, 1998, from Ardèche (Privas, Saint-Bauzile), collected in diatomite deposits of a volcanic lake dated from Upper Miocene time (8.5 mybp). In the author's opinion, this taxon is not closely related to any extant species, and represents evidence of an ancient carabid fauna living in Miocene age forests, in a temperate-humid climate. The species was associated with faunas no longer living in the region (*Macrotermes* and Corydalidae, among insects; *Hipparion,* mastodonts and *Dinotherium*, among mammals), but in ecological conditions corresponding to those present to-day between 25°N and 30°N (South-East Asia, for instance), where many *Carabus* species live in subtropical conditions. At the same time, but on the opposite side of Eurasia, another *Carabus* species, belonging to the subgenus *Ohomopterus* (described in *Apotomopterus*), lived in Japan: its fossil remains are dated to at least 9.0 mybp (Hiura, 1971).

One elytron of a second specimen, from Cantal (Murat, Sainte-Reine), but from a more recent diatomite deposit, dating from 5.3 mybp, is more informative from phylogenetic, ecologic and faunal points of view. Owing to its morphological features, it can be attributed to the recent Asiatic-European species *Carabus (Tachypus) cancellatus* Illiger (Deuve, 1998b). This finding, associated with the few Pleistocene European *Carabus* remains known so far (see Breuning 1932-36; Deuve, 1994) (*C. thuerachi* Flach, 1884, from the Pleistocene of Germany; *C. dzieduszyckii* Lomnicki, 1894, *C. praearvensis* Lomnicki, 1894, *C. praeviolaceus* Lomnicki, 1894, and *C. maeandroides* Lomnicki, 1894, from the Pleistocene of Ukraine; *C. nitens humerosus* Lapouge, 1902, *C. nemoralis malacopterus* Lapouge, 1902, *C. sylvestris arietinus* Lapouge, 1902, *C. violaceus orcinus* Lapouge, 1902, from the Pleistocene of Belgium; and *C. maeander* Fischer, 1822, a species presently living in Northeastern Asia and North America, but found several times in deposits of the last Glacial period in Europe), demonstrates the occurrence in Europe, since the Upper Miocene, of assosiations of *Carabus* and *Calosoma* species very similar to those living today in the same area. This fact is very important, because it confirms the limited cladogenetic effects of the Plio-Pleistocene paleogeographical and paleoclimatic events on carabids characterized by slow rates of evolution (Prüser & Mossakowski, 1998). It shows only slight morphological modifications in this group, as explained by Matthews (1979) with reference to fossil remains of *Carabus* from Late Tertiary beds of Alaska.

8.5.4. Origins of the *Carabus* species in Europe

The Darwinian concept of centre of origin (Croizat *et al.*, 1974), and concepts such as vicariance and dispersal (Platnick & Nelson, 1978), have been some of the major questions in historical biogeography, which merit consideration also today (Briggs, 2000; Estabrook, 2001). The attempt to determine the centre of origin of single, extant species, seems to be impossible, and sometimes useless (Coope, 1979a,b), and a conceptual model inconsistent with the principles of common ancestry and vicariance. On the contrary, reconstruction of biogeographical history of homogeneous, monophyletic lineages (Croizat's generalized tracks, very similar to Jeannel's *lignées phylétiques*) can furnish reliable information for interpreting modern distributions of the extant biota. In our opinion, and in that of several authors, this concept may be analyzed as four different questions, i.e.: 1, what is the origin of a taxon?; 2, what is the centre of origin of a taxon?; 3, what is the origin of the present distribution of a taxon, in relation to that of sympatric taxa?, and, 4, why do many taxa of different groups present similar (or identical) patterns of distribution, or chorotypes? European *Carabus* species provide some clues for seeking answers to these questions, as follows.

1. The origin of a taxon may be recognized as an event of allopatric speciation that, from a common ancestor, produced both the taxon itself, and its adelphotaxon. In the European *Carabus* fauna, excellent examples of this process are offered by allopatric or parapatric, closely related taxa, such as the Cantabrian *C. auriculatus* and the Pyrenean *C. pyrenaeus*, several allopatric Alpine *Orinocarabus* species, or *C. pseudomonticola* in the Eastern Pyrenees and *C. vagans* in the South-western Alps, as peripheral isolates from the widely distributed *nemoralis* and *cancellatus* complexes. For such taxa, paleogeographic and paleoclimatic data, when available, may provide excellent information about causes and times of isolation (vicariance), and have been widely used to set the molecular clock.
2. For such taxa, a primary centre of origin may be recognized in one section of the area where they presently live. On the contrary, this is not possible for species presently having a very wide range, or, on the contrary, for relict, isolated and very localized species. The first type of distribution is represented in Europe by taxa such as *C. cancellatus*, *C. granulatus* and many others. Excellent representatives of the second type of distribution are, among others, *C. olympiae* and *C. cychroides*. The first is presently recognized as a member of the *Chrysocarabus* lineage, morphologically and geographically widely isolated from its relatives, and localized presently in a well known Pleistocene refugium of the western Pre-Alps. The second species is a high altitude element, represented today by two fully isolated populations, living each on a few hectares on two separated massifs of the Cottian Alps. Furthermore, it is sympatric and syntopic with the close relative *C. depressus*, widely distributed through the Alps. For these taxa, nothing (not even molecular data, about *C. cychroides*: Casale *et al.*, 1998) permits conclusions about centres of origin, and the original shape and size of geographical distributions of the cited species.
3. Hypotheses about origins of the past and present distributions of taxa, connected with those of the other organisms living in the same area ('What is a fauna?', in Mayr's sense), call for analysis of several facts. European *Carabus* species may be highly informative about this topic, as follows.

8.5.5. The early history of *Carabus* in the light of Palaearctic-Nearctic connections[2]

Palaearctic understanding of the history of European *Carabus* is hardly possible without knowledge about the early history of the genus as a whole and its subsequent stages and routes of dispersal and vicariance. In this respect, the historical connections and faunal exchange between the Palaearctic and Nearctic regions seem to be of key importance.

Excluding the introduced species from discussion, there are 12 native Nearctic species, and we know something of their relationships and geographical distribution of their (consubgeneric) related species. We know also that the Nearctic Carabus fauna is small. We know that the East Asian-Siberian *Carabus* fauna is enormous, and that it declines as one goes westward toward Western Europe. We know that Western Europe and North America were joined, probably until the end of the Eocene Epoch. A classic evidence for that is demonstrated by the present distribution of the relic family Plethodontidae (Amphibia) in the Americas and the Mediterranean area. Moreover, there are fossil remains of *Carabus* species described both from Europe and USA (see Deuve, 1994). Put otherwise, until that time, what is now Western Europe and North America were geographically one. And we know that more recently (Miocene on) Western North America and Eastern Siberia were joined from time to time by an area referred to as Beringia. Taking these matters into account, it should be possible to infer source areas and times of arrival for the elements of the Nearctic *Carabus* fauna (Table 8.9).

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[2] This section was written by George Ball

Table 8.9. Western Hemisphere species of *Carabus* arranged by putative time of arrival (from most to least recent) from postulated source areas (source: G. Ball, *in litt.*).

No	Species	Origin
01.	C. (Carabus) granulatus Linné, 1758	Introduced; Recent; W. Palaearctic
02.	C. (Archicarabus) nemoralis O.F. Muller, 1764	Introduced; Recent; W. Palaearctic
03.	C. (Tachypus) auratus Linné, 1761	Introduced; Recent; W. Palaearctic
04.	C. (Diocarabus) truncaticollis Eschscholtz, 1833	Immigrant; Pleistocene; E. Palaearctic
05.	C. (Megodontus) vietinghoffi Adams, 1812	Immigrant; Pleistocene; E. Palaearctic
06.	C. (Homoeocarabus) maeander Fischer, 1820	Immigrant; Plio/Pleistocene; E. Palaearctic
07.	C. (Neocarabus) taedatus Fabricius, 1787	Autochtonous; Miocene?; E. Palaearctic?
08.	C. (Diocarabus) chamissonis Fischer, 1820	Autochtonous; Miocene?; E. Palaearctic?
09.	C. (Hemicarabus) serratus Say, 1823	Autochtonous; Miocene?; E. Palaearctic
10.	C. (Lichnocarabus) vinctus Weber, 1801	Autochtonous; Eocene?; E. Nea/W. Palaearctic
11.	C. (Lichnocarabus) goryi Dejean, 1831 (=limbatus Say, 1823)	Autochtonous; Eocene?; E. Nea/W. Palaearctic
12.	C. (Tanaocarabus) sylvosus Say, 1823	Autochtonous; Eocene?; E. Nea/W. Palaearctic
13.	C. (Tanaocarabus) finitimus Haldeman, 1852	Autochtonous; Eocene?; E. Nea/W. Palaearctic
14.	C. (Tanaocarabus) forreri Bates, 1882	Autochtonous; Eocene?; W. Nea/E. Nea./W. Palaearctic
15.	C. (Tanaocarabus) hendrichsi Bolivar y Pieltain, Rotger & Coronado, 1967	Autochtonous; Eocene?; W. Nea/E. Nea./W. Palaearctic)

With a rich Palaearctic East Asian-Siberian fauna, we assume that movement of immigrant species or autochtonous species that are members of groups with a predominantly Eastern Palaearctic distribution, has been into the Nearctic Region from the Palaearctic Region, that this movement has been via Beringia, and that it has taken place comparatively recently, with degree of recency being determined by degree of distinction. Thus, immigrant species with arctic/sub-arctic ranges (*C. vietinghoffii*, and *C. truncaticollis*) are assumed to have arrived more recently, and autochtonous, more temperate species (*C. serratus*) to have arrived earlier, under a northern climatic regime that was more temperate than the present one. So, it may be postulated that species 04-09 in Tab. 8.9, are Beringian derivatives. In contrast, the autochtonous species that are more southern and eastern seem not to have had a Beringian connection with the Palaearctic Region. Rather, they (through their ancestors) are more likely to have had a connection with Western Europe, and achieved their present position in the Nearctic Region when North America was still a part of what is now Western Europe. That would put their ancestral stocks (for *Tanaocarabus* and the species pair *goryi-vinctus*) in Western Europe in early Tertiary time, and this is the main point of this long presentation, and the connection with the historical biogeographical analysis of the European *Carabus* fauna.

Since *Tanaocarabus* has no extant representatives in the Palaearctic Region, this lineage must have become extinct there – but it must have once been in Western Europe. The *goryi-vinctus* lineage may still have (probably does have) extant relatives, but again, this lineage had to be in Western Europe early in the Tertiary Period. Probably, relatives of these taxa have to be searched in basic Palaearctic lineages, widely distributed presently in Europe, such as *Oreocarabus* (see Breuning, 1932-1937). We need not go into detail about differentiation in the Nearctic Region of the invasive ancestral stocks.

In summary, it may be postulated that *Carabus* arose in what is now warm temperate Eastern Asia, probably in Late Cretaceous time, after Gondwana and Laurasia split apart, sundering Pangaea. The *Carabus* stock differentiated by speciation and climatic adaptation, with lineages spreading westward at different times and under different circumstances. At least two lineages spread as far as the territory that would come to lie to the west of the Atlantic Ocean when the Atlantic Basin formed. Later, with development of the Beringian connection and northward drift of the northern continents, various lineages reached the Nearctic

Region, spreading southward and eastward as times and circumstances allowed. The early-arriving more temperate-adapted lineages became cut off from their Palaearctic counterparts.

For the autochtonous species (those that are known only from the Western Hemisphere, and presumably originated there), No. 07-15, the Nearctic 'source area' refers to where splitting of the immediate common ancestor occurred, whereas the W. Palaearctic component refers to the ancestral source area (of *C. vinctus-goryi*; and members of subgenus *Tanaocarabus*) and not to the descendant species.

For *Tanaocarabus*, with four species, the situation is still more complex. The immediate ancestor of the species pair *sylvosus-finitimus* evidently differentiated in Eastern North America, whereas the ancestor of the species pair *forreri-hendrichsi* differentiated in Western North America – almost certainly in northern Mexico. However, that ancestor must have come from the Eastern part of the Nearctic Region.

8.5.6. Biogeographical patterns and underlying processes

Some data and some opinions, able to explicate the methods used in drawing conclusions about ages and origin of distributions of the main *Carabus* lineages in Europe, were expressed above. Broadly accepted is the opinion that the best way in reconstructing the origin of distributions, and chorological affinities among taxa, is offered by phylogenetic analyses of sufficiently broad and homogeneous species groups. In spite of analysis of morphological and molecular data (see Chapter 7. *Phylogeny*), a definitive consensus about the phylogeny of many lineages of *Carabus* present in the European fauna is not yet available. Lapouge, in his monumental Genera Insectorum (1929-1932), was the pioneer in connecting phylogenetic inferences ('généalogie') with the distribution patterns of the examined taxa. The tables of 'primitive' and 'derived' morphological characters as described by Lapouge may be models for modern cladistics. Moreover, some of his phylogenetic trees – for instance, the *Heterocarabus, Chaetocarabus, Pseudocechenus, Platycarabus* lineage (in agreement with the 'genus *Chaetocarabus*' sensu Ishikawa, 1984: see Casale *et al.*, 1998); or the lineage including *C. genei* in the *Eurycarabus* complex – have been re-evaluated and confirmed by modern classifications, some of which were based on molecular characters.

Some other principles (recently discussed by Casale & Vigna Taglianti, 1999), merit explanation. The concepts of dispersal (accepted by Croizat *et al.*, 1974), vicariance, and speciation events are self-explanatory (Erwin, 1981): dispersal power (i.e. ability of dispersal by individuals, or groups of individuals), vicariance (i.e. development of geographic or environmental barriers, able to isolate two or more genetic pools), and differentiation (both cladogenetic and anagenetic), seem to be irrefutable, demonstrated facts. Another fact, is that earth and climate changed in the past, and are changing in the present, more quickly and dramatically than some organisms: Europe, and all the Mediterranean area, furnish a good example of this reality, and of the influence that these changes exerted in different, proximate areas, on the diversity of life and faunal assemblages.

At different times, phytogeographers and zoogeographers have recognized patterns of distribution for plants and animals living in the Euro-Mediterranean region. As for other areas, the result has been a series of biogeographical provinces and/or postulated biogeographic relationships, the details of which were not accepted by all eco-geographers, botanists and zoologists. In this area also, the conflicting approaches between dispersalists, more attentive to ecological, dynamic recent factors, and historical biogeographers, more influenced by paleogeographical aspects, are evident. Phytogeographers and vertebrate zoologists are mostly representative of the first group. Soil fauna workers, including many entomologists – mostly carabidologists, adherent to the Jeannelian school – are as a rule partisans of the second approach.

At the moment, and in spite of recent efforts (Salomon, 2001), it seems evident that a unified theory on the development of recent biota and its geographical distribution does not exist. Therefore it is important to avoid simplistic reductionism. The taxon pulse model proposed for carabids by Erwin (1981), as a unidirectional series of habitat shifts and specialization (different, in this unidirectionality, from Wilson's taxon cycle theory), provides a satisfactory, narrative explanation at least at higher levels and over longer intervals of time.

Concerning European *Carabus* species and associations, from the historical point of view, some aspects merit particular attention. They will be illustrated in terms adopted recently by Casale & Vigna Taglianti (1999), dealing with the Anatolian carabid fauna. The available facts are: highly varied ecological associations (and associated structural and functional adaptations); faunal associations; topographical associations; geological history of the area, and fossil evidence of Tertiary forests, with some scarce remains of *Carabus* species, which lived and evolved in those forests. Also available are data about diversity (number of species and subspecies) and divergence, both in morphological features and life history. The taxa involved provide patterns which emerge from a combination of diversity, divergence and geographical distribution within Europe, and a relationship of the European taxa – or populations – to taxa occurring elsewhere. These patterns must be interpreted in terms of evolutionary processes.

The first objective fact that we have available, is the diversity in Europe of the genus *Carabus* as a whole (see section 8.3. and Fig. 8.2). As pointed out above, the richness of specific and subspecific taxa is evident. The drifting of microplates and the early evolution of the Euro-Mediterranean area seem to have contributed elements of the early carabid assemblages, represented today by markedly isolated carabid lineages. A more careful examination of taxa and their geographical patterns of distribution permits postulating the history and evolution of some of the most ancient representatives of the genus *Carabus* in Europe. In particular: the original position during the Mesozoic Era of a section of the European paleo-continent on the northern side of the Tethyan Sea, probably allowed in this area the occurrence of the most ancient *Carabus* lineages since the Eocene Epoch, ancestors of both European and Nearctic elements preceding formation of the Atlantic Basin. Subsequently, in the Oligocene age, closing of the Ural Sea between the Angarian (Asian) and the Baltic areas, allowed the immigration to Europe of other ancient *Carabus* elements, and highly enriched the diversity of the genus in the Western Palaearctic.

Nevertheless, land movement, as an explanation of the current distribution of carabids in restricted areas, is a factor which must be used with prudence: for instance, in the biogeographical analysis of carabids of Sardinia, Casale & Vigna Taglianti (1996) recognized, among some 350 species known at the time, not more than 5 species (isolated at generic rank), the occurrence of which can be explained only by the well documented drift of the island in the western Mediterranean area.

The processes explaining speciation, diversity, and present distribution of most insect taxa in Europe, including *Carabus* species, are evidently both *vicariant*, i.e. eco-geographic or climatic events which split an original distribution, with subsequent isolation of genetical pools in ancestor phyletic lineages; and *dispersal* subsequently of species (by flight in long-winged species, or individuals: Lindroth, 1979), using available land connections, or over narrow sea barriers, and then movements of various stocks as dictated by changing climate and changing topography (Platnick & Nelson, 1978).

The ancient connections between the Balkan Peninsula and Asia Minor in Upper Oligocene and in Miocene time again, and extensive connections of Europe with Asian territories in different phases of the Miocene, allowed the immigration of sub-tropical, forest-dwelling lineages, ancestors of taxa today represented by distinctive endemics (of the subgenera *Procerus*, *Chrysocarabus* and *Macrothorax*, for instance), mostly localized in regions of Southern and Eastern Europe. During Upper Miocene to Early Pliocene time, land connections (particularly impressive during the Messinian Mediterranean salinity crisis), new orogenic phases, and changes of climate and vegetation, contributed to important faunistic changes. These changes included cladogenetic events and increased diversity, by means of spreading of thermophilic lineages from North Africa, Asia Minor, West and Central Asian regions to Europe, and phases of isolation and differentiation.

Subsequently, Pleistocene climatic changes and fluctuations, with the availability of refugia during the glacial and interglacial (hot) phases, new patterns of vegetation, extension of steppes, and new land connections (made possible by marked sea level changes of the Mediterranean in the glacial peaks), produced the present pattern of the carabid fauna. Additionally, Pleistocene isolation and survival of relicts, modification of several patterns of distribution, and adaptive specialisation to different environments, contributed to development of the modern *Carabus* fauna in Europe. Furthermore, immigrations to East Europe of Asian-European or Siberian, taiga, tundra or steppe dweller elements are traced to the last glacial interval (18.000 ybp). More recently, in post-glacial time (last 10.000 years), extension occurred of geographical ranges of silvicolous species into deglaciated or ice-free places that had become re-forested: lowlands, slopes, valleys and ridges in the main European mountain chains.

If historical, long-term processes provide a satisfactory, narrative reconstruction of the composition of the extant carabid fauna as a whole, some other information, and other processes, are necessary to explain in detail the present distribution of *Carabus* species in the area. These other processes involve different ways of life, and related adaptive features and modifications. This additional information is provided by an ecological (both auto-ecological and synecological) approach to the faunal assemblages.

Macroptery is known in only three *Carabus* species (*C. granulatus*, *C. clatratus*, and, locally, *C. italicus*). These species correspond with Darlington's hygrophiles, or with Erwin's waterside or lowland generalists, or plesiotypes. However, macroptery does not necessarily result in a high dispersal power and a large distribution area. Among the above cited species, the first two present a widespread Eurasian distribution, but *C. italicus* is endemic to Italy.

In contrast, almost all other *Carabus* species in Europe are represented by brachypterous or micropterous forms, corresponding with Darlington's mesophile geophiles, or with Erwin's apotypes. Many of these present a markedly reduced or scattered range of distribution, and low dispersal power, in spite of the ability of some to colonize wide altitudinal ranges: among others, we cite *C. solieri*, a species living at altitudes from 200 to 2200 m, in forests as in alpine pastures, but endemic to the Western Alps and to the Ligurian Apennines, and in some sections of its range markedly localized and unable to colonize apparently suitable, contiguous biotopes (Casale & Cavazzuti, 1975).

On the contrary, many flightless species are widely distributed: *Carabus auratus*, *C. auronitens*, and *C. coriaceus*, although represented in Europe by subspeciated or semi-speciated forms, are good examples of brachypterous species with a wide geographical range, high dispersal power, and ability in colonizing, by walking, available terrain. Being however flightless, heavy, and large-sized insects, the representatives of the genus demonstrate little aptitude as colonizers of islands by passive means. This is demonstrated by the low number of extant species present in the Mediterranean and circum-European islands, a subject on which further data are provided below. In other words, brachyptery not always results in low dispersal power, or low genetic flow, and vice versa. In Europe, brachypterous species demonstrated a very efficient, impressive ability in re-colonizing alpine valleys and high altitude ridges and moraines in recent millennia, or lowland areas reforested in recent centuries (see Chapter 6). Conversely, two of the three *Carabus* species that maintained winged individuals (*C. clatratus* and *C. italicus*) show – such as many carabids in tropical areas – reduced or scattered ranges of distribution; they demonstrate to-day only restricted dispersal power, and are declining owing to loss of habitat. This datum, and the recent discovery of the remains of an extinct Miocene age species adapted to sub-tropical forests (*C. neli* Deuve, 1998, cited above), suggest massive extinctions of *Carabus* species induced by the Upper Miocene climatic deterioration in Europe, and their substitution by lineages tied to a temperate, seasonal climate.

Therefore, it seems clear that the diversity and composition of the extant European *Carabus* fauna has been influenced not only by historical events, but also by ecological constraints, and availability of varied habitats (marshes, open lands, forests, high mountains) and trophic resources. In this context, some evolutionary processes seem important. Among these, evolution towards a larger size in some groups (some European *Carabus* species of the subgenera *Procrustes* and *Procerus* are among the largest in size in the genus), seems to be a favourable adaptation in attacking and eating large-sized prey (for example, some terrestrial gastropod molluscs). Such specialisations are present in cychrisized or macrocephalic forms, co-existing, some of both types in the same subgenus (such as *Platycarabus*), and are in agreement with phylogenetic hypotheses (Casale *et al.*, 1998).

Competition, and exclusion among species occurring in one and the same habitat, seem to be prominent features of European *Carabus* associations. For example, nine *Carabus* species (and three *Cychrus* species) are syntopic in the same biotope of the high Sessera Valley, at 1500-1600 m, in the Pennine Alps (*C. granulatus*, *C. cancellatus*, *C. monticola*, *C. concolor*, *C. glabratus*, *C. intricatus*, *C. depressus*, *C. germarii*, *C. olympiae*) (Casale & Vigna Taglianti, 1992). None of these is closely related to any of the others, and some of these exhibit different periods of activity and breeding, larval development, different habitat choices to forests or alpine pastures, respectively, or feed on different prey.

As a rule, sister species tend to be distributed allopatrically or parapatrically. Among the best studied examples, *C. depressus* and *C. creutzeri* are sympatric in the Central and Eastern Alps, but ecologically fully segregated – the first on crystalline soil, the second on limestone – and are not syntopic (Brandmayr & Zetto Brandmayr, 1988). Thus, although living in the same area, they do not hybridize in nature (Casale *et al.*, 1998).

Another impressive example of allopatric occurrence of closely related species is provided by two *Orinocarabus* species in the Western Alps, where *C. putzeysianus bisioi*, in a small area of syntopy with *C. fairmairei*, lives segregated on narrow, stony ridges at 2800-3000 m, while the second species colonizes alpine pastures from 1800 to 2800 m (Cavazzuti & Meli, 1999).

This situation, however, cannot be generalized: *C. (Platycarabus) depressus* and *C. (Platycarabus) cychroides* are fully syntopic in the two massifs of the Western Alps (in which the second is localized), present the same period of activity, and eat the same prey; nevertheless, the pre-zygotic and post-zygotic barriers seem to be very efficient, because only a few natural hybrids generated by the two species are known.

These facts, associated with the shift to cold, wet or high altitude habitats by hygrophilic elements in hot, dry periods, suggest that some older elements of the montane fauna once occupied forested lowlands and were displaced from there when changing climate allowed differently adapted species to enter the lowland habitats. A few European *Carabus* species presently seem to be exclusively high altitude dwellers. In fact, several *Orinocarabus, Chrysocarabus, Platycarabus* species are able to reach or exceed 2000-2500 m in the southern massifs, colonize moist forests of beech or fir-tree at 1000-1500 m in Central Europe.

Owing to the facts presented above, the comparison of association ('communities', or 'taxocoenoses') structures seems to be less informative from the viewpoint of historical biogeography. Many of these associations are, at least in the highly dynamic and varied Euro-Mediterranean area, a kaleidoscopic assemblage of taxa (many endemic), with different origins and relationships (see section 8.4 and Appendix 8.2). It seems evident, in fact, that particular caution must be exercised in attributing ecological constraints to caraboid species (*Carabus* included), whose ways of life are scarcely known. This attribution seems to be favored by ecologists working with carabid beetles; but a very abundant literature (Lövei & Sunderland, 1996) demonstrates that many so-called specialized carabids can adapt, at least in temperate regions, to different and changing habitats (about the European *Carabus* species, see Chapters 5. *Species Accounts* and 6. *Biology and Ecology*). Closely related species (or adelphotaxa), with the same morphological modifications (*C. granulatus* and *C. menetriesi*, *C. ulrichii* and *C. italicus*, *C. nemoralis* and *C. pseudomonticola*), present markedly different geographical ranges, and colonize a wide or narrow altitudinal range, respectively, or biotopes very different in environmental conditions. Some of these species also modify their life cycles and activity periods, in agreement with different latitudes and altitudes. Consequently, and owing to the occurrence of numerous endemics, in the European regions, some faunal structures, in apparently similar environments, are markedly different from each other in *Carabus* species composition; or, conversely, some are very similar in different environments.

8.6. GEOGRAPHICAL HISTORY OF EUROPEAN *CARABUS* SPECIES: A SCENARIO

The preceding data illustrate some aspects of the diversity of the European *Carabus* fauna, in terms of paleogeographic and paleoclimatic events, heterochronic phases of colonisation, overlap of taxa of different origin, local speciation and subspeciation, and ability, for some species, to adapt their way of life to changing ecological conditions. The complexity of the data shows how difficult it is to provide a detailed picture of the evolution of the genus *Carabus* in the area, in terms of historical biogeography. Nonetheless, using the available information about the beetles, their inferred relationships, and their geographical distribution, some hypotheses are possible, compatible with both paleogeographic and paleoclimatic data.

1. The most ancient *Carabus* elements in Europe date probably to the Eocene epoch, preceding the formation of the Atlantic Basin: the occurrence of the most isolated *Carabus* species in the Nearctic Region, probably derived by Holarctic lineages – and overlapped presently to some recent, Pleistocene Behringian immigrants – support this hypothesis (see section 8.5.5). Since Oligocene time, the closing of the Ural Sea Basin, alpine orogenic phases, and extensive land connections available both between the Angarian and the Baltic area, and among different sections of the future European paleo-continent, made possible dispersal of the most basal *Carabus* lineages, ancestors of the modern subgenera. Notable in this context, is that the modern representatives of the subgenus *Tachypus*, recognized as the first group at the base of the genus (see Chapter 7. *Phylogeny*), are at present, typically Euro-Sibirian (*C. cancellatus*), or European elements. Therefore, owing to reasons previously stressed, nothing permits localizing exactly the area in which these early cladogenetic events happened. Angara, however, has been probably the main center of origin of most *Carabus* lineages, as demonstrated by the overall pattern of diversity of the extant lineages of the genus.

   Two other evidently basal lineages (in the sense of the phylogeny proposed in this contribution (see Chapter 7. *Phylogeny*), i.e. *Limnocarabus* and *Hygrocarabus*, have today only a few extant representatives, the first in Eurasia (*C. clatratus)* and the second in Europe (the sister taxa *C. variolosus* and *C. nodulosus).* The phylogenetic relationships of *Hygrocarabus* are not yet definitively ascertained. *Limnocarabus* could be a representative of the very diverse Angarian *Apotomopterus* lineage, if the *Spinulati* (in the sense of Ishikawa and Deuve) is confirmed as a monophyletic unit. If so, *C. (L.) clatratus* (in the widest sense, including the East Asian subsp. *C. c. maacki*), should be recognized as a more recent, Plio-Pleistocene immigrant to Europe from Asia.

2. Since Early Miocene time, the less specialized basal lineages, ancestors of the modern *Carabus*, were probably present in extensive sections of the European paleo-continent: both *Archeocarabi* (*Archicarabomorphi* plus *Lipastromorphi* partim, recognized as a paraphylum), including ancestors of the modern subgenera *Carabus*, *Eucarabus*, *Morphocarabus*, and *Archicarabus*); and *Metacarabi* (*Lobifera* partim, including ancestors of the modern subgenera *Hemicarabus*, *Oreocarabus*, *Orinocarabus*, *Mesocarabus*, *Tomocarabus* and *Ctenocarabus*).

   Since the end of Early Miocene time (23 mybp) to the beginning of Upper Miocene time (8.5 mybp), new extensive land connections, closing of the Tethyan Sea, formation of the Paleo-Mediterranean basin, and climatic changes (with further extension of tropical and sub-tropical, lowland and montane forests), permitted increased diversity, thanks to the more recently derived, specialized Asiatic-European lineages of the longimandibularan *Neocarabi*. These lineages produced, in different sections of the Euro-Mediterranean area, the ancestors of the modern subgenera *Chaetocarabus* (with its Anatolian *Heterocarabus* adelphotaxon), *Platycarabus*, *Iniopachys*, *Chrysocarabus*, *Macrothorax*, *Procerus, Procrustes* and *Megodontus* (the last-named, in the narrow sense of the present monograph, excluding *Pachycranion*). The available paleo-maps of the period between 20.0 and 10.0 mybp, and in particular those of Mid Miocene age (Rögl & Steininger, 1983), together with the paleo-climatic and paleo-ecological evidence are compatible with the origin of the ancestors of the modern taxa, not only by processes of allopatric (vicariance) speciation, but also owing to structural specialization to live in montane forests and eat special prey, such as gastropod molluscs, with subsequent morphological modifications, such as brachyptery, reduced dispersal power, and shifting to large size, macrocephaly, or cychrization.

   Examples of very large sized carabids ('procerization') in the Euro-Mediterranean area are several representatives of the subgenera *Procerus*, *Megodontus* and *Procrustes.* Macrocephaly ('licinization') and cychrization co-exist in the subgenus *Platycarabus,* the extant species of which originated in Central Europe, Alps, Carpathians, and the Dinaro-Balkanian area, from a common, *Tribax*-like ancestor (Casale *et al.*, 1998).

The southern Mediterranean (North African) lineages, ancestors of the present representatives of the subgenera *Macrothorax*, *Cathoplius* and *Eurycarabus*, expanded their ranges in Northern Africa. Since 10 and 7 mybp, a representative of the common ancestor of the extant subgenera *Eurycarabus* and *Nesaeocarabus* was responsible for a single event of colonization of the Canary islands from the western (Atlantic) coast of Africa: this hypothesis is supported by both morphological, molecular, and geological data (Prüser *et al.*, 2000).

3. During the Mediterranean salinity crisis (7.1-5.3 mybp, definitively interrupted by the opening of the Gibraltar strait), important climatic changes, with reduction of tropical forests, more xeric conditions, and marked seasonality, profoundly modified the biota extant at that time. Possible extinctions occurred of species adapted to tropical environments (documented by fossil evidences: *C. neli* Deuve, 1998). In contrast, range extension occurred for *Carabus* species more adapted to temperate conditions.

   At that time, probably the main features of the presently extant Euro-Mediterranean *Carabus* fauna emerged. This hypothesis is supported not only by remains of *Carabus* cf. *cancellatus* in Southern France, (5.3 mybp: Deuve, 1998b), but also by the history of the colonization of the Western Mediterranean areas by some *Carabus* representatives (see Prüser & Mossakowski, 1998). In this period, extensive land connections, through different parts of the Western Mediterranean area, allowed dispersal by flightless insects. These dispersals produced the present patterns of distribution of several western Mediterranean *Carabus* lineages. Among these were the early colonization of southwestern Europe, from northern Africa, by *Ctenocarabus* species, and of Southern Europe, the Balearic islands, Sicily and Sardinia by *Macrothorax* and *Eurycarabus* species. This spreading left evidence in various specialized extant forms which have speciated, semi-speciated or sub-speciated. Examples are, in particular, the Corso-Sardinian *C. (E.) genei* and the Sicilian *C. (M.) planatus*, the latter strikingly localized today in mesophilic, montane forests in the north of the island); and several markedly distinct subspecies of *C. (M.) rugosus* and of *C. (C.) melancholicus.*

   The history of colonization of the western Mediterranean area by *C. (M.) morbillosus*, and the origin of its presently scattered populations on the mainland and in several isles and islets, are less clear, and merit further investigation. At least the Calabro-Sicilian subspecies, *C. morbillosus alternans*, and the Sicilian subspecies, *C.* (*Eurycarabus*) *f. faminii* are markedly distinct from all North-African populations known so far of both species, and therefore their colonization of Sicily could date to a rather remote past. However, several populations of *C. morbillosus* in southern Spain, Corsica, Sardinia, some small Mediterranean islests, southern France and central Italy, which are scarcely or not differentiated, have, at least in part, more recent origins, some of which are anthropogenic (Casale *et al.*, 1987). It is also to be stressed that, apparently, in Messinian (Lower Pliocene) time, only one lineage of European *Carabus* – the subgenus *Mesocarabus* – colonized Africa from Europe, dispersing from the Iberian Peninsula to North Africa. This event is marked by the presence of the extant species, *C. (M.) riffensis* Fairmaire, 1872, presently localized in the Rif massif (northern Morocco).

4. In Early Pliocene (5.0 mybp) time, extensive transgressive phases, and the formation of the present Mediterranean Sea, interrupted the main land connection between Europe and North Africa, and at about 3.5 mybp, some areas inland, such as the Padanian Plain, were invaded by the sea, while tropical and sub-tropical conditions prevailed in large sections of Europe. Based on the evidence provided above, supported by molecular data, we assume that the main cladogenetic events, including speciation, in the genus *Carabus*, concluded at about this time. Only limited semi-speciation or sub-speciation may be recognized in the following millennia, in which, however, the geographical ranges of several European species were modified profoundly; many species probably became extinct; and some species extended their ranges to Europe from Northern and Central Asia.

5. The Plio-Pleistocene climatic deterioration, marked especially by glaciation, remodelled profoundly the geographic and orographic features of Europe. On this topic, a very extensive literature is available: boundaries of the ice surfaces, geo-morphological effects on the landscape, dates of glacial maxima and inter-glacial phases, and changes of climate and vegetation are documented extensively. As for island biogeography, evolution of biota in the Quaternary Epoch has been, and is presently, one of the most exploited fields of investigation by biogeographers, ecologists, and general biologists.

   Concerning carabids, and the theory of Pleistocene refugia, it would be instructive, especially for the uninitiated, to study one of the last papers written by one of the leaders on the topic (Lindroth, 1979). But many more recent contributions on the natural history of the genus *Carabus* are cited in the section 6.6.2. *Differentiation and population history* of Chapter 6. *Biology and ecology.*

   Some aspects, however, merit review here. Recently, for instance, Focarile (1987), and Casale & Vigna Taglianti

(1992), dealing with the carabids of the Western Alps, questioned again both the concept and the limits of the term *refugium*, with reference to the European southern chains and massifs. The questions were: refugium for what taxa? and from what environmental circumstances? For mesophilic, forest-dwelling species, relicts of tropical and sub-tropical Tertiary faunas, that survived in 'glacial refugia' during the catathermic peaks? Or for microthermophilic species, previously adapted to tundra, or high altitude habitat, during hot, xeric, inter-glacial periods (the Present included), in areas that very correctly Lindroth distinguished as 'interglacial refugia'?

In the southern massifs, and also in some areas of central and northern Europe, action of the Ice Age was not so destructive as claimed by some authors. Suitable for colonization by insects, as emphasized by Lindroth and Holdhaus, have been *nunataks* (ridge tops and mountain tops emergent from ice cover). Additional sites near glaciers have been available, also, such as: alpine valleys, forests fringing glacial fronts, and broader bands of vegetation that escaped cover by glacial ice.

Entomologists familiar with some *Orinocarabus* species, able to colonize denuded moraines and ridges up to 3000 m, or to climb on vertical, stony walls, and adapted to hibernate for ten months per year, may rightly suppose that several carabid species were adapted to survive markedly adverse conditions associated with proximity to glacial ice. The conclusion was that, at least in some areas and for epigean, vagile insects, the processes of isolation and vicariance were not so dramatic and extended in time. This conclusion explains why the hypothesis of intense Pleistocene speciation is not accepted presently for insects with slow rates of evolution, such as *Carabus* species.

More generally, the climatic deterioration modified landscape, environment, and diversity of life, and caused probably extinction of relict species adapted to subtropical conditions.

But some events increased diversity of other insect lineages, as well as some of *Carabus*. In Europe, cold and dry conditions favoured development of extensive areas of tundra and steppe during the glacial maxima, while evergreen forests (taiga) and temperate deciduous forests were fragmented and allowed the immigration of cold-adapted insect faunas from Northern and Central Asia to Eastern Europe (see, for a recent analysis of the palaeoecological data in last glacial maximum, 18000 ybp, and the mid-Holocene, 6000 ybp (Prentice *et al.*, 2000). Such changes during the last two million years are reflected in at least six events, as follows.

(1) Survival of relict, isolated (morphologically and geographically) species, some in very reduced refugial areas, adapted to either moist, montane forests, or to high altitude environments, and presently with reduced or very reduced geographical ranges. *C. olympiae* and *C. cychroides*, are good examples; but also *C. solieri* in the southwestern Alps, *C. planicollis* in the Transylvanian Mountains, and other species, provide excellent evidence of a Late Tertiary (i.e., pre-Quaternary) *Carabus* fauna, and show scarce or no dispersal power in recolonizing proximate areas which became suitable postglacially.

(2) Vicariance, i.e. isolation of gene pools by fragmentation of geographical ranges, with subsequent cladogenetic events (further data are provided for this topic in the section 6.6.2. *Differentiation and population history* of Chapter 6. *Biology and ecology*).

Semi-speciation and sub-speciation in the *C. monilis* complex in Central and Southern Europe, is a classic example stressed by Thiele (1977). But many other taxa offer analogous, excellent examples of Pleistocene differentiation, with different degrees of both morphological divergence and genetic distances, in relation to different ages and times of isolation, and different dispersal power in different populations. Examples are: the carefully investigated *auronitens-punctatoauratus* complex (for which a recent, extensive literature is available, see Chapter 5); the *hampei*, *violaceus*, *intricatus-lefebvrei*, *lusitanicus-macrocephalus* complexes; several close *Orinocarabus* representatives, vicariant in different sections of the Alpine chain, the taxonomic rank (specific or sub-specific) of which is questioned (see, as example, the homogeneous *heteromorphus-cenisius-fairmairei* group); some *Platycarabus* species sub-speciated in Alpine, Dinaric and Carpathian refugia; and several others.

Concerning this subject, a paradigmatic example is provided by *C. solieri*, as illustrated by Rasplus *et al.* (2000), and supported by molecular data. The two highly differentiated subspecies, *solieri solieri* and *solieri bonnetianus*, seem to have originated in two different glacial refugia, separated by the Younger Dryas glacial maximum.

The *Carabus* populations occurring as fossils in late glacial deposits in the British Isles, however, are morphologically identical to the extant conspecific populations, with only moderate differences in their present geographical ranges (Coope, 1979a,b).

(3) New spreading, by relatively few *Carabus* species, through the Mediterranean area during the glacial maxima, as new land connections between proximate is-

lands, islets, peninsulas and mainland became possible, owing to the impressive decrease in sea level (as much as -120 m) in different periods. These sea-level oscillations, however, did not allow further land connections between Africa and Europe.

In these catathermic phases, some silvicolous Apennine species reached Sicily from southern Italy, leaving – probably owing to genetic drift and founder effect – moderately differentiated forms (i.e. *C. lefebvrei*), or undifferentiated populations (i.e. *C. convexus*, among others). The same origins have the more or less differentiated forms of *C. coriaceus* present today in the Aegean Islands, with the Ionian (both Greek and Italian) forms of *C. coriaceus* close to *C. coriaceus mediterraneus*, and several populations of *Carabus* species living in the islets that fringe the Dalmatian coast and western Anatolia. Furthermore, suitable land connections between the Bosporus and Dardanelles, until 7.500 ybp, made possible the immigration to the Balkans of a few Anatolian species of the subgenera *Archicarabus*, *Heterocarabus*, *Lamprostus* and *Procerus* (Casale & Vigna Taglianti, 1999), or vice-versa.

(4) At least in some phases of the glacial stadia, and in the phases of re-colonization by arboreal vegetation in the inter-glacial, or last post-glacial stadia, extensive spreading was possible of several tundra, steppe, or taiga adapted species, from Siberia and western Asia to eastern Europe. Evidence of this spreading is provided by the extant populations of several species of the subgenera *Trachycarabus*, *Diocarabus*, *Aulonocarabus* and *Pachycranion*. Among these, *C. maeander* is impressive. A boreal species localized presently in northeastern Asia and North America only, fossilized remains were found in several deposits of the last Glacial stage in Europe. The simultaneous availability of both steppe, open habitat, and extensive land connection in Glacial periods, was particularly favourable to representatives of the subgenus *Pachystus*, which reached Europe and the eastern Mediterranean area from western Asia. This lineage colonized respectively both eastern Europe with the extant, polytypic *C. hungaricus*, Greece and Aegean islands from Asia Minor with *C. graecus* (and its derived, moderately differentiated from, *C. (P.) trojanus*), and the Italian Peninsula from the Balkans, with *C. (P.) cavernosus* (represented today by the subspecies *C. c. variolatus*, localized to the montane pastures of some massifs in Southern Apennines.

Therefore, if this picture is correct, the present distribution of *C. cavernosus* – such as the trans-Ionian distribution of *C. (Oreocarabus) preslii* – has to be recognized as a relict of an originally circum-Adriatic, or trans-Adriatic, Quaternary distribution, and not a very ancient, Tertiary pattern of distribution in the classic sense of Gridelli (1950).

(5) In Holocene time (last 10.000 years), new events modified the previous geographical ranges of many species, and are the subjects of investigation by ecological biogeographers, population ecologists and geneticists, rather than by historical biogeographers (see Chapters 6 and 7). Of particular interest is the spreading of silvicolous or montane species, provided with a more or less high dispersal power, and able to extend their geographic ranges in the reforestation phases subsequent to the last glacial age, or to follow the pioneer vegetation in colonizing the moraines at high altitude. This process produced similar patterns of distribution in different species. A carefully studied example (Weber, *in litt.*) is offered by the adelphotaxa *C. (Hygrocarabus) variolosus* and *C. (H.) nodulosus*, which present today a geographical range markedly coincident with that of the polytypic *C. (Platycarabus) irregularis* (see maps in Chapter 5). Probably, as strictly silvicolous taxa, they survived in two glacial age forest refugia, in the Dinarian and the Carpathian mountain chains, respectively. From the Dinarian refugium, *C. nodulosus* and *C. irregularis* spread westward and then northward; from the Carpathian refugium *C. variolosus* and *C. irregularis* spread north-westward. This ability to re-colonize available re-forested lands in the last millennia, or in the last several centuries, is documented by several, recent contributions. In particular, the *auronitens-punctatoauratus* complex offers an excellent model for research on: morphological differentiation (with taxonomic implications), genetics, dynamic and age structure of populations and metapopulations, identification of glacial refugia, and ways and times of dispersal (Assmann, 1995; Assmann *et al.*, 1994; Hockmann *et al.*, 1998; Niehues *et al.*, 1996; Reimann, 2000; Schwoppe *et al.*, 1998; Terlutter, 1991). Furthermore, *C. auronitens* was able to colonize, from central Europe, two reduced sections of the southern side of the Alps, following the re-forested slopes of the Dora Baltea valley in northwestern Italy, and the Adige valley in northeastern Italy, respectively (Casale *et al.*, 1982), just as *C. nemoralis* succeeded in doing.

Other species, however, showed a very reduced dispersal power at present: not only several cited, impressively localized, steno-endemic and relict taxa, but also others – with a present wide distribution – in some sections of their range. *C. glabratus* is a good example of a eurytopic species with a low dispersal power in Central Europe (Assmann, 1998).

(6) Finally, man has served as a biogeographic factor for European *Carabus* species, not only in reducing geo-

graphic ranges owing to modification or destruction of suitable habitats, but also in increasing ranges by providing passive transportation. The successful trans-continental introductions of *C. granulatus*, *C. auratus* and *C. nemoralis*, from Europe to North America, are the most famous examples. But more reduced movements among coasts, isles and islets of the Mediterranean area (by species such as *C. morbillosus* and *C. coriaceus*), or among inland territories (by species such as *C. septemcarinatus* and *C. varians*), are documented and cited (see Chapter 5. *Species accounts*). The very recent discovery of an introduced population of *C. montivagus* in the eastern Italian Alps (Vigna Taglianti *et al.*, 2000), confirms that probably other cases of anthropogenic introductions occur, but have not been ascertained yet.

APPENDIX 8.1. Distribution, taxonomic and chorological characteristics of *Carabus* species in Europe

Abbreviations:

IC – Island; **FC** – Fennoscandia (including Kola Peninsula and Russian Karelia, southern boundary coincides with the gulfs of Dvina and Onega, and with the southern shores of the lakes Ladoga and Onega); **WC** – Western and Central Europe (France, north of Garona River, Benelux, Alps, Germany, Switzerland, Italy north of Po River, Austria, Czech and Slovac republics, Poland); **PC** – Pannonian-Carpathian Region (Hungary, Romania, Northern Serbia, Ukrainian Carpathians); **RU** – Russian Plain (East European Russian Plain – Byelorussia, Estonia, Lithuania and Latvia, Ukraine except for the Carpathians, all the European part of Russia southwards to the Kumo-Manych Basin (the line Rostov-Kizlyar Bey)); **UR** – The Ural Mountains; **CR** – Crimean Peninsula; **BA** – Balkan Peninsula, nothern boundary along the rivers Danube, Sava and Izontso, including Northeast Italy (Triest region); **AP** – Apennine Peninsula (south of Po River, including Corsica, Sardinia and Sicily); **IB** – Iberian Peninsula (Spain, Portugal and France south of Garona River).

Suprasubgeneric groups:

SPIN – Spinulati (subgenus *Limnocarabus*); **DIGI** – Digitulati & Lipastromorphi (*Morphocarabus*, *Carabus* s.str., *Eucarabus*, *Tachypus*); **ARCH** – Archicarabomorphi (*Archicarabus*); **MULA** – Multistriati A (*Hemicarabus*, *Diocarabus*, *Aulonocarabus*, *Mesocarabus*, *Orinocarabus*, *Oreocarabus*, *Tomocarabus*, *Eurycarabus*, *Pachystus*); **MULB** – Multistriati B (*Ctenocarabus*, *Rhabdotocarabus*, *Hygrocarabus*, *Chaetocarabus*, *Platycarabus*, *Heterocarabus*, *Sphodristocarabus*, *Megodontus*, *Pachycranion*, Iniopachys, *Chrysocarabus*, *Chrysotribax*, *Macrothorax*, *Lamprostus*, *Procrustes*, *Procerus*)

Range characteristics and chorotypes:

In the present study we use two types of arealogical classification of the species. First, each species is classified to a certain 'chorotype' which assumes the main area where the species is distributed (sensu Vigna Taglianti *et al.*, 1993, 1999, with some changes). Second, a descriptive and more detailed 'range characteristics' ('chorotype') is assigned to each species. For instance, the abbreviation of the type **EEU-URAL: Ural(S)** means 'species of Eastern European-Uralian chorotype', distributed in the Southern Ural. The methodology of the arealogical classifications of the species ranges is described in Chapter 8. The following abbreviations are used to properly characterise the distribution of each species:

Chorotypes:

ASE = Asiatic-European, **SIB** = Siberian, **SIE** = Sibero-European, **EUR** = European, possibly extended (*C. coriaceus*) to part of Asia Minor, **CEU** = C-European, **SEU** = S-European (see sub-divisions below), **WEU** = W-European (see sub-divisions below), **EEU** = E-European (see subdivisions below), **NAF** = N-African, **WME** = W-Mediterranean, **EME** = E-Mediterranean.

CAUC = Caucasian (eventually extended to the mountains of S-Crimea), **CAUC-CRIM** – Caucasian-Crimean species, eventually extending to the southernmost steppe part of European Russia, **ANAT** = Anatolian (extended to the Balcanian peninsula), **POCA** = Ponto-Caucasian (extended to some parts of SE-Europe).

EEU-CARP = E-European-Carpathian (extended sometimes to the neighbouring hilly regions of western Ukraine), **EEU-PANN** = E-European-Pannonian (Pannonian Plain, western Romania and northern regions of the Balkan peninsula), **EEU-SEEU** = E-European-SE-European (distributed from the southern steppes of European Russia to the Pannonian Plain in the east and Balkans in the south), **EEU-SWRU** = E-European-SW-Russian (southwestern region of the Russian Plain, i.e. Central-Chernozem region, Ukraine, Moldova, sometimes in the adjacent regions of Romania and Poland), **EEU-CRUS** = E-European-C-Russian (middle region of European Russia, that is forest-steppe and steppe zone between Dnieper and Volga rivers), **EEU-URAL** = E-European-Uralian (endemic to the Ural mountain range).

WEU-PYRE = W-European (Pyrenees), **WEU-IBER** = W-European (Iberian peninsula, extended eventually to Rif), **WEU-IBEN** = W-European (northern part of Iberian Peninsula), **WEU-IBEC** = W-European (central part of Iberian peninsula), **WEU-IBES** = W-European (southern part of Iberian peninsula).

SEU-ALAP = S-European (Alpino-Apennine), **SEU-ALPW** = S-European (endemic to W-Alps, eventually extended to the Ligurian Apennines), **SEU-ALPC** = S-European (endemic to Central Alps), **SEU-ALPE** = S-European (endemic to E-Alps, eventually extended to the Dinaric Alps), **SEU-ALPI** = S-European (Alpine element, more or less extended to the Padanian Plain and/or Dinaric Alps), **SEU-ALCA** = S-European (Alpino-Carpathian), **SEU-APPE** = S-European

(Apennine), **SEU-APDI** = S-European (Apennino-Dinaric, i.e. trans-adriatic/trans-ionian element), **SEU-CADI** = S-European (Carso-Istrian-Dinaric, eventually extended to C- and E-Pre-Alps), **SEU-DIBA** = S-European (Dinaric-Balcanian, eventually extended to E-Alps), **SEU-CABA** = S-European (Carpatho-Balcanian), **SEU-TYRR** = S-European (Tyrrhenian), **SEU-SACO** = S-European (Sardo-Corsican endemic), **SEU-SICI** = S-European (Sicilian endemic), **SEU-CRET** (endemic to Crete, eventually extended to some Aegean Islands), **SEU-GRNC** = S-European (endemic to North and Central Greece), **SEU-THES** = S-European (endemic to Thessalia), **SEU-PELO** = S-European (endemic to Peloponnesos), **SEU-FRAS** = S-European (endemic to S-France).

Range characteristics:

Eur – European, **EEur** – E-European, **CEur** – C-European (and so on); **Balk** – Balkanian, **Alpi** – Alpinian (distributed in the Alps), **Carp** – Carpathian, **Apen** – Apennine, **Iber** – Iberian, **NAfr** – N-African, **Anat** – Anatolian, **Pont** – Pontic (territories around the Black Sea), **Cauc** – Caucasian **Sib** – Siberian, **WSib** – W-Siberian (and so on), **Asi** – Asian, **EAsi** – E-Asian (the Palearctic part of East Asia!).

Combinations of range characteristics:

Each chorotype can consist of one chorological category, e.e. **EEur** or two or three categories, for instance **CEur-SEEur** (distributed in Central and Southeastern Europe), or **EEur(E)-Sib-EAsi** (distributed in the easternmost parts of Eastern Europe, Siberia and East Asia (from Japan to Korea and Northern China).

Abbreviations in brackets:

C – central, **S** – southern, **W** – western, **E** – eastern, **P** – pan (=whole), respectively **SE** – southeastern, **NW** – northwestern and so on.

SG	SPE	SPECIES	GROUP	SUBGENUS	RANGE CHARACTERISTICS	CHOROTYPE	IC	BI	FE	WC	PC	RU	UR	CR	BA	AP	IB	TOT
1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
01	001	CLATRATUS	SPIN	Limnocarabus	Eur-Sib-EAsi	**ASE**	0	1	1	1	1	1	1	1	1	1	0	9
02	001	AERUGINOSUS	DIGI	Morphocarabus	EEur(E)-Sib	**SIB**	0	0	0	0	0	1	1	0	0	0	0	2
02	002	BESSERI	DIGI	Trachycarabus	EEur(SW)	**EEU-SWRU**	0	0	0	0	1	1	0	0	0	0	0	2
02	003	BOSPHORANUS	DIGI	Trachycarabus	Crim-Cauc	**CAUC-CRIM**	0	0	0	0	0	0	0	1	0	0	0	1
02	004	COMPTUS	DIGI	Morphocarabus	Carp	**EEU-CARP**	0	0	0	0	1	0	0	0	0	0	0	1
02	005	ERRANS	DIGI	Trachycarabus	Eeur(SW)	**EEU-SWRU**	0	0	0	0	0	1	0	0	0	0	0	1
02	006	ESTREICHERI	DIGI	Trachycarabus	EEur(CS)-Wsib	**EEU**	0	0	0	0	0	1	1	0	0	0	0	2
02	007	EXCELLENS	DIGI	Morphocarabus	EEur(SW)	**EEU-SWRU**	0	0	0	1	1	1	0	0	0	0	0	3
02	008	HAERES	DIGI	Trachycarabus	EEur(C)	**EEU-CRUS**	0	0	0	0	0	1	0	0	0	0	0	1
02	009	HAMPEI	DIGI	Morphocarabus	Carp	**EEU-CARP**	0	0	0	0	1	0	0	0	0	0	0	1
02	010	HENNINGI	DIGI	Morphocarabus	EEur(E)-CSib	**SIB**	0	0	0	0	0	1	1	0	0	0	0	2
02	011	HUMMELI	DIGI	Morphocarabus	EEur(NE)-Asi	**SIB**	0	0	0	0	0	1	1	0	0	0	0	2
02	012	KARPINSKII	DIGI	Morphocarabus	Ural(S)	**EEU-URAL**	0	0	0	0	0	0	1	[illegible]	0	0	0	1
02	013	KOLLARI	DIGI	Morphocarabus	Pann-Carp	**EEU-CARP**	0	0	0	0	1	0	0	0	1	0	0	2
02	014	MONILIS	DIGI	Morphocarabus	WEur-CEur	**EUR**	0	1	1	1	0	0	0	0	0	0	1	4
02	015	ODORATUS	DIGI	Morphocarabus	EEur(NE)-Sib	**SIB**	0	0	0	0	0	1	1	0	0	0	0	2
02	016	PERRINI (=CAMPES.)	DIGI	Trachycarabus	EEur(S)	**CAUC-CRIM**	0	0	0	0	0	1	1	1	0	0	0	3
02	017	REGALIS	DIGI	Morphocarabus	EEur(E)-CSib	**SIB**	0	0	0	0	0	1	1	0	0	0	0	2
02	018	ROTHI	DIGI	Morphocarabus	Carp	**EEU-CARP**	0	0	0	0	1	0	0	0	0	0	0	1
02	019	RYBINSKII	DIGI	Trachycarabus	EEur(W)	**EEU-CARP**	0	0	0	0	0	1	0	0	0	0	0	1
02	020	SCABRIUSCULUS	DIGI	Trachycarabus	EEur(W)-CEur-SEEur	**EEU-SEEU**	0	0	0	1	1	1	0	0	1	0	0	4
02	021A	SCHEIDLERI	DIGI	Morphocarabus	CEur	**EEU-PANN**	0	0	0	1	1	0	0	0	1	0	0	3
02	021B	VERSICOLOR	DIGI	Morphocarabus	Balk	**SEU-DIBA**	0	0	0	0	0	0	0	0	1	0	0	1
02	022	SIBIRICUS	DIGI	Trachycarabus	EEur(E)-CSib	**SIB**	0	0	0	0	0	1	1	0	0	0	0	2
02	023A	ZAWADZKII	DIGI	Morphocarabus	Carp(N)	**EEU-CARP**	0	0	0	1	1	0	0	0	0	0	0	2
02	023B	ZHERICHINI	DIGI	Morphocarabus	Eeur(E)-Sib	**SIB**	0	0	0	0	0	0	1	0	0	0	0	0
03	001	GRANULATUS	DIGI	Carabus *s.str.*	Eur-Sib-EAsi	**ASE**	0	1	1	1	1	1	1	1	1	1	1	10
03	002	MENETRIESI	DIGI	Carabus *s.str.*	CEur-EEur(NC)-WSib	**EEU**	0	0	1	1	0	1	0	0	1	0	0	4
04	001	ARVENSIS	DIGI	Eucarabus	Eur-Sib-EAsi	**SIE**	0	1	1	1	1	1	1	0	1	0	0	7
04	002	CATENULATUS	DIGI	Eucarabus	Alpi-Dina	**SEU-CADI**	0	0	0	0	1	0	0	0	1	1	0	3
04	003A	CRISTOFORII	DIGI	Eucarabus	Iber(NE)	**WEU-PYRE**	0	0	0	0	0	0	0	0	0	0	1	1
04	003B	DEYROLLEI	DIGI	Eucarabus	Iber(NW)	**WEU-IBEN**	0	0	0	0	0	0	0	0	0	0	1	1
04	004	ITALICUS	DIGI	Eucarabus	Alpi-Apen	**SEU-ALAP**	0	0	0	1	0	0	0	0	1	1	0	3
04	005	OBSOLETUS	DIGI	Eucarabus	Pann-Carp	**EEU-CARP**	0	0	0	1	1	0	0	0	0	0	0	2

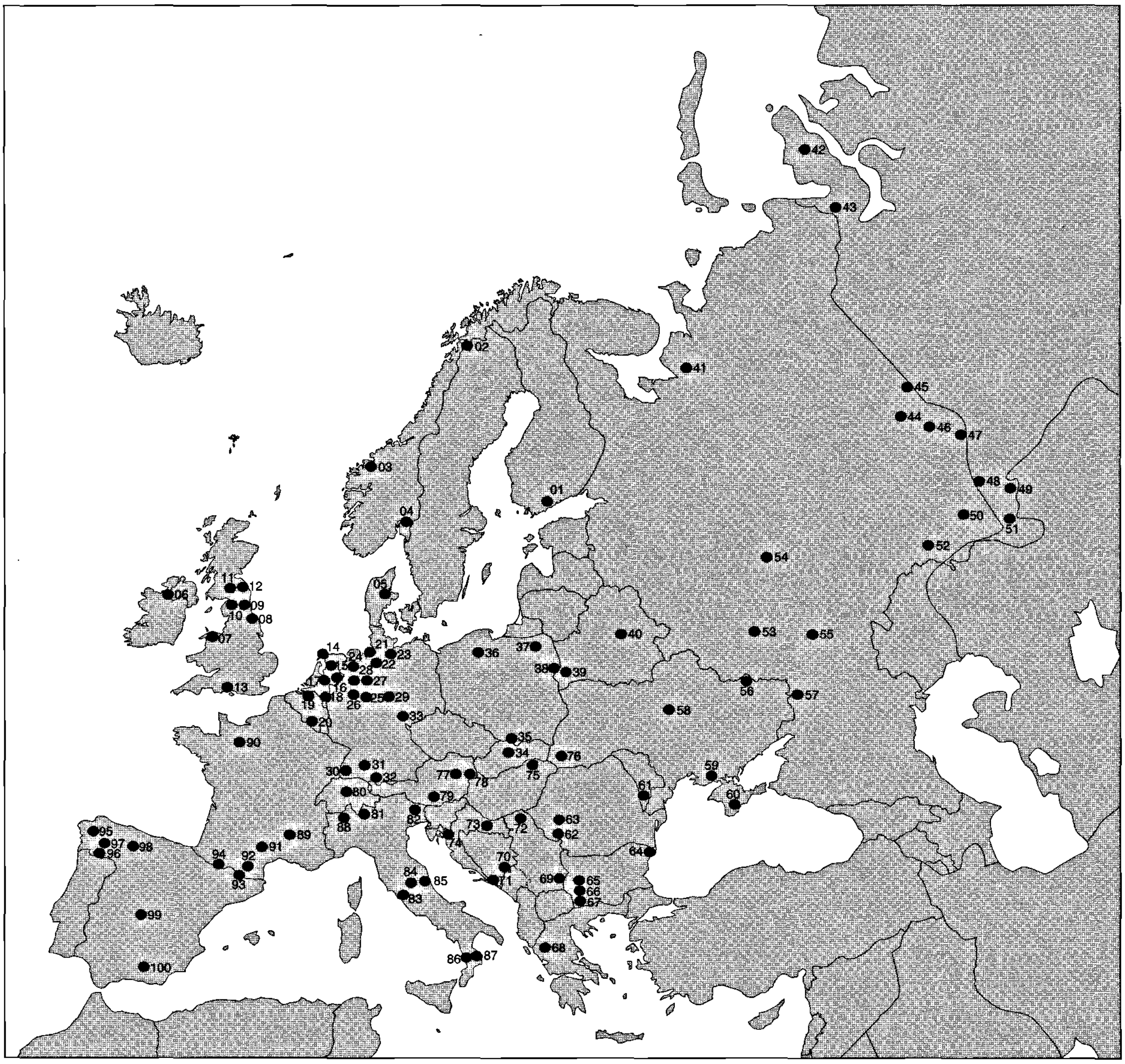
1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
04	006	PARREYSSII	DIGI	Eucarabus	Balk(NW)	**SEU-CADI**	0	0	0	0	0	0	0	0	1	0	0	1
04	007	STSCHEGLOWI	DIGI	Eucarabus	EEur(C)-Wsib	**EEU**	0	0	0	0	0	1	1	1	0	0	0	3
04	008	ULRICHII	DIGI	Eucarabus	CEur-SEEur	**CEU**	0	0	0	1	1	1	0	0	1	0	0	4
05	001	AURATUS	DIGI	Tachypus	WEur	**CEU**	0	1	1	1	0	0	0	0	0	0	1	4
05	002	CANCELLATUS	DIGI	Tachypus	Eur-CSib	**SIE**	0	1	1	1	1	1	1	1	1	1	1	10
05	003	VAGANS	DIGI	Tachypus	Alpi(W)	**SEU-ALPW**	0	0	0	1	0	0	0	0	0	0	0	1
06	001	ALYSIDOTUS	ARCH	Archicarabus	Alpi(W)	**SEU-TYRR**	0	0	0	1	0	0	0	0	0	1	0	2
06	002	MONTICOLA	ARCH	Archicarabus	Alpi(W)	**SEU-ALPW**	0	0	0	1	0	0	0	0	0	1	0	2
06	003	MONTIVAGUS	ARCH	Archicarabus	SEEur	**SEU-CABA**	0	0	0	1	1	0	0	0	1	0	0	3
06	004	NEMORALIS	ARCH	Archicarabus	WEur-CEur	**EUR**	0	1	1	1	1	1	1	1	1	1	1	10
06	005	PSEUDOMONTICOLA	ARCH	Archicarabus	Iber(NE)	**WEU-PYRE**	0	0	0	0	0	0	0	0	0	0	1	1
06	006	ROSSII	ARCH	Archicarabus	Apen	**SEU-APPE**	0	0	0	0	0	0	0	0	0	1	0	1
06	007	STEUARTII	ARCH	Archicarabus	Iber(NW)	**WEU-IBEN**	0	0	0	0	0	0	0	0	0	0	1	1
06	008	WIEDEMANNI	ARCH	Archicarabus	Balk(SE)-Anat	**ANAT**	0	0	0	0	0	0	0	0	1	0	0	1
07	001	NITENS	MULA	Hemicarabus	NCEur	**SIE**	0	1	1	1	1	1	1	0	0	0	0	6
08	001	LOSCHNIKOVII	MULA	Diocarabus	EEur(E)-CSib	**SIB**	0	0	0	0	0	1	1	0	0	0	0	2
08	002	TRUNCATICOLLIS	MULA	Diocarabus	EEur-Sib	**SIB**	0	0	0	0	0	1	1	0	0	0	0	2
09	001	CANALICULATUS	MULA	Aulonocarabus	EEur(NE)-Sib-EAsi	**SIB**	0	0	0	0	0	1	1	0	0	0	0	2
10	001	DUFOURII	MULA	Mesocarabus	Iber(SW)	**WEU-IBEC**	0	0	0	0	0	0	0	0	0	0	1	1
10	002	LUSITANICUS	MULA	Mesocarabus	Iber(P)	**WEU-IBER**	0	0	0	0	0	0	0	0	0	0	1	1
10	003	MACROCEPHALUS	MULA	Mesocarabus	Iber(N)	**WEU-IBEN**	0	0	0	0	0	0	0	0	0	0	1	1
10	004	PROBLEMATICUS	MULA	Mesocarabus	NEur-CEur-WEur	**EUR**	1	1	1	1	1	1	0	0	1	1	1	9
11	001	ADAMELLICOLA	MULA	Orinocarabus	Alpi(C)	**SEU-ALPC**	0	0	0	1	0	0	0	0	0	0	0	1
11	002	ALPESTRIS	MULA	Orinocarabus	Alpi(CE)	**SEU-ALPE**	0	0	0	1	0	0	0	0	0	0	0	1
11	003	BERTOLINII	MULA	Orinocarabus	Alpi(C)	**SEU-ALPE**	0	0	0	1	0	0	0	0	0	0	0	1
11	004	CARINTHIACUS	MULA	Orinocarabus	Alpi(E)-Balk(W)	**SEU-ALPE**	0	0	0	1	0	0	0	0	1	0	0	2
11	005	CASTANOPTERUS	MULA	Orinocarabus	Alpi(C)	**SEU-ALPC**	0	0	0	1	0	0	0	0	0	0	0	1
11	006	CENISIUS	MULA	Orinocarabus	Alpi(W)	**SEU-ALPW**	0	0	0	1	0	0	0	0	0	0	0	1
11	007A	CONCOLOR	MULA	Orinocarabus	Alpi(C)	**SEU-ALPW**	0	0	0	1	0	0	0	0	0	0	0	1
11	007B	LEPONTINUS	MULA	Orinocarabus	Alpi(CW)	**SEU-ALPC**	0	0	0	1	0	0	0	0	0	0	0	1
11	008	FAIRMAIREI	MULA	Orinocarabus	Alpi(C)	**SEU-ALPW**	0	0	0	1	0	0	0	0	0	0	0	1
11	009	HETEROMORPHUS	MULA	Orinocarabus	Alpi(W)	**SEU-ALPW**	0	0	0	1	0	0	0	0	0	0	0	1
11	010	LATREILLEANUS	MULA	Orinocarabus	Alpi(W)	**SEU-ALPW**	0	0	0	1	0	0	0	0	0	0	0	1
11	011	LINNAEI	MULA	Orinocarabus	CEur-EEur(W)-Balk(N)	**SEU-ALCA**	0	0	0	1	1	1	0	0	0	0	0	3
11	012	PUTZEYSIANUS	MULA	Orinocarabus	Alpi(W)	**SEU-ALPW**	0	0	0	1	0	0	0	0	0	0	0	1
11	013	SYLVESTRIS	MULA	Orinocarabus	CEur	**SEU-ALCA**	0	0	0	1	1	0	0	0	0	0	0	2

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
12	001	AMPLIPENNIS	MULA	Oreocarabus	Iber(NW)	**WEU-IBEN**	0	0	0	0	0	0	0	0	0	0	1	1
12	002	GHILIANII	MULA	Oreocarabus	Iber(C)	**WEU-IBEC**	0	0	0	0	0	0	0	0	0	0	1	1
12	003	GLABRATUS	MULA	Oreocarabus	CNEur-WSib	**EUR**	0	1	1	1	1	1	1	0	1	1	0	8
12	004	GUADARRAMUS	MULA	Oreocarabus	Iber(C)	**WEU-IBEC**	0	0	0	0	0	0	0	0	0	0	1	1
12	005	HORTENSIS	MULA	Oreocarabus	NCEur-SEEur	**EUR**	0	0	1	1	1	1	1	0	1	1	0	7
12	006	PRESLII	MULA	Oreocarabus	Apen(SW)-Balk(W)	**SEU-APDI**	0	0	0	0	0	0	0	0	1	1	0	2
13	002	BESSARABICUS	MULA	Tomocarabus	EEur(S)-Kaza	**SIE**	0	0	0	0	0	1	1	1	0	0	0	3
13	003	CONVEXUS	MULA	Tomocarabus	Eur-Anat-Wsib	**SIE**	0	0	1	1	1	1	1	0	1	0	1	7
13	004	MARGINALIS	MULA	Tomocarabus	EEur(C)-WSib	**EEU**	0	0	0	1	1	1	1	1	0	0	0	5
14	001	FAMINII	MULA	Eurycarabus	NAfr-Sici	**NAF**	0	0	0	0	0	0	0	0	0	1	0	1
14	002	GENEI	MULA	Eurycarabus	Sard-Cors	**SEU-SACO**	0	0	0	0	0	0	0	0	0	1	0	1
15	001	CAVERNOSUS	MULA	Pachystus	Apen(CW)-Balk(WC)	**SEU-APDI**	0	0	0	0	0	0	0	0	1	1	0	2
15	002	CRIBELLATUS	MULA	Pachystus	EEur(E)-CSib(S)	**SIB**	0	0	0	0	0	0	1	0	0	0	0	1
15	003	GRAECUS	MULA	Pachystus	Balk-Anat	**EME**	0	0	0	0	0	0	0	0	1	0	0	1
15	004	HUNGARICUS	MULA	Pachystus	Pann-EEur(S)	**EEU-SEEU**	0	0	0	1	1	1	0	1	0	0	0	4
15	005	TROJANUS	MULA	Pachystus	Balk(S)	**SEU-CRET**	0	0	0	0	0	0	0	0	1	0	0	1
16	001	GALICIANUS	MULB	Ctenocarabus	Iber(W)	**WEU-IBEC**	0	0	0	0	0	0	0	0	0	0	1	1
17	001	MELANCHOLICUS	MULB	Rhabdotocarabus	Iber-NAfr	**WEU-IBER**	0	0	0	1	0	0	0	0	0	0	1	2
18	001	NODULOSUS	MULB	Hygrocarabus	CEur	**CEU**	0	0	0	1	0	0	0	0	0	1	0	2
18	002	VARIOLOSUS	MULB	Hygrocarabus	CEur-SEEur	**EEU-PANN**	0	0	0	1	1	1	0	0	1	0	0	4
19	001	ARCADICUS	MULB	Chaetocarabus	Balk(S)	**SEU-GRNC**	0	0	0	0	0	0	0	0	1	0	0	1
19	002	INTRICATUS	MULB	Chaetocarabus	CEur-SEEur	**EUR**	0	0	0	1	1	1	0	0	1	0	0	4
19	003	KRUEPERI	MULB	Chaetocarabus	Balk(S)	**SEU-THES**	0	0	0	0	0	0	0	0	1	0	0	1
19	004	LEFEBVREI	MULB	Chaetocarabus	Apen	**SEU-APPE**	0	0	0	0	0	0	0	0	0	1	0	1
19	005	MERLINI	MULB	Chaetocarabus	Balk(S)	**SEU-PELO**	0	0	0	0	0	0	0	0	0	1	0	1
20	001	DEPRESSUS	MULB	Platycarabus	Alpi(N)	**SEU-ALPI**	0	0	0	1	0	0	0	0	0	0	0	1
20	002	CREUTZERI	MULB	Platycarabus	Alpi(CE)	**SEU-ALPE**	0	0	0	1	1	0	0	0	1	0	0	3
20	003	CYCHROIDES	MULB	Platycarabus	Alpi(W)	**SEU-ALPW**	0	0	0	1	0	0	0	0	0	0	0	1
20	004	FABRICII	MULB	Platycarabus	Alpi-Carp	**SEU-ALCA**	0	0	0	1	1	0	0	0	0	0	0	2
20	005	IRREGULARIS	MULB	Platycarabus	CEur-SEEur	**EUR**	0	0	0	1	1	0	0	0	1	0	0	3
21	001	MARIETTI	MULB	Heterocarabus	Balk(SE)-Anat(N)	**ANAT**	0	0	0	0	0	0	0	0	1	0	0	1
22	001	VARIANS (=JANTHIN.)	MULB	Sphodristocarabus	Cauc(W)	**CAUC**	0	0	0	0	0	0	1	0	0	0	0	1
23	001	AUROLIMBATUS	MULB	Megodontus	EEur(S)-CSib	**SIE**	0	0	0	0	0	1	1	0	0	0	0	2
23	002	CAELATUS	MULB	Megodontus	Balk(W)	**SEU-CADI**	0	0	0	0	0	0	0	0	1	0	0	1
23	003	CROATICUS	MULB	Megodontus	Balk(W)	**SEU-CADI**	0	0	0	0	0	0	0	0	1	0	0	1
23	004	EXARATUS	MULB	Megodontus	Cauc-EEur(S)	**CAUC**	0	0	0	0	0	0	1	0	0	0	0	1

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
23	005	GERMARII	MULB	Megodontus	CEur-SEEur	**SEU-ALPI**	0	0	0	1	0	0	0	0	1	1	0	3
23	006	GYLLENHALI	MULB	Megodontus	Crim	**CAUC-CRIM**	0	0	0	0	0	0	0	1	0	0	0	1
23	007	PLANICOLLIS	MULB	Megodontus	Carp	**EEU-CARP**	0	0	0	0	1	0	0	0	0	0	0	1
23	009	SEPTEMCARINATUS	MULB	Megodontus	Cauc-Anat(NE)	**CAUC**	0	0	0	0	0	1	0	0	0	0	0	1
23	010	VIOLACEUS	MULB	Megodontus	CNEur	**EUR**	0	1	1	1	1	1	1	0	1	1	1	9
24	001	ERMAKI	MULB	Pachycranion	EEur(NE)-WSib	**SIB**	0	0	0	0	0	1	1	0	0	0	0	2
24	002	SCHOENHERRI	MULB	Pachycranion	EEur(C)-CSib	**SIB**	0	0	0	0	0	1	1	0	0	0	0	2
25	001	AURICULATUS	MULB	Iniopachys	Iber(N)	**WEU-IBEN**	0	0	0	0	0	0	0	0	0	0	1	1
25	002	PYRENAEUS	MULB	Iniopachys	Iber(NW)	**WEU-PYRE**	0	0	0	0	0	0	0	0	0	0	1	1
26	001	AURONITENS	MULB	Chrysocarabus	CEur	**CEU**	0	0	0	1	1	0	0	0	1	0	1	4
26	002	LINEATUS	MULB	Chrysocarabus	Iber(N)	**WEU-IBEN**	0	0	0	0	0	0	0	0	0	0	1	1
26	003	OLYMPIAE	MULB	Chrysocarabus	Alpi(W)	**SEU-ALPW**	0	0	0	1	0	0	0	0	0	0	0	1
26	004	SOLIERI	MULB	Chrysocarabus	Alpi(W)	**SEU-ALPW**	0	0	0	1	0	0	0	0	0	1	0	2
26	005	SPLENDENS	MULB	Chrysocarabus	Iber(NW)	**WEU-PYRE**	0	0	0	0	0	0	0	0	0	0	1	1
26	006	RUTILANS	MULB	Chrysocarabus	Iber(NW)	**WEU-PYRE**	0	0	0	0	0	0	0	0	0	0	1	1
26	007	HISPANUS	MULB	Chrysocarabus	WEur(W)	**SEU-FRAS**	0	0	0	1	0	0	0	0	0	0	0	1
28	001	MORBILLOSUS	MULB	Macrothorax	NAfr-Sici-Iber(SE)	**WME**	0	0	0	1	0	0	0	0	0	1	1	3
28	002	PLANATUS	MULB	Macrothorax	Sici	**SEU-SICI**	0	0	0	0	0	0	0	0	0	1	0	1
28	003	RUGOSUS	MULB	Macrothorax	Iber(S)-NAfr	**WEU-IBER**	0	0	0	0	0	0	0	0	0	0	1	1
29	001	TOROSUS	MULB	Lamprostus	Balk(SE)-Anat	**ANAT**	0	0	0	0	0	0	0	0	1	0	0	1
30	001	BANONI	MULB	Procrustes	Balk(S)	**SEU-CRET**	0	0	0	0	0	0	0	0	1	0	0	1
30	002	CORIACEUS	MULB	Procrustes	Eur-Anat(W)	**EUR**	0	0	1	1	1	1	0	0	1	1	0	6
31	001	DUPONCHELII	MULB	Procerus	Balk(S)	**SEU-PELO**	0	0	0	0	0	0	0	0	1	0	0	1
31	002	GIGAS	MULB	Procerus	SEEur	**SEU-DIBA**	0	0	0	1	1	0	0	0	1	0	0	3
31	003	SCABROSUS	MULB	Procerus	Balk(SE)-Crim-Cauc-Anat	**POCA**	0	0	0	0	0	0	0	1	1	0	0	2
31	004	SOMMERI	MULB	Procerus	Balk(S)	**ANAT**	0	0	0	0	0	0	0	0	1	0	0	1
	Number of species						1	11	15	58	37	42	32	12	44	25	28	
	Number of subgenera						1	10	12	20	19	19	15	10	20	15	14	

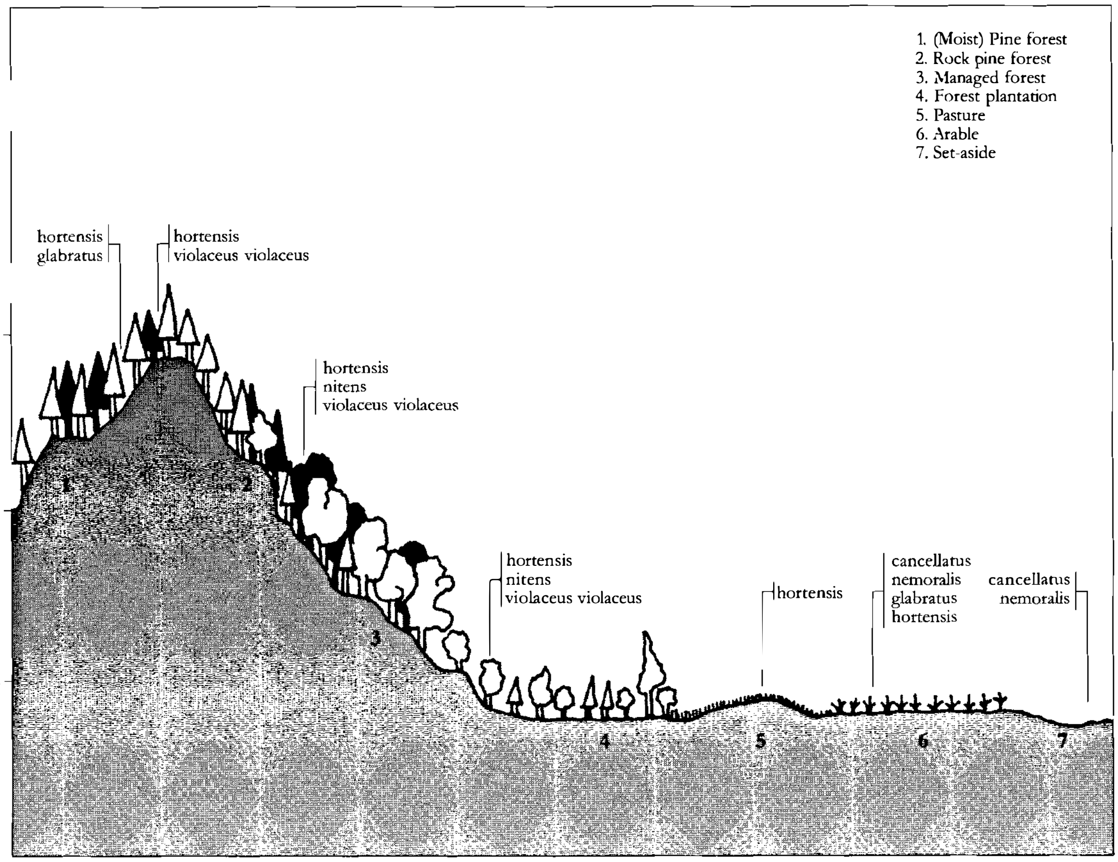
APPENDIX 8.2. Distribution map of 100 local faunas and schematic pictures of all local gradients (=transects)[3]

The numbers on the map correspond to the number of each local gradient (from T-01 to T-100) on the following pages. For an overview of the number of species, compare Fig. 8.9. For further explanation, see section 8.4.2, p. 346.

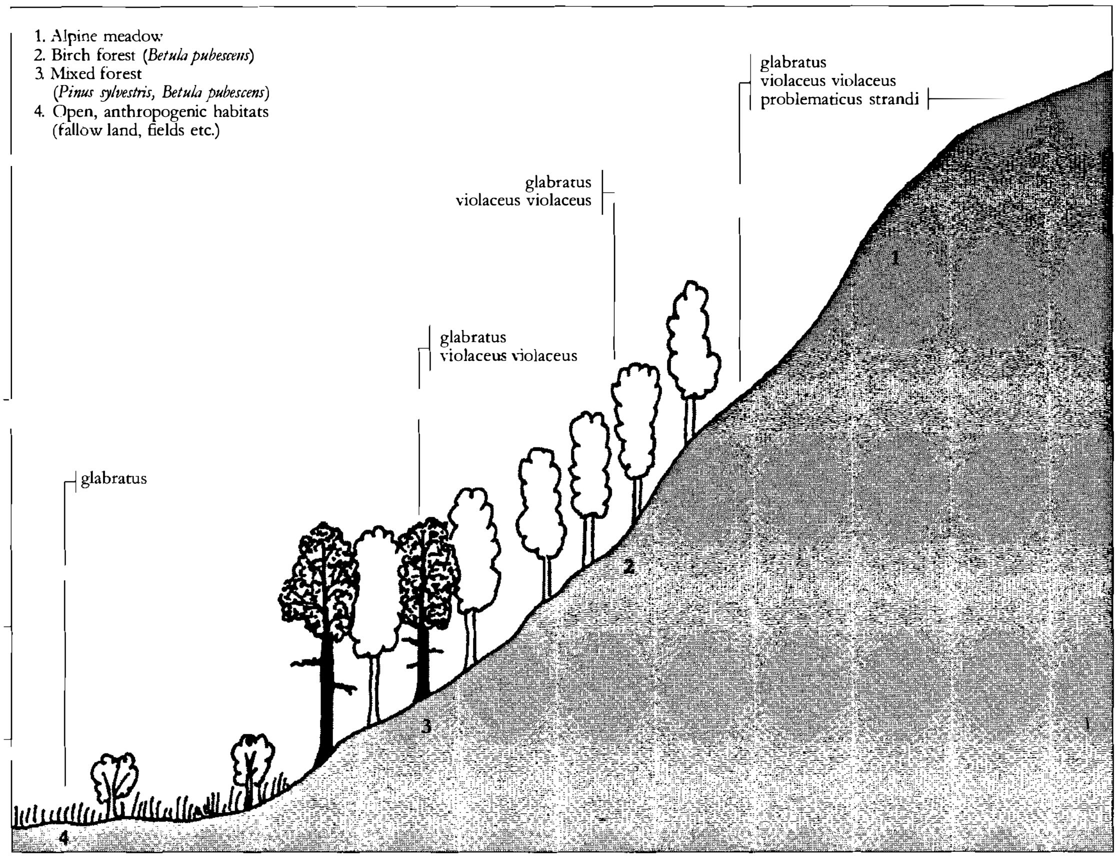


01: S. Finland; 02-04: Norway; 05: Denmark; 06: Ireland; 07-13: Britain; 14-18: The Netherlands; 19-20: Belgium; 21-33: Germany; 34: Slovakia; 35-38: Poland; 39-57: Russia; 58-60: Ukraine; 61: Moldova; 62-63: Romania; 64-67: Bulgaria; 68: N. Greece; 69-74: Former Yugoslavia; 75-76: Hungary/Ukraine; 77-79: Austria; 80-81: Switzerland; 82-88: Italy; 89-94: France; 95-100: Iberian Peninsula.

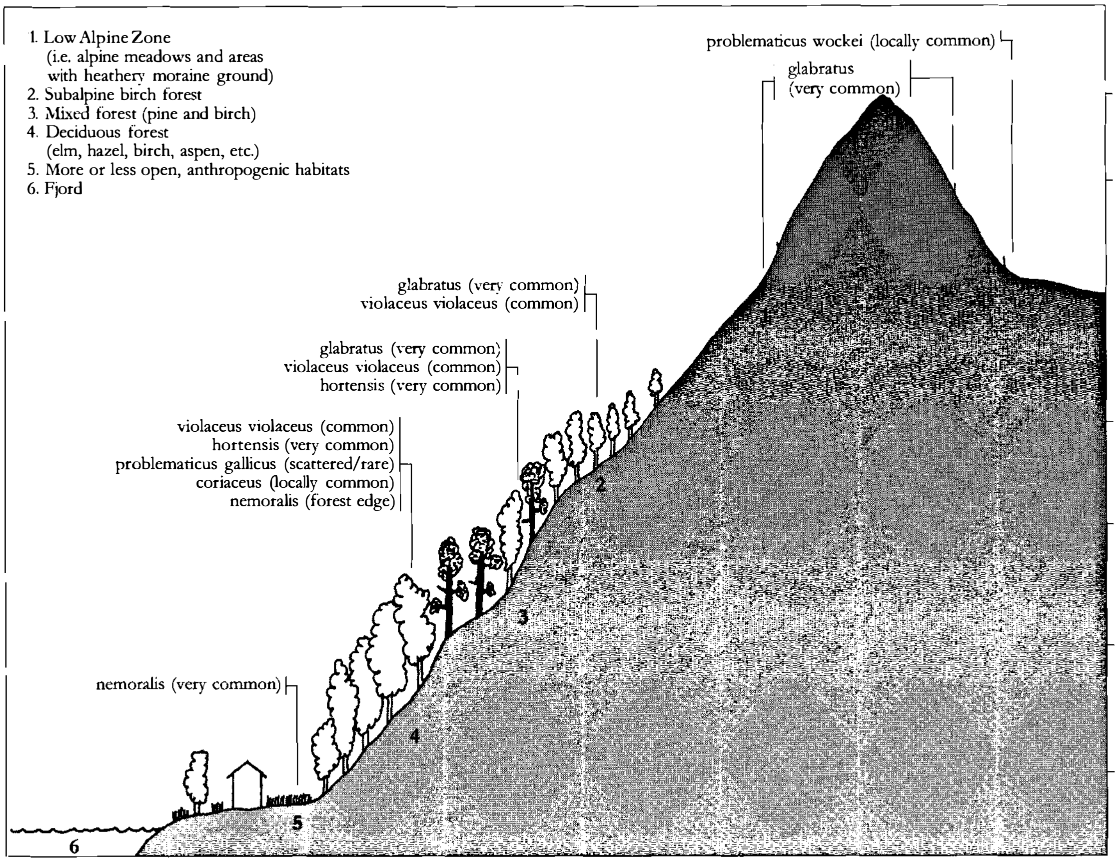
[3] The figures T-01 to T-100 were obtained from highly heterogeneous sources. Very few could be taken directly from published figures, but the main part were delivered in form of pencilled sketches or summarised data lists. Others were taken from data from pitfall trapping. In order to harmonise these data that are meant to present local *Carabus* faunas in an easy way, most figures were re-made by the publisher. However, we did not uniform the transects in a strict way. The transects reflect to a certain degree the different styles of the original contributions. In two cases (T-62 and T-76), situation maps are presented instead of a gradient. After the geographical information in the figures and texts, we mention the name of the contributor to the respective figure. We stress that these investigators who all cooperated generously, are in no way responsible for eventual mistakes that could be generated in the proces of harmonising and/or transferring data from their publications into the figure. The editors of the present book take full responsibility for eventual misinterpretations of any kind.



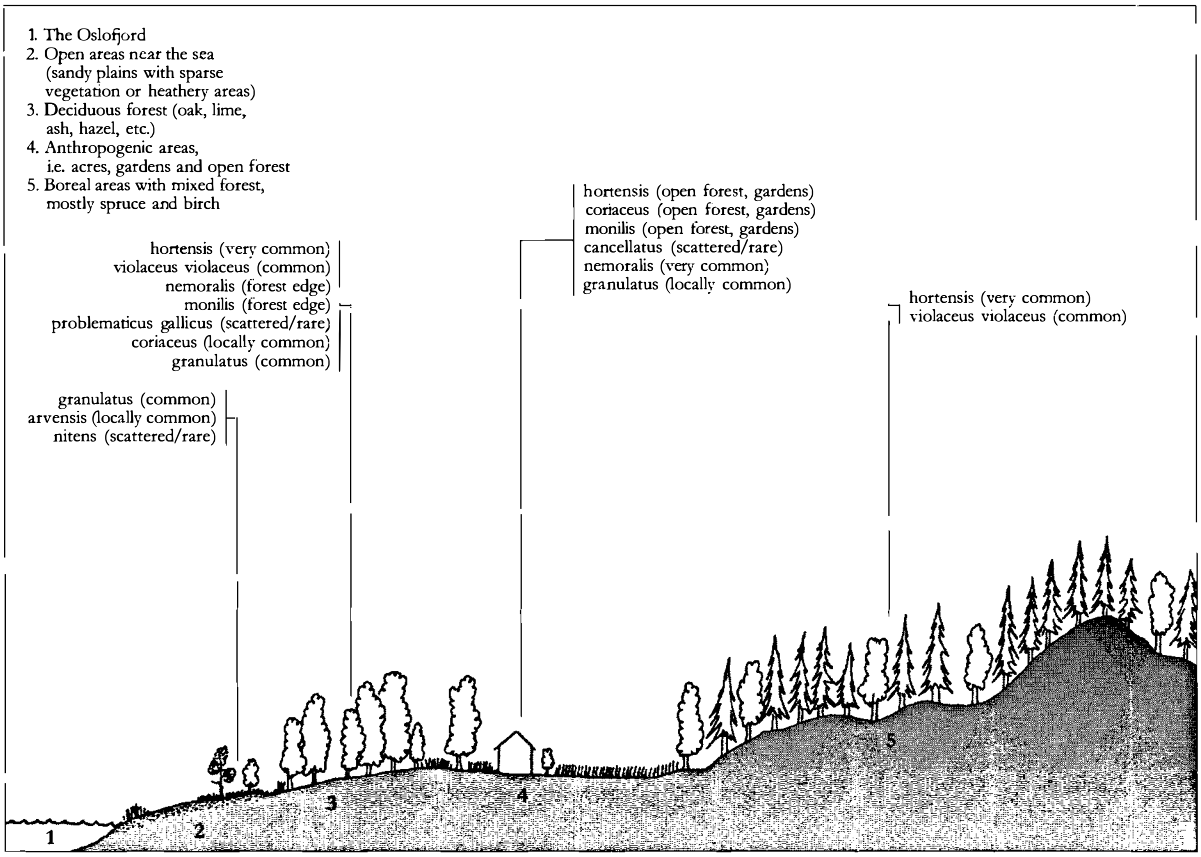
T-01. Southwest Finland:
Compiled by H. Turin from various pitfall investigations in lowlands and hills, in field-forest complexes in Ålandia (Niemelä et al., 1988; Niemelä & Halme, 1992) and Nylandia (Kinnunen, Tiainen & Tukia, 1999; Kinnunen & Tiainen, 1999; Kinunen, Holopainen & Pakala, 1999).



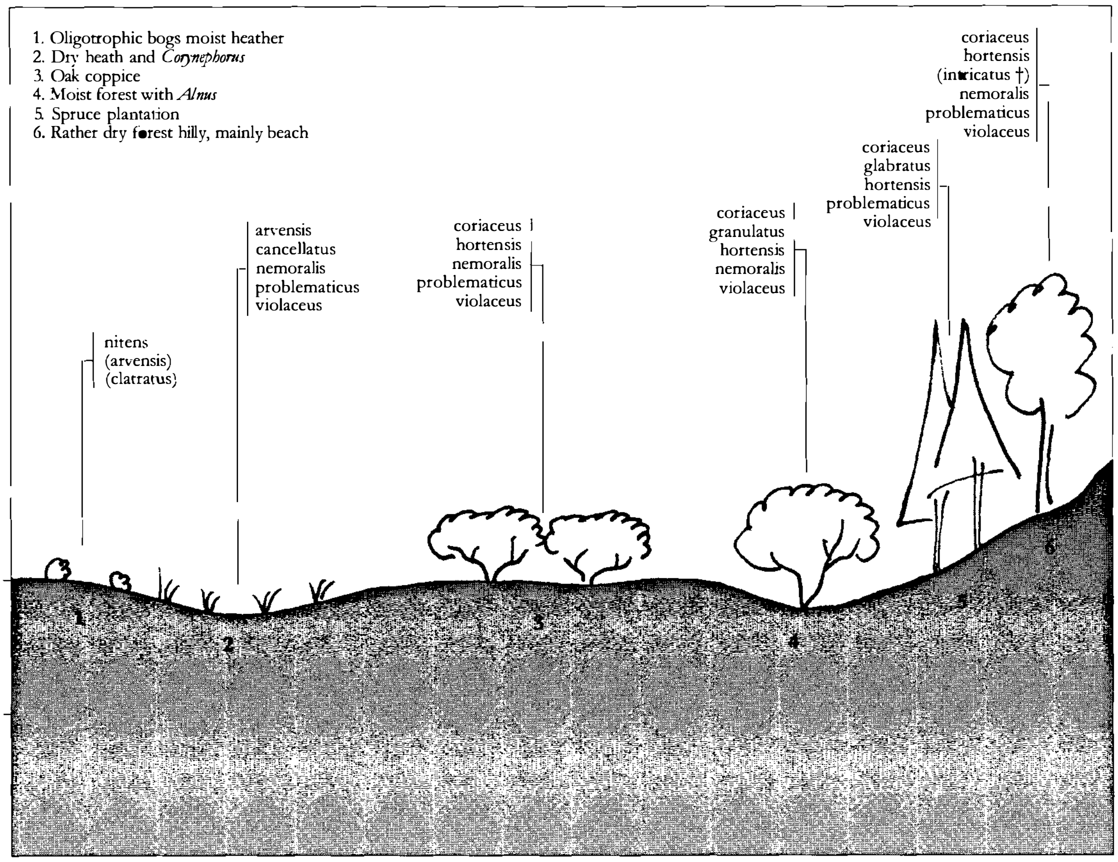
T-02. Northern Norway:
Continental parts of Troms county (69°N). O. Hanssen & J. Andersen, after Andersen (unpublished data), Lindroth (1945) and Strand (1946).



T-03. Western Norway: *Inner fjord areas of Möre & Romsdal county (63°N). O. Hanssen & J. Andersen, after Hanssen (unpublished data) and Lindroth (1945).*

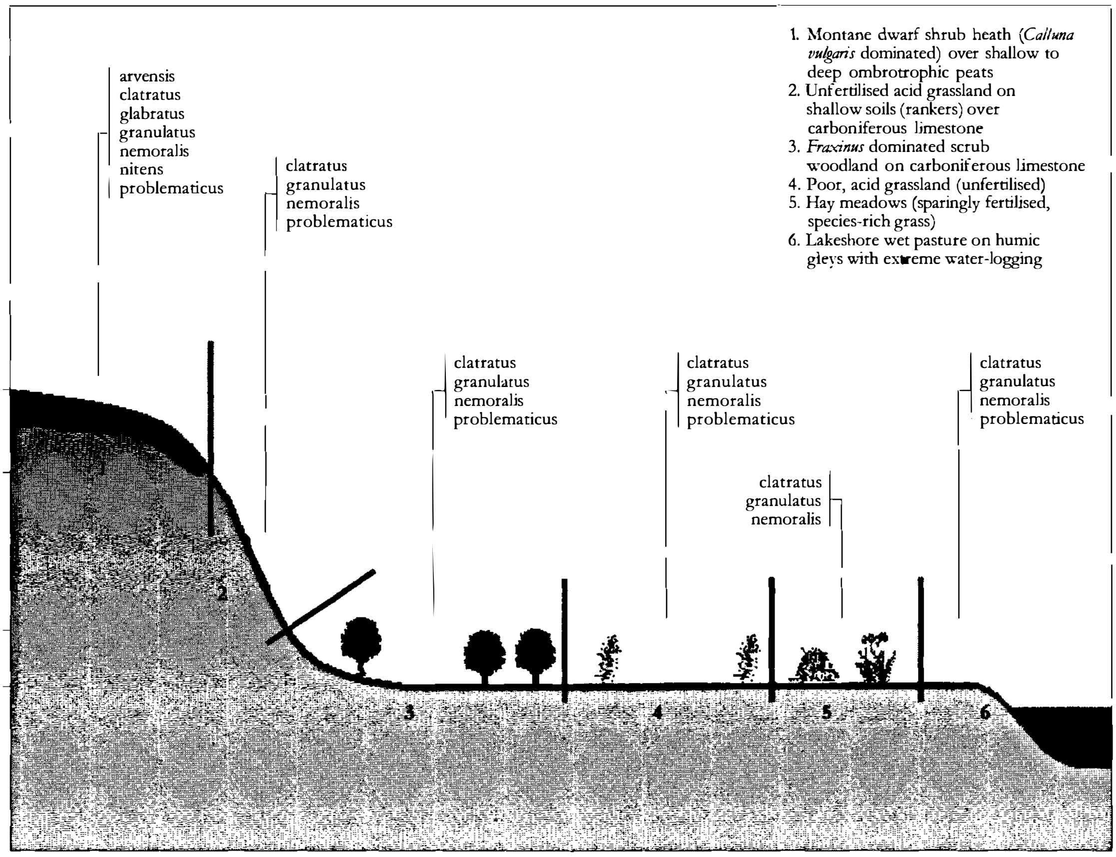


T-04. Southern Norway: *Lowlands in Östfold county (59°N). O. Hanssen & J. Andersen, based on unpublished data.*



T-05. Denmark:

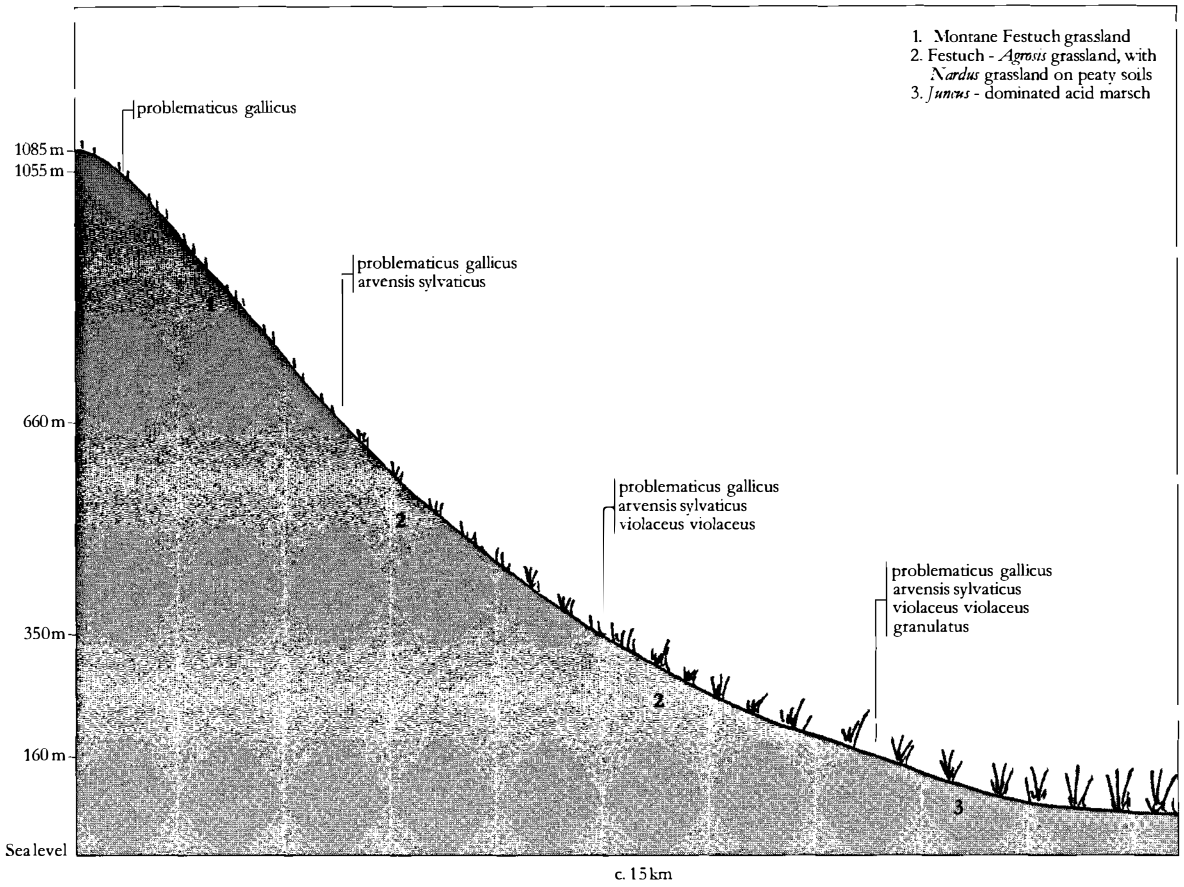
Mid and NW Jutland, compiled by P. Jørum, based on unpublished data from the Silkeborg area and Hald Ege in Mid-Jutland, and Heste have at Kalø in East Jutland and Bangsholt (1983).



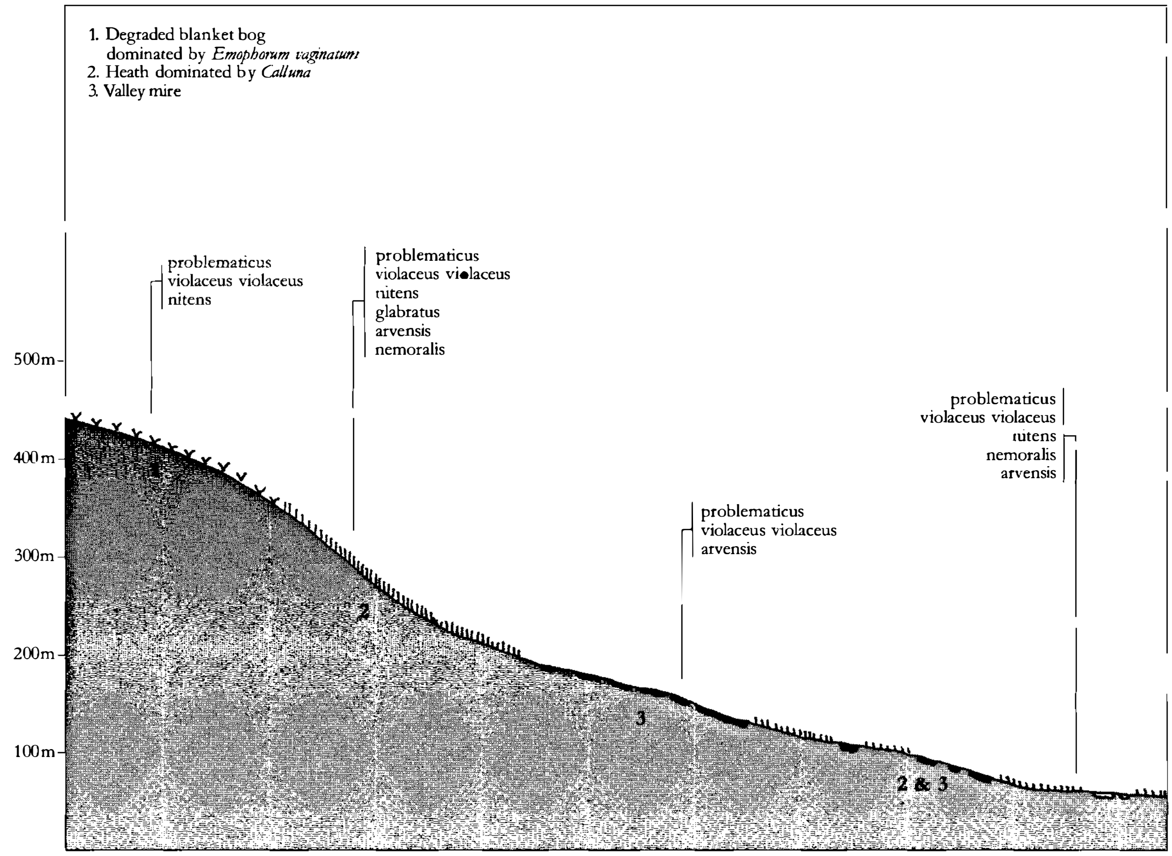
T-06. Northern Ireland:

Cuilcagh mountain in County Fermanagh. R. Anderson, from unpublished data and Anderson (2000).

Prevailing influences are water-logging and poor drainage, exposure with a precipitation of 2000 mm down to 1400mm along the 8-km transect.

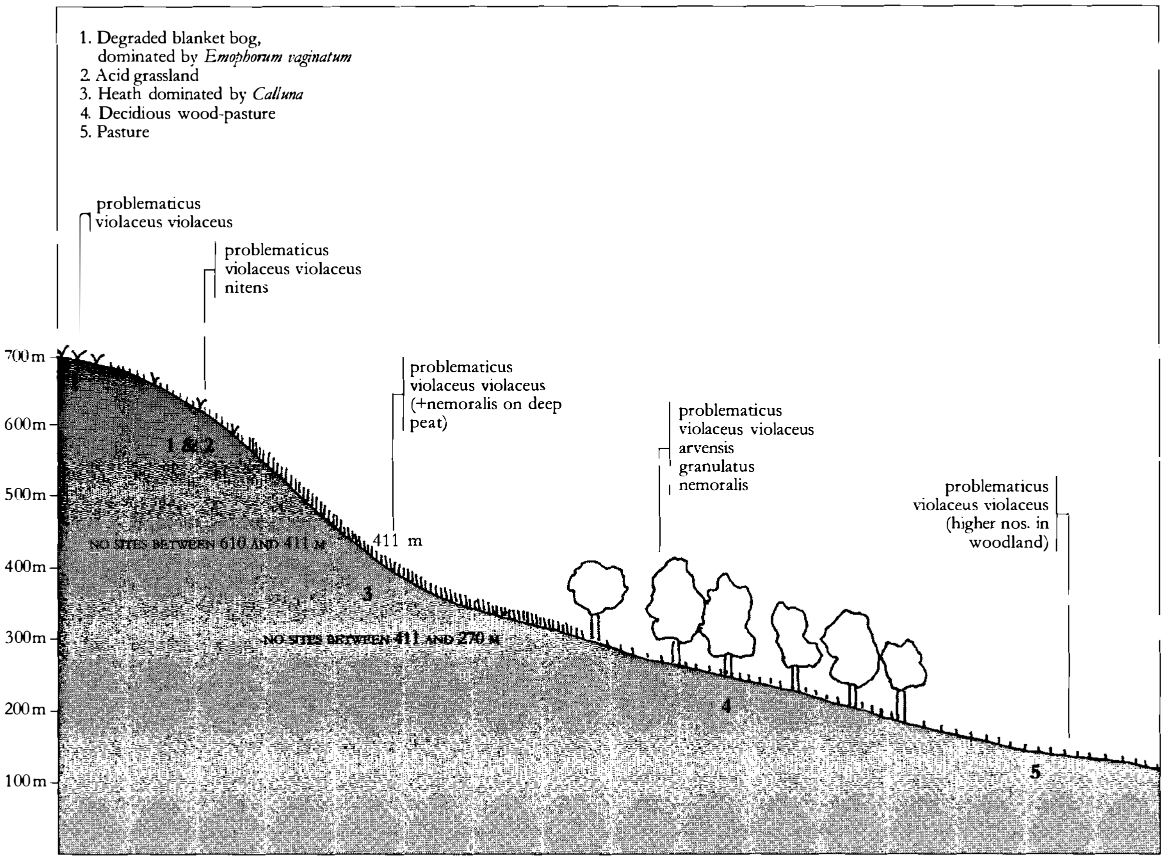


T-07. Britain: *Snowdon mountain in Wales. M. Telfer, from original pitfall data collected by A. Buse.*

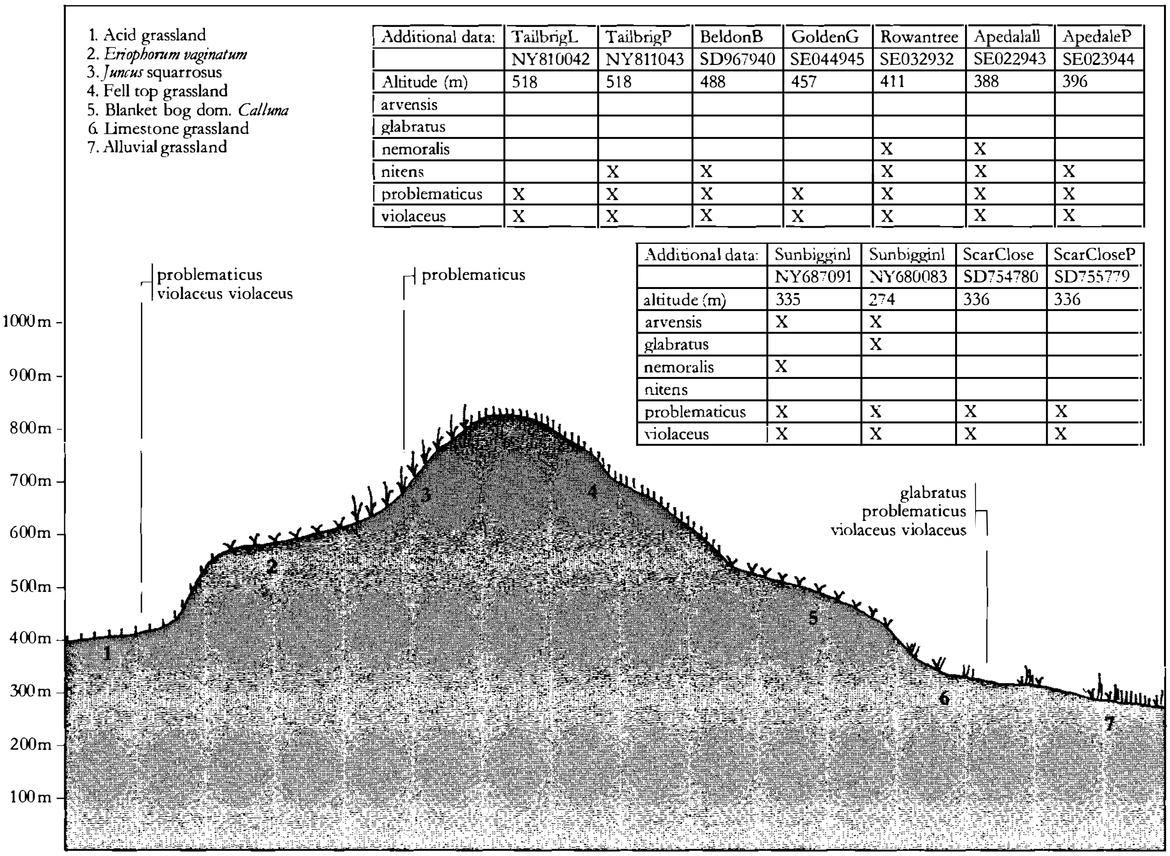


T-08. Britain: *North York Moors Reserve. J. Butterfield and M. Telfer, compiled from original data by J. Butterfield.*

In fact, this is not a real transect, but a number of sites within a 15 km range.



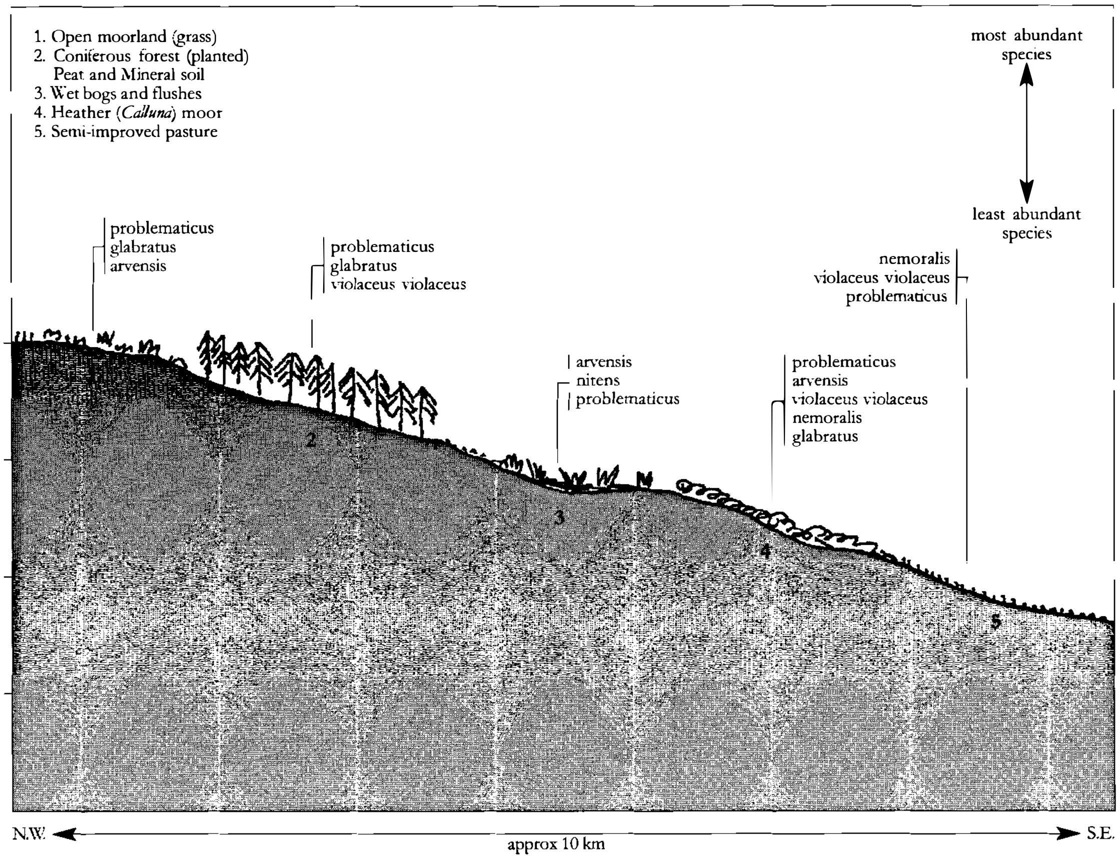
T-09. Britain:
Weardale (25 km from Capel Fell). J. Butterfield and M. Telfer, compiled from original data by J. Butterfield.



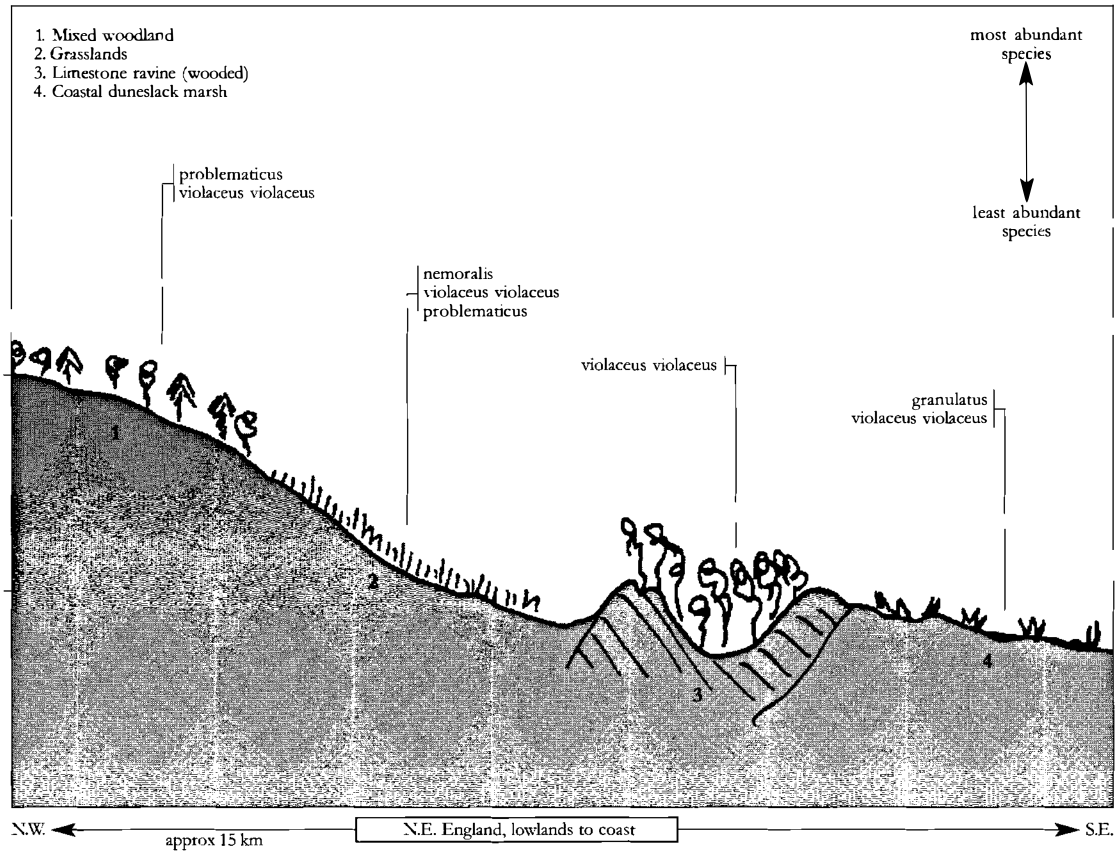
Additional data:	TailbrigL	TailbrigP	BeldonB	GoldenG	Rowantree	Apedalall	ApedaleP
	NY810042	NY811043	SD967940	SE044945	SE032932	SE022943	SE023944
Altitude (m)	518	518	488	457	411	388	396
arvensis							
glabratus							
nemoralis					X	X	
nitens		X	X		X	X	X
problematicus	X	X	X	X	X	X	X
violaceus	X	X	X	X	X	X	X

Additional data:	Sunbigginl	Sunbigginl	ScarClose	ScarCloseP
	NY687091	NY680083	SD754780	SD755779
altitude (m)	335	274	336	336
arvensis	X	X		
glabratus		X		
nemoralis	X			
nitens				
problematicus	X	X	X	X
violaceus	X	X	X	X

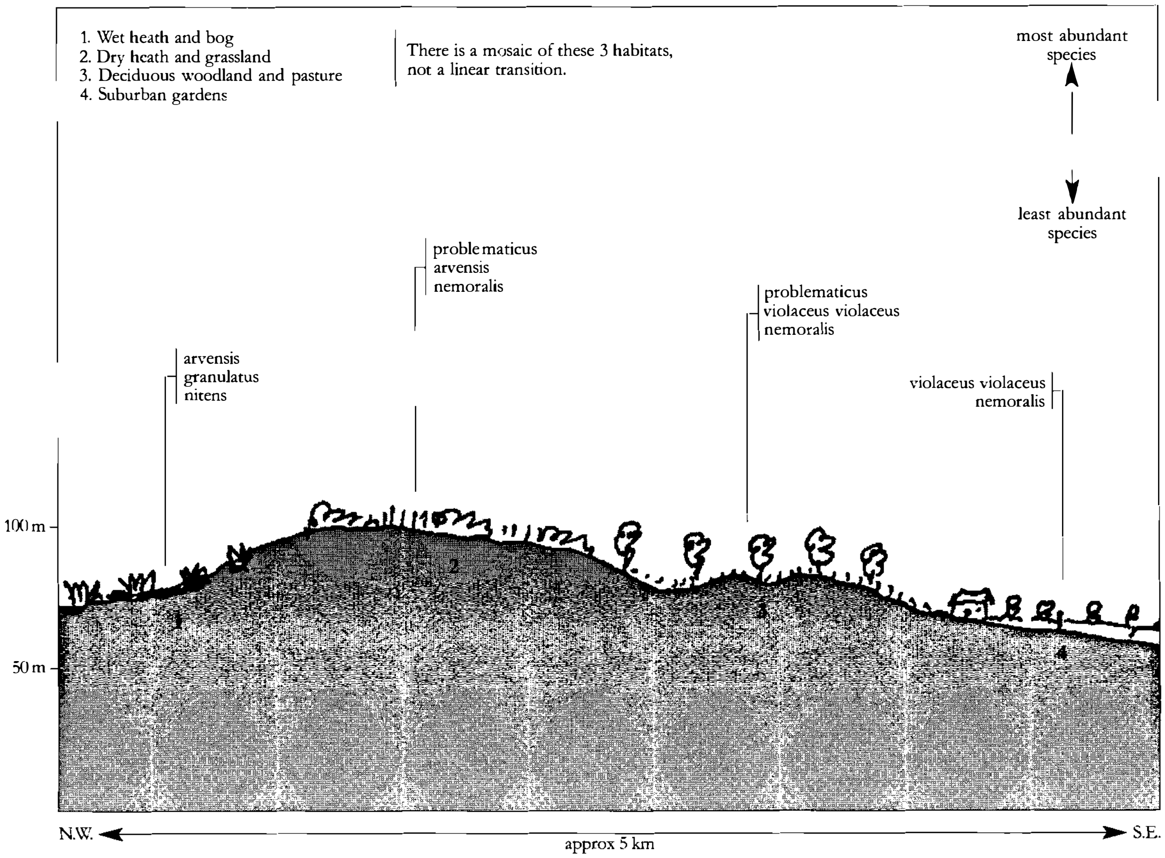
T-10. Britain:
Great Dun Fell and Moor House national Reserve. J. Butterfield and M. Telfer. compiled from original data by J. Butterfield. Length 6 km.



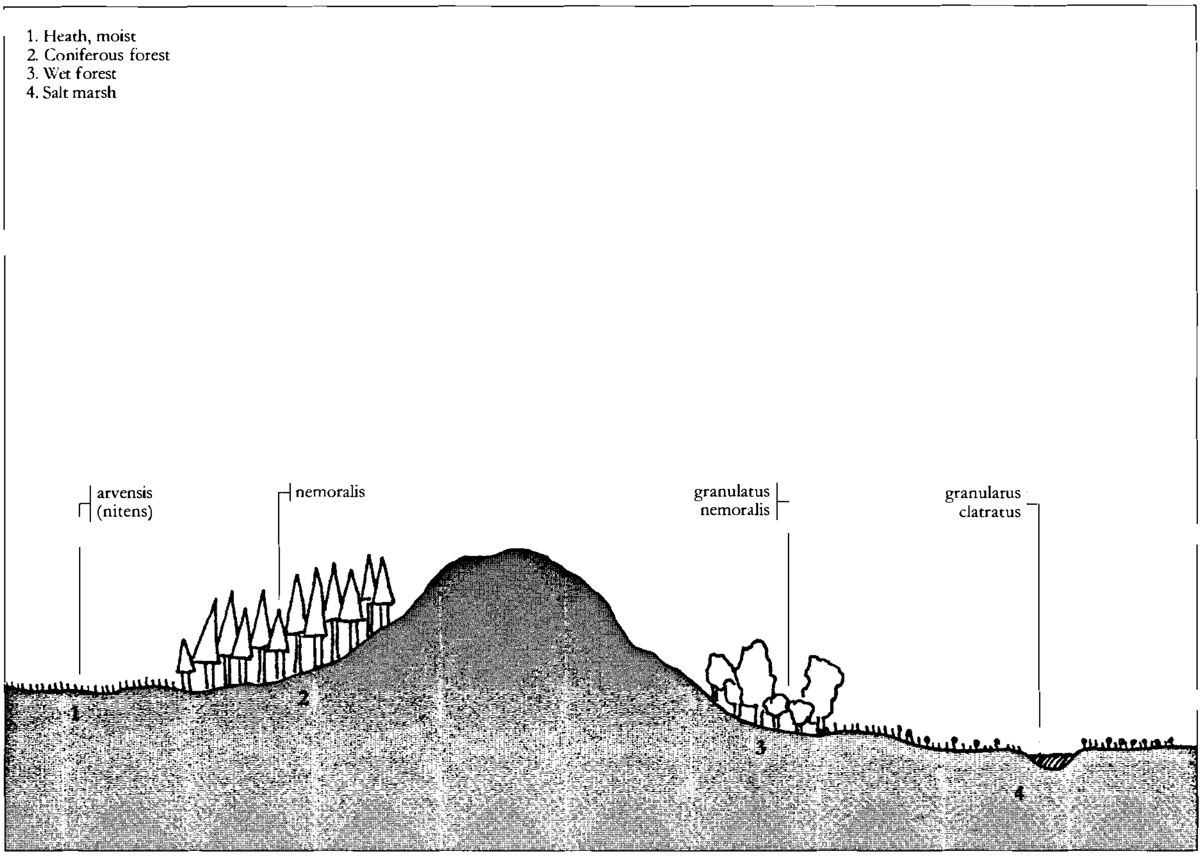
T-11. Britain: *Upland near Redesdale (Kielder area) in* N.E. *England. M. Luff, from unpublished data by Eyre and Luff. Length about 10 km.*



T-12. Britain: *Redesdale; lowlands to coast, in* N.E. *England. M. Luff, from unpublished data by Eyre and Luff. Length about 15 km.*

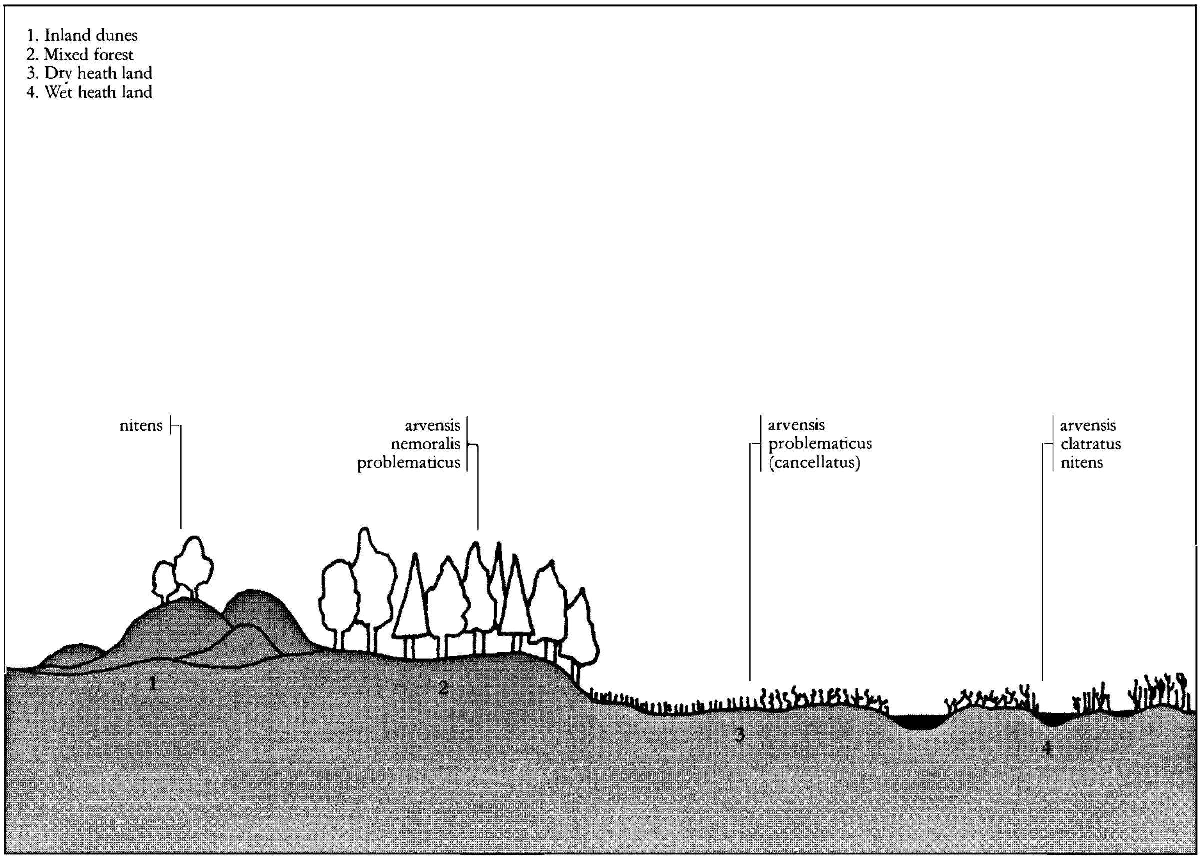


T-13. Britain: *Transect from the New Forest Reserve. M. Luff, from unpublished data by Luff and Allen. Length about 5 km.*



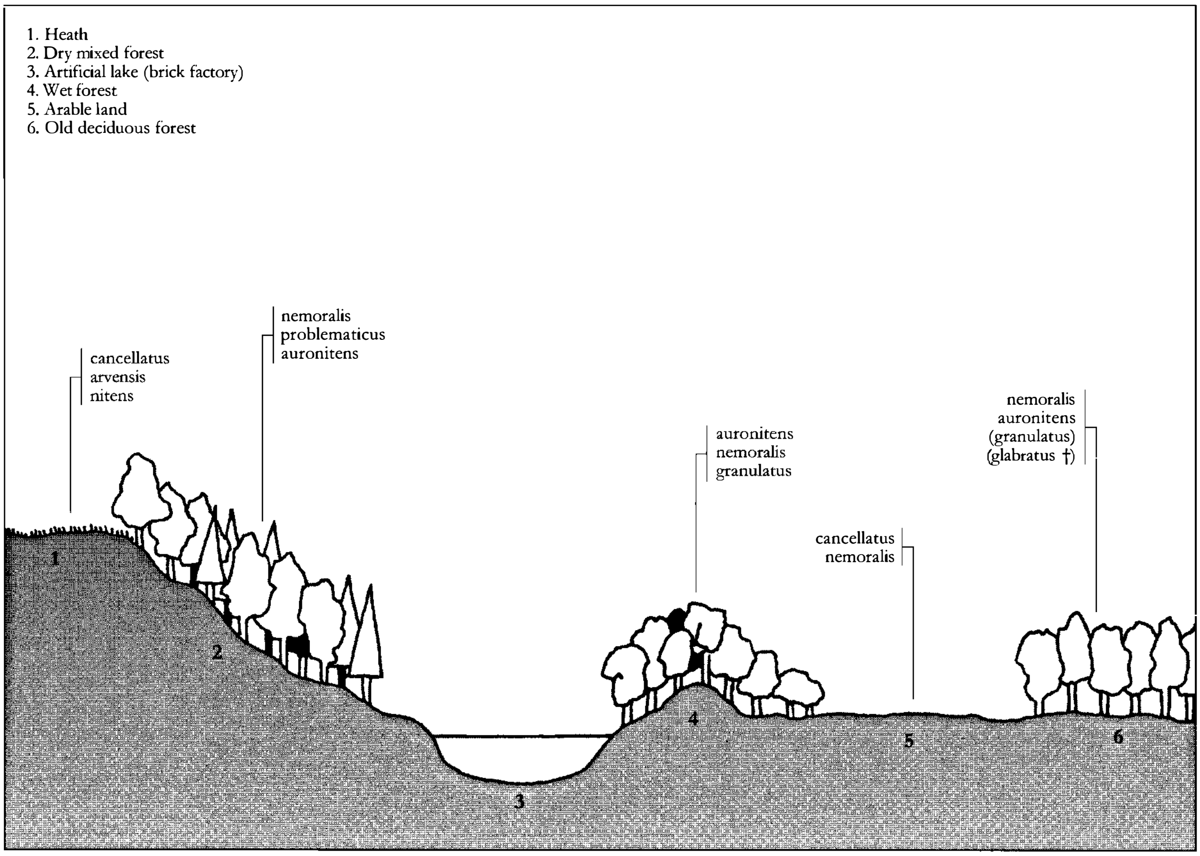
T-14. The Netherlands: *Island of Terschelling (West-Frysian Islands) in the North. H. Turin, from pitfall data and Turin (2000).*

Some "common" species, e.g. C. auratus and C. problematicus, have not yet been recorded from most Frysian islands. C. nitens is probably seriously endangered in most of the Frysian Islands.



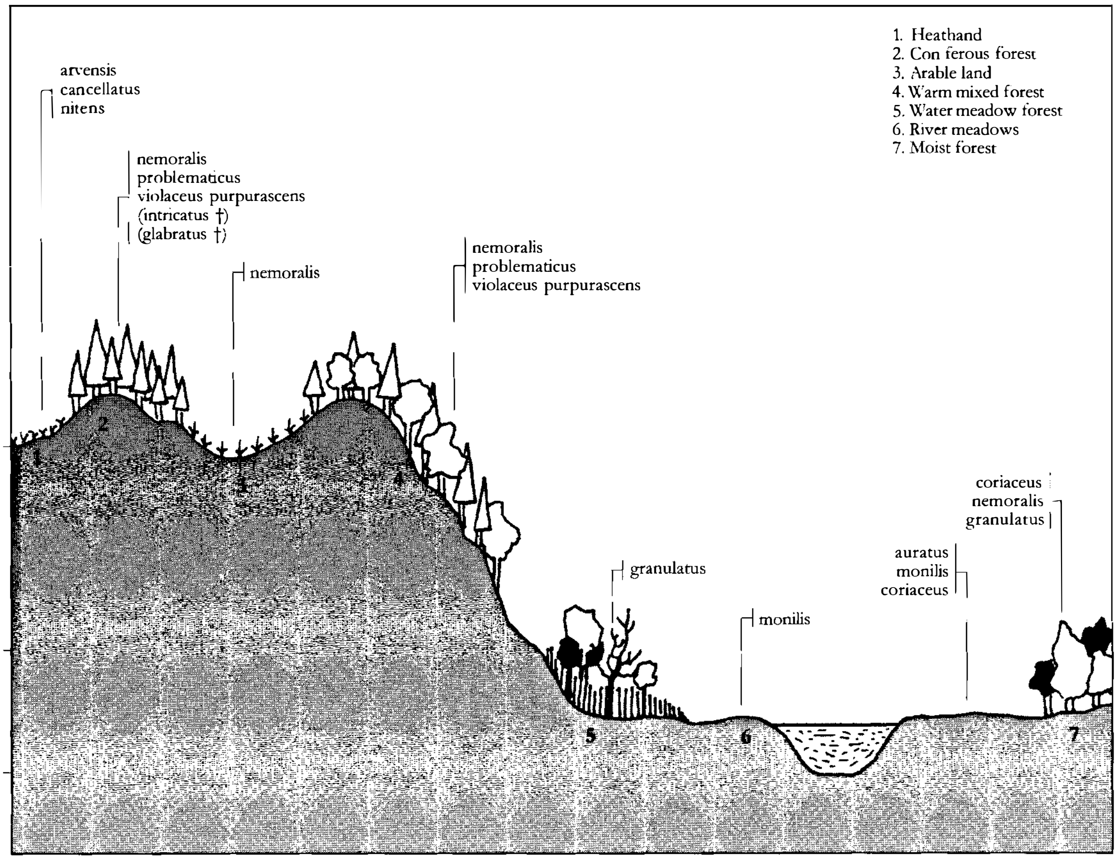
T-15. The Netherlands: *Dwingelderveld, a national 6000 ha wet-heathland reserve (province of Drenthe). H. Turin, from pitfall data of the former Biological Station, Wijster (P.J. den Boer; Th. van Dijk), and from Van Essen (1993). Length of approximately 5 km.*

In this reserve, in the early nineties of the last century, C. nitens became very abundant after cutting Calluna- and Erica-heath, with C. arvensis as dominant species. C. nitens is also present in the inland dunes with Corynephorus and shows here no preference for peaty soil (van Essen, 1993).



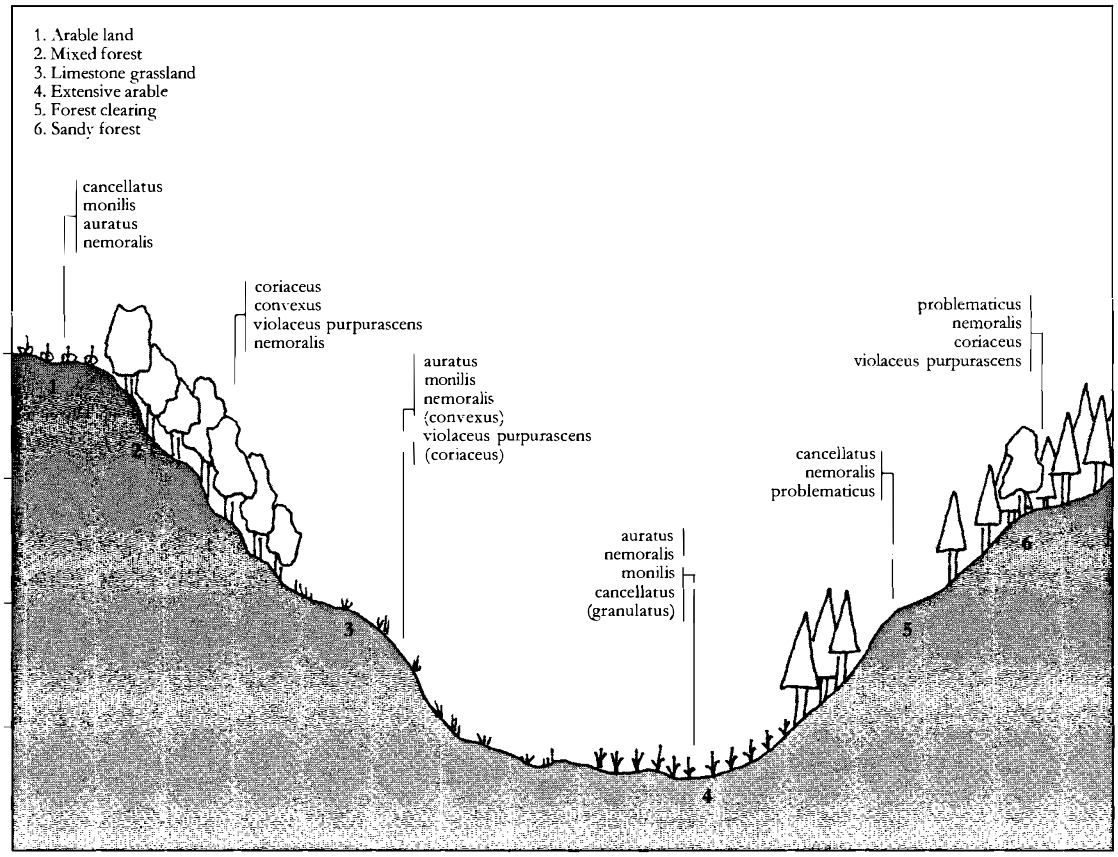
T-16. The Netherlands: *Twente north of Enschede (province of Overijssel). H. Turin, compiled from personal observations, pitfall data and from Turin (2000). Length of about 3 km.*

In a fragmented old, small-scale agricultural landscape with various types of forest and small patches of heathland. C. glabratus occurred in an old forest near Denekamp (10 km more to the N.) until about 1930, but is now extinct.



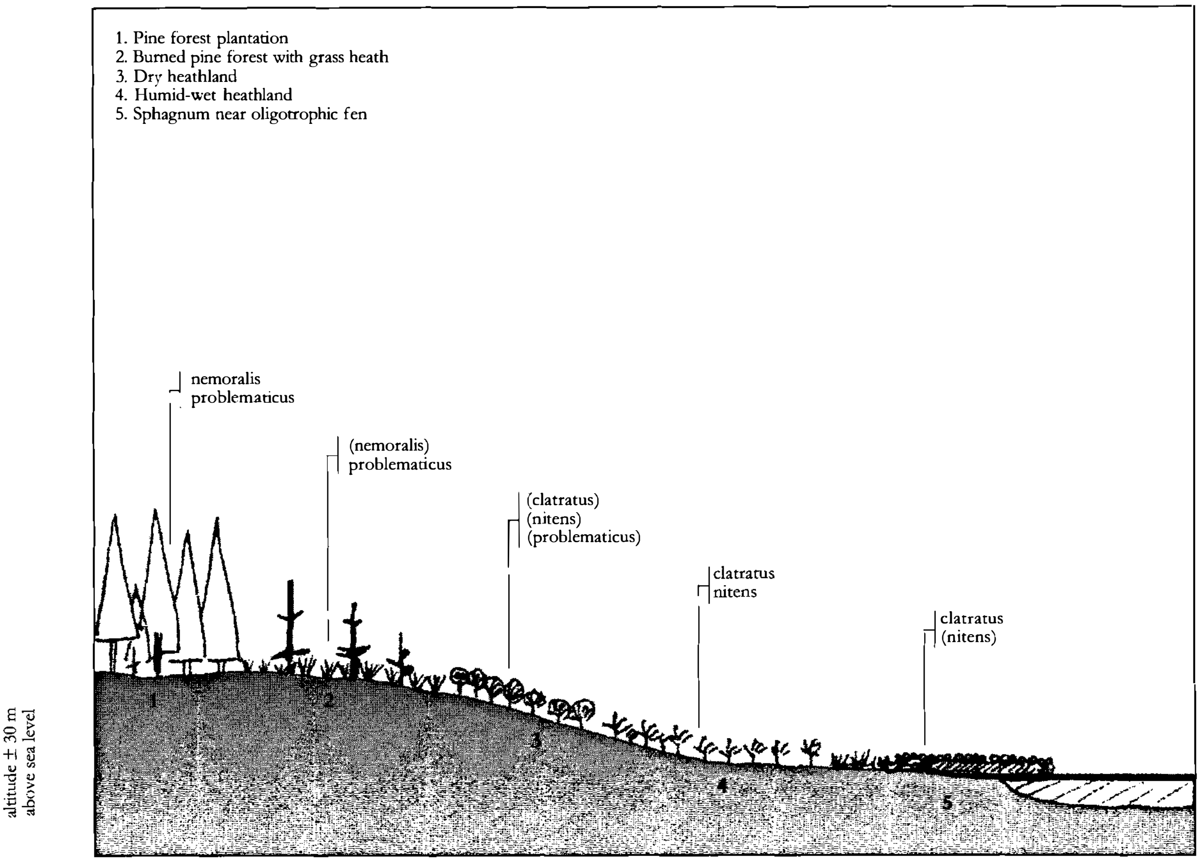
T-17. The Netherlands: *Southern Veluwe, situated on the gradient from the central lateral moraine to the Rhine basin. H. Turin, from various pitfall data and from Turin (2000: fig 158, p. 124). Length approximately 10 km.*

Both C. glabratus and C. intricatus occurred in this area until the thirties and fourties of last century respectively, but are now extinct. C. cancellatus and C. nitens are rare.

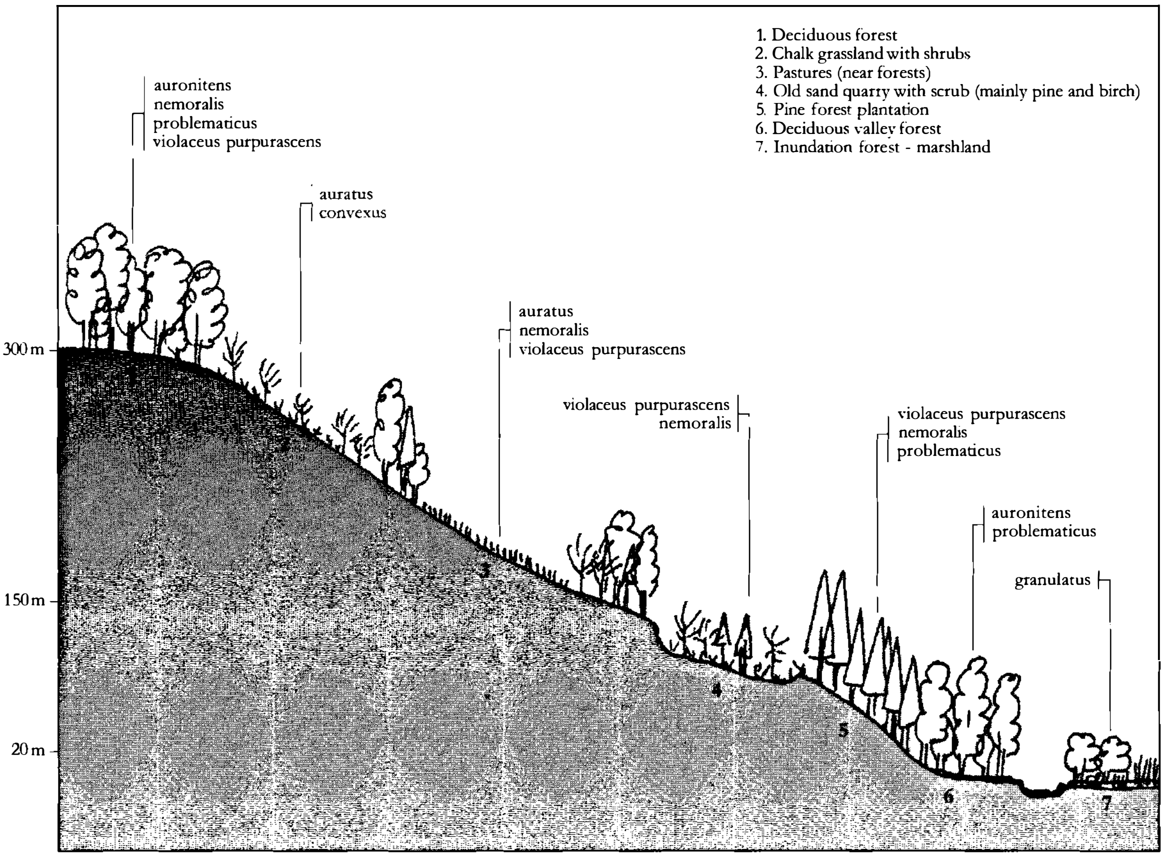


T-18. The Netherlands: *Southern Limburg, limestone hills near Wijlre and Schin op Geul. H. Turin, compiled from unpublished pitfall data and Turin (1983, 2000). Length about 3 km.*

In a small-scale, highly fragmented landscape. C. convexus which always was rare, is probably extinct now (last record 1977).

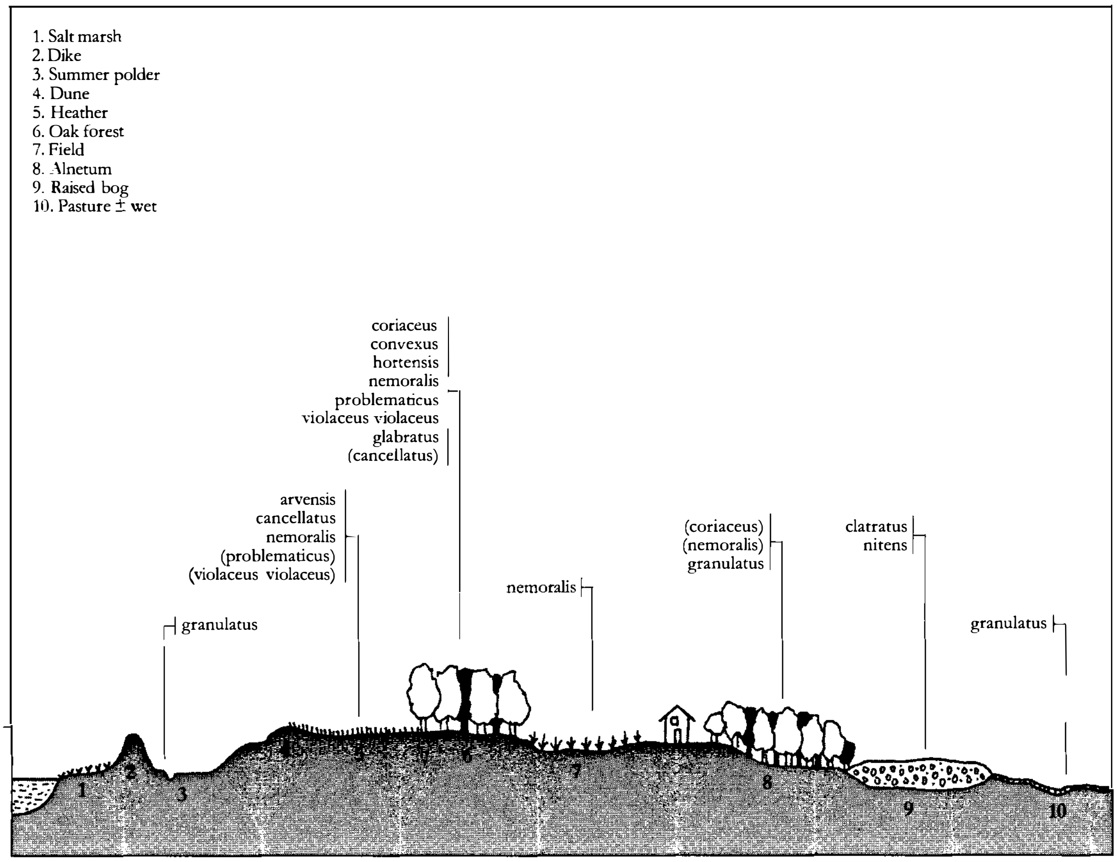


T-19. Belgium:
Campine area in Northern Flanders (lowlands, sandy soil). K. Desender, from unpublished data. Length about 300 m; compiled from two transects of Brecht and Kalmthout, N. of Antwerp.

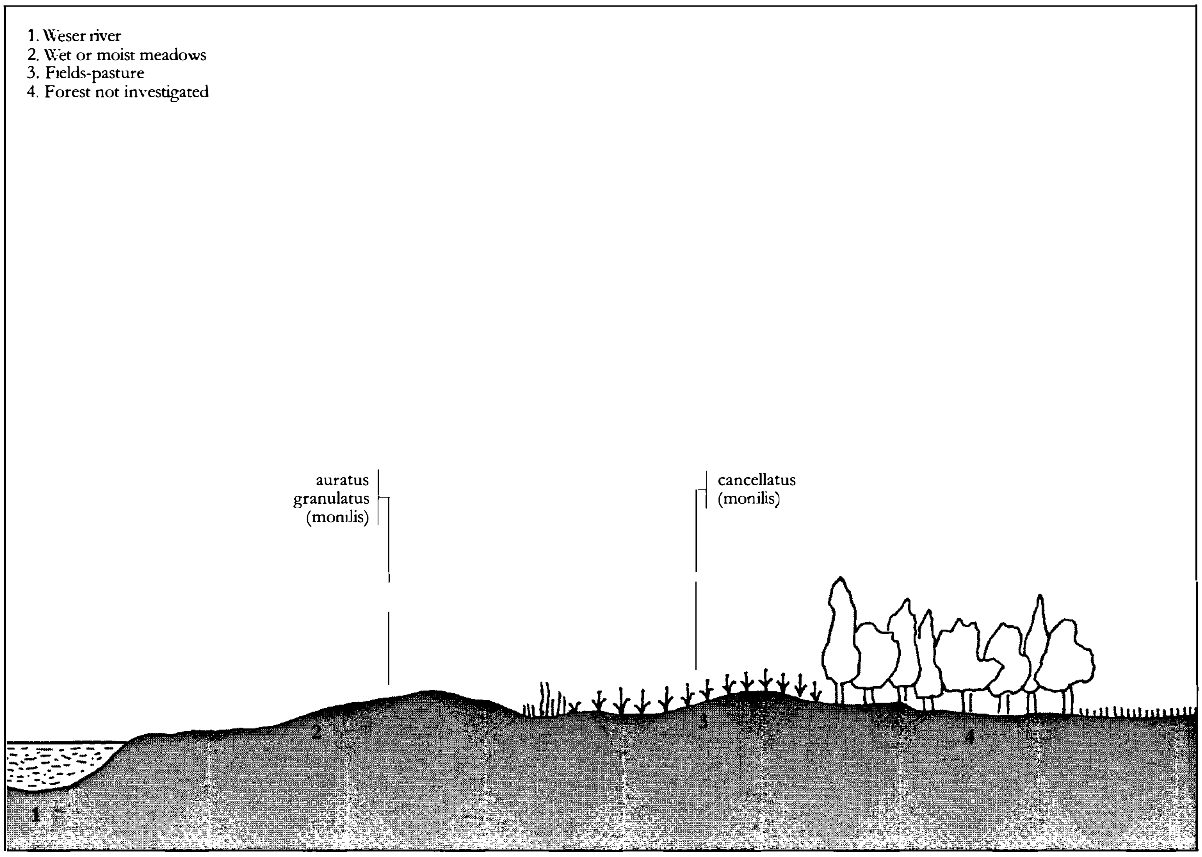


T-20. Belgium:
Gaume region in S.E. Wallonia (lowlands, sandy soil). K. Desender, from unpublished data. Length approximately 20 km.

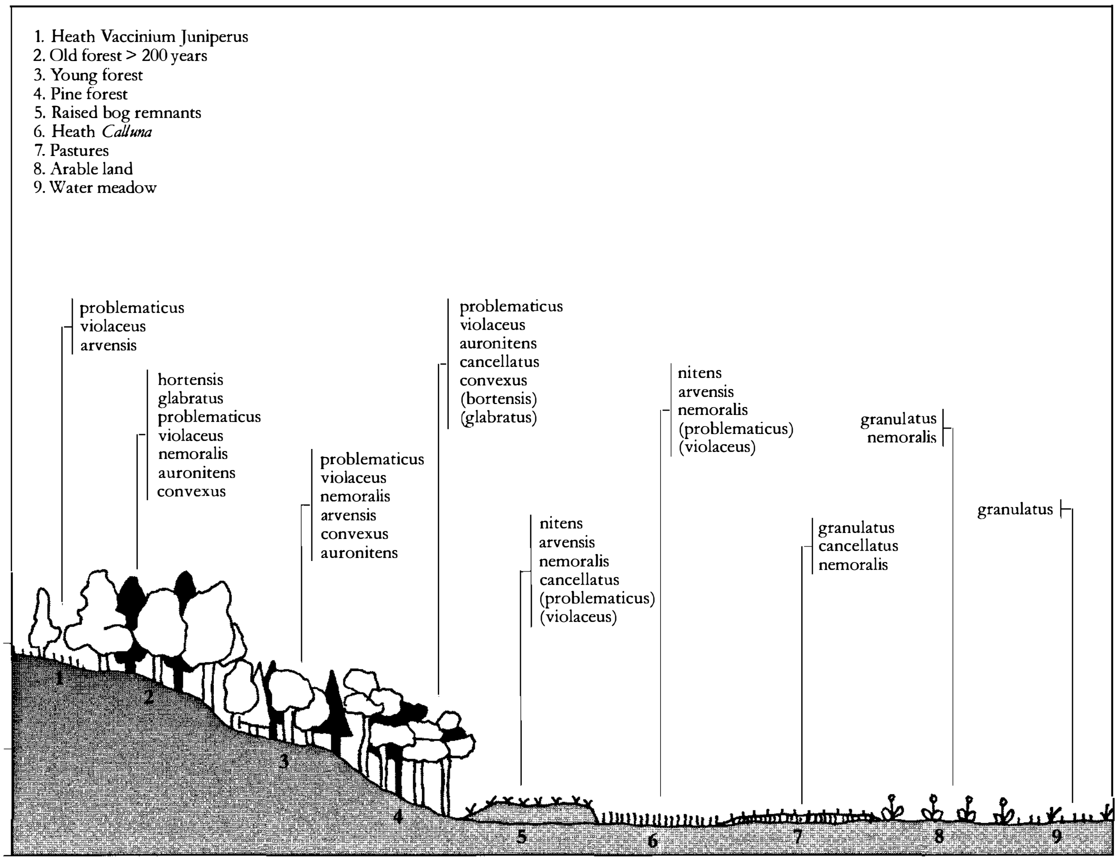
Cultivated fields are not included, because they have not been investigated.



21. Germany:
Bremerhaven area, near Bremen.
D. Mossakowski, compiled from various (unpublished) pitfall data.

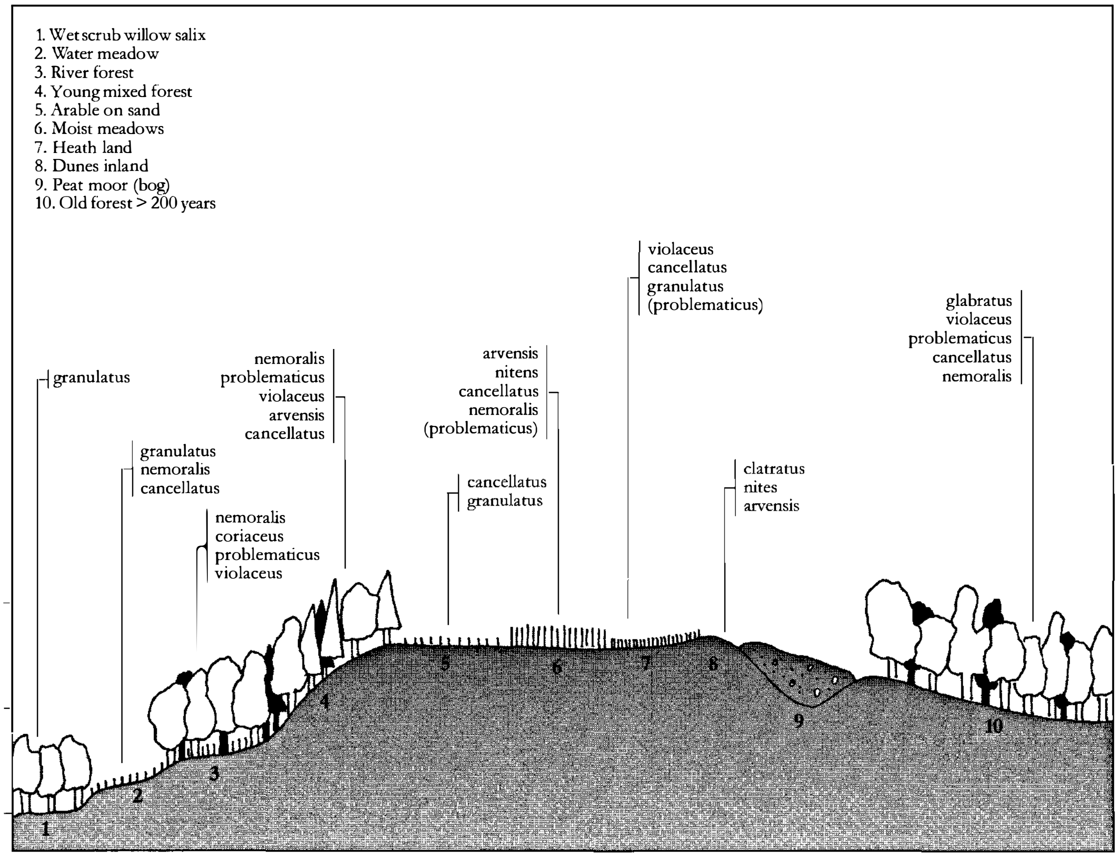


T-22. Germany:
Weser river area, near Bremen.
D. Mossakowski, compiled from various (unpublished) pitfall data.



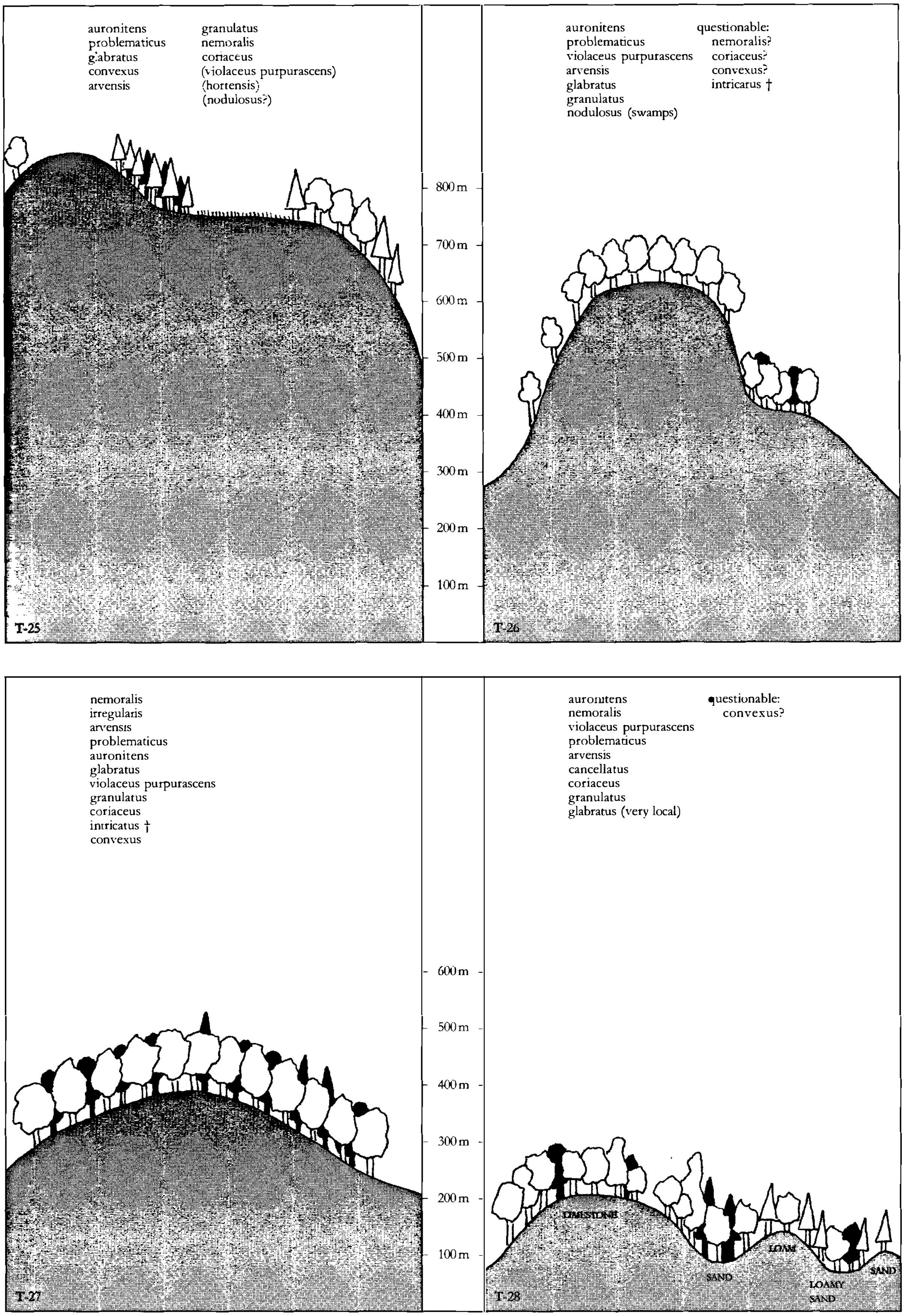
T-23. Germany: *Lüneburgerheide near Wilsede (Wildeseder Berg, 169 m). Th. Assmann, from unpublished data. Length ca 7 km.*

C. glabratus in old forest remnants "Heinköpen" (see also Assmann, 1999; Assmann and Güther, 2000).



T-24. Germany: *Ems river area, N. of Meppen (Lower Saxonia). Th. Assmann, from unpublished data. Length ca 15 km.*

C. glabratus in old forest remnant "Sprakeler Holz" (see also Assmann and Güther, 2000).



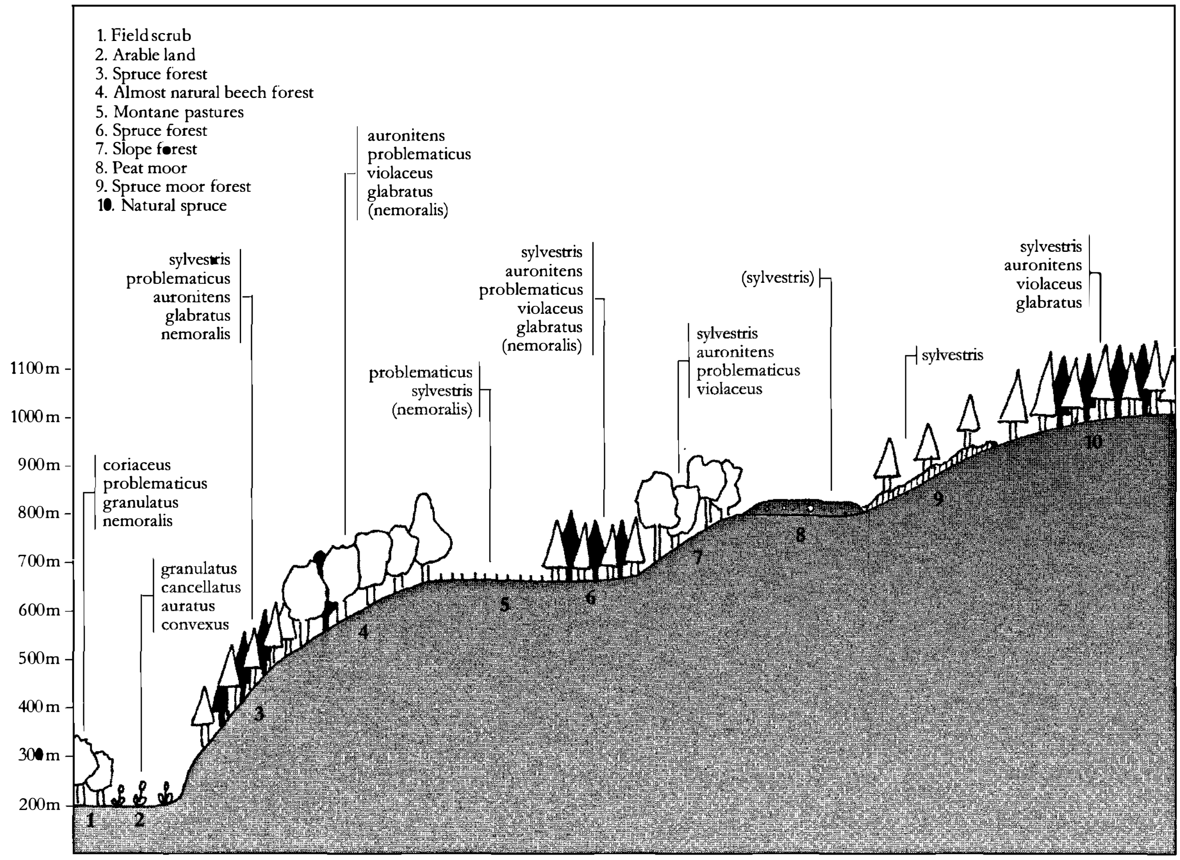
T-25-28.
Germany:
Forest "transect" fom Westphalia, drawn on the same altitude scale, by F. Weber, compiled from various unpublished pitfall data. Total length approximately 130 km and it consists (from high to low) of four localities. Because of its length and the lack of open biotopes, it is not a real transect, but a number of sites along the range. For a more complete picture of the species in this area, see the overall transect in the introduction (fig. I-1).

T-25: *Hoch-Sauerland area*

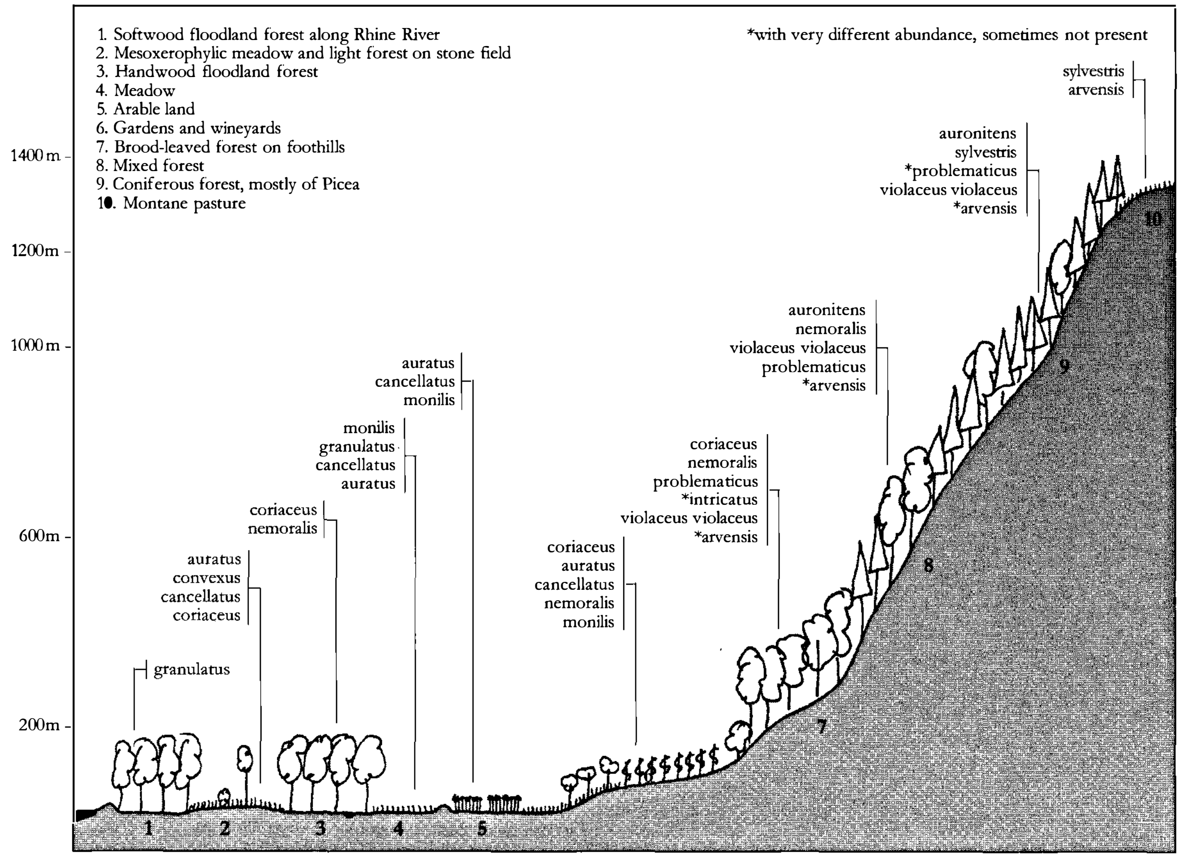
T-26: *Arnsbergerwald*

T-27: *Teutoburgerwald-Weserbergland*

T-28: *Münsterland area*

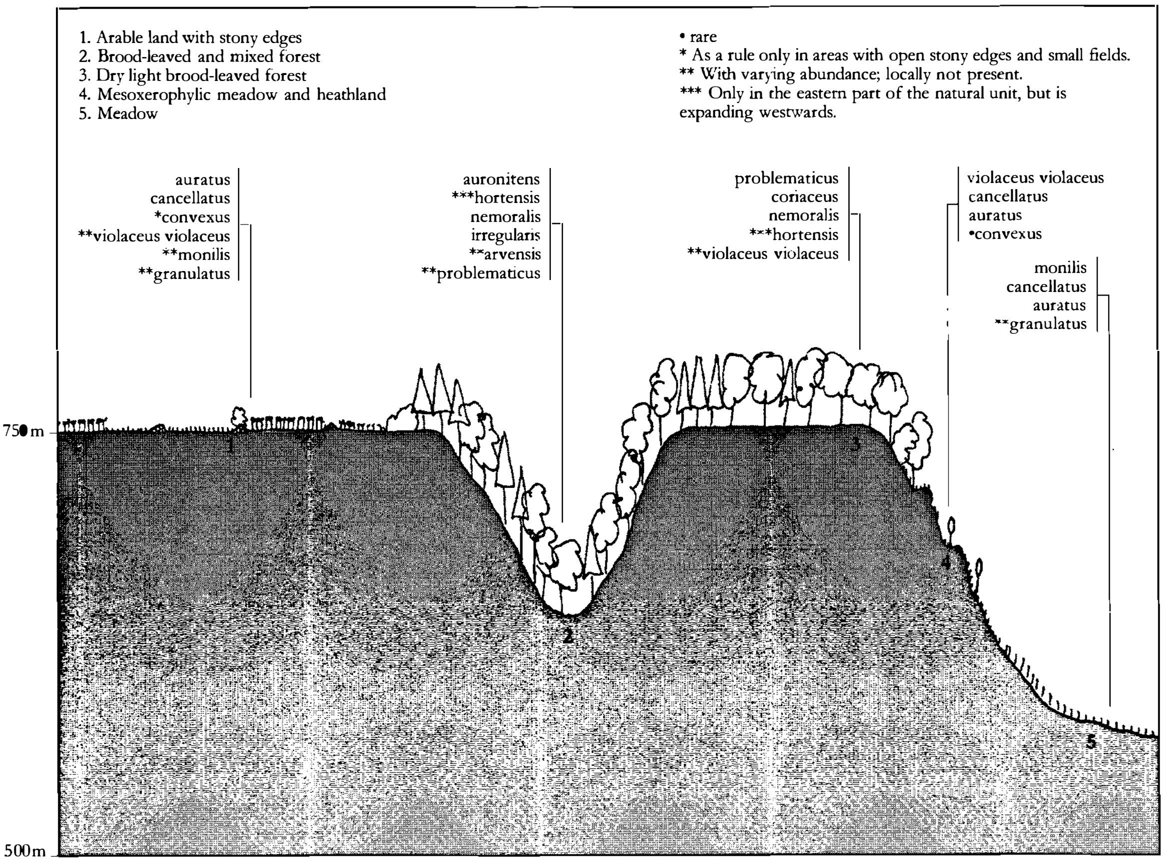


T-29. Germany: *Harz mountains in SE Saxonia. Th. Assmann, from unpublished data. Length ca 15 km, with C. glabratus in old forest remnant "Sprakeler Holz" (see also Assmann and Schnauder, 1998).*

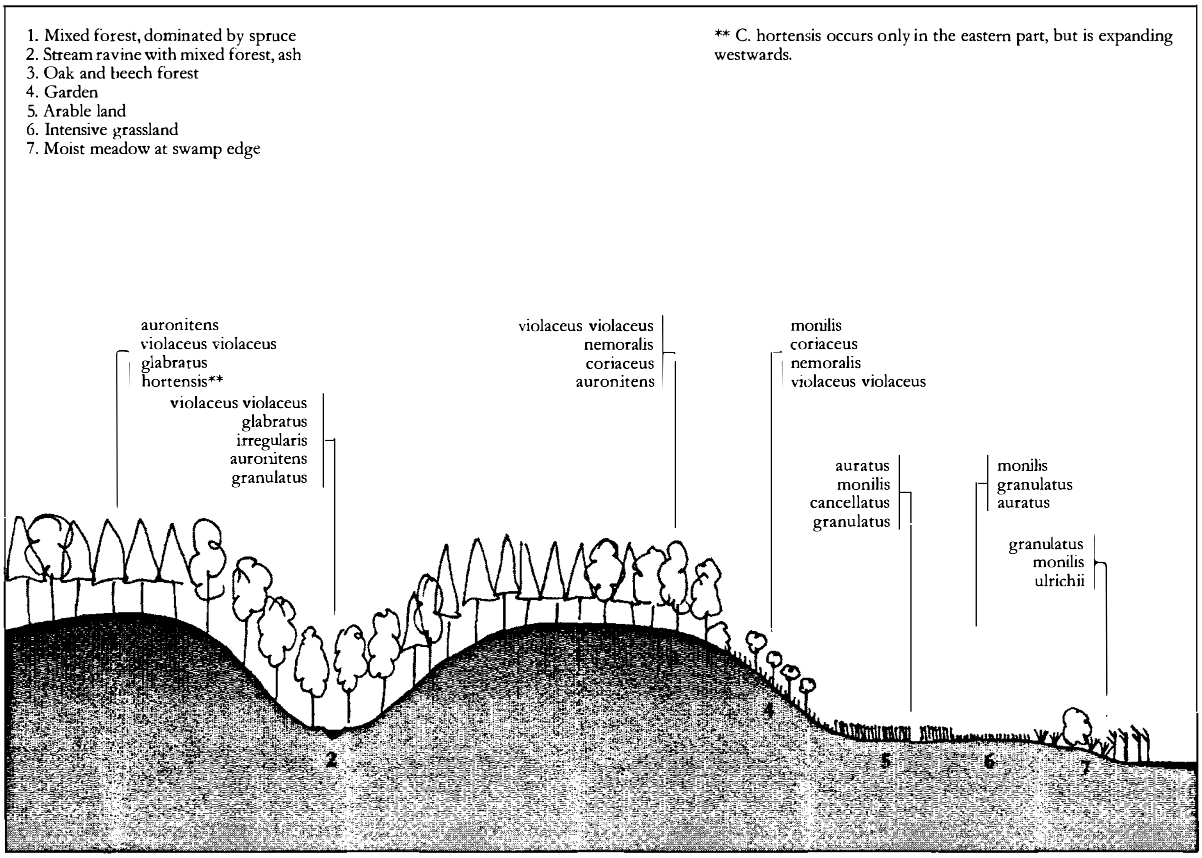


T-30. Germany: *Schwarzwald (Baden-Württemberg) to the southern valley of the river Rhine at the French border. J. Trautner, from unpublished data. Length ca 10 km.*

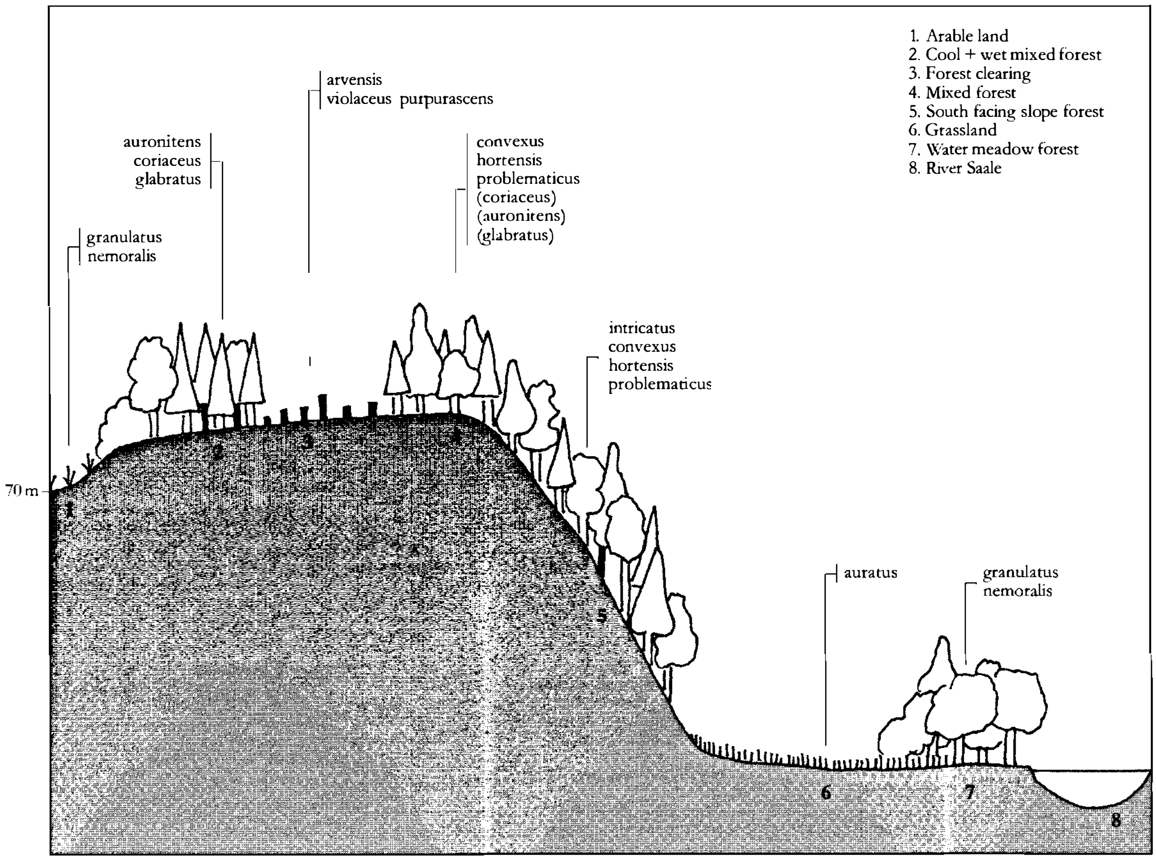
C. nodulosus has not been included in the transect, because its status is not clear. The few records from small forest brooks in the area, concern mostly older records.



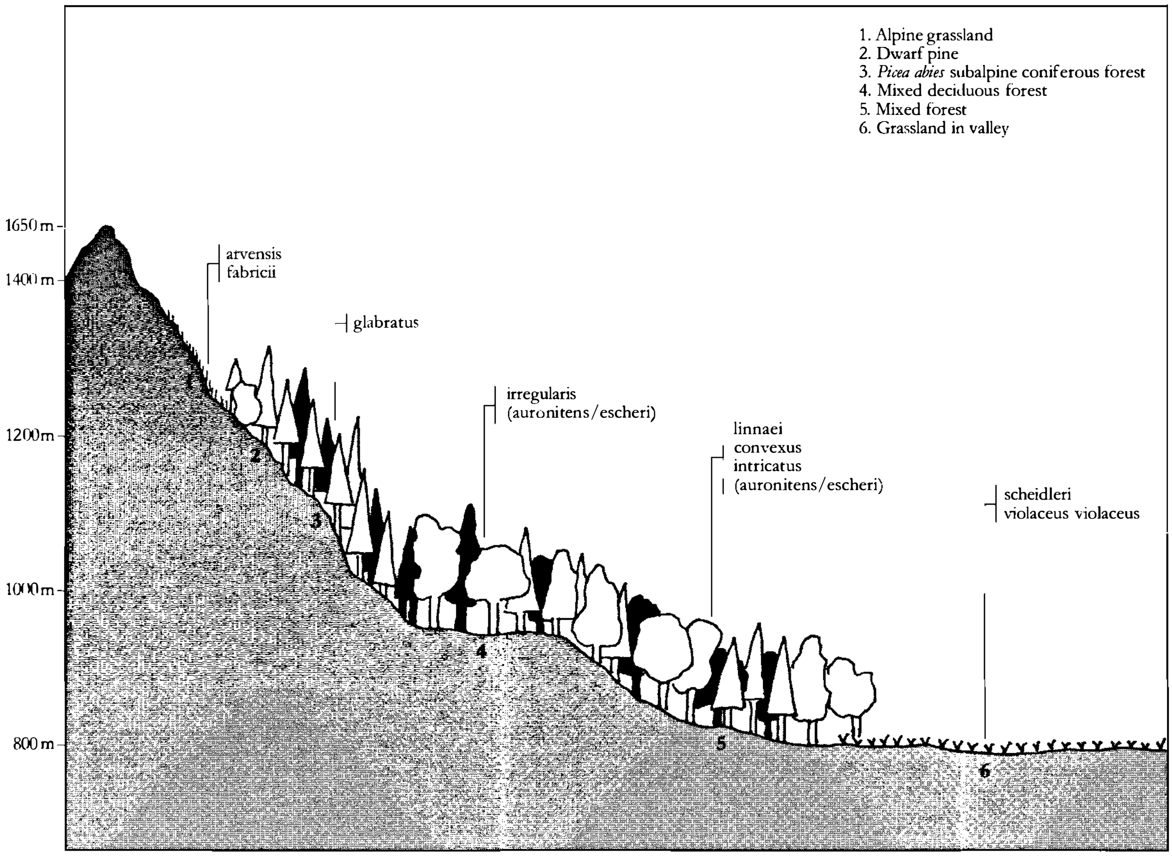
T-31. Germany:
Schwabische Alb, west of Ulm (Baden-Württemberg).
J. Trautner, from unpublished data.
Length ca 5 km.



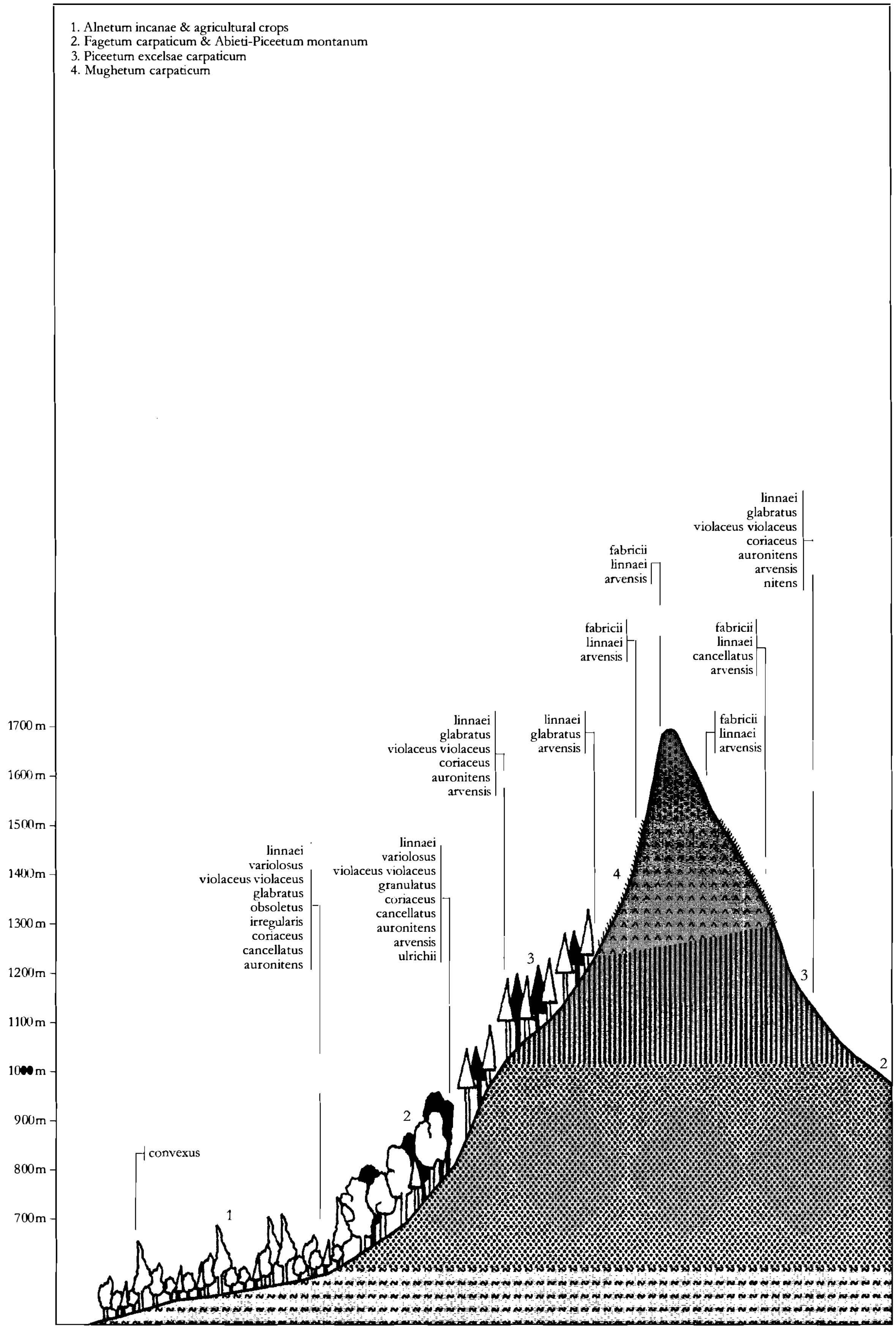
T-32. Germany:
Oberschwaben; the southern foothills of the Alps near Ravensburg.
J. Trautner, from unpublished data.
Length ca 5 km.



T-33: Germany: *Central German hills along the valley of the river Saale, south of Jena. E. Arndt, from unpublished data. Length ca 400 m.*

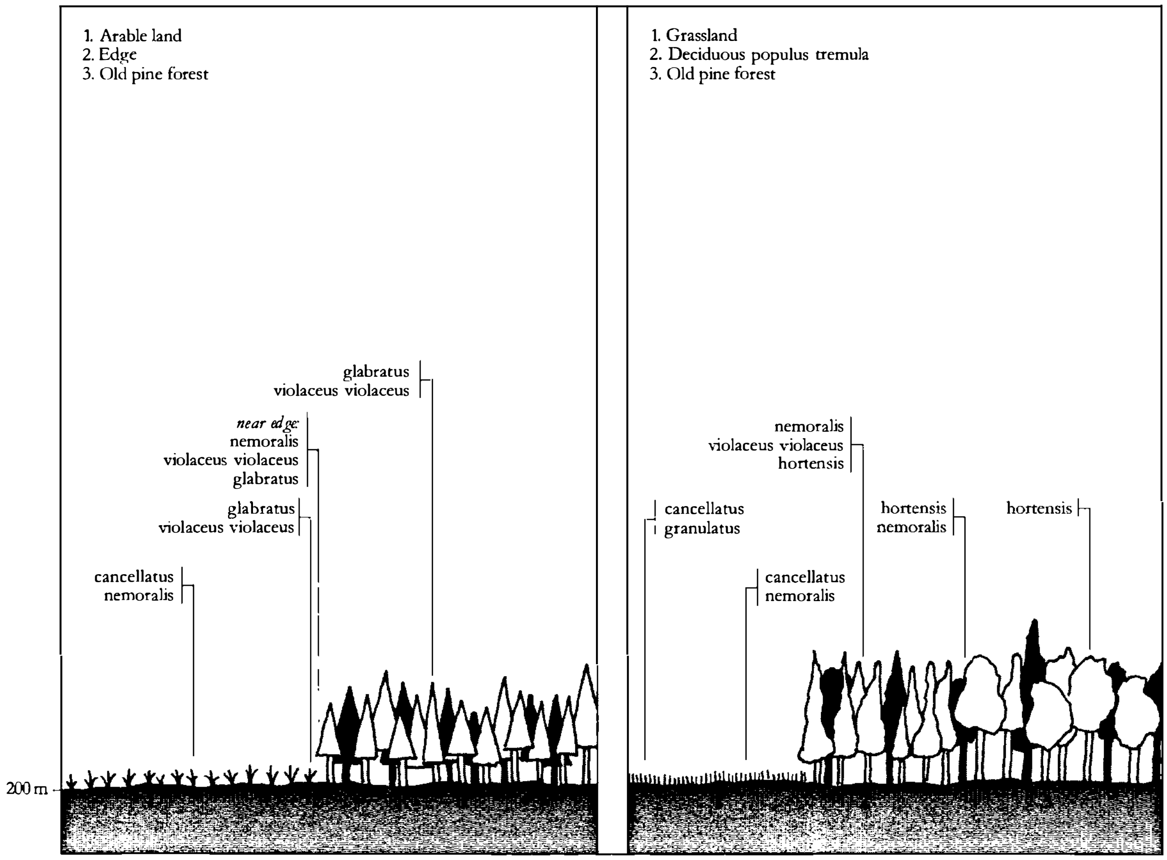


T-34. Slovakia: *Montane western Nizke Tatry near Banska Bystrica. E. Arndt, from unpublished data. Length ca 1500 m.*

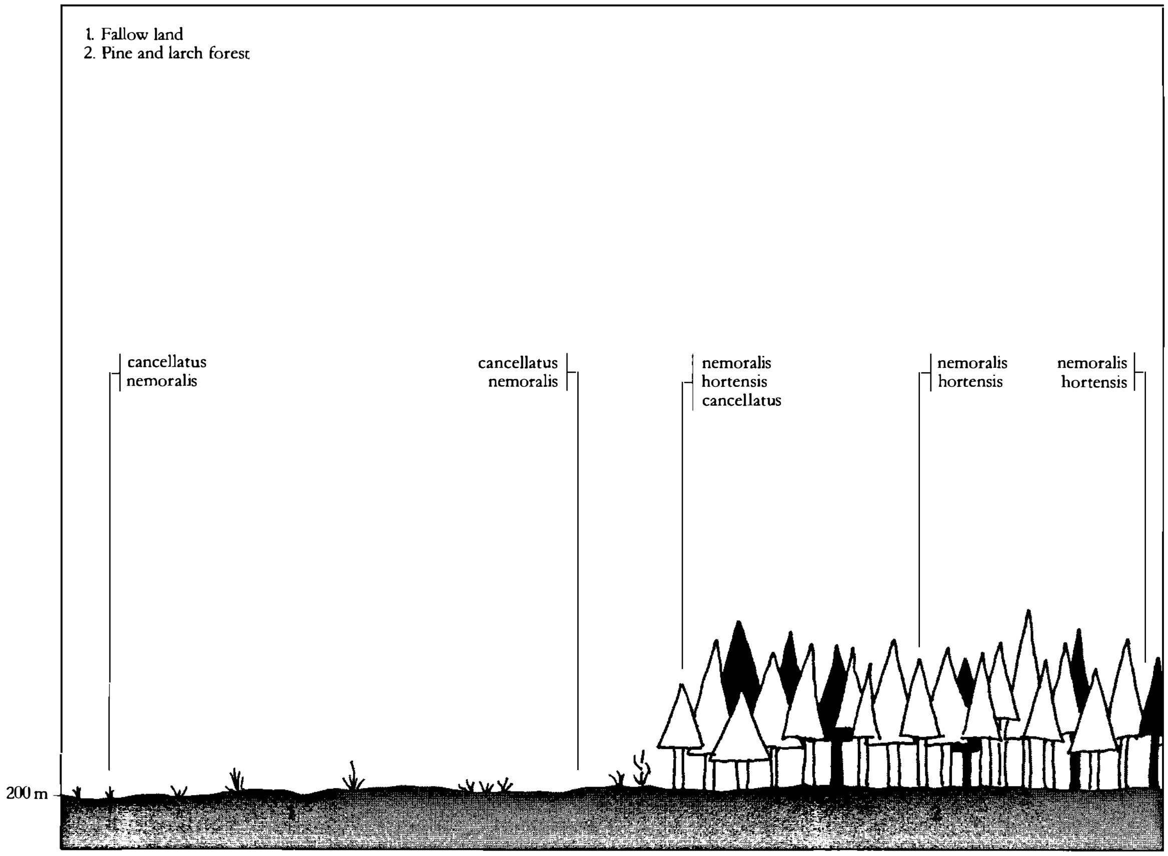


T-35. Poland: *Babia Góra (West Carpathians). Y. Pawlowski, from original data, mainly collected in the period 1959-1964 (Pawlowski, 1967; 1972), partly confirmed in 1995-1998. Length about 10 km.*

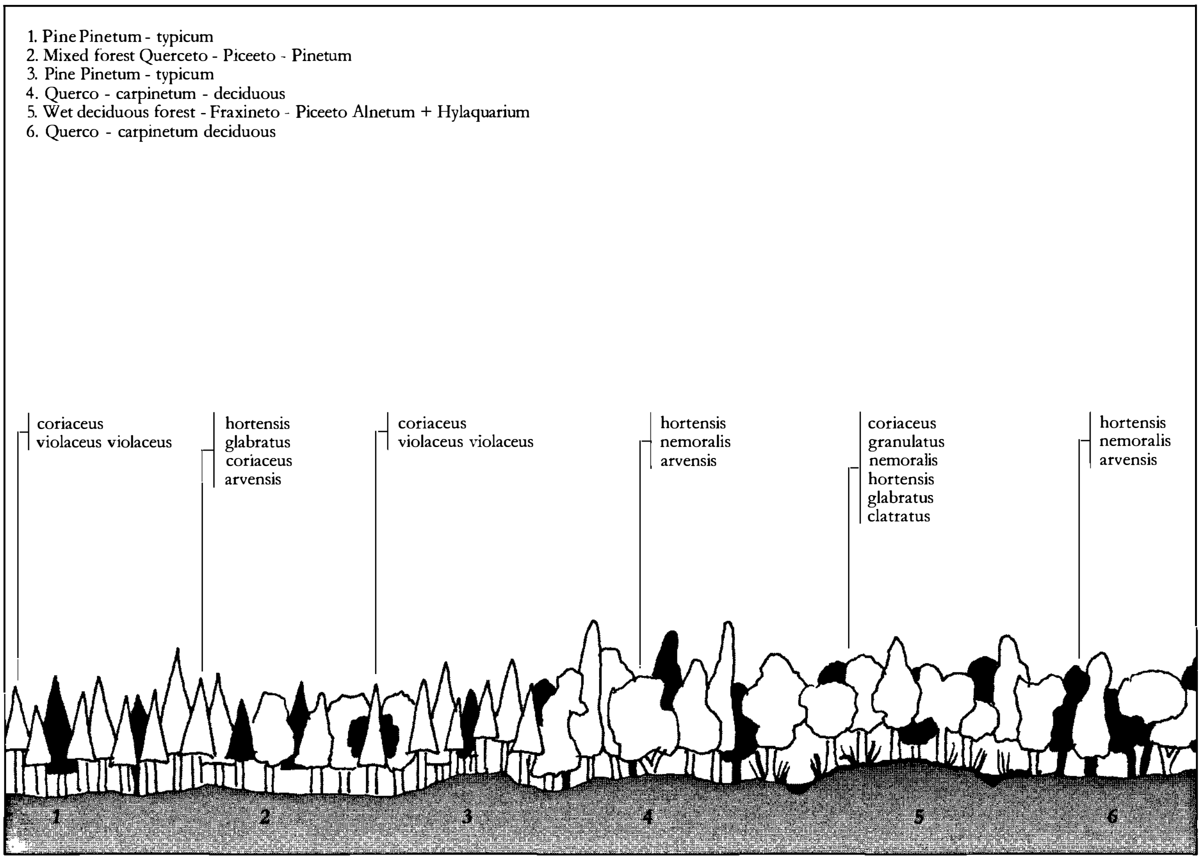
C. nitens was recorded only once and is now probably extinct. Also extinct are C. intricatus (from the lower parts) and C. sylvestris (from the upper region); both have been recorded from Babia Góra in the 19th century (before 1880). C. fabricii (in Poland only found here) is probably endangered in refugia between 1600-2170 m).



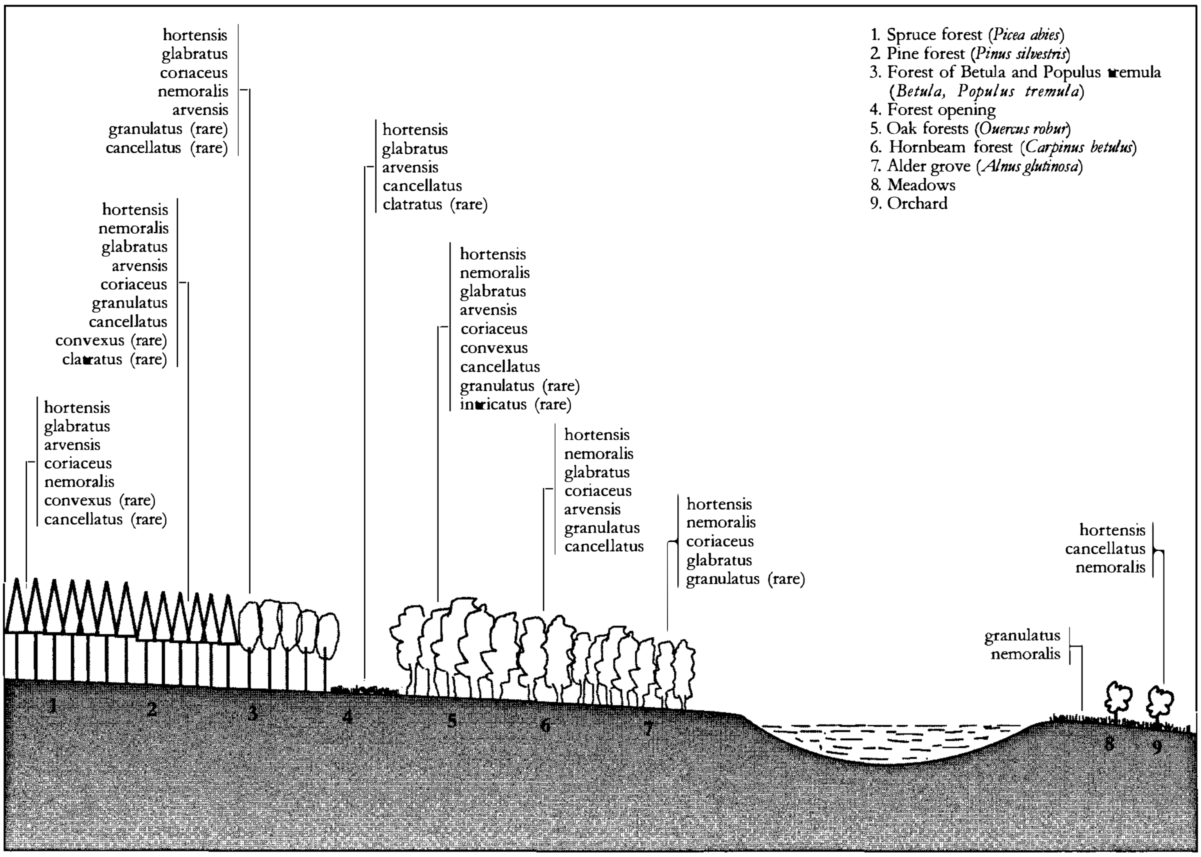
T-36. Poland:
Człuchow Forest (NW Poland).
J. Skłodowski, from original data.



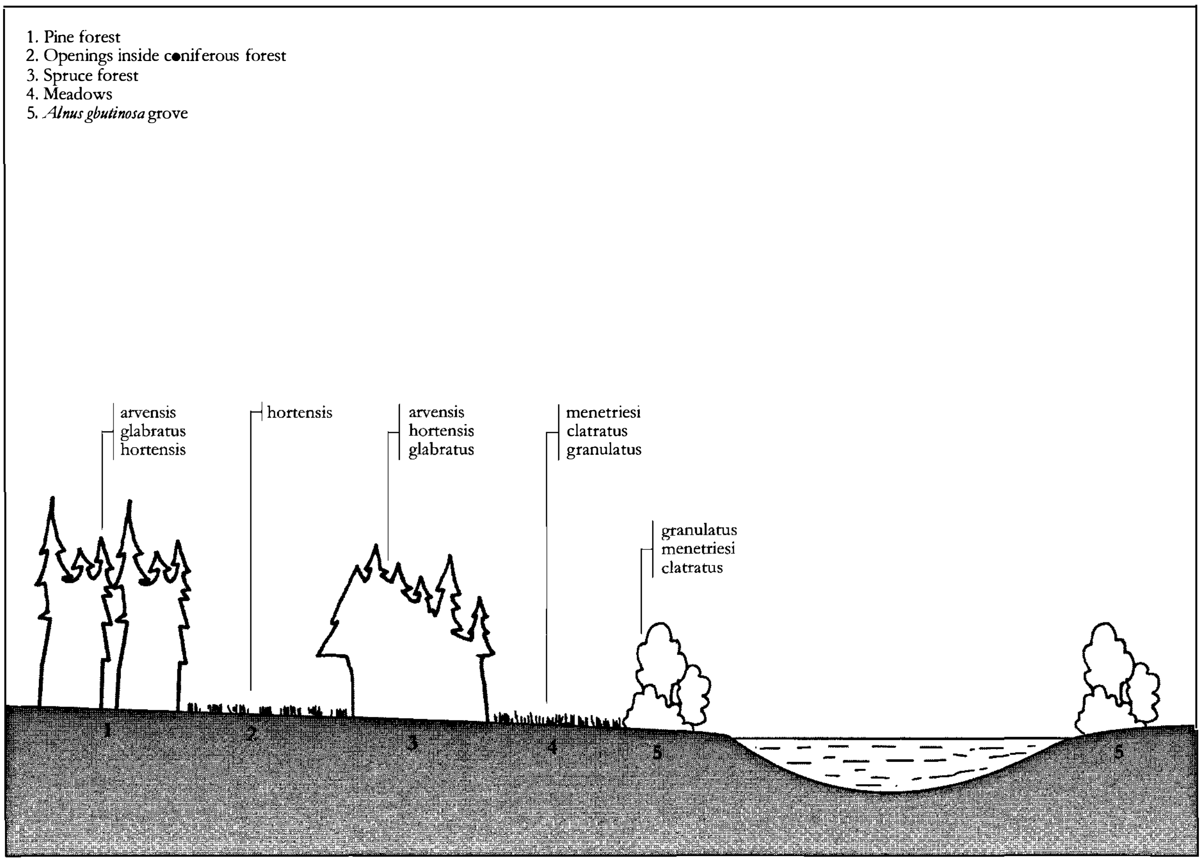
T-37. Poland:
Borecki forest (NE Poland).
J. Skłodowski, from original data.



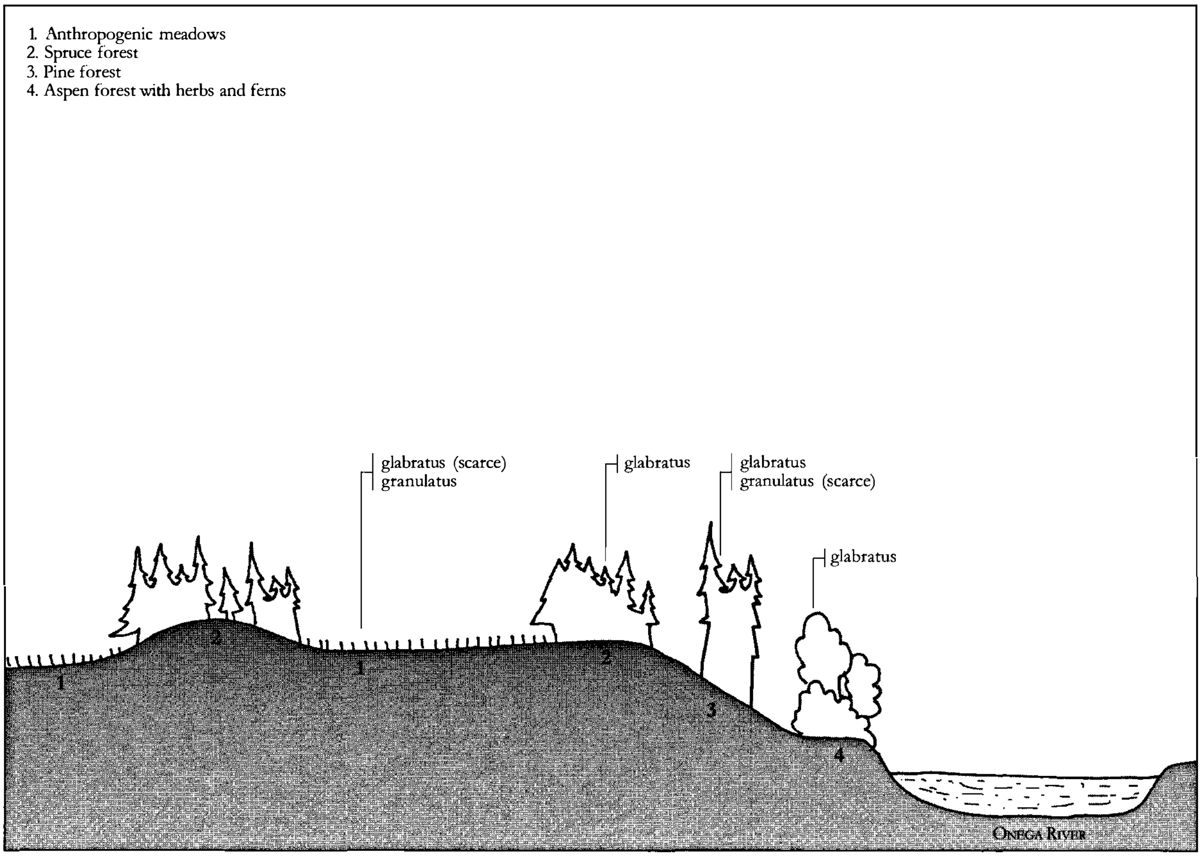
T-38. Poland:
Bialowieza forest in eastern Poland.
J. Skłodowski, from original data (see also T-39).



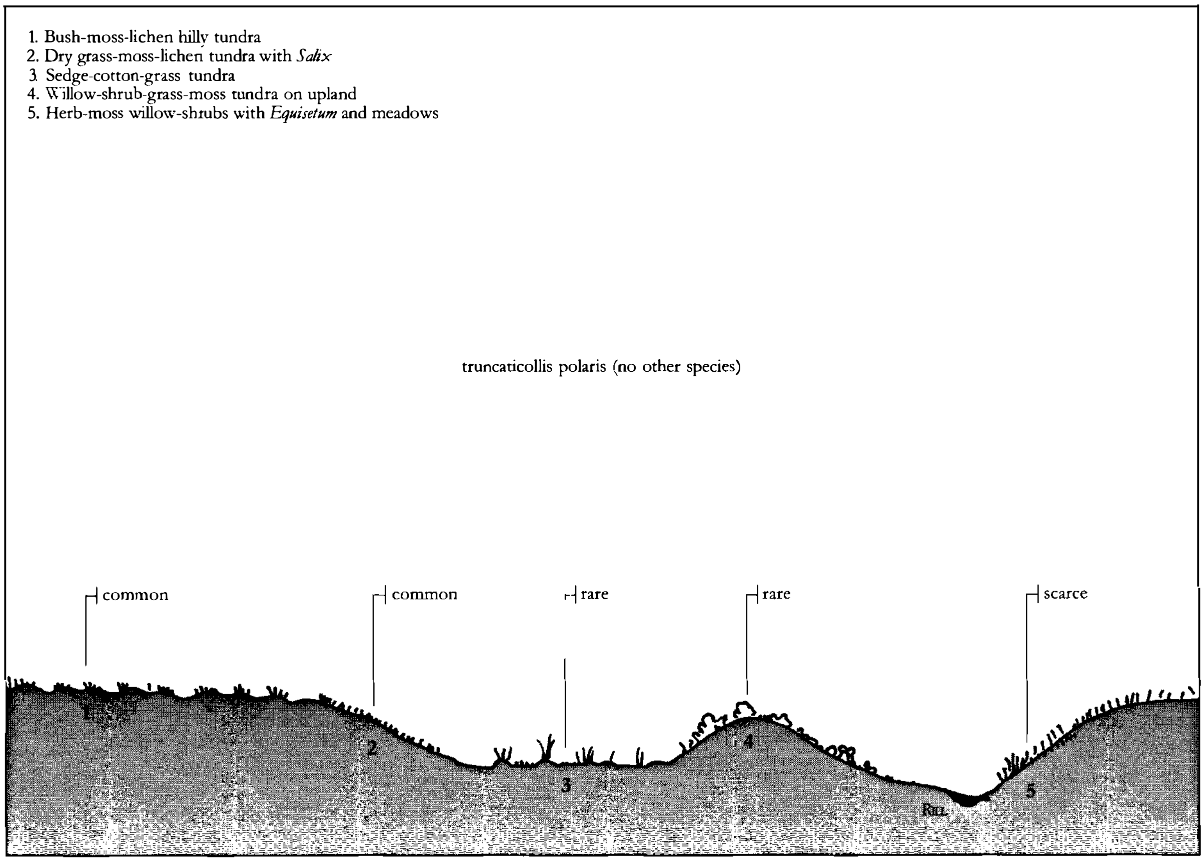
T-39. Byelorussia:
Byelovezha Reserve in western Beyelorussia.
L. Penev, after Arzamasau (1966).
It concerns the same forest complex as transect T-38.



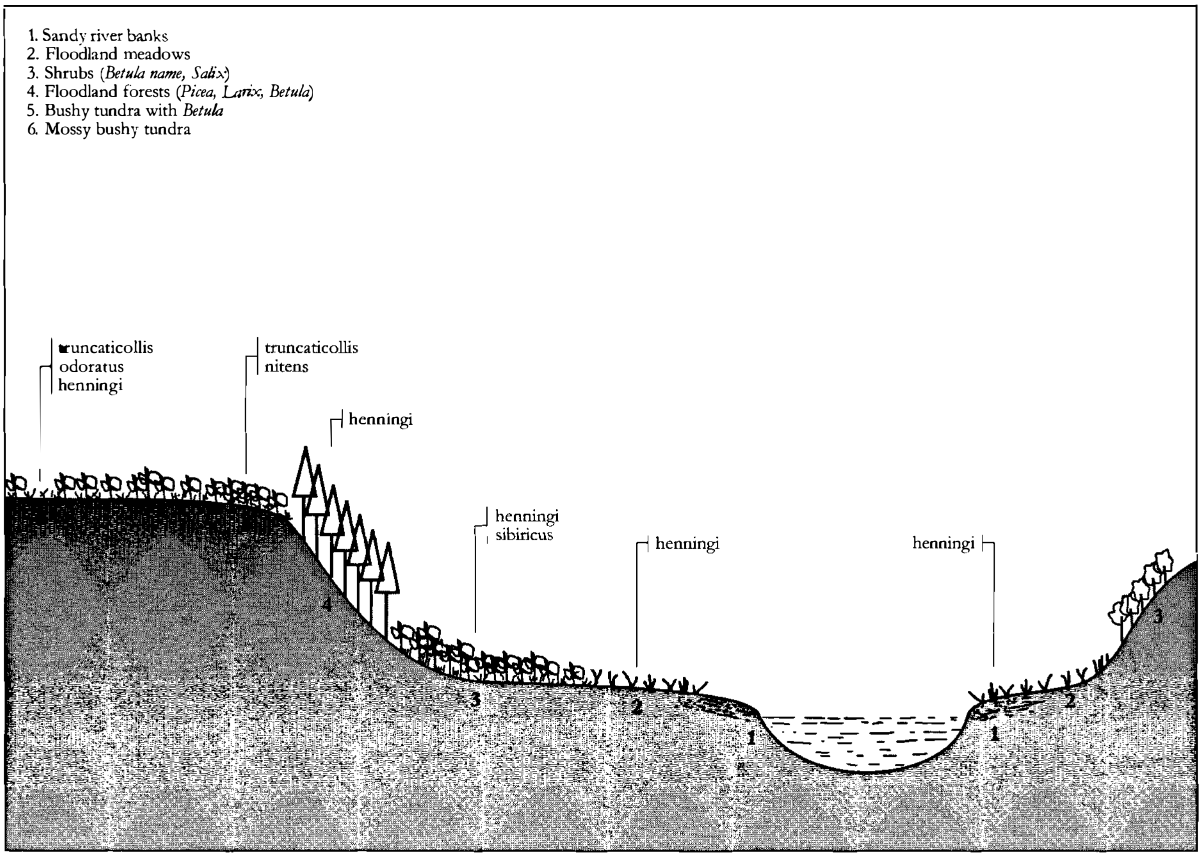
T-40. Byelorussia: *Berezina Reserve in central Byelorussia. L. Penev, after Khot'ko et al. (1988).*



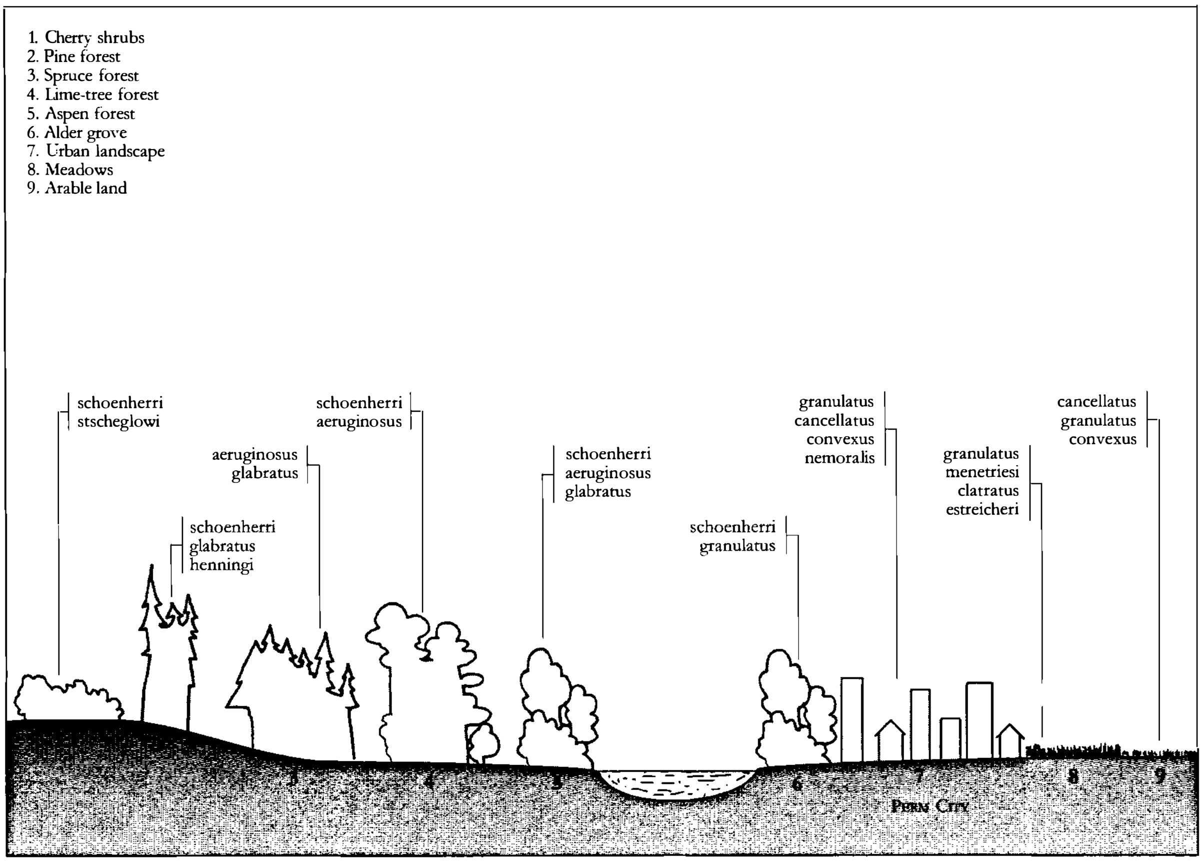
T-41. Russia: *Onega District (Gribanikha Village) in the Arkhangelsk Province (northern part of European Russia). K. Makarov, after data provided by S. Gryuntal.*



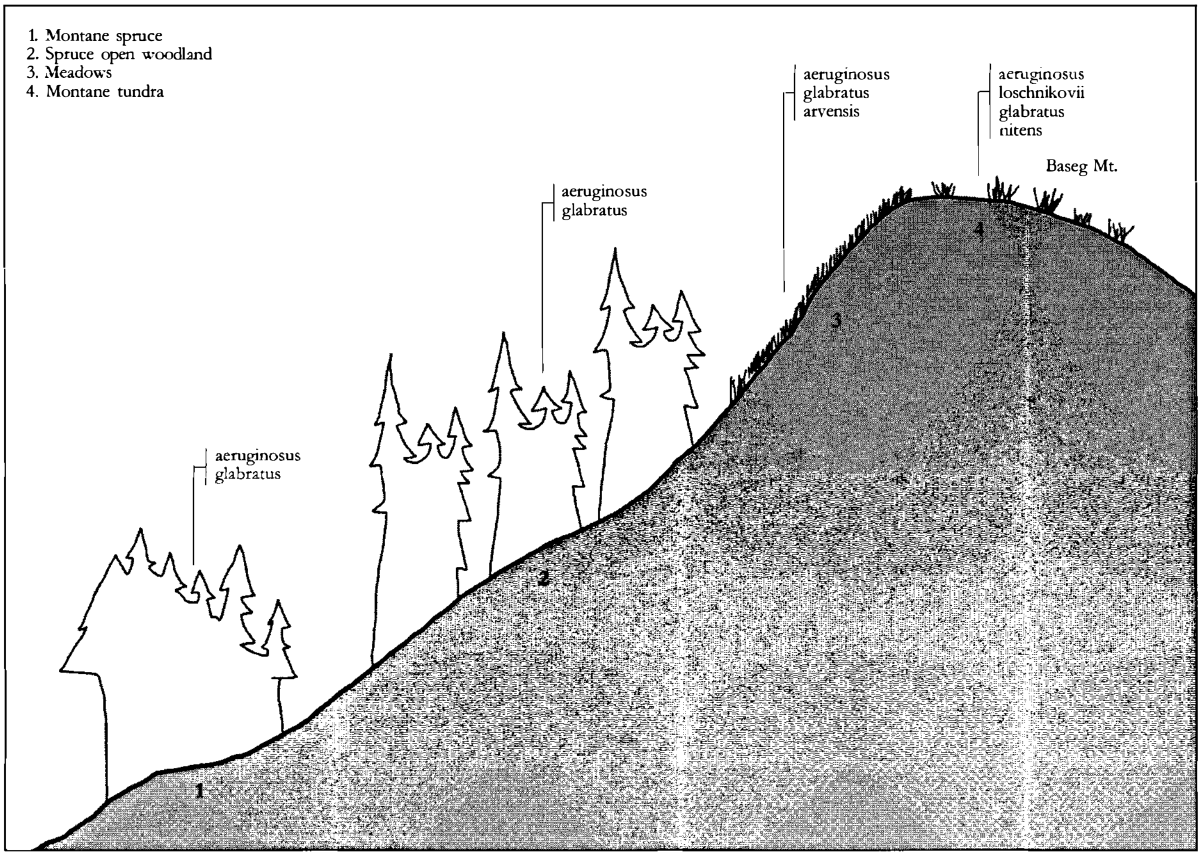
T-42. Russia: *A high northern locality (near Yaibari, 71°04' N) in the Yamal Peninsula, in adjacent non-European West Siberia, very close to the north-easternmost part of Europe. K. Makarov, after Ryabitsev (1998).*



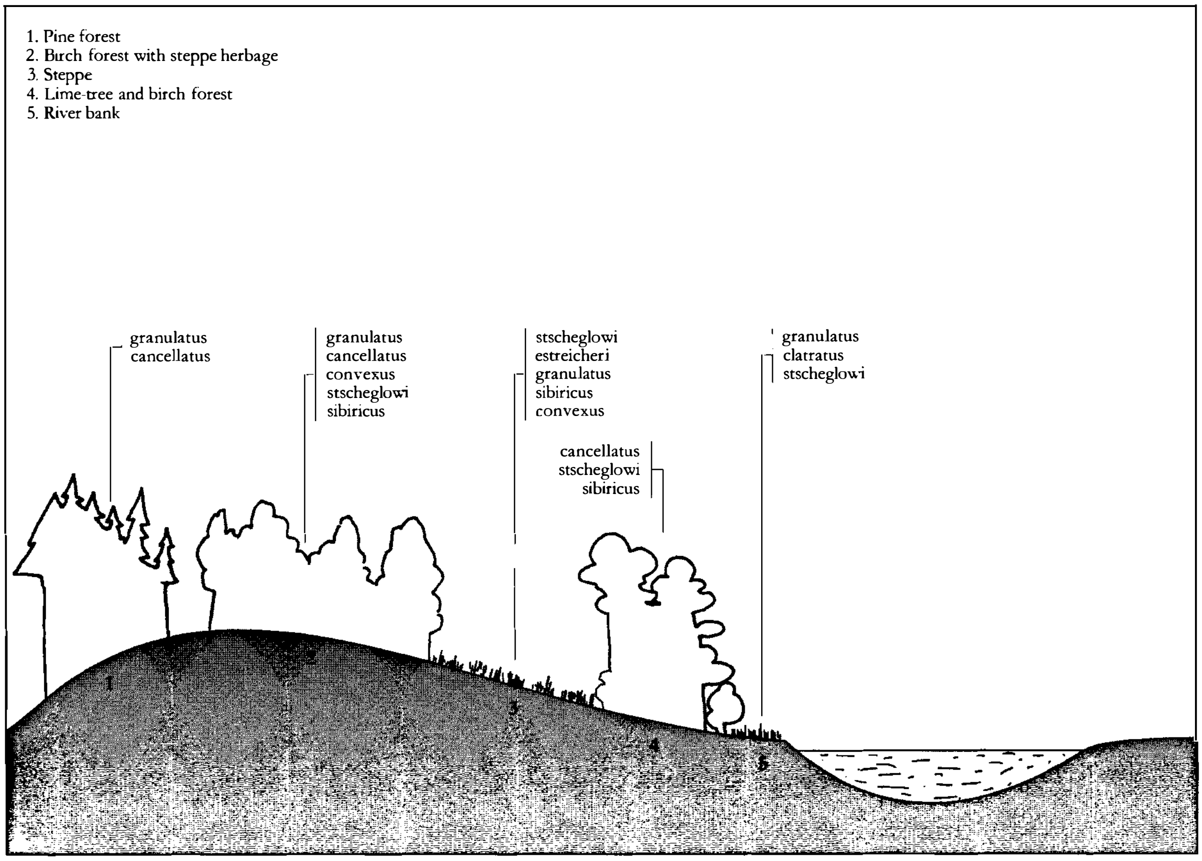
T-43. Russia: *Polar Ural, South Yamal Peninsula, at the middle flow of the Khadyta-Yakha river. L. Penev, after Korobeinikov (1987).*



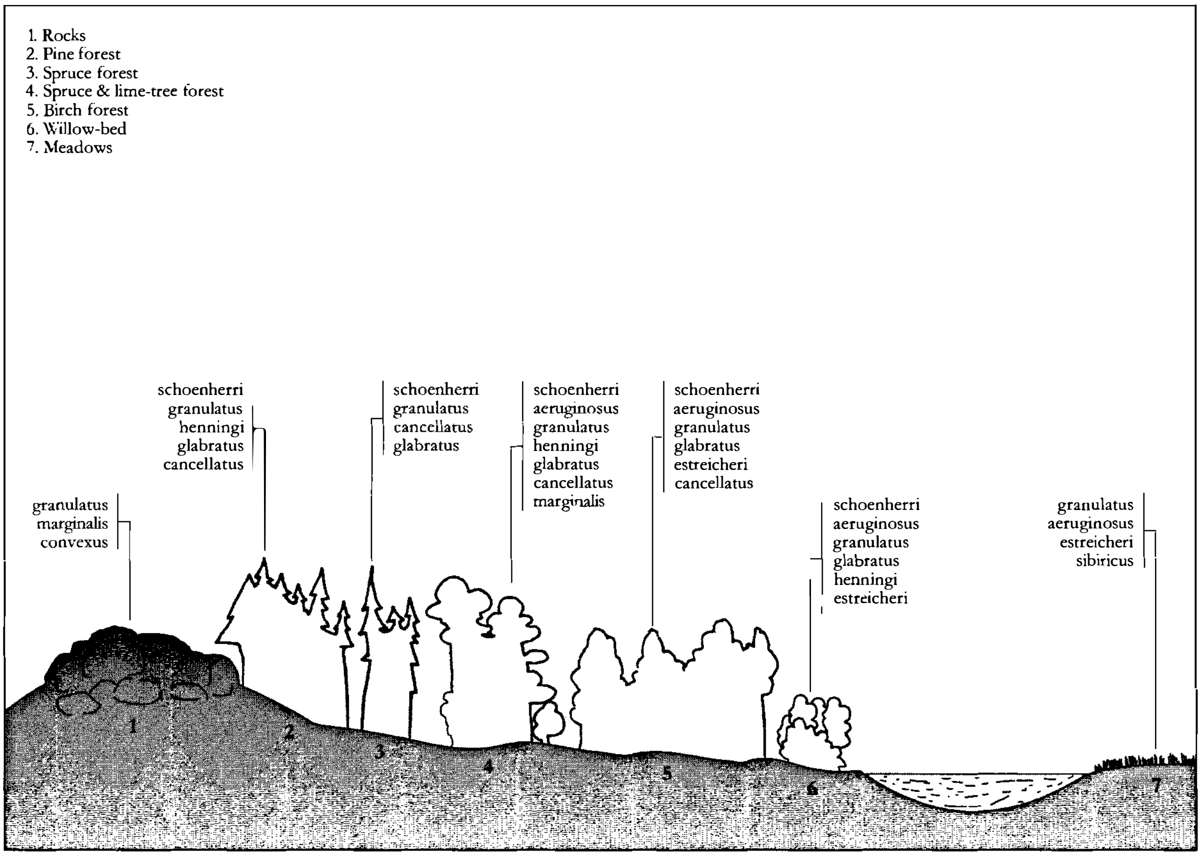
T-44. Russia: *Perm city and its environments. L. Penev, after data compiled by V. Koz'minykh and S. Esyunin, from Kozyrev et al. (1995), Kozyrev and Koz'minykh (1997) and Voronin (1999).*



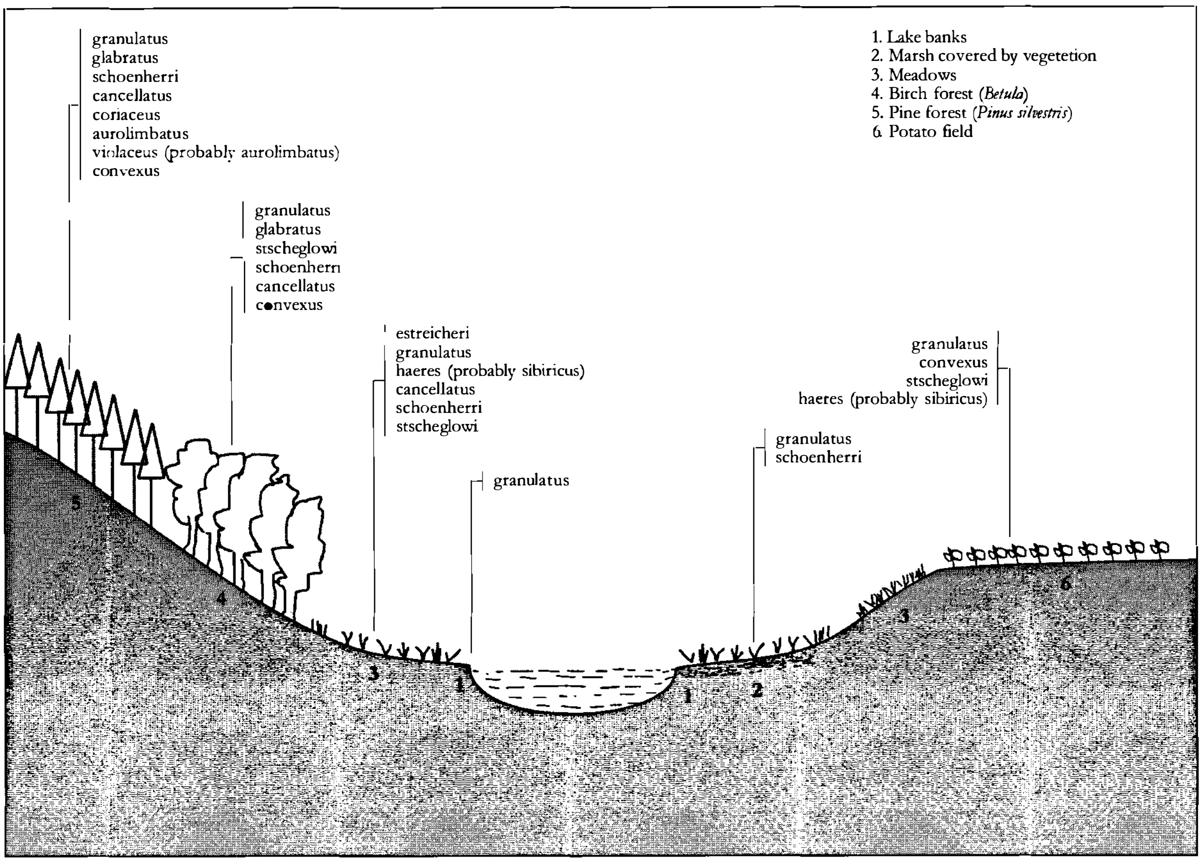
T-45. Russia: *Transect from the Baseg mountain range in the Middle Urals (Perm Province, Gornozavodsk District). L. Penev, after data compiled by V. Koz'minykh and S. Esyunin from A. Kozyrev et al. (unpublished) and Voronin (1999).*



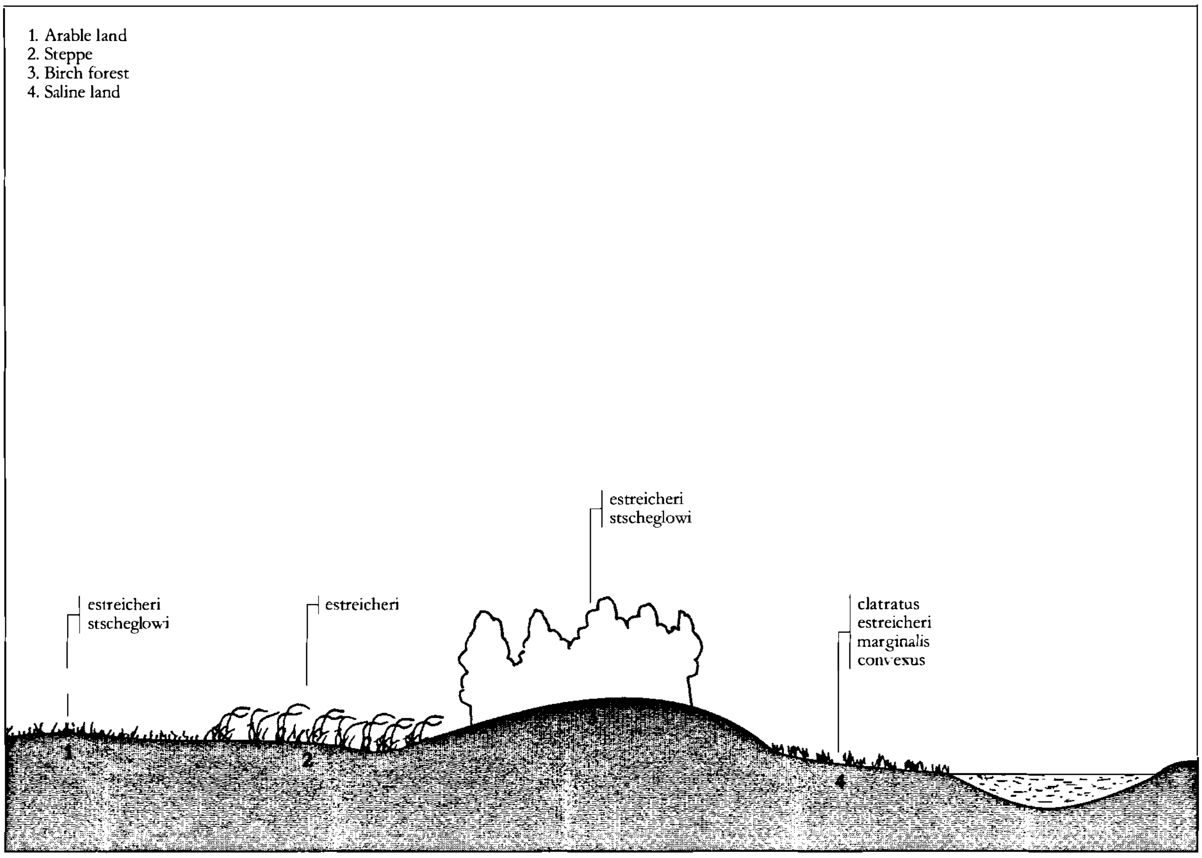
T-46. Russia: *Spasskaya Gora Reserve in the Middle Urals (Perm Province, Kungur District). L. Penev, after data compiled by V. Koz'minykh and S. Esyunin from Zinovyev (1997) and Koz'minykh and Esyunin (1991).*



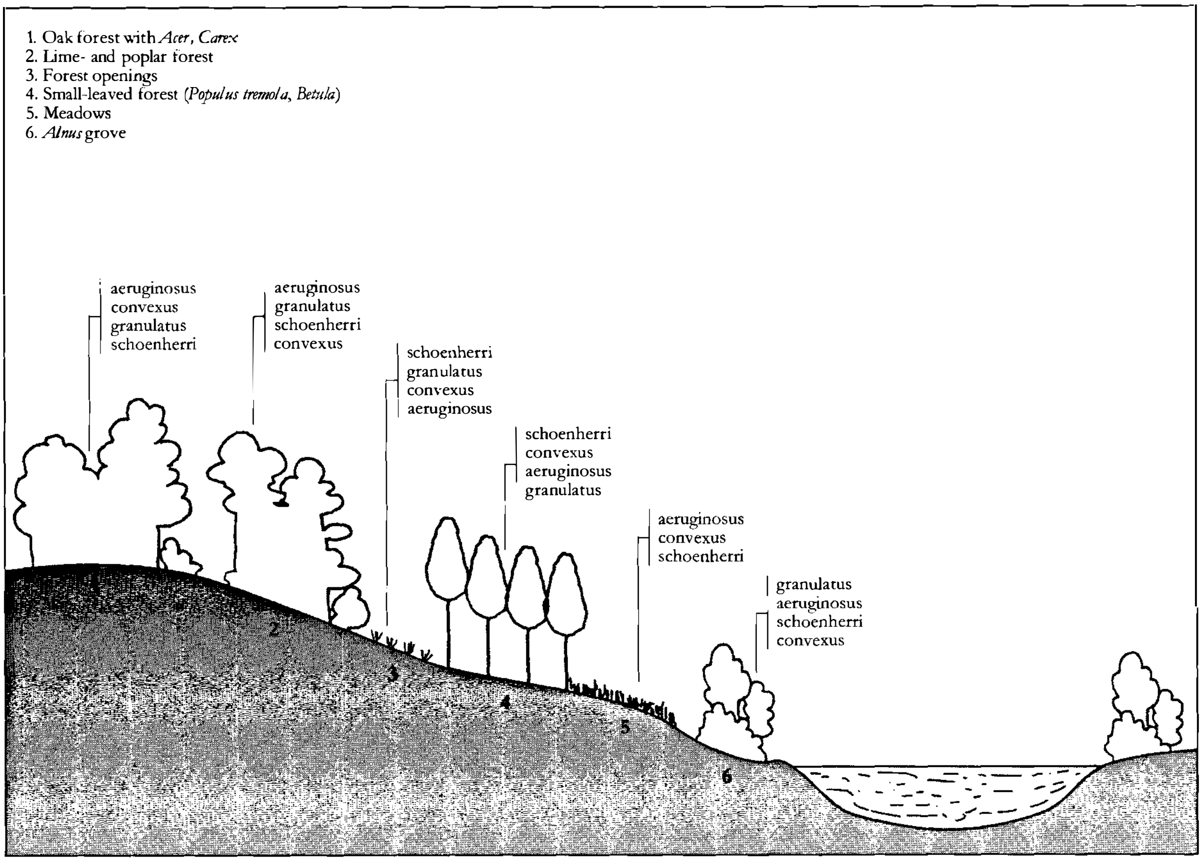
T-47. Russia: *Predural'ye Reserve in the Middle Urals (Perm Province, Kishert District). L. Penev, after data compiled by V. Koz'minykh and S. Esyunin from Voronin (1999, 2000) and A. Kozyrev et al. (unpublished).*



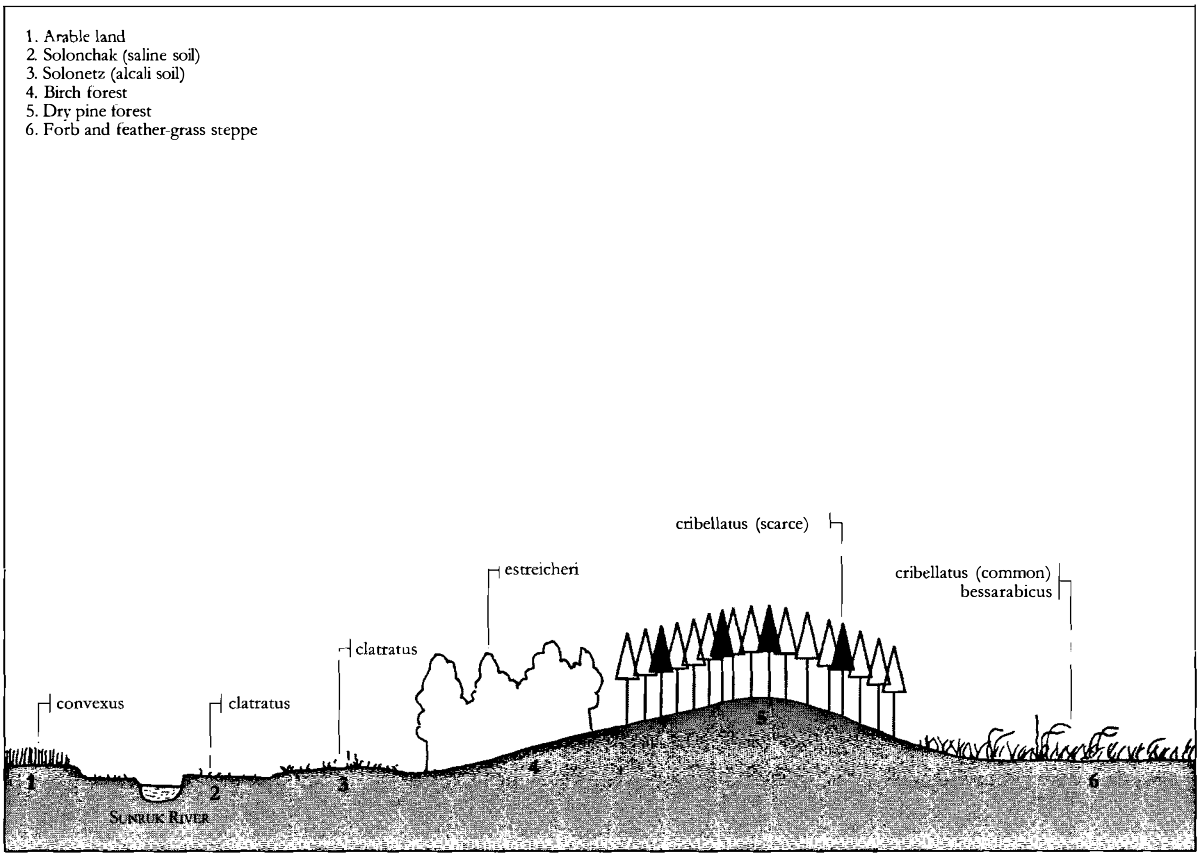
T-48. Russia: *Ilmen Reserve in the South Urals (Chelyabinsk Province, Miass District). L. Penev, after Korobeinikov (1979).*



T-49. Russia: *Troitsk Reserve in southern Transuralia (Chelyabinsk Province, Troitsk District). L. Penev, after unpublished data provided by I '. Koz'minykh and S. Esyunin.*

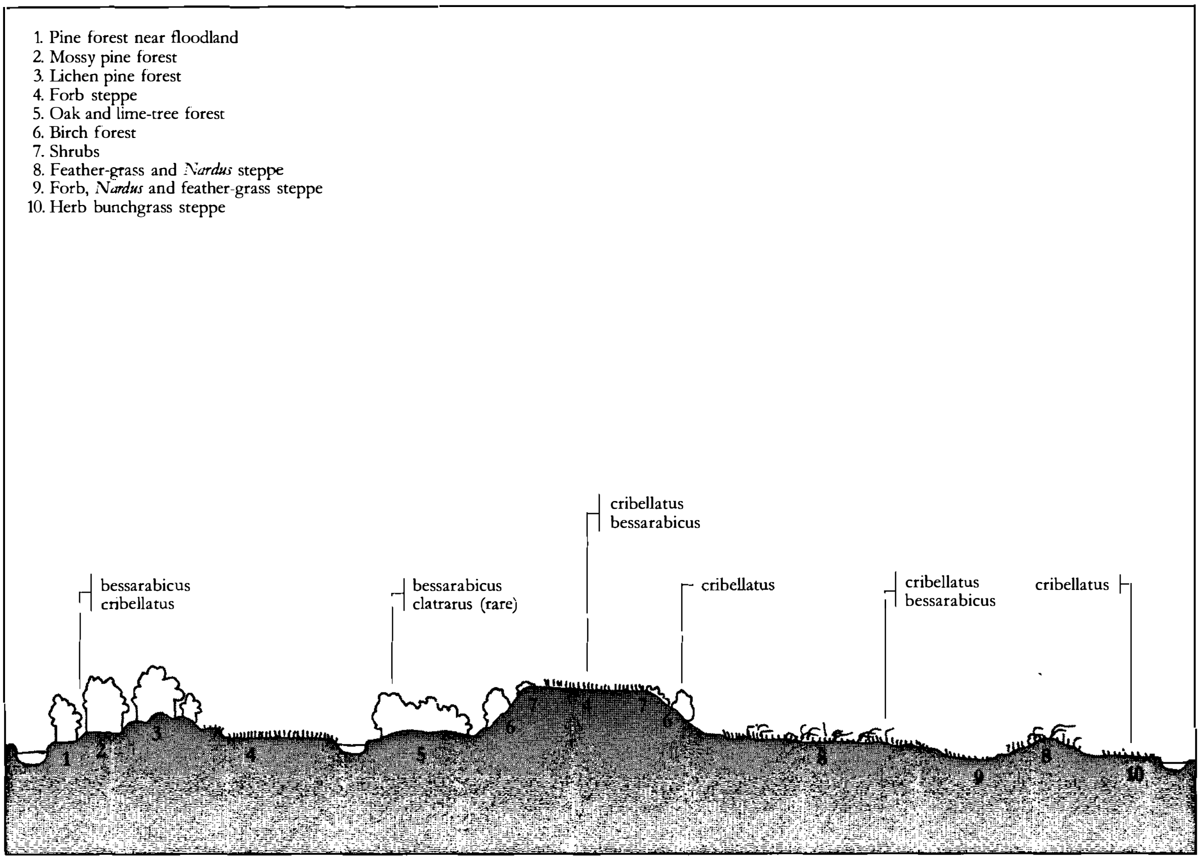


T-50. Russia:., *South Uralian Nature Reserve near Belyaqutovo (Burzian Distr., Republic Bashkiria). L. Penev, after Kasheverov (1986).*

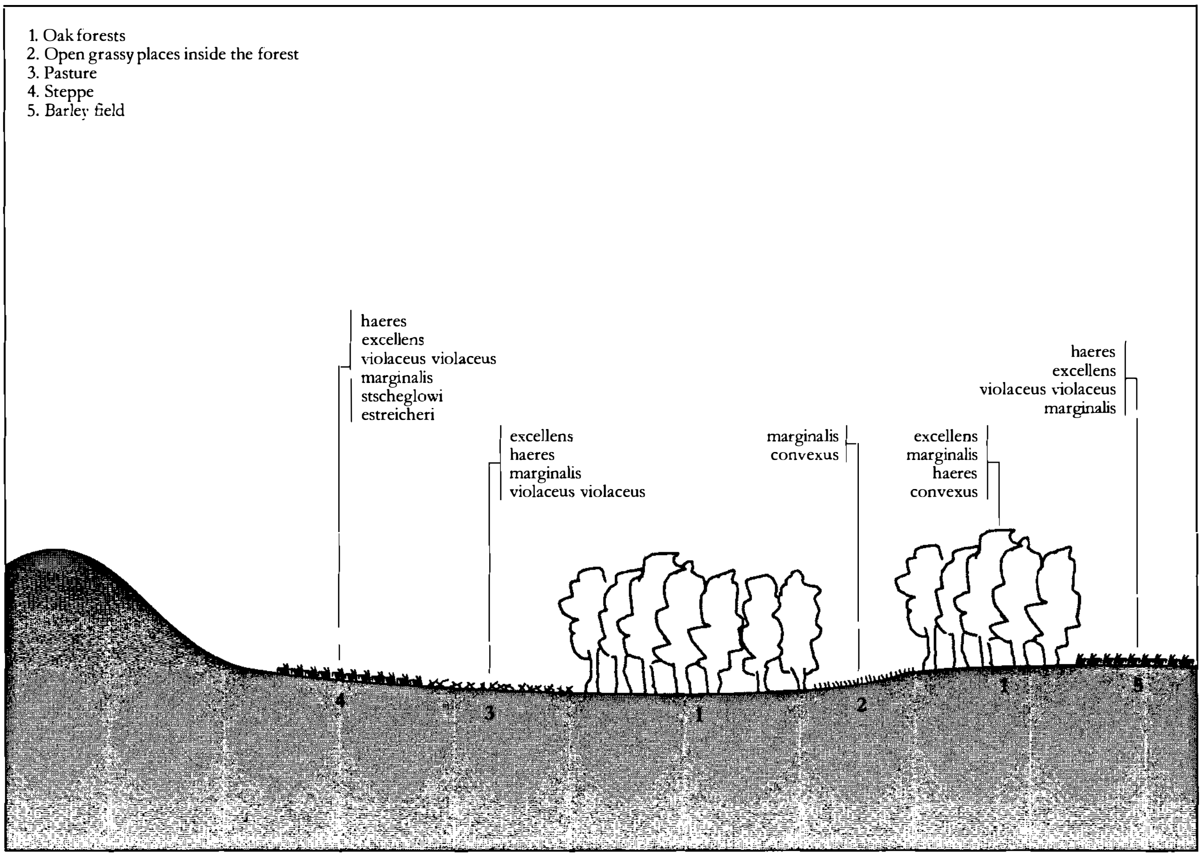


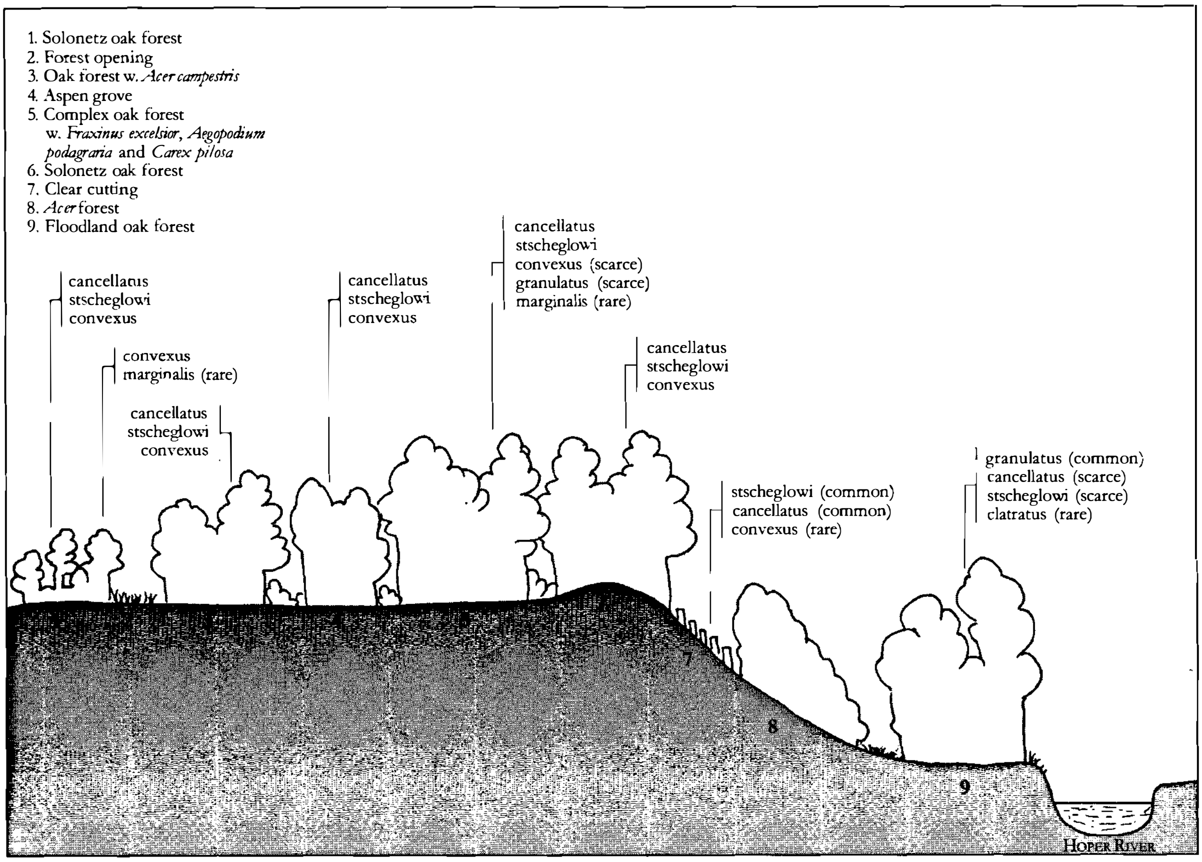
T-51. Russia: *Environments of Bolotovsk in the southeastern part of European Russia (Orenburg Province, Bolotovsk District). K. Makarov and L. Penev, after Lapshin (1969) and Sharova & Lapshin (1971).*

T-52. Russia: *Buzuluk District, the southeastern part of European Russia (Orenburg Province). K. Makarov, after Nagumanova (PhD Thesis, unpublished).*



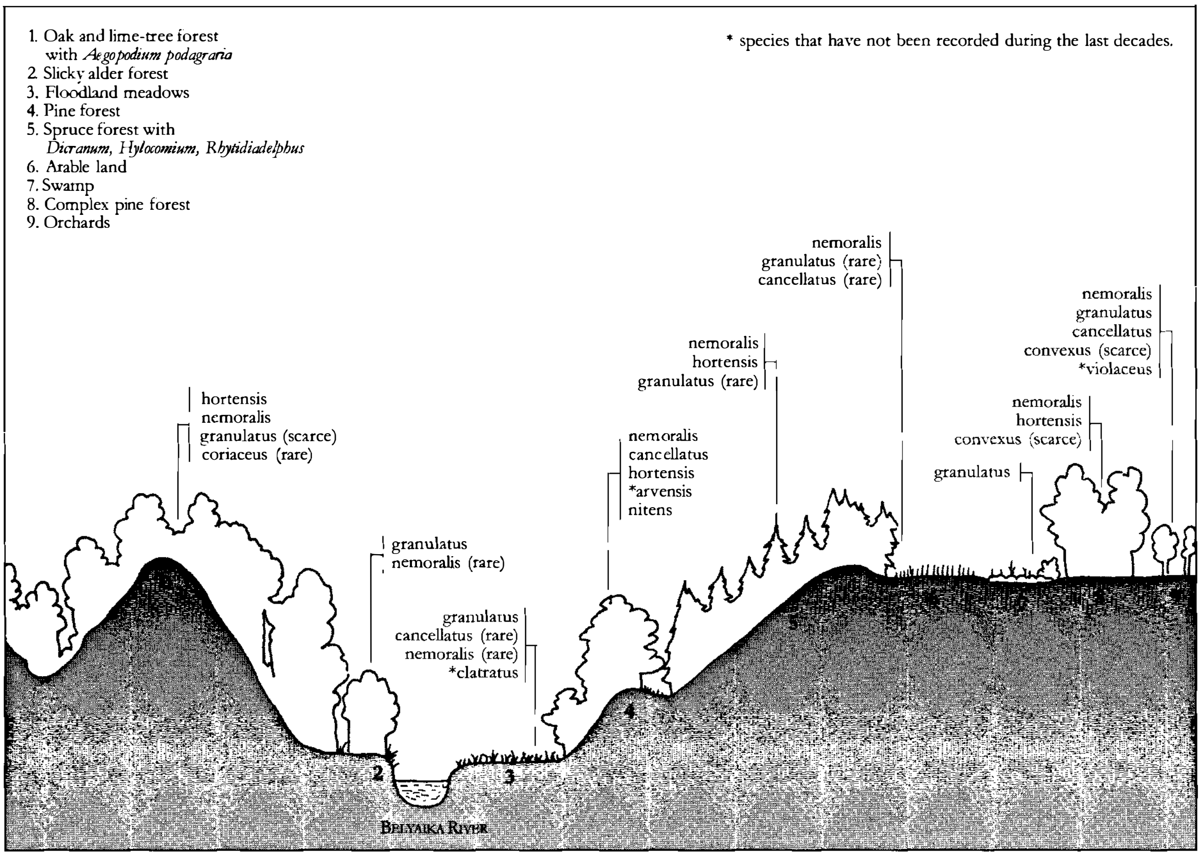
T-53. Russia: *Central-Chernozem Reserve near Kursk in the central part of European Russia (Kursk Province, Kursk District). L. Penev, after Arnoldi et al. (1972) and personal observations.*





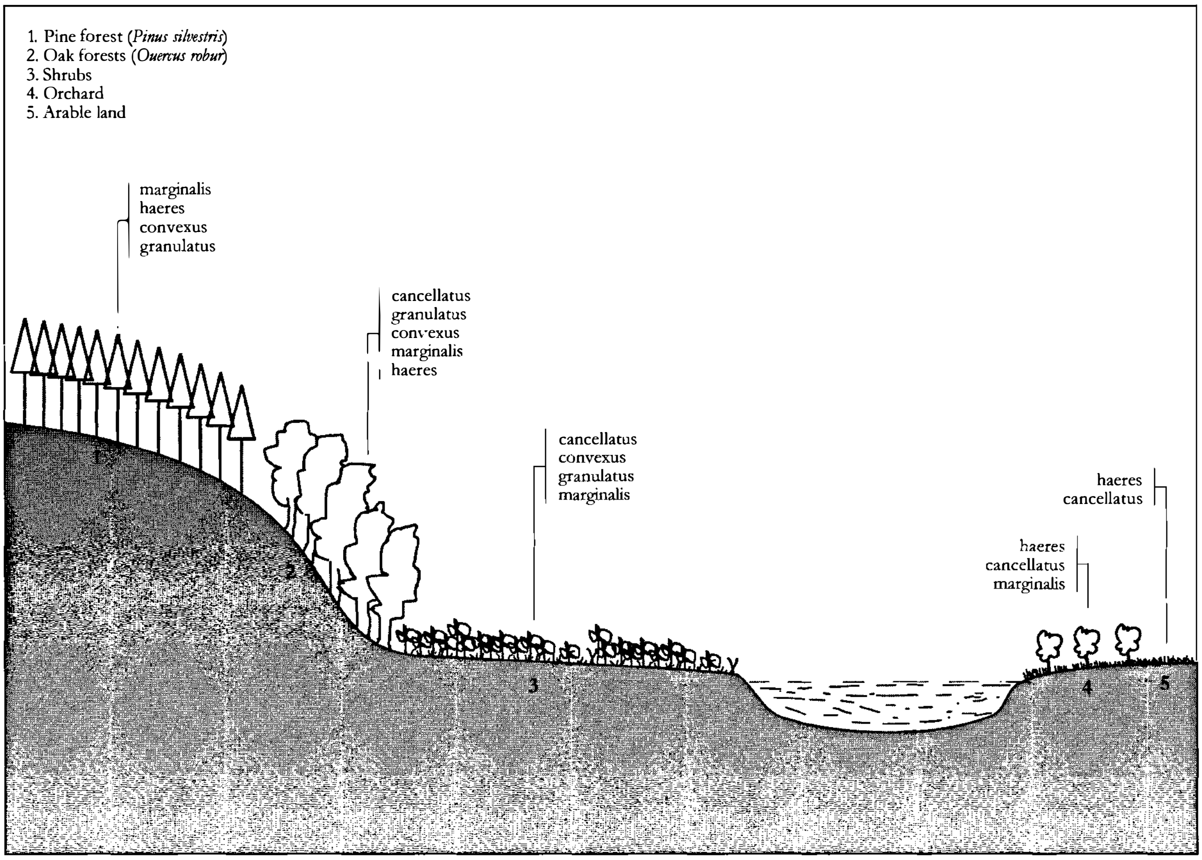
T-54. Russia:

Tellerman forest (Voronezh Province, Borisoglebsk District), Central Russia. K. Makarov, after original data provided by S. Gryuntal.

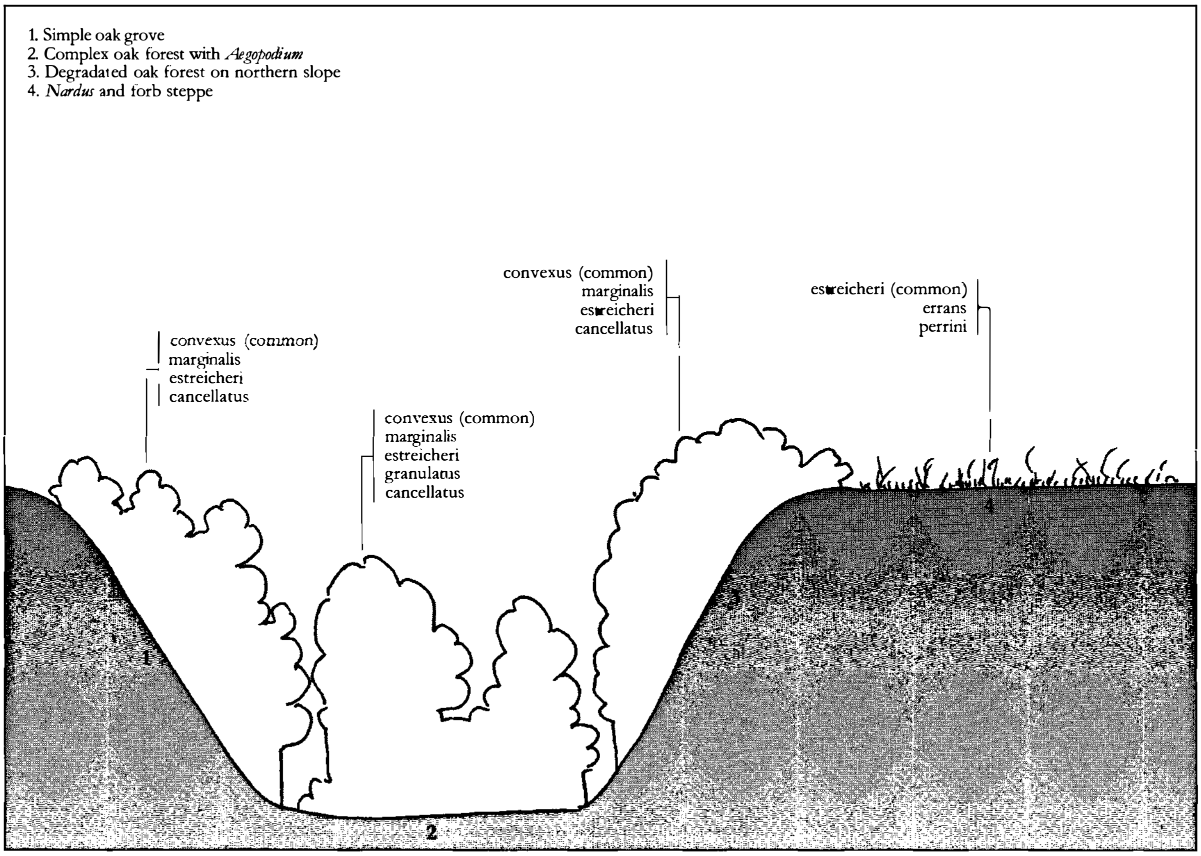


T-55. Russia:

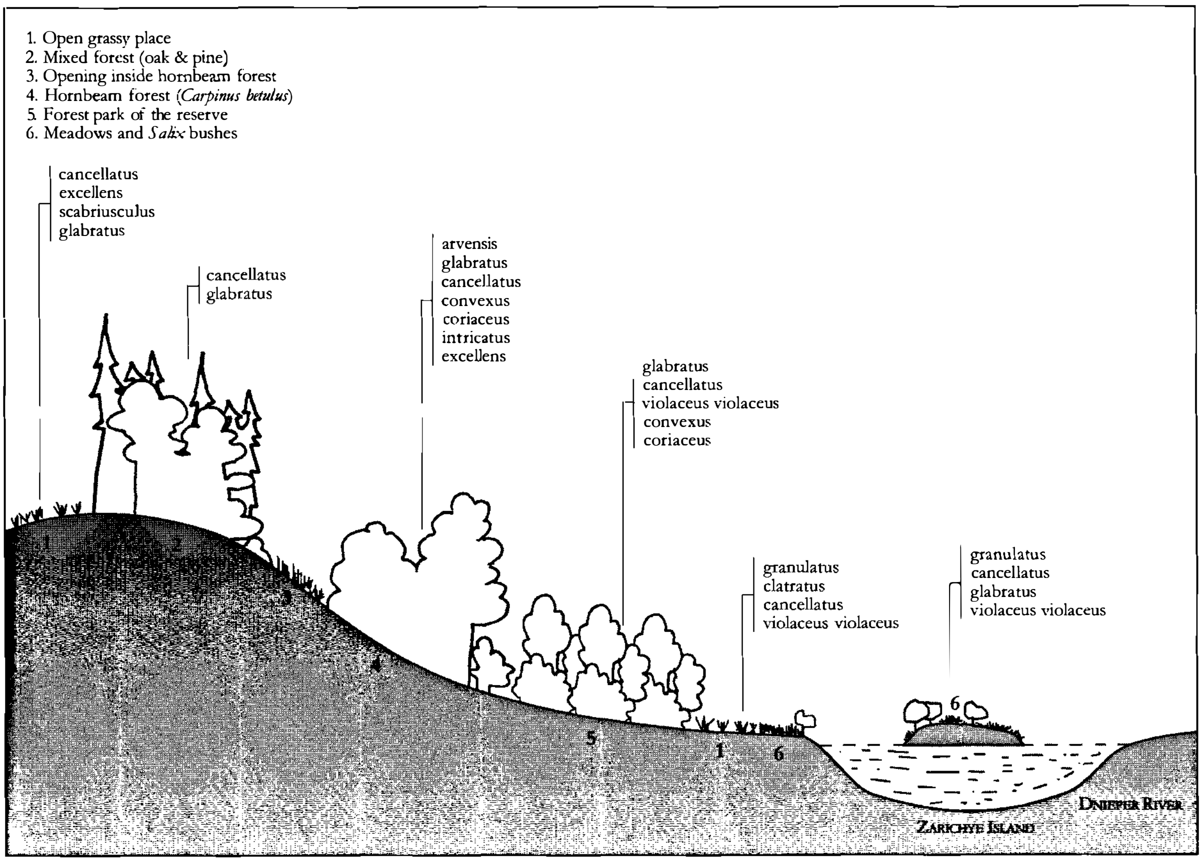
Pavlovskaya Sloboda (Moscow Province, Istra District), Central Russia. K. Makarov, after data provided by I. Sharova and personal observations.



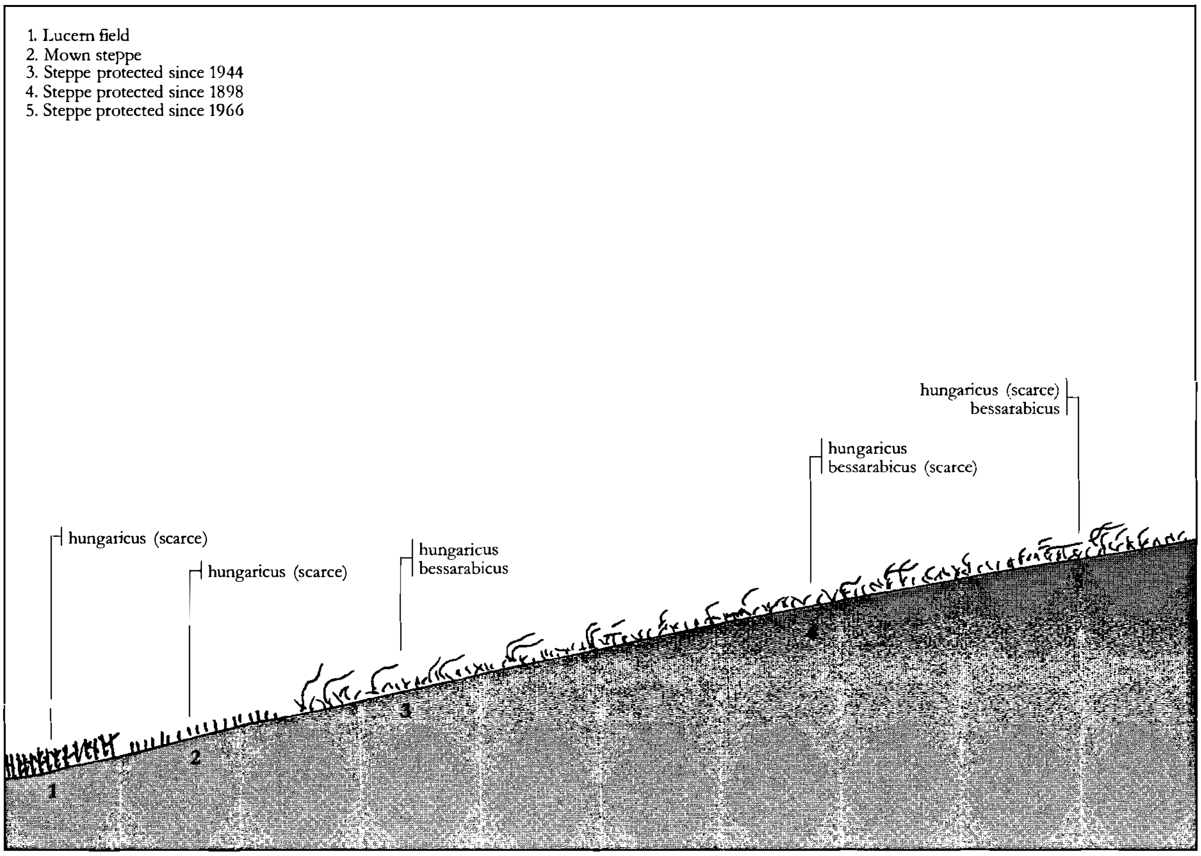
T-56. Russia: *Vorskla Reserve in Central Russia (Belgorod Province, Borisovka District). L. Penev, after Grinfeld (1948) and personal onservations.*



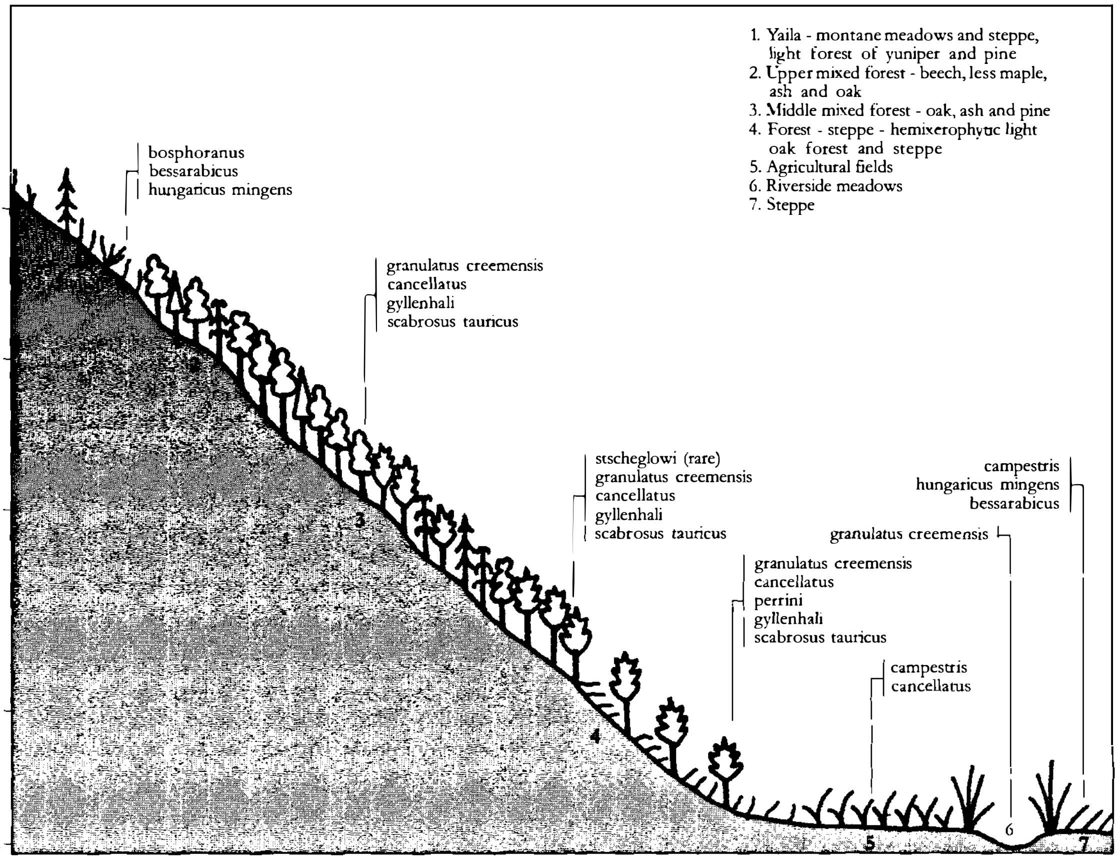
T-57. Russia: *Millerovo flat-bottom valley (ravine forest) in the southern part of European Russia (Rostov Province, Millerovo District). K. Makarov, after data provided by S. Cherednikov.*



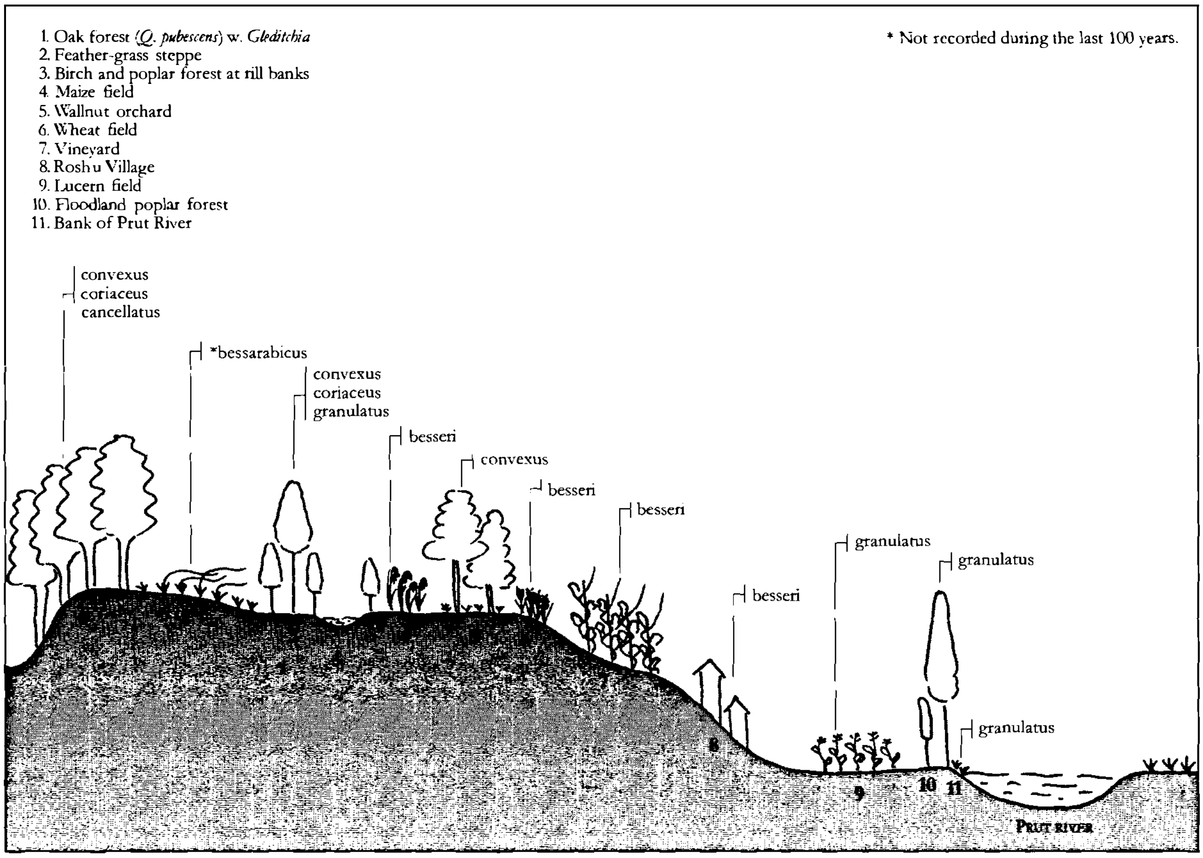
T-58. Ukraine: *Kanev Reserve in Central Ukraine. L. Penev, after Kryshtal (1956) and personal observations.*



T-59. Ukraine: *Askania Nova Reserve in South Ukraine. K. Makarov and L. Penev, after Pavlova (1974).*

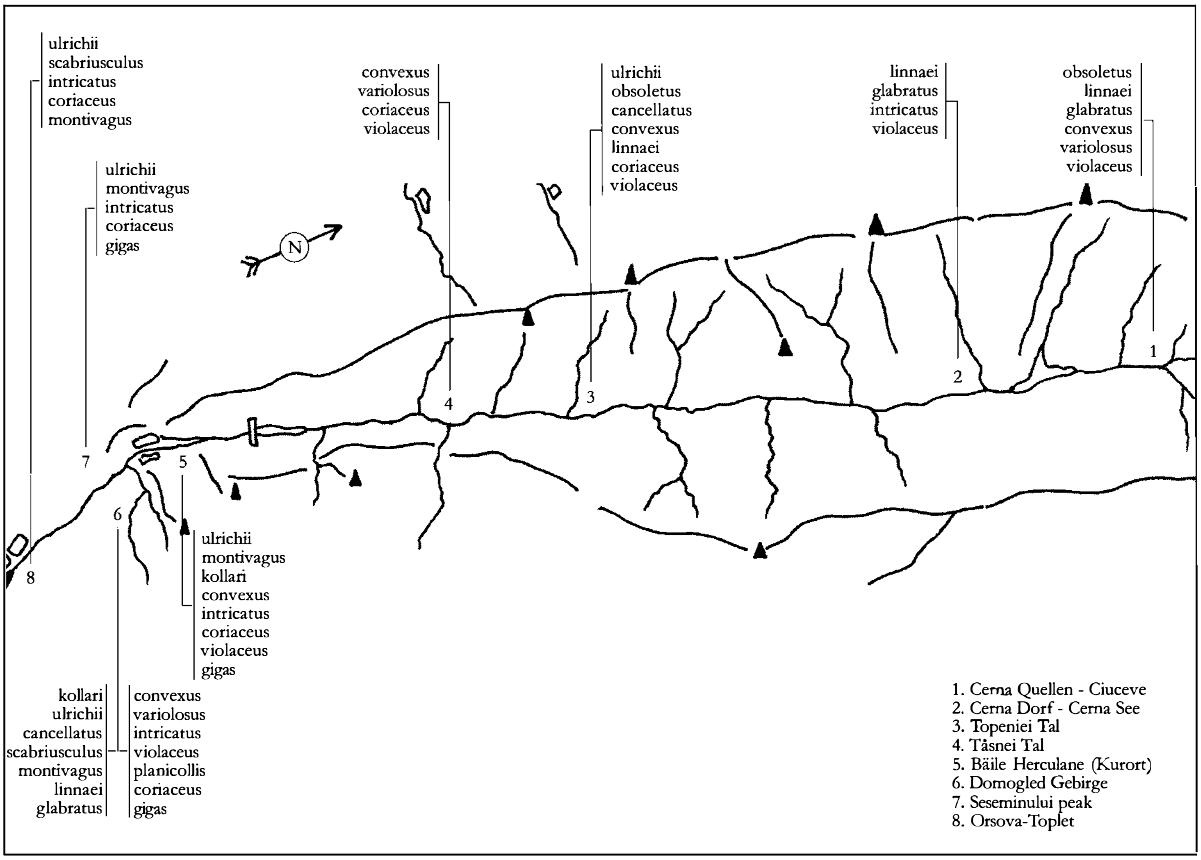


T-60. Ukraine:
Steppe to montane Crimea peninsula in South Ukraine. A. Putchkov; from original unpublished data.

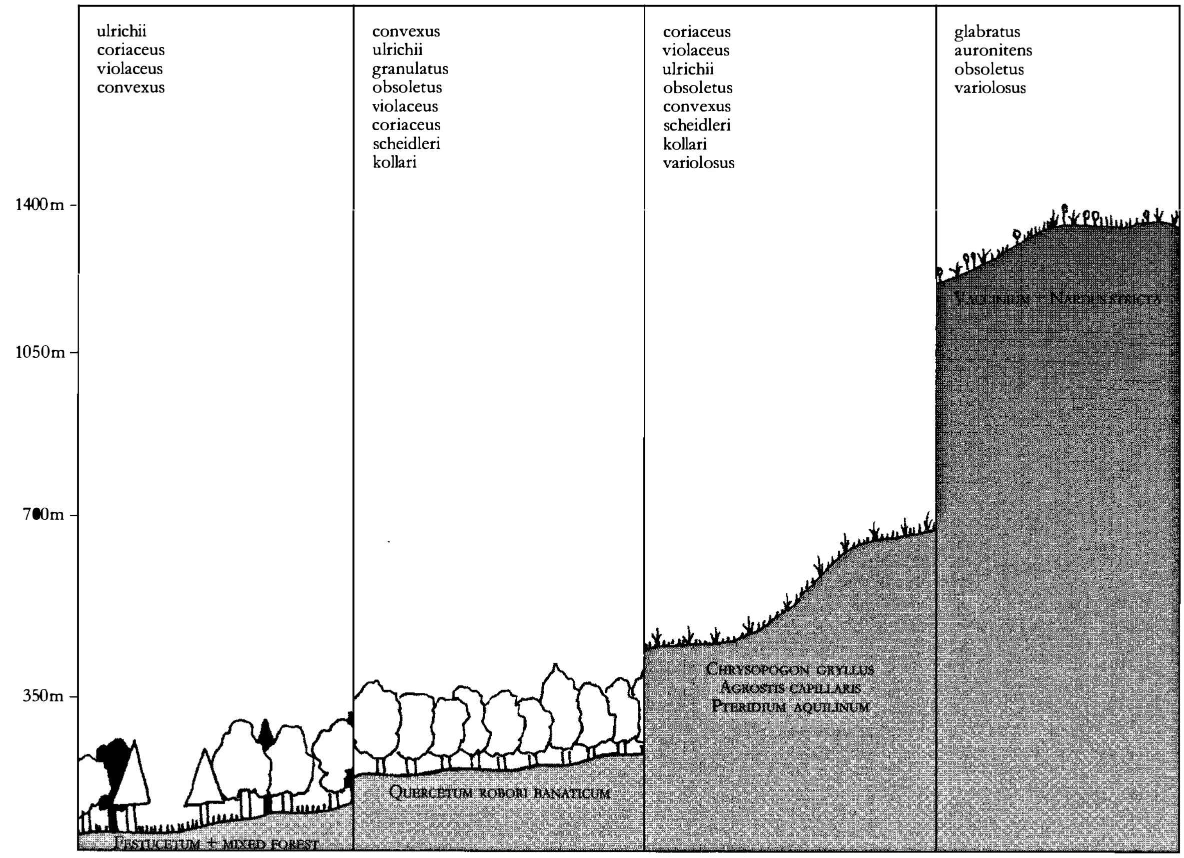


T-61. Moldova:
Flood plain of the Prut river in the environments of the Village of Roshu. Karpova and Matalin (1993).

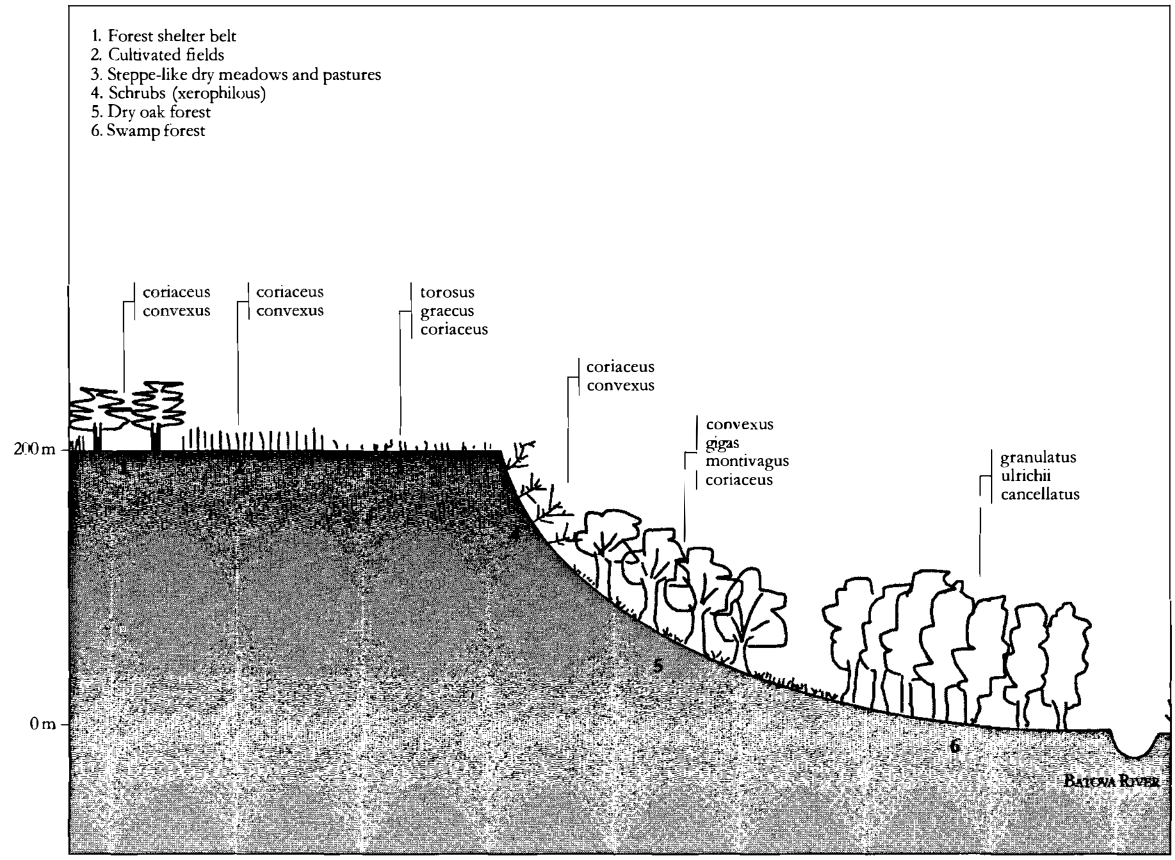
GENERAL PART



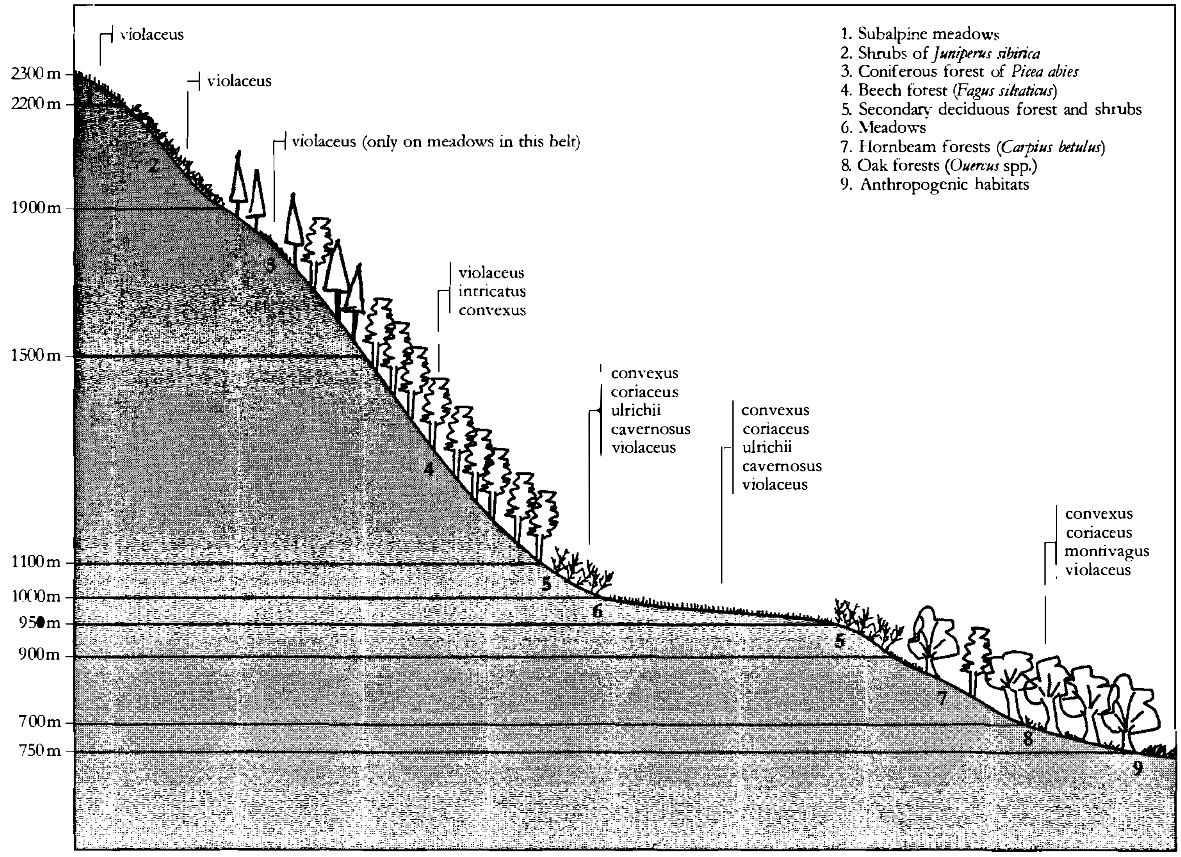
T-62. Romania:
Cernei valley (Banat), after Lie (1998), advised by F. Prunar.



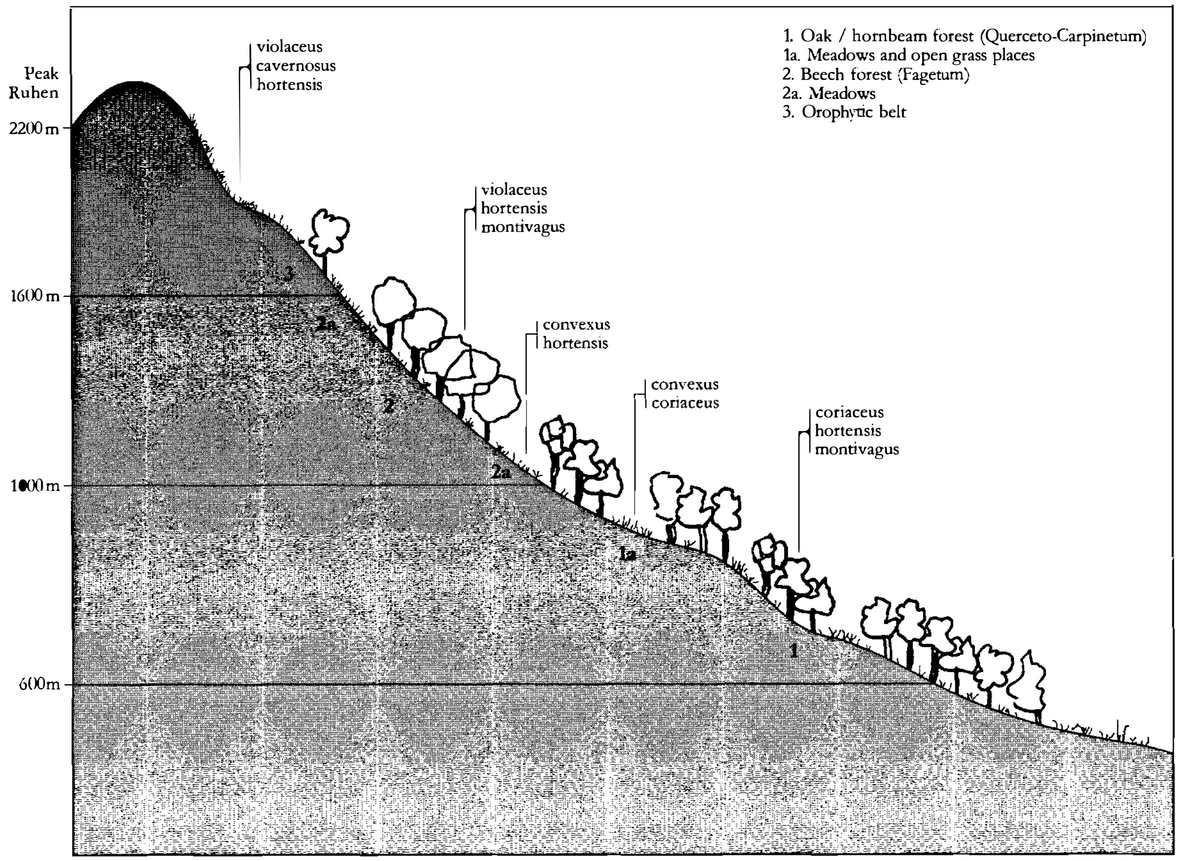
T-63. Romania:
Banat (Buziaş, Caraşova, Muntele Semenic, Timişoara), compilation by F. Prunar and H. Turin, from original data by F. Prunar.



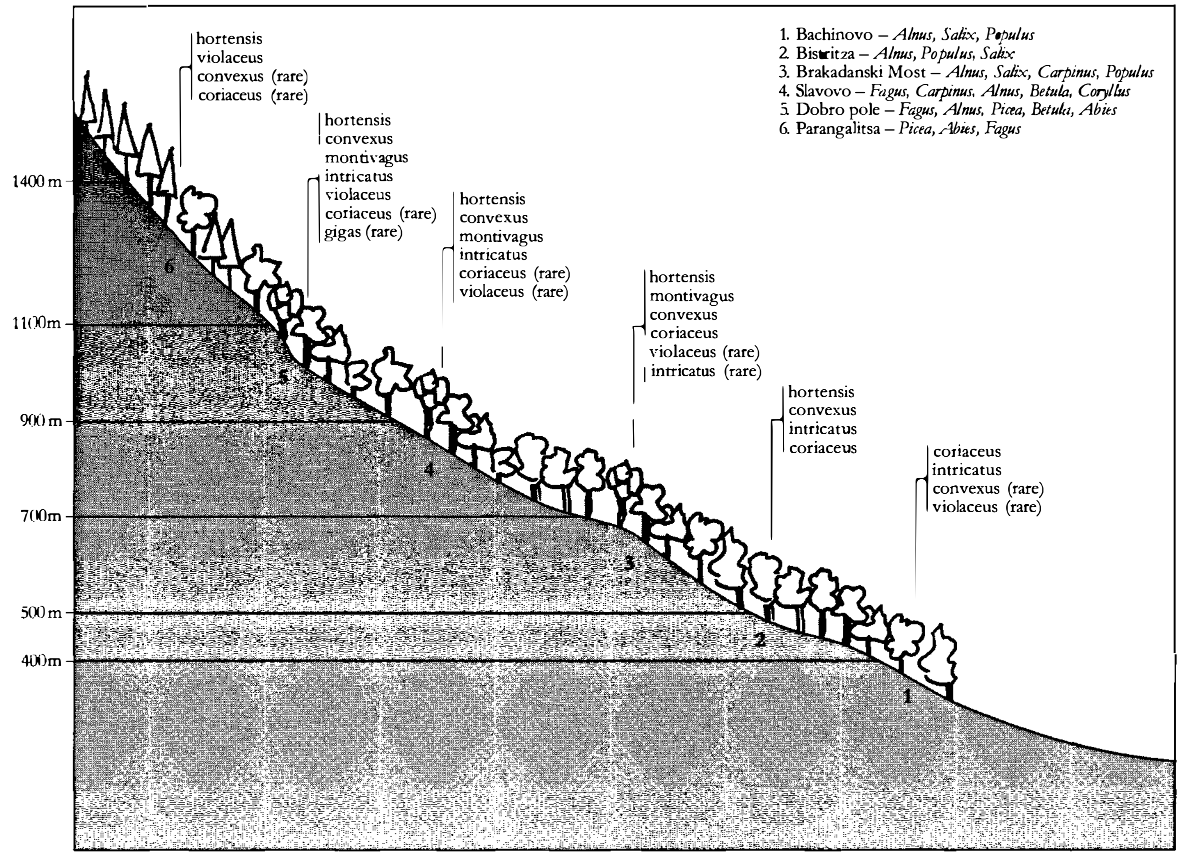
T-64. Bulgaria: *Northeastern Bulgaria, Dobrogean Plateau (between Kranevo and Balchik), near the Black Sea coast. V. Popov, after personal observations and Popov and Krusteva (1999).*



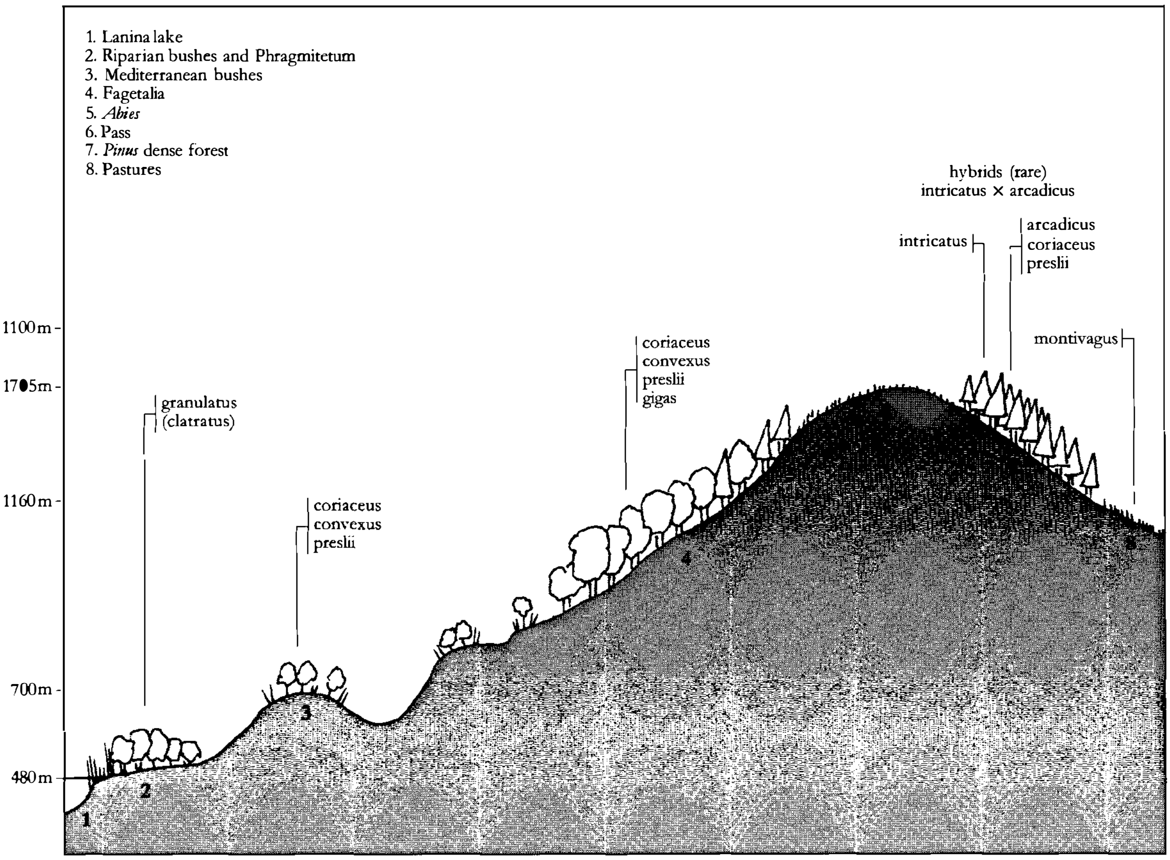
T-65. Bulgaria: *Western Bulgaria, Vitosha Mt., northern macroslope. V. Popov, after personal observations and Krusteva et al. (1995).*



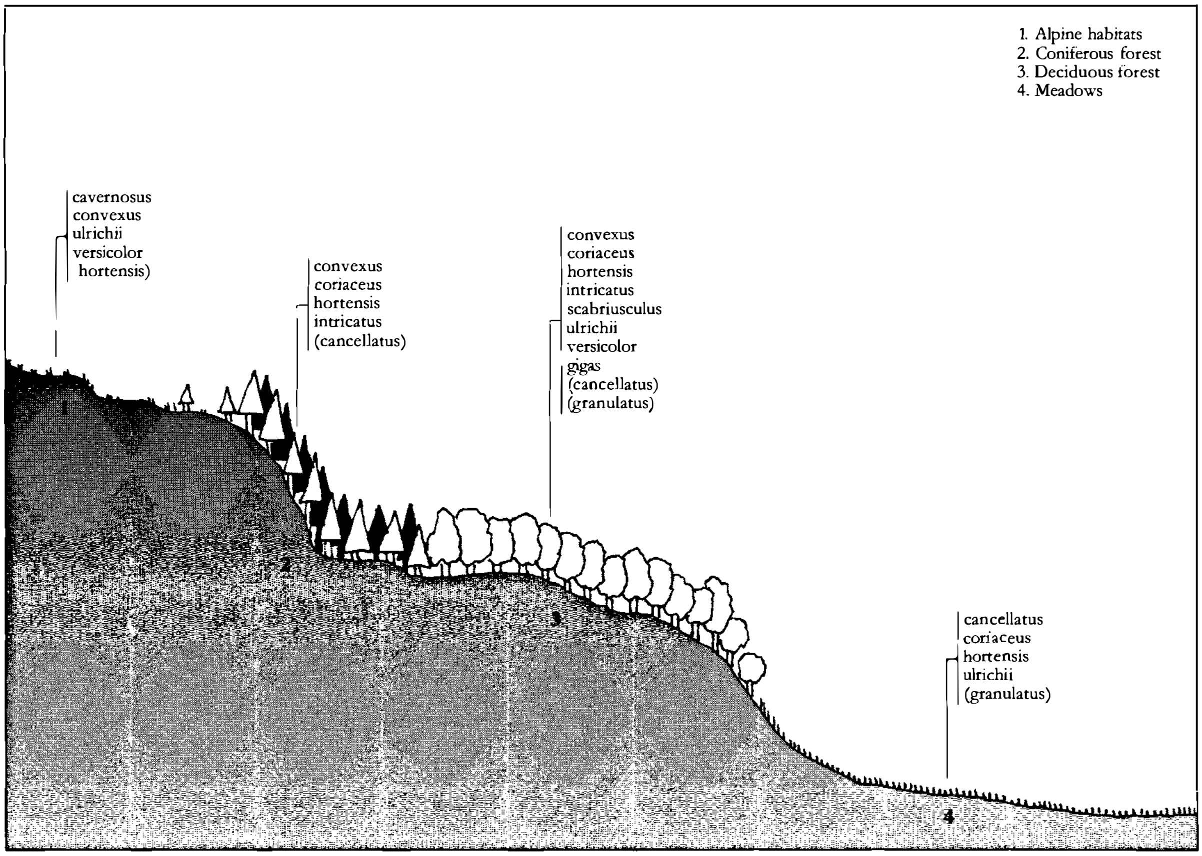
T-66. Bulgaria: *Western Bulgaria, Osogovo Mt., northern macroslope. L. Penev, after data provided by B. Guéorguiev.*



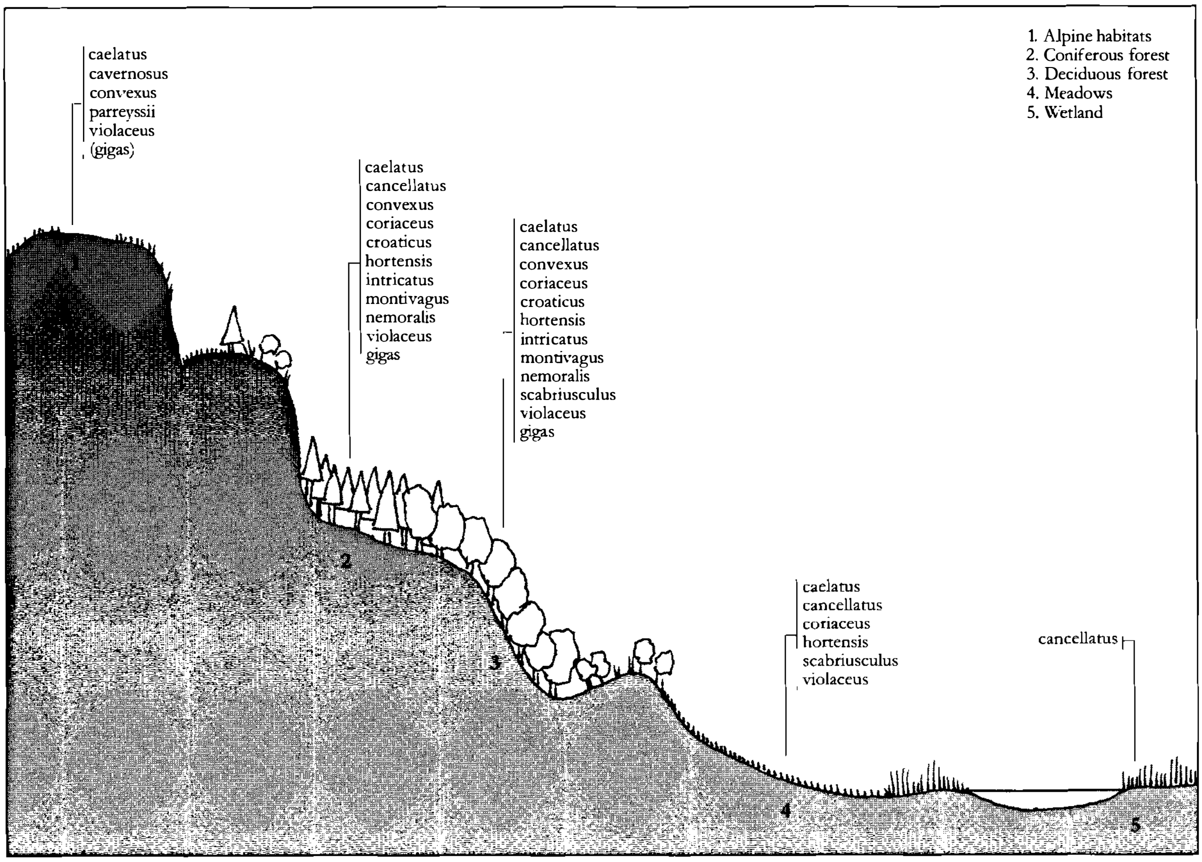
T-67. Bulgaria: *Southwestern Bulgaria, Rila Mt., Bistritsa river above Blagoevgrad, ca. 20 km long. L. Penev and V. Peneva, from unpublished data.*



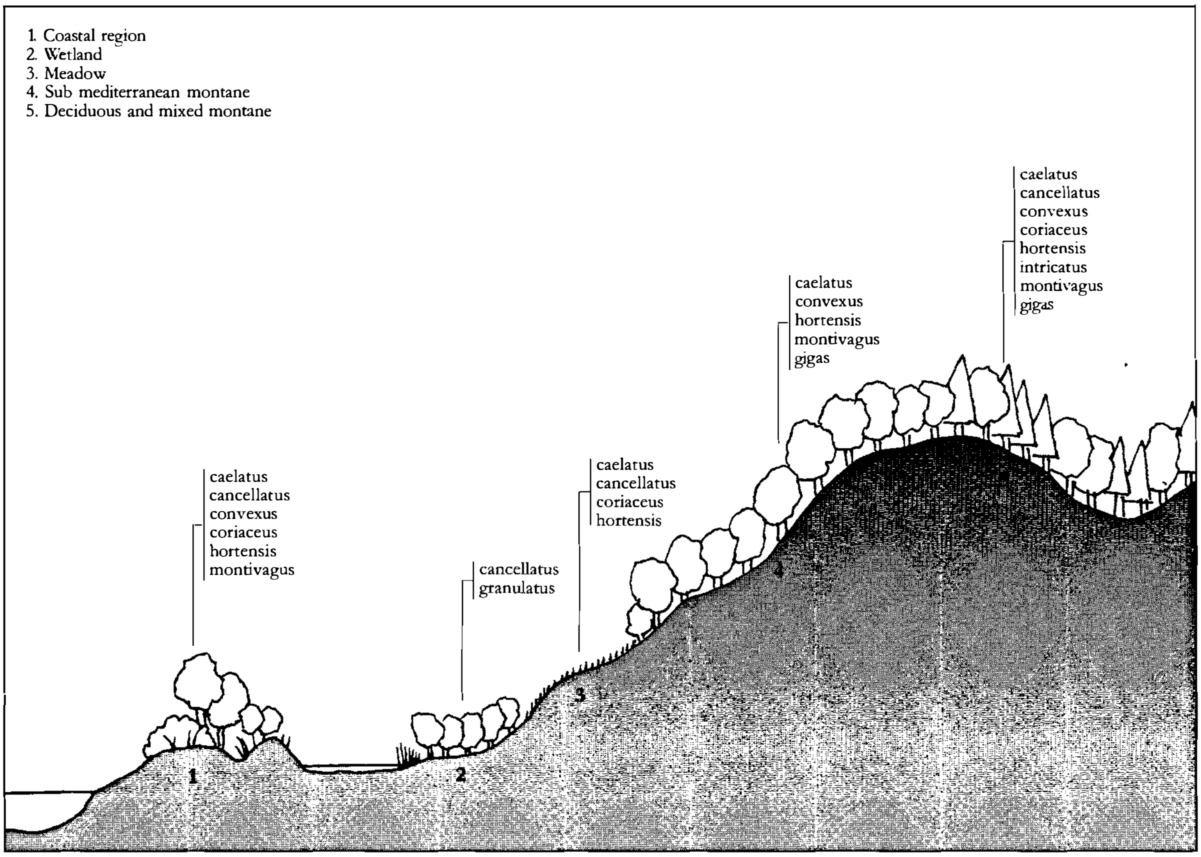
T-68. Greece: *Pindos chain near lake Ioanina (Ipiros). A Casale, from original unpublished data.*



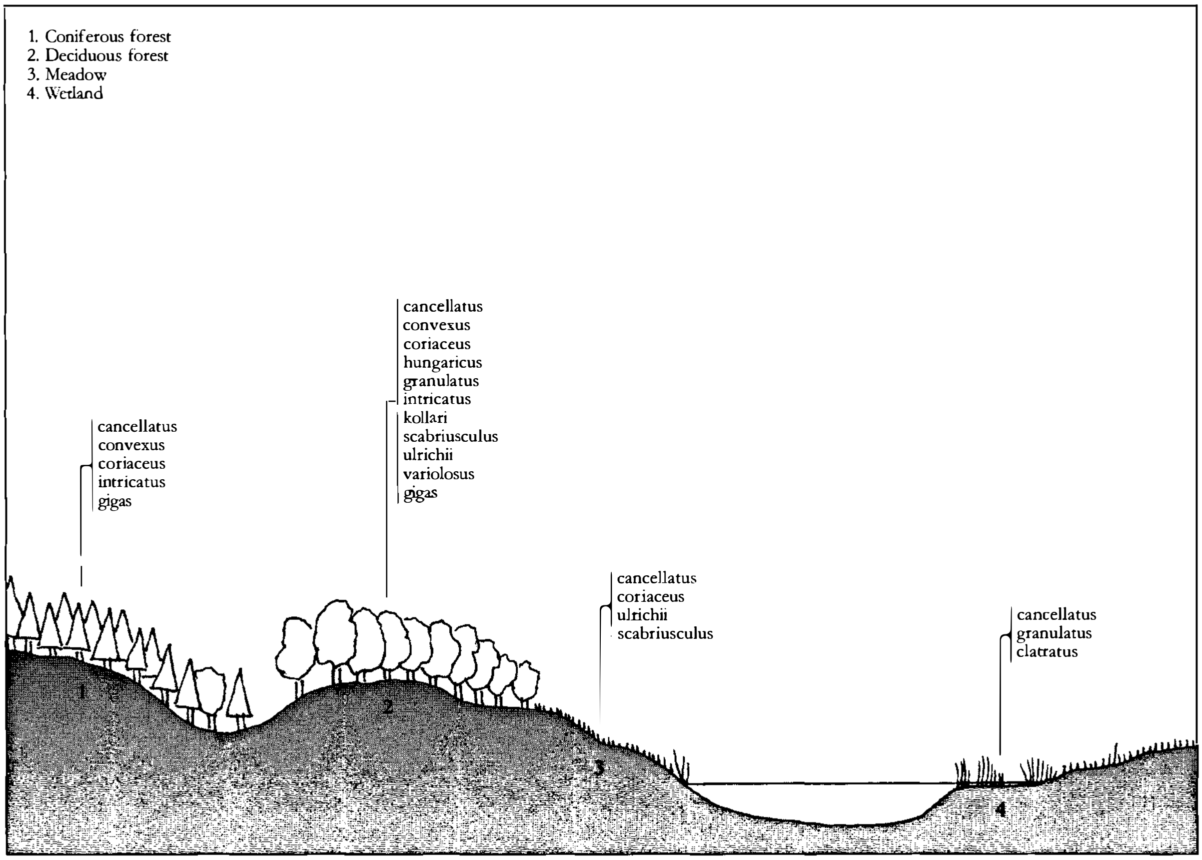
T-69. Former Yugoslavia: *Southeast Serbia. H. Turin and A. Casale, after Pavicevic and Mesaros (1997), Casale et al. (1982) and various small papers.*



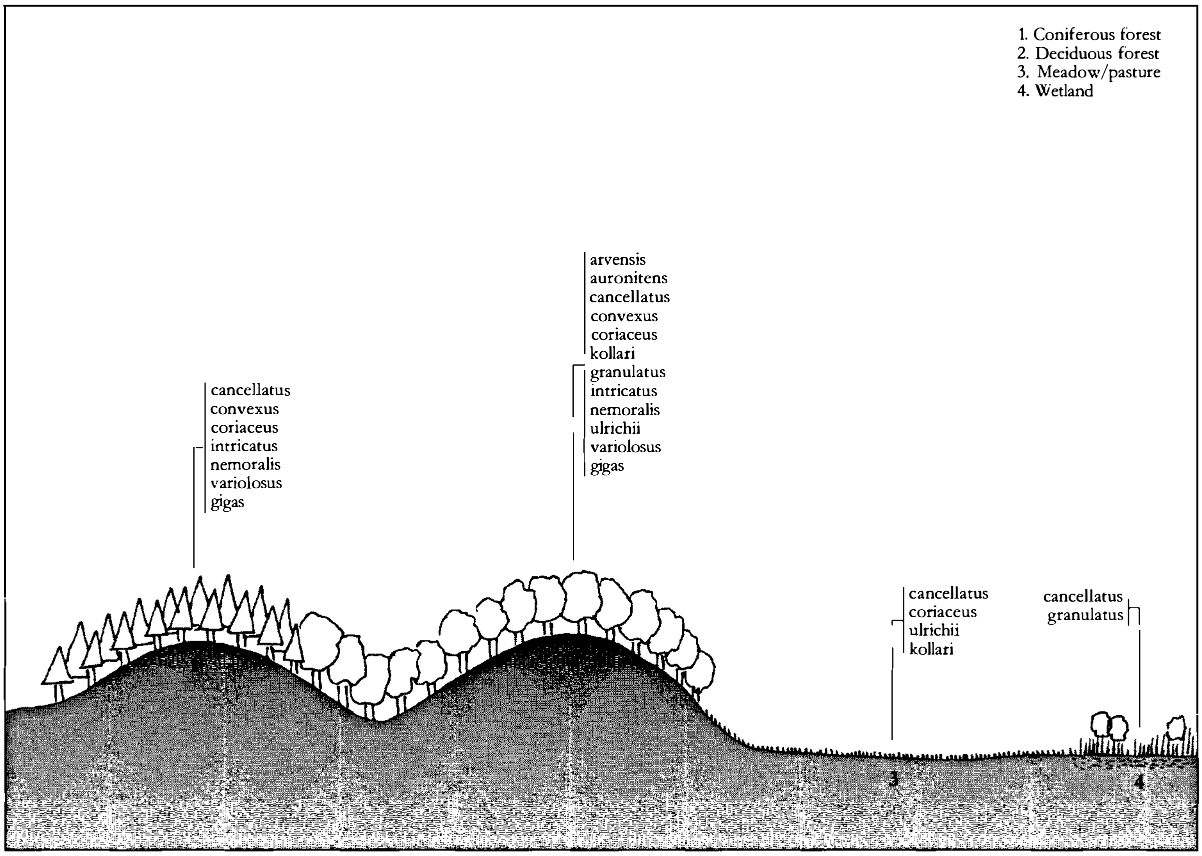
T-70. Former Yugoslavia: *Alpine Montenegro. H. Turin and A. Casale, after Pavicevic and Mesaros (1997), Casale et al. (1982) and various small papers.*



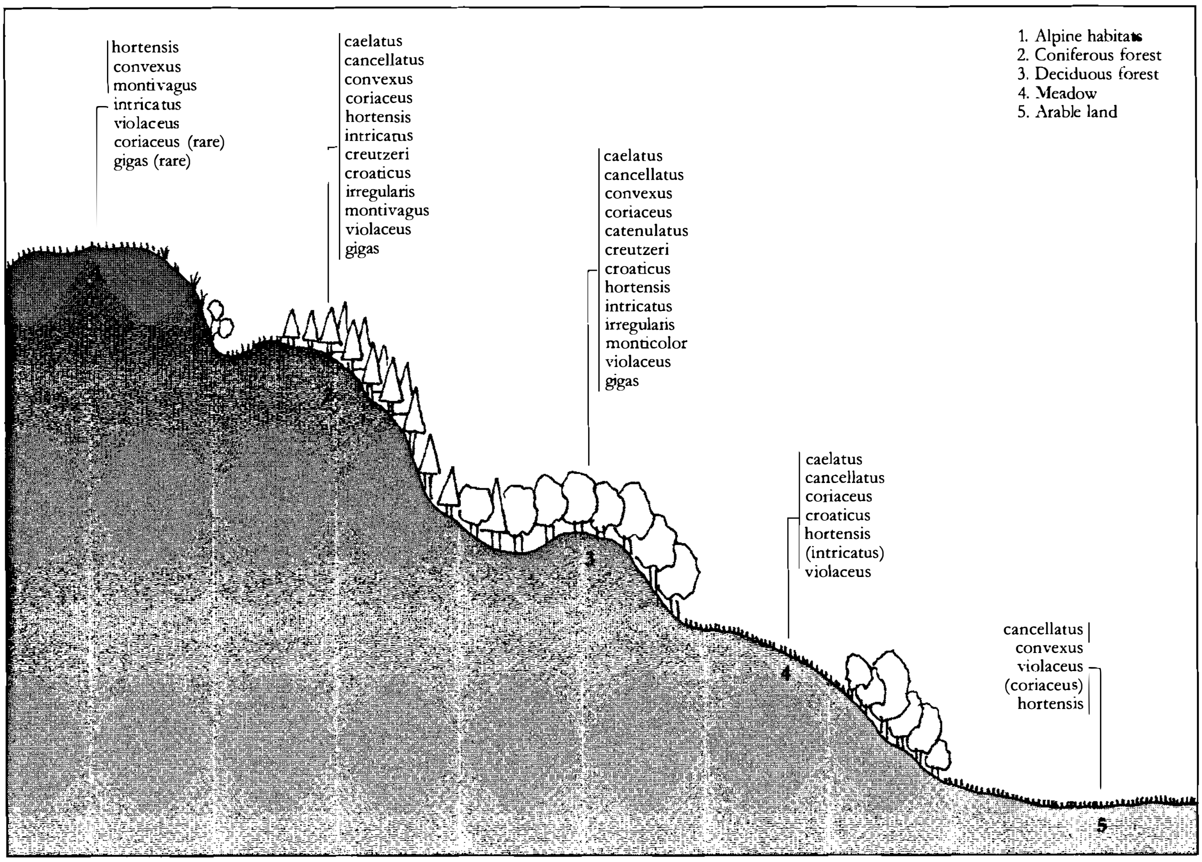
T-71. Former Yugoslavia: *Coastal Herzegovina. H. Turin and A. Casale, after Pavicevic and Mesaros (1997), Casale et al. (1982) and various small papers.*



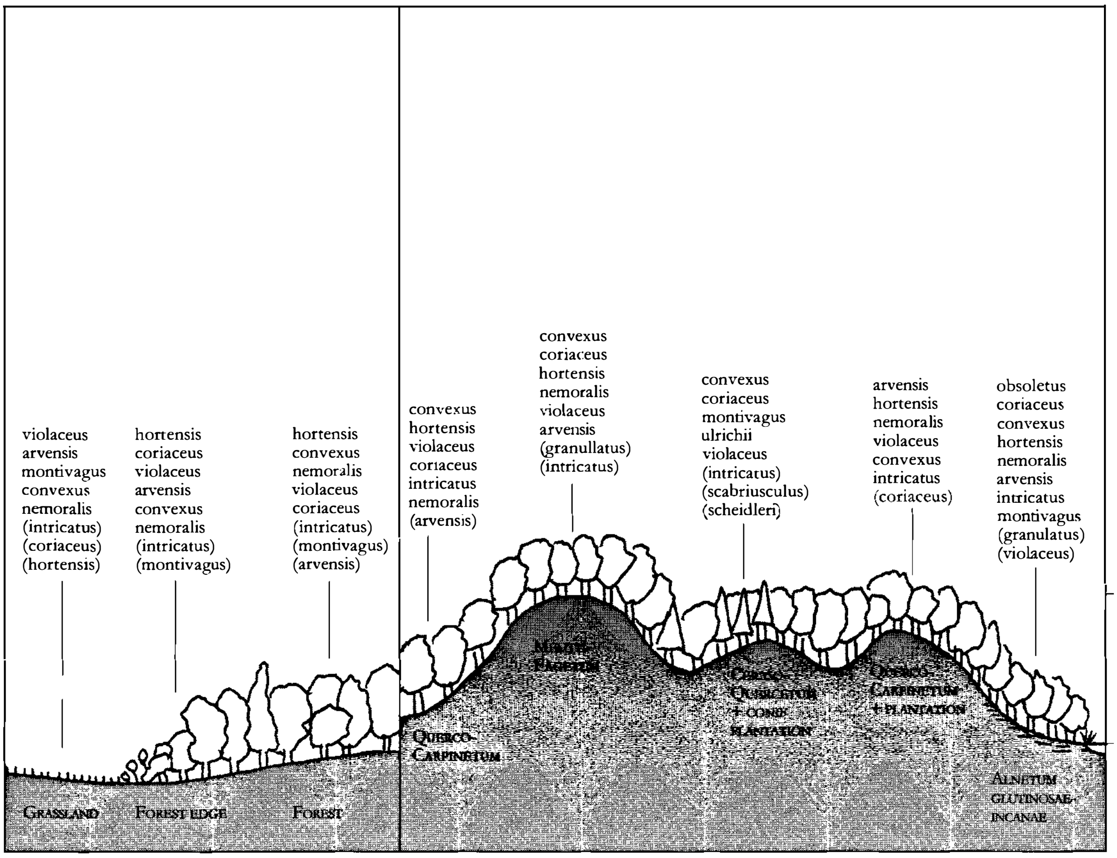
T-72. Former Yugoslavia: *Vojvodina. H. Turin and A. Casale, after Pavicevic and Mesaros (1997), Casale et al. (1982) and various small papers.*



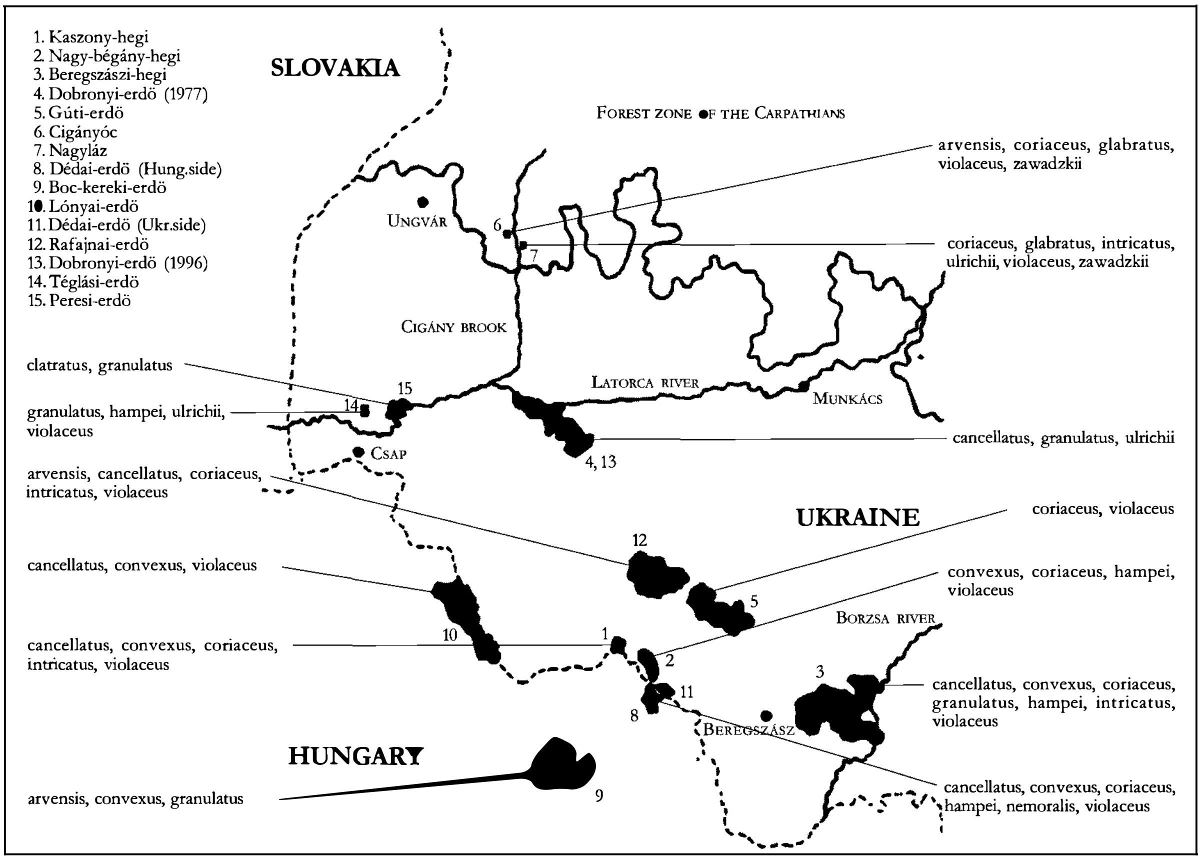
T-73. Former Yugoslavia: *Eastern Croatia. H. Turin and A. Casale, after Pavicevic and Mesaros (1997), Casale et al. (1982) and various small papers.*



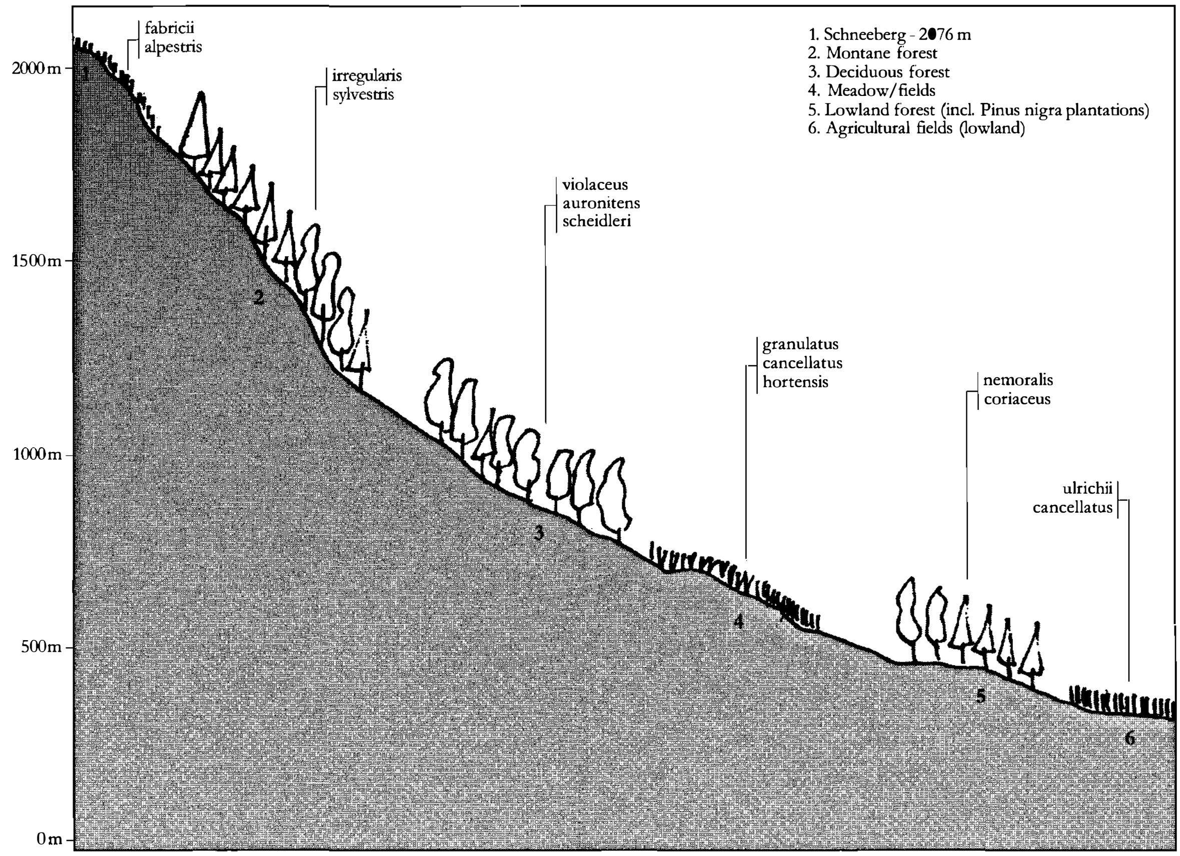
T-74. Former Yugoslavia: *Istra-Kvarner. H. Turin and A. Casale, after Pavicevic and Mesaros (1997), Casale et al. (1982) and various small papers.*



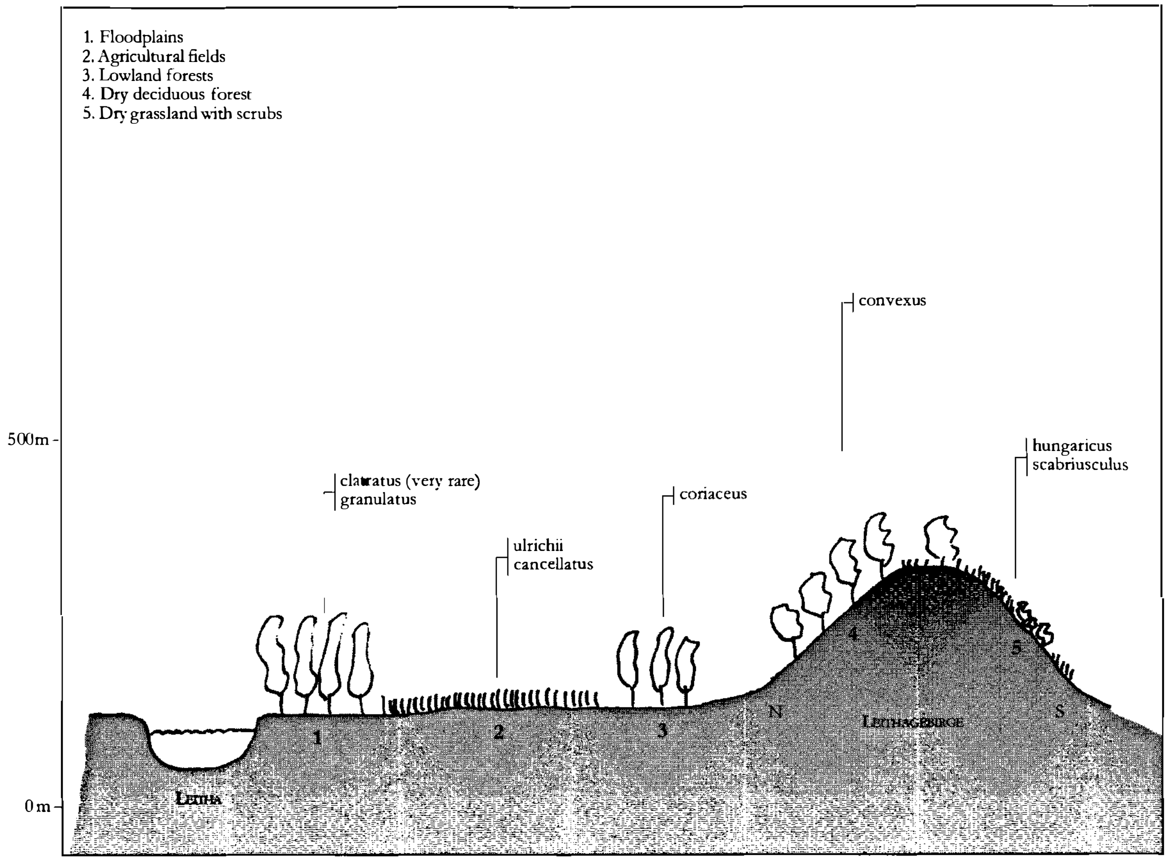
T-75. Hungary: *Aggetelek Reserve. H. Turin and T. Magura, after Magura and Molnár (1996), Magura et al. (1997; 2000)*



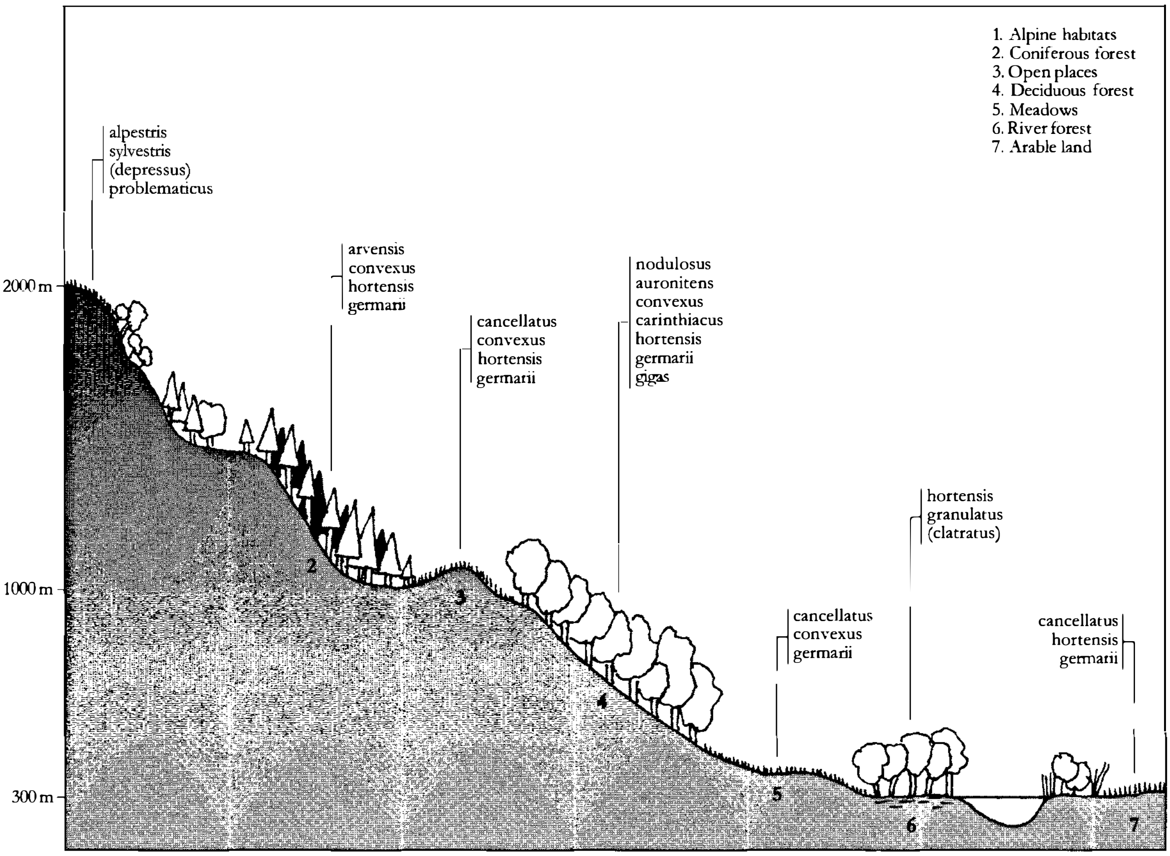
T-76. Hungary-Ukraine: *Beregi-síkság to Carpathians. T. Magura, after Ködöböcz and Magura (1999)*



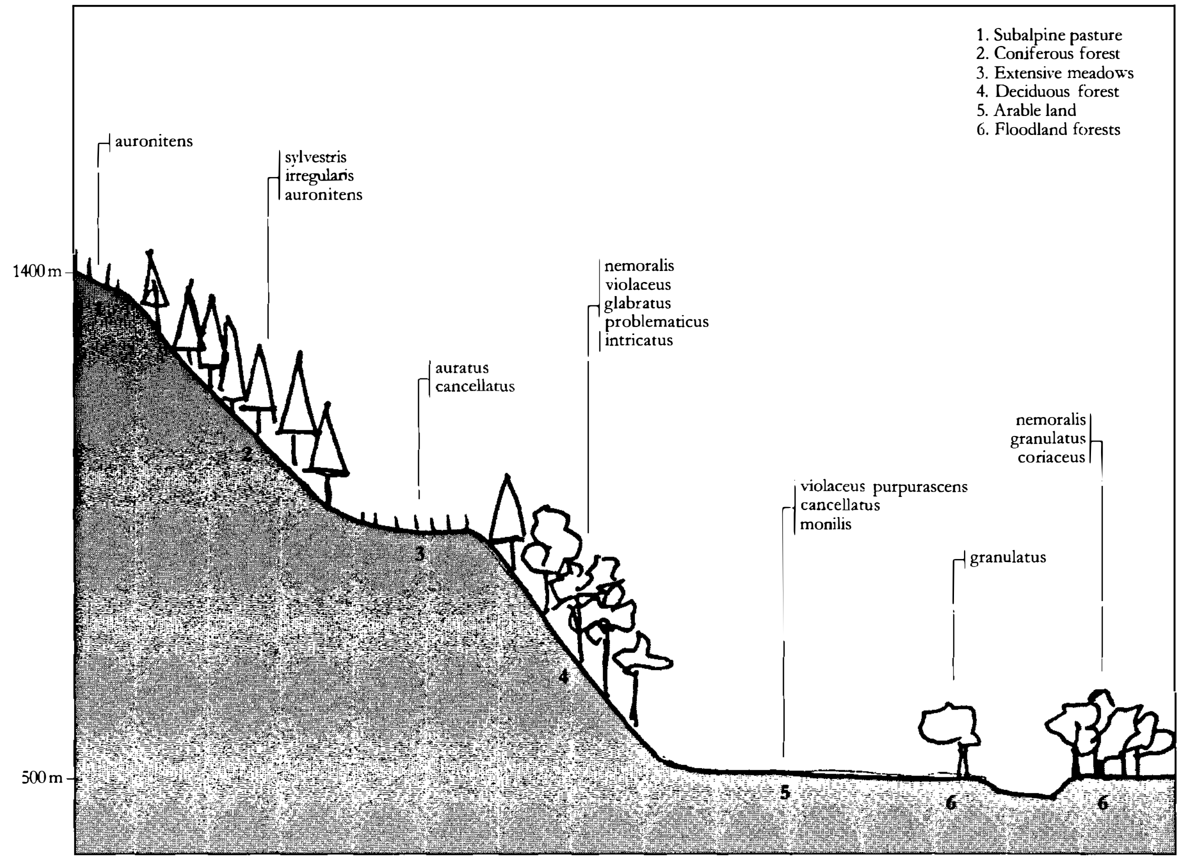
T-77. Austria: *Schneeberg (Lower Austria). K.-P. Zulka, after original data and Franz (1970)*



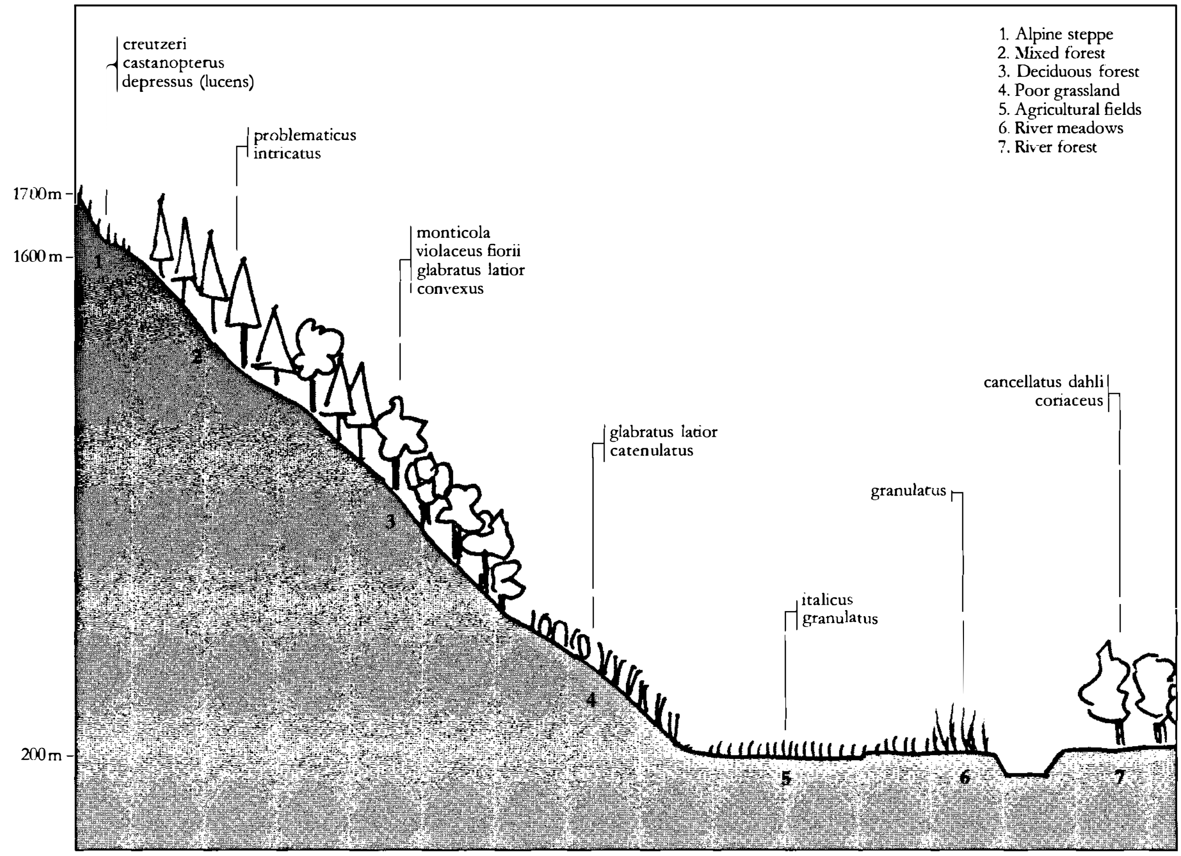
T-78. Austria:
Leithagebirge (Lower Austria).
K.-P. Zulka, after original data and Franz (1970)



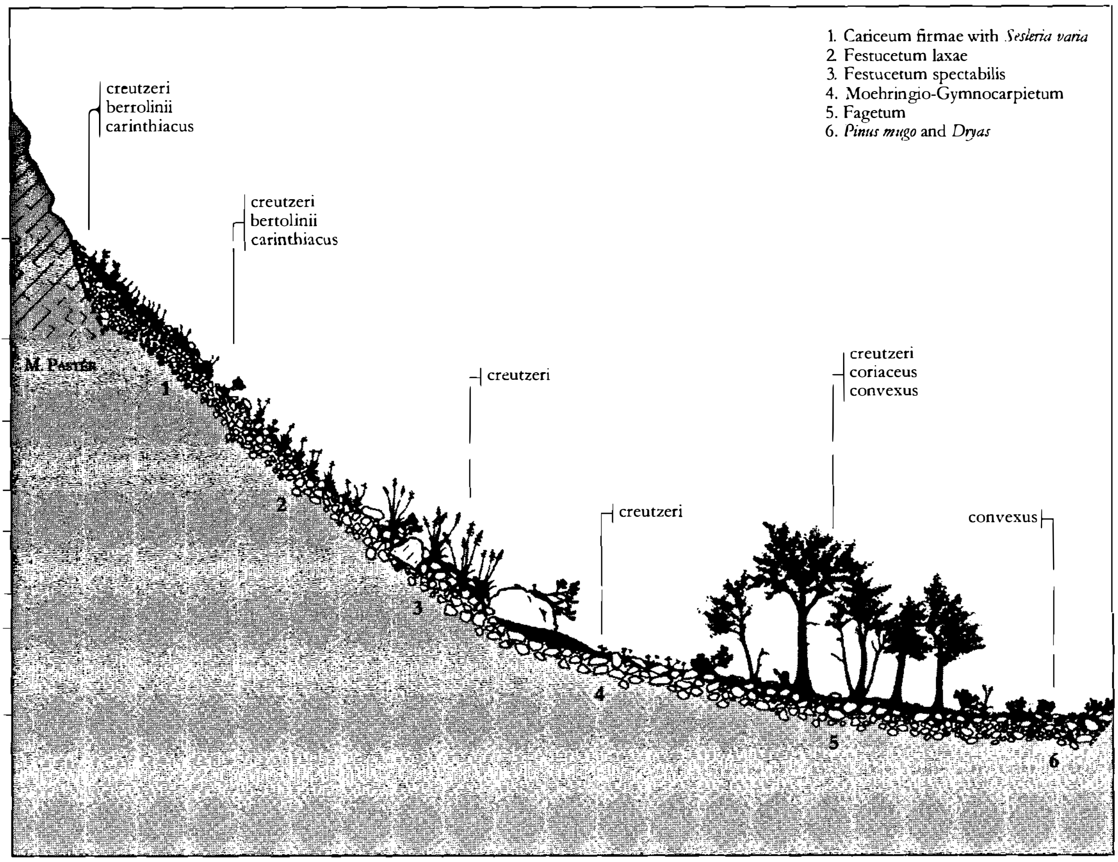
T-79. Austria:
Carinthia, Villacher Alp (Dobratsch).
H. Turin from original data and Penterman (1989a, b)



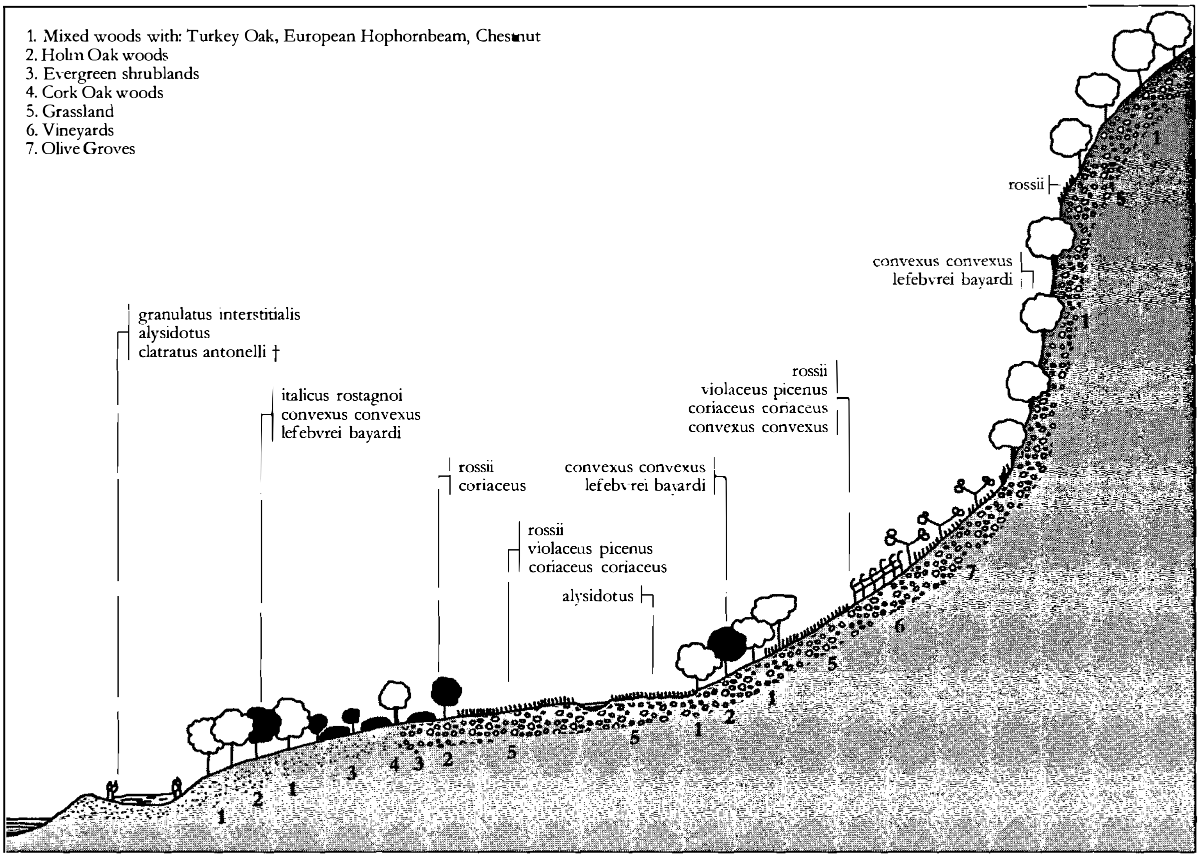
T-80. Switzerland: *Napfgebiet, Emmental. W. Marggi, from original data.*



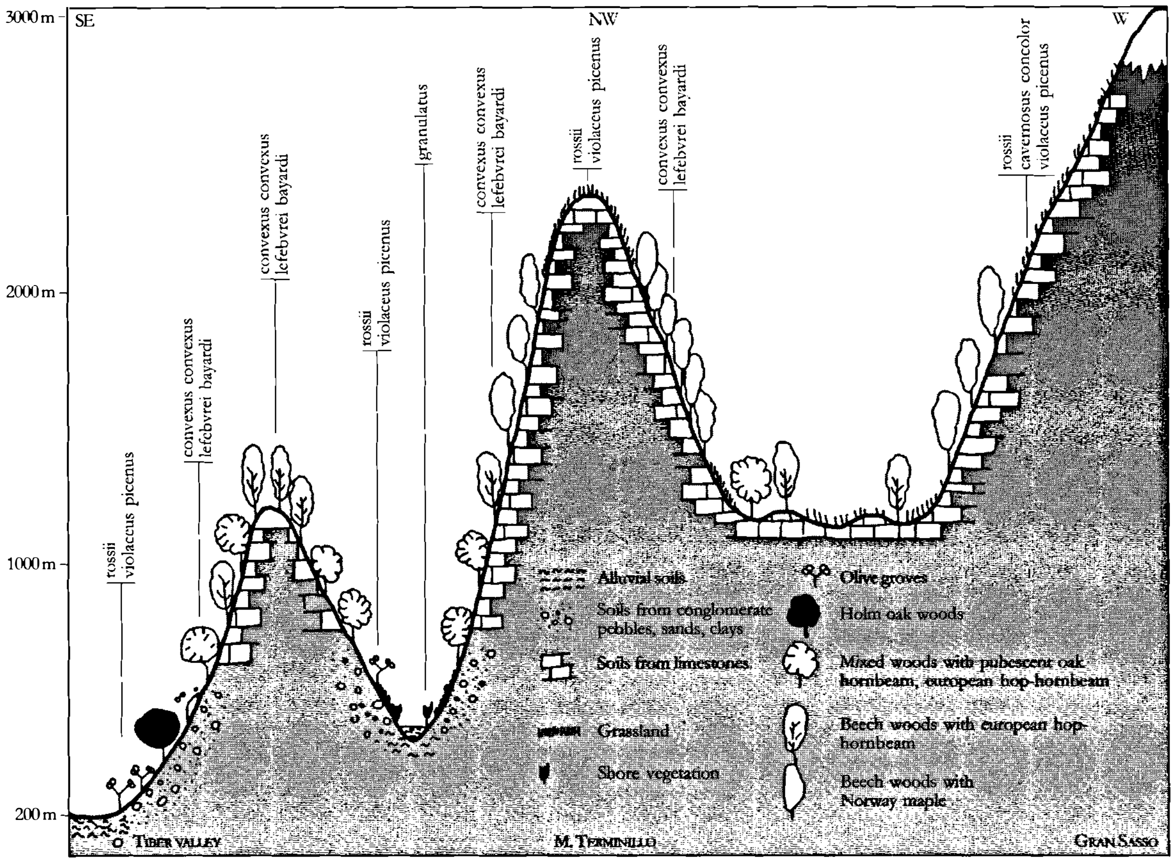
T-81. Switzerland: *Tessin. W. Marggi, from original data.*



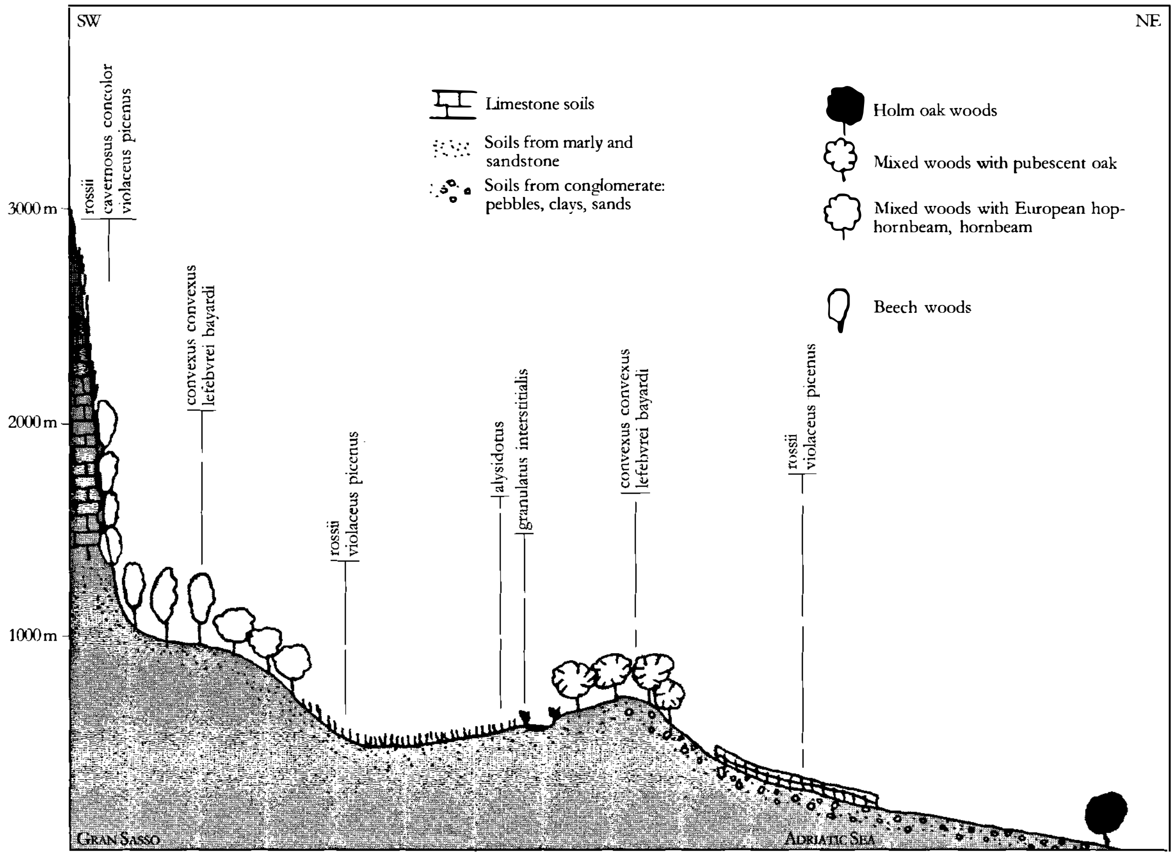
T-82. Italy:
Friuli, Venezia Gulia, Prescudin. R. Pizzolotto and P. Brandmayr, from original data.



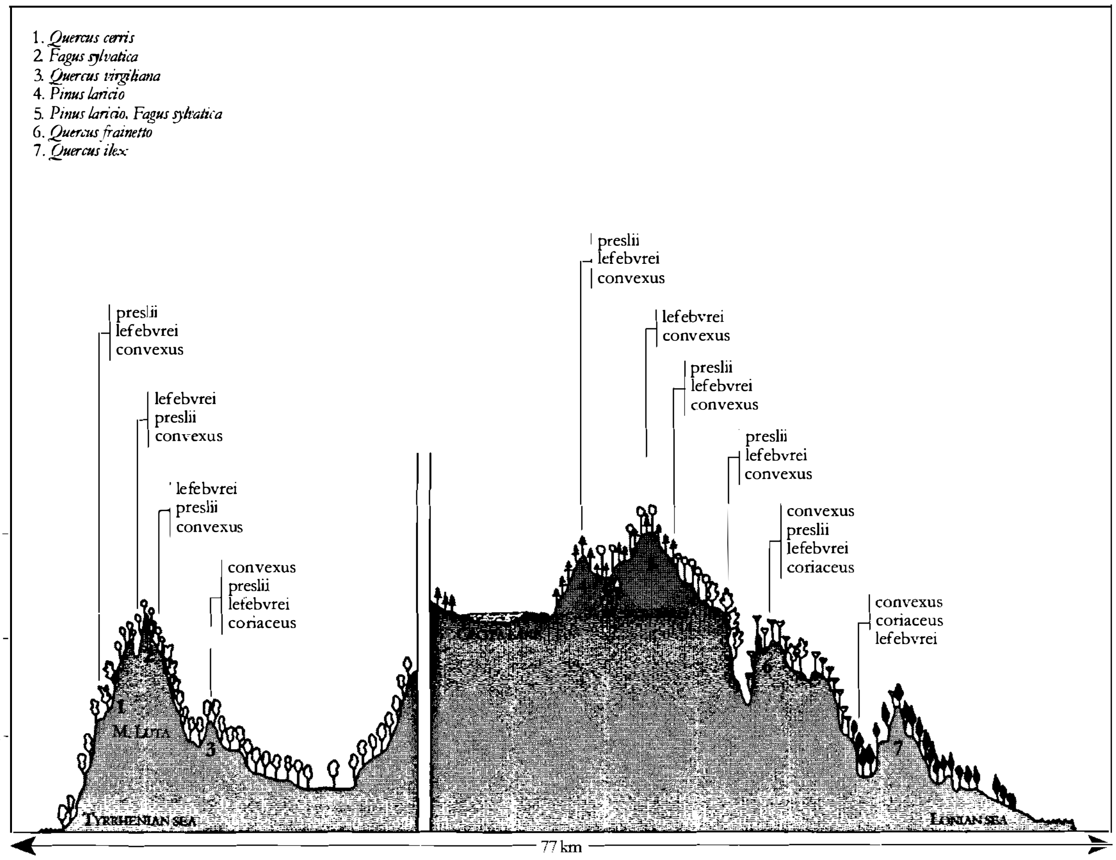
T-83. Italy:
Central Apennines (West). S. De Felici and A. Vigna Taglianti, from original data.



T-84. Italy: *Central Apennines (Central). S. De Felici and A. Vigna Taglianti, from original data.*

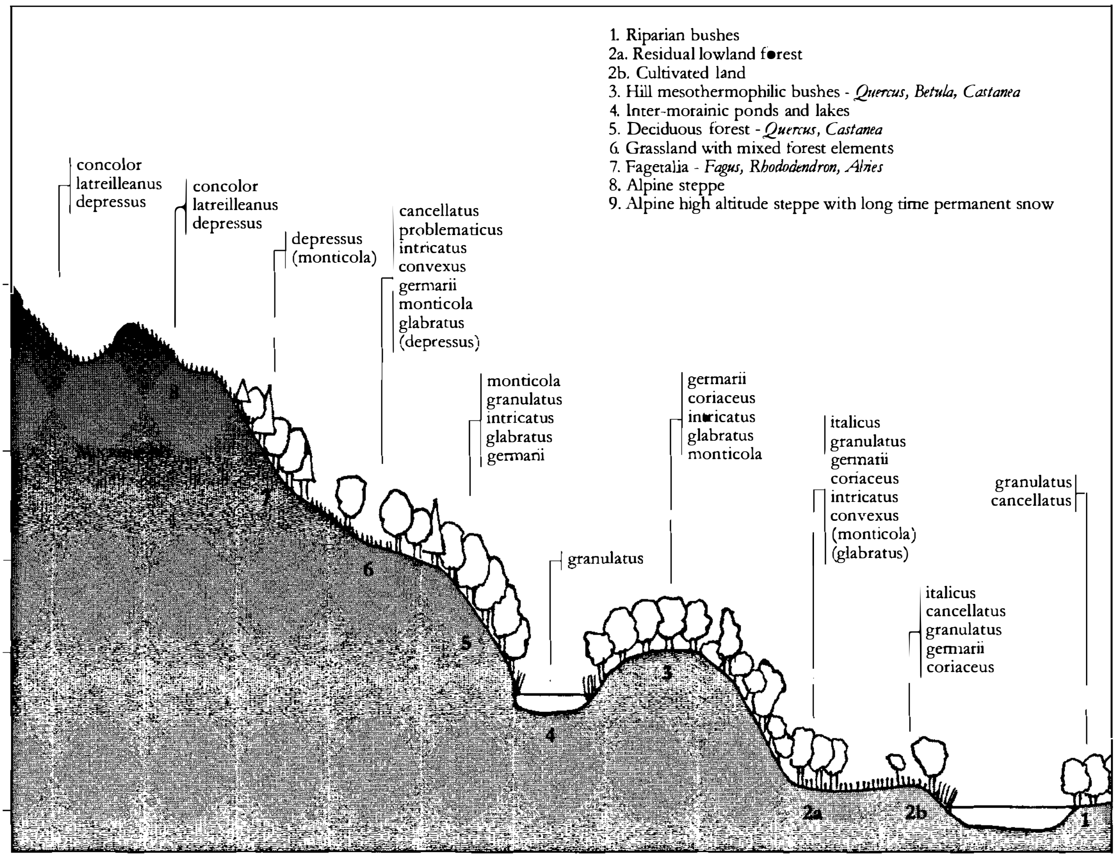


T-85. Italy: *Central Apennines (East). S. De Felici and A. Vigna Taglianti, from original data.*

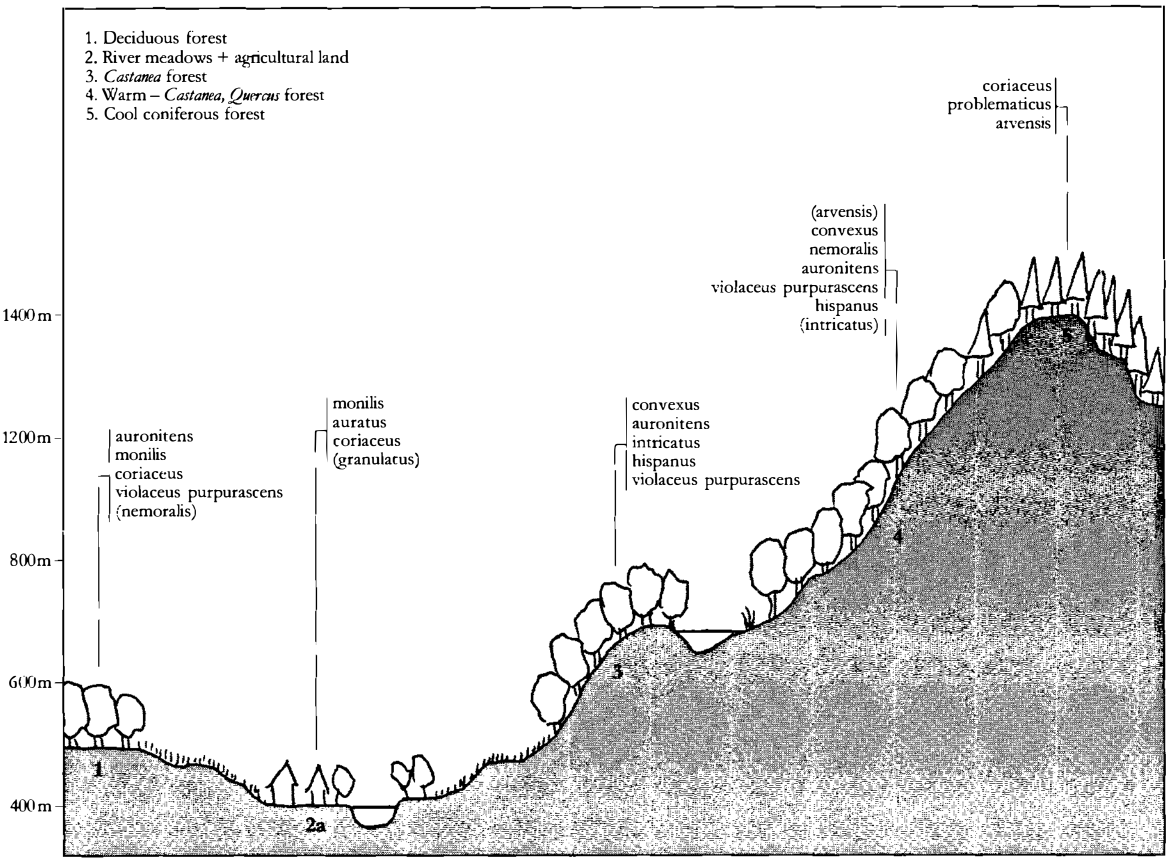


T-86. Italy:
Calabria near Cosenza (West).
R. Pizzolotto and P. Brandmayr, from original data.

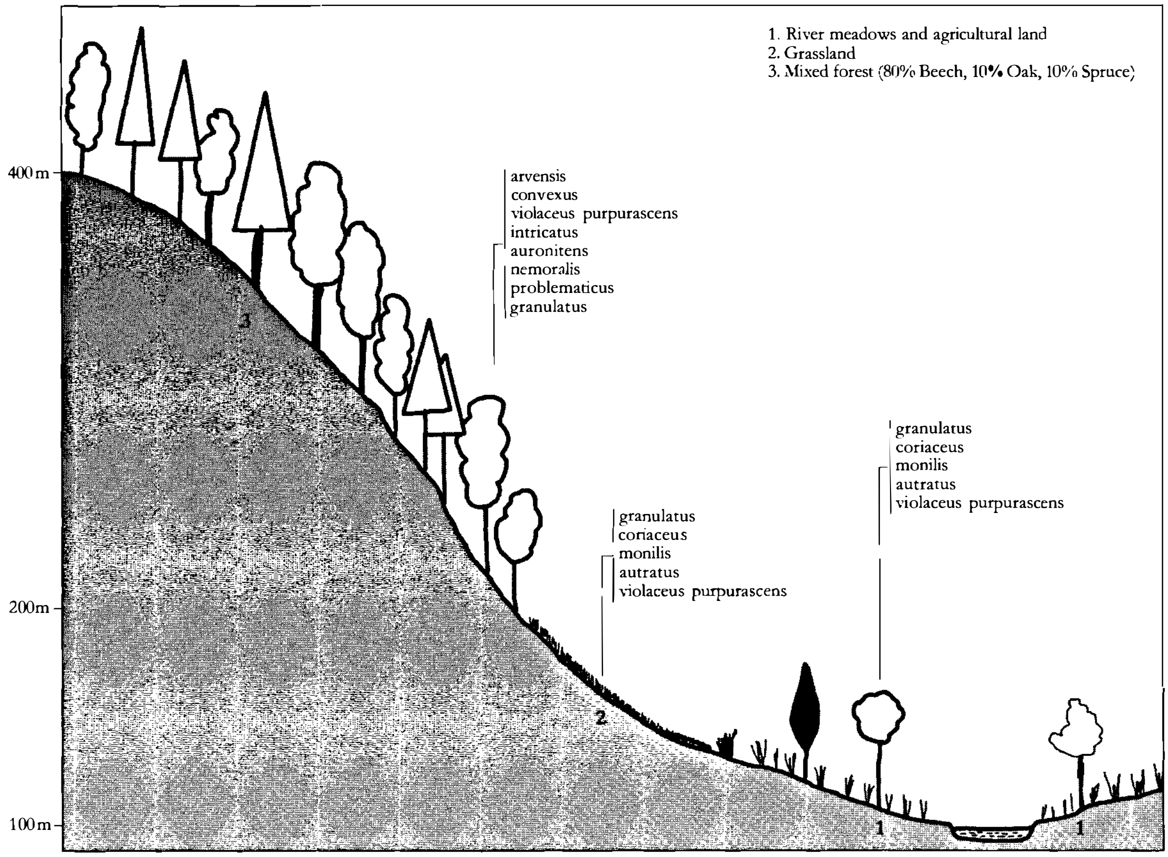
T-87. Italy:
Calabria near Cosenza (East).
R. Pizzolotto and P. Brandmayr, from original data.



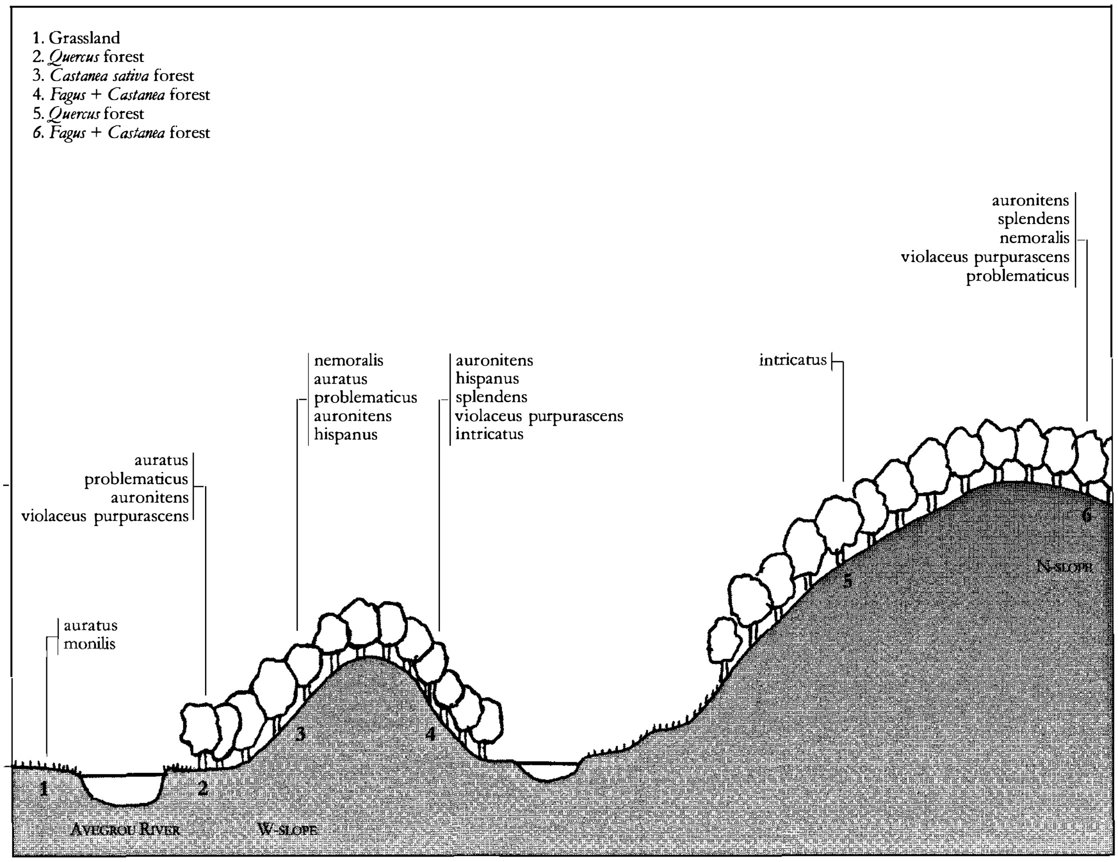
T-88. Italy:
Piemonte, hills and Alps N.E. of Ivrea (Torino).
A. Casale, from original unpublished data.



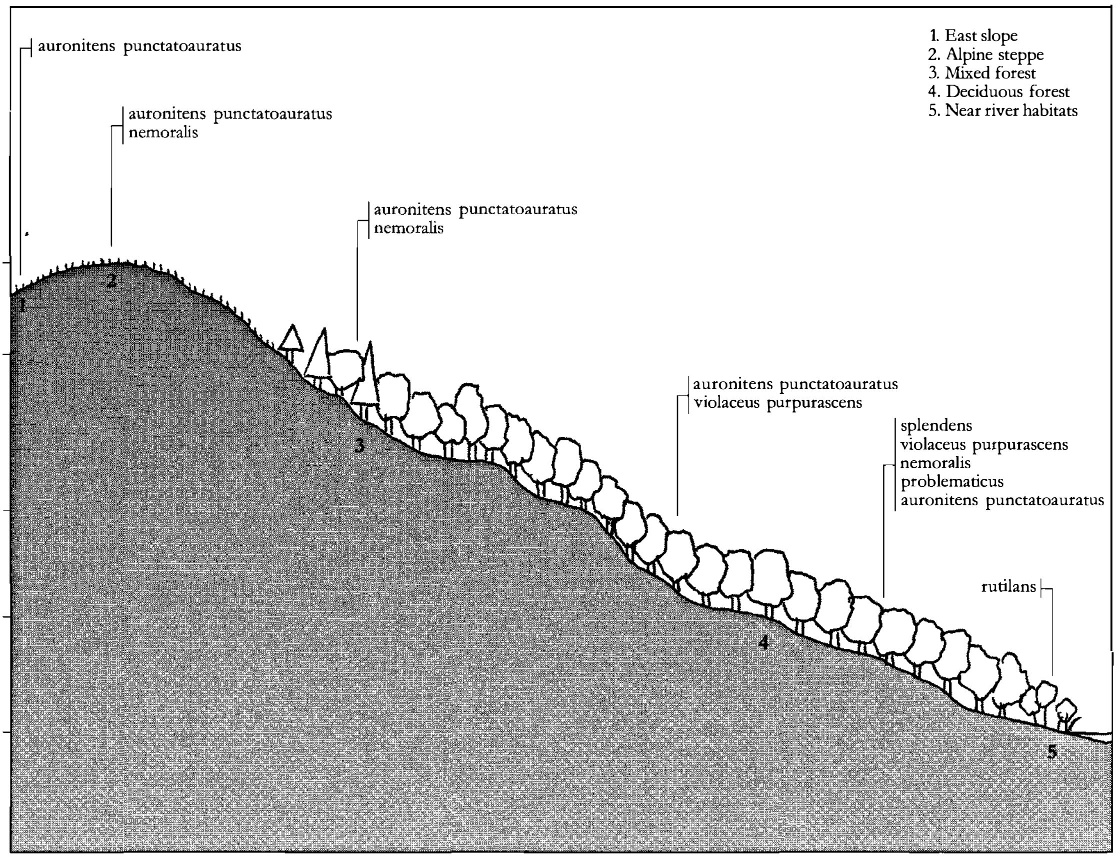
T-89. France:
Southern Ardèche (Haute Loire / Cevennes).
H. Turin, from original data.



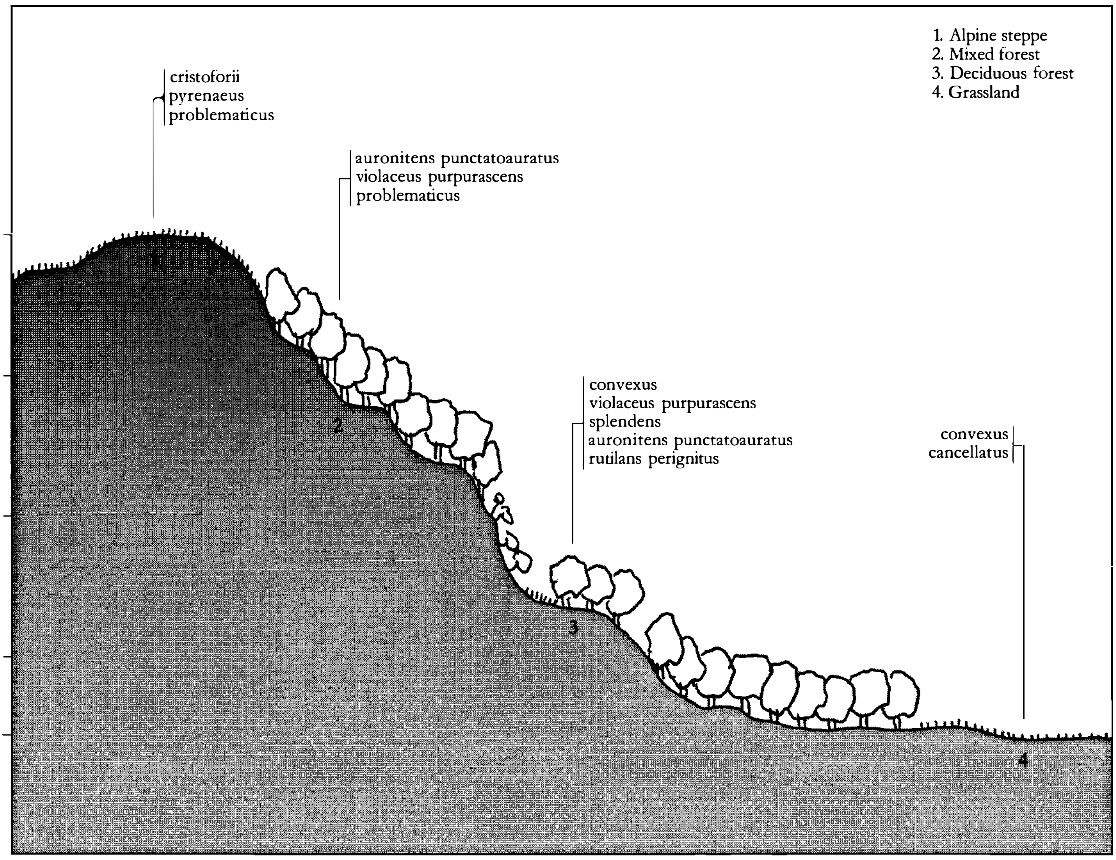
T-90. France:
Forêt d'Ecouves (Normandie).
S. Rémond, from original data.



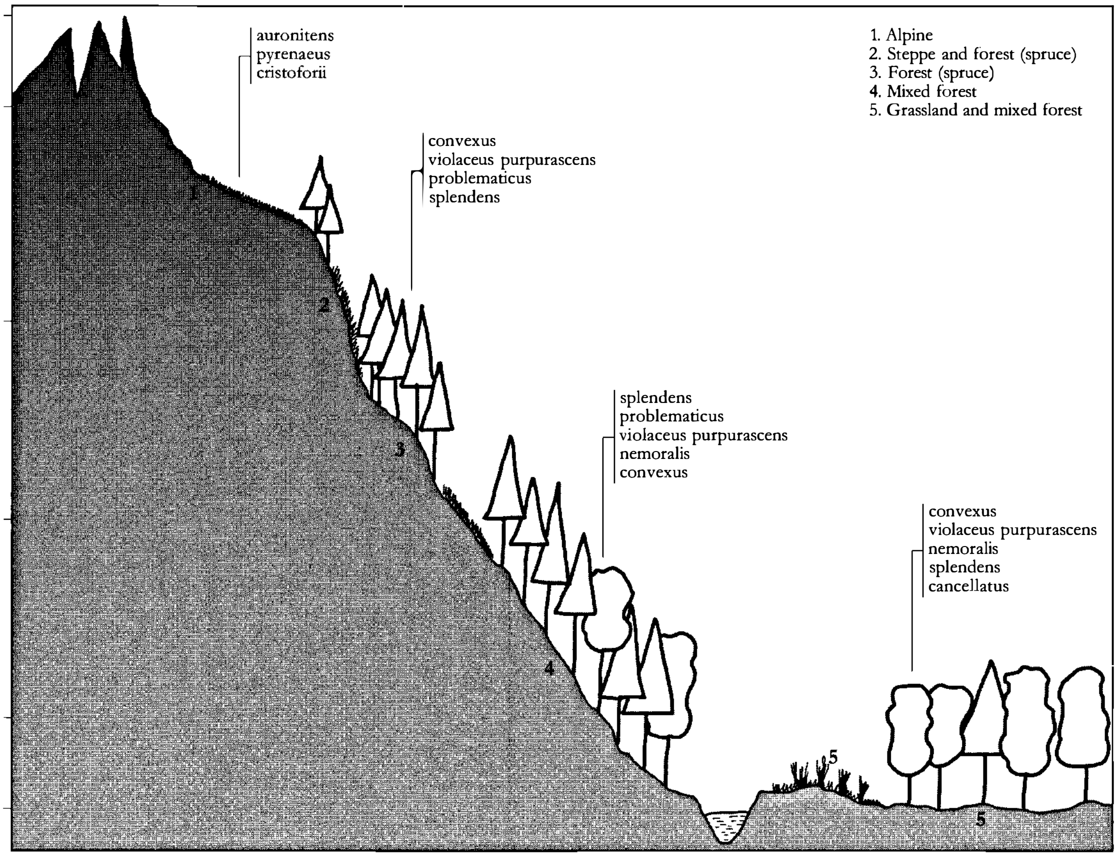
T-91. France:
Aveyron.
D. Mossakowski,
from original data.



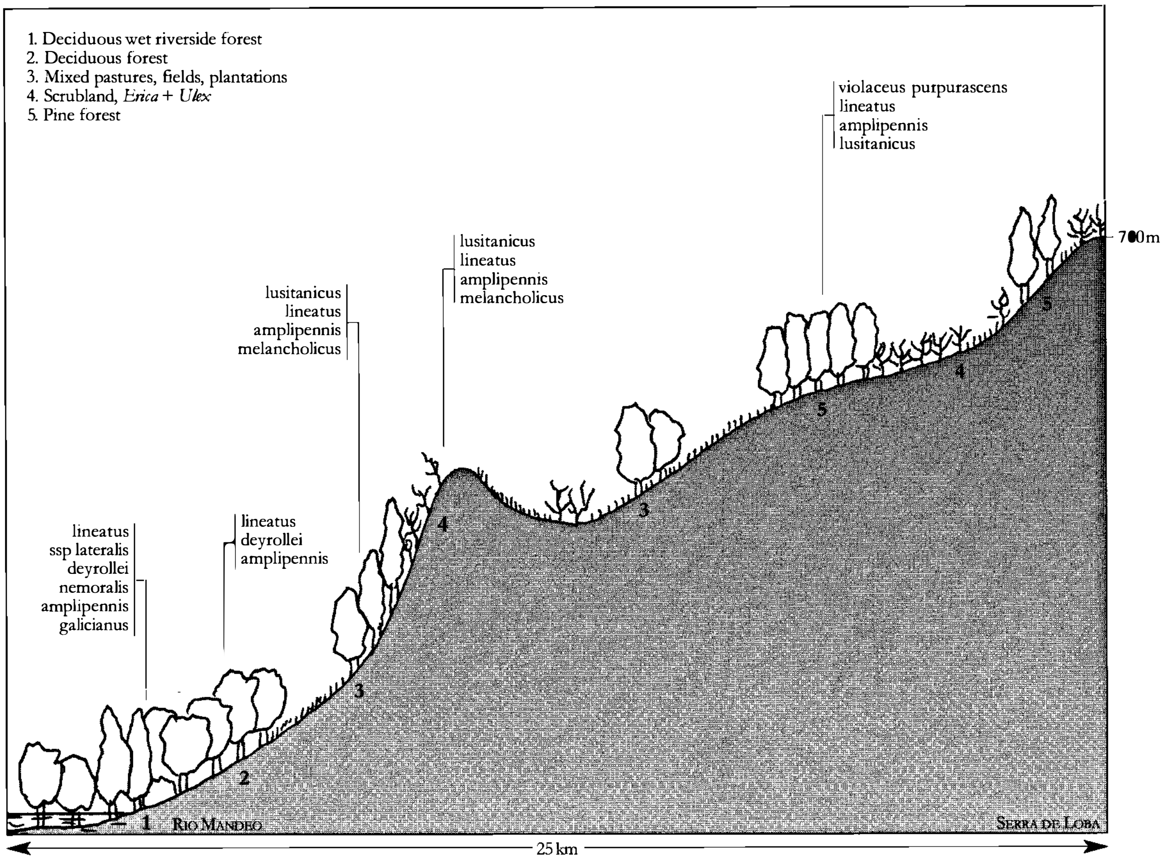
T-92. France:
Ax-les-Thermes
(East Pyrenees).
D. Mossakowski,
from original data



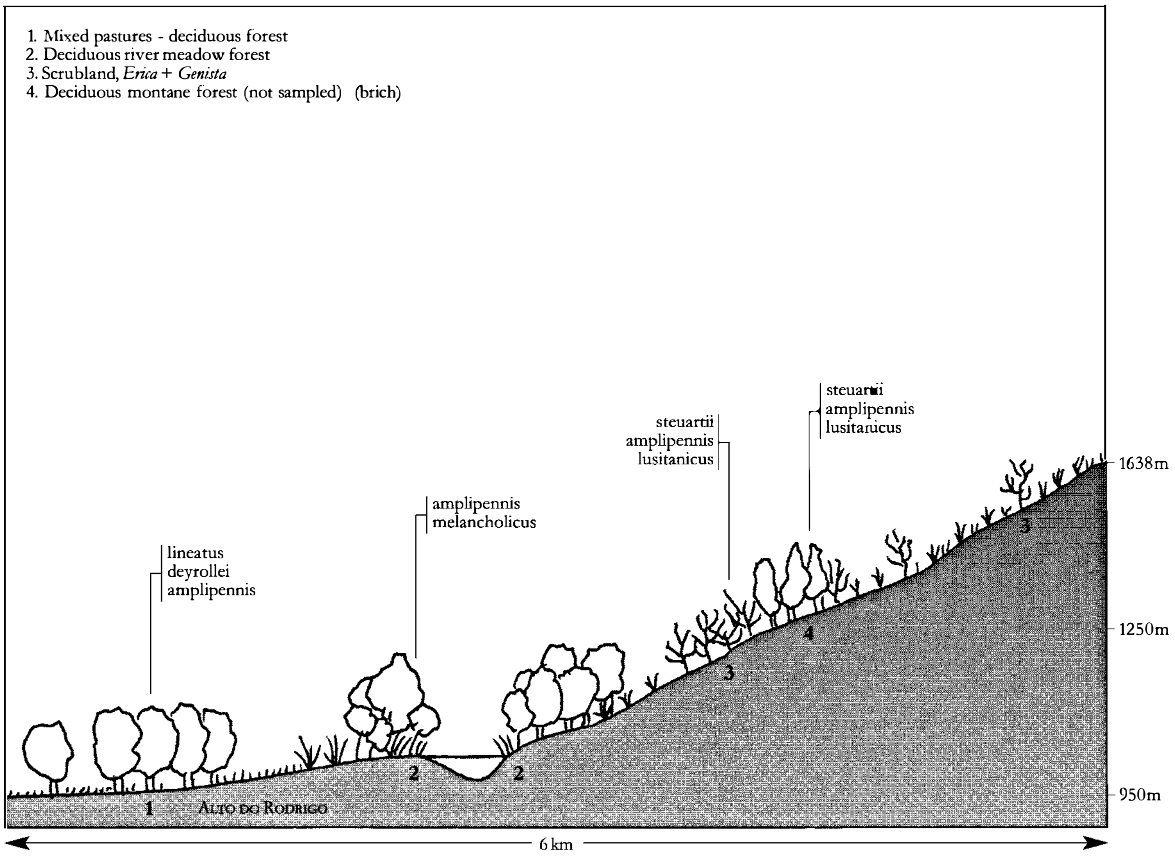
T-93. France: *Near Andorra (East Pyrenees). D. Mossakowski and A. Casale, from original data.*



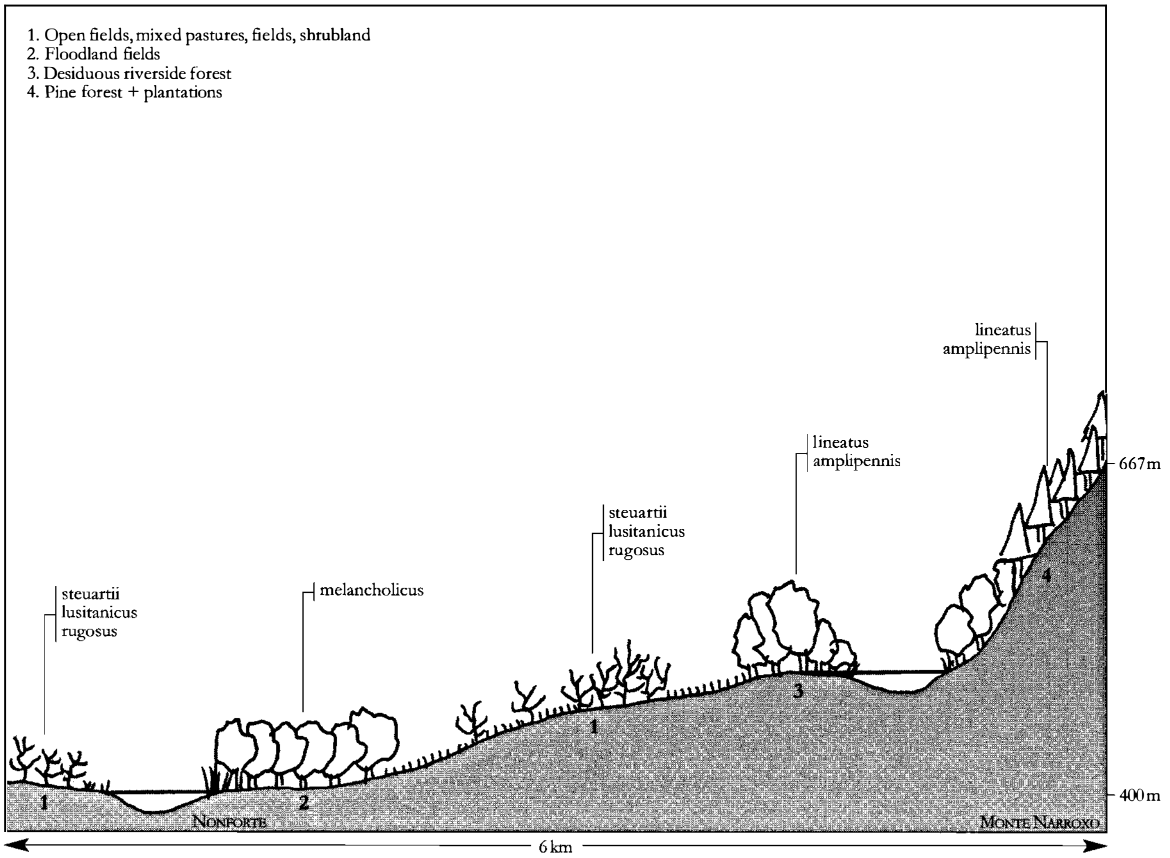
T-94. France: *Pic du Midi de Bigorre (Central Pyrenees). S. Rémond, from original data.*



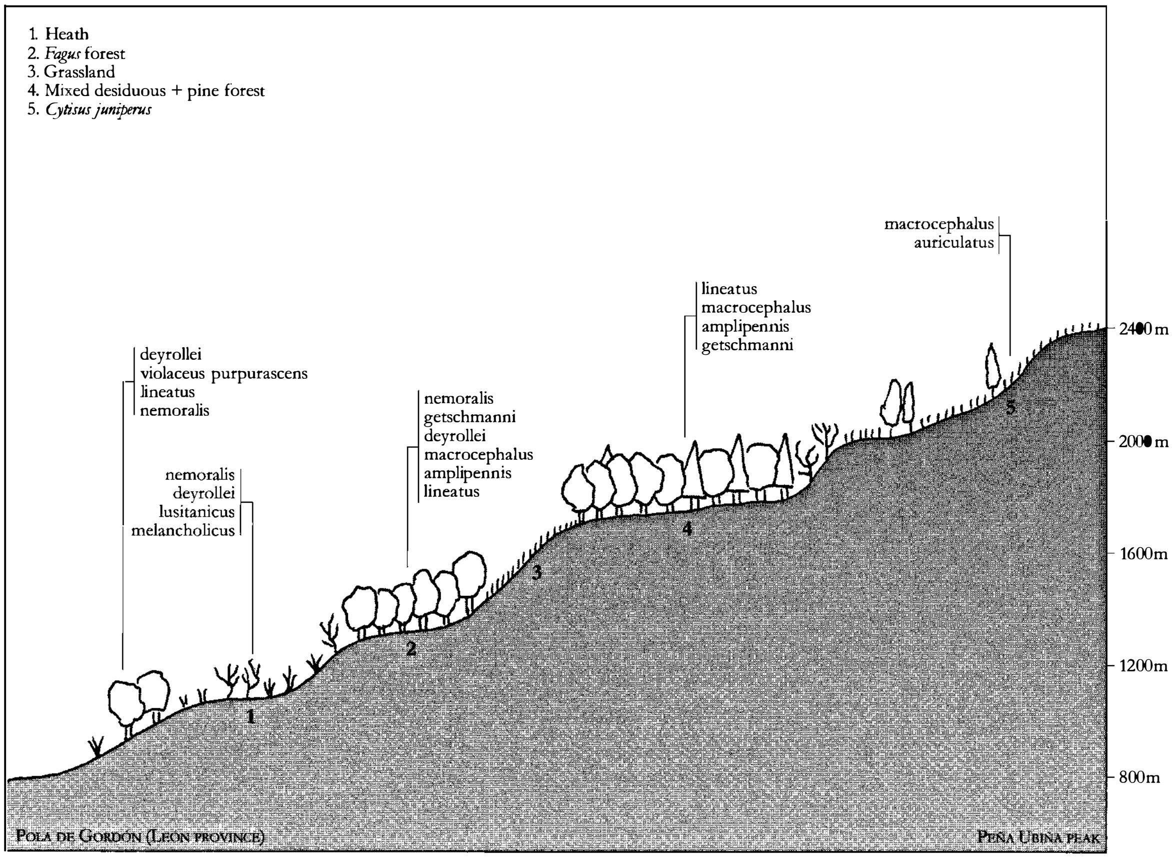
T-95. Iberian Peninsula:
Rio Mandeo - Serra da Loba (Galicia northwest, Northern Spain). J.P. Valcarcel, after original data.



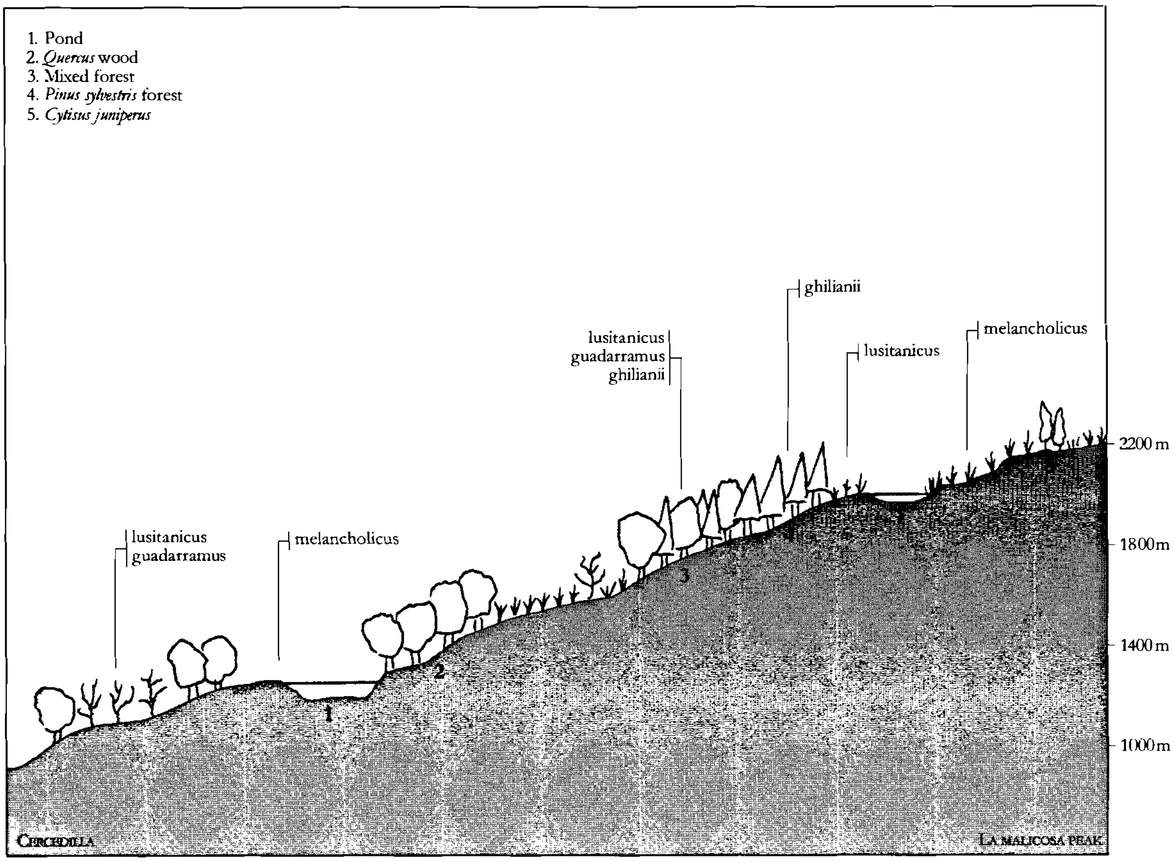
T-96. Iberian Peninsula:
Ovrense, Alto do Rodicio (Galicia south, Northern Spain). J.P. Valcarcel, after original data.



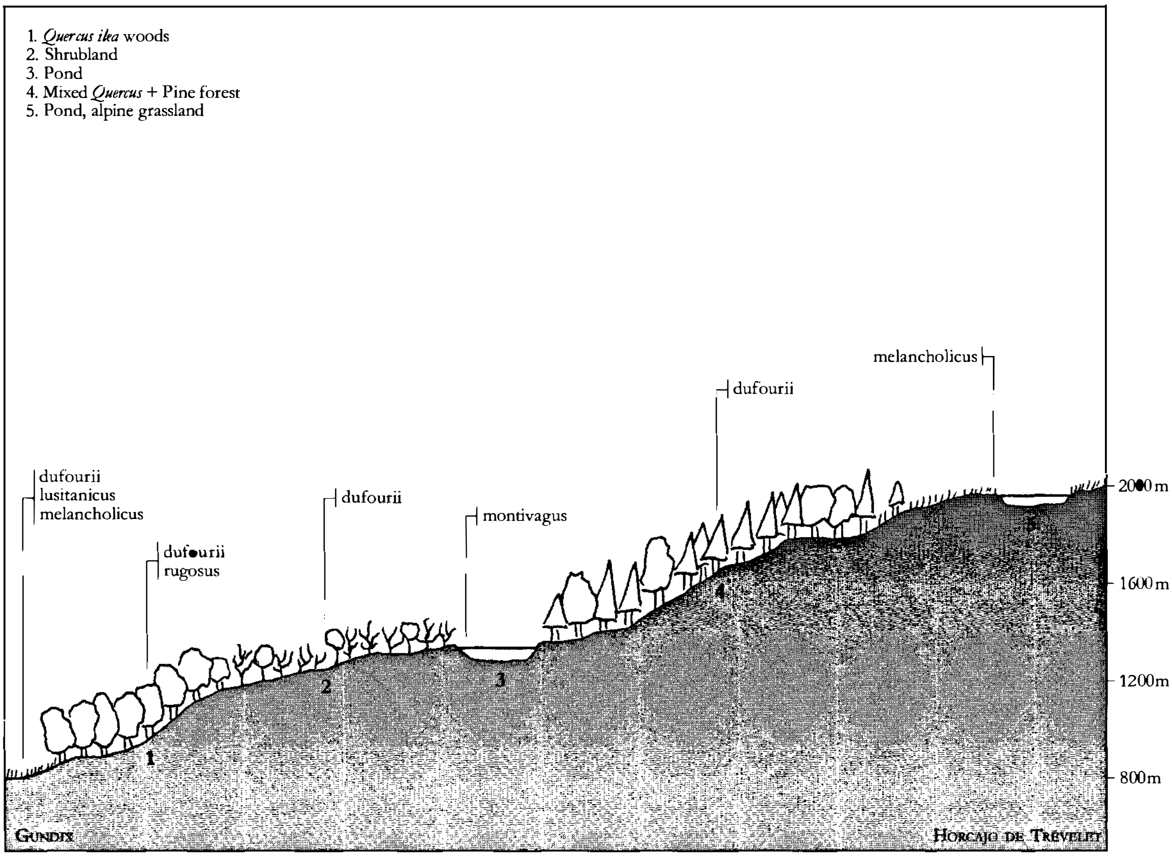
T-97. Iberian Peninsula: *Lugo, Nonforte (Galicia south, Northern Spain). J.P. Valcarcel, after original data.*



T-98. Iberian Peninsula: *East Cantabrian Mts, Pena Ubina (Northern Spain). J. Serrano, after original data and literature.*



T-99. Iberian Peninsula: *Sierra de Guadarrama (Central Spain). J. Serrano, after original data and literature.*



T-100. Iberian Peninsula: *Northeast Sierra Nevada (Southern Spain). J. Serrano, after original data and literature.*

Chapter 9 Conservation biology

Th. Assmann

9.1. DECLINE – EXAMPLES AND OUTLINE OF THE PROBLEM

As with several other insect groups (Samways, 1994), a considerable decline in the populations of many *Carabus* species can be observed (e.g. Turin & den Boer, 1988; Desender & Turin, 1989; Balletto & Casale, 1991). Usually the decline in species is accounted for by changes in land use, caused by changing socio-economic conditions in recent decades in Europe. Faunistic investigations demonstrate, however, that some European *Carabus* species had already suffered a population decline by the end of the 19th century. This can be demonstrated by three examples:

(1) *C. nodulosus* is doubtlessly one of the species in question. Breuning (1926, p. 22) wrote that it 'seems in many cases to be in the process of dying out' (translated). In the previous century this species occurred as far north as the region of Hamburg (Lohse, 1954). Although individual populations existed in northern Central Europe until the 1960s, some of these could no longer be found in recent decades, despite intensive searches (e.g. Westphalia: Weber & Weber, 1966; Lower Saxony: Gersdorf & Kuntze, 1957). The northernmost population now occurs in southern Westphalia. *C. nodulosus* is a stenotopic species occurring in swamp woodlands. The decline is most probably caused by the destruction of its habitats by intensified commercial forestry (e.g. drainage) and, at least in Italy (Trieste) by urbanisation and water pollution (Casale, *pers. comm.*).

(2) In the last century *C. intricatus* was still prevalent in Central Europe (e.g. Horion, 1941). However, since the turn of the century, a drastic reduction of its populations began in northern Central Europe. This ended with its complete extinction in the north-west German lowlands. Populations still exist today in north-east Germany, but these are limited to dry, warm localities (Richter & Jacob, 1980; Stegemann, 1981; Arndt, 1989). The decline in the species is therefore attributed to changes in the Central European climate (e.g. Gries *et al.*, 1973). The last known population from the lowlands of Lower Saxony was recorded in the woodland 'Hasbruch' near Oldenburg, a large former wood-pasture (Gersdorf & Kuntze, 1957). Falke *et al.* (2000) state that the local climatic factors in a wood-pasture are probably more suitable for this tree-climbing and thermophilic species, because of the increased solar insolation (cf. the similar argumentations by Trautner (1996), for *Calosoma sycophanta*, which is also in decline in Central Europe, and by Assmann & Falke (1997), for the buprestid *Aphanisticus pusillus*). However, wood-pasture structures are increasingly in decline in Central Europe, due to a ban on forest pasture. The high density of *C. intricatus* in a dry, warm coppice forest in Baden-Württemberg also corresponds to this assumption (Hochhardt & Ostermann, 1998). It is therefore well possible that two important factors combined, have led to a reduction in the populations of Central Europe: (1) climatic change and (2) changes in the local climate of woodlands, due to different forms of cultivation. Furthermore, other forest-related changes in the woodlands can have a negative effect on populations (cf. Chapter 5).

(3) A noticeable decline within this century can also be observed in the East European species *C. marginalis.* This species has already become extinct in Germany, but records from the 20th century prove its former occurrence (Arndt, 1989). In Poland the formerly wide-spread beetle has declined to remnant populations in the east (found in a very small area of about 1 ha, in the communal forests of the city of Warsaw: Szyszko, 1987, *pers. comm.*). *C. marginalis* lives in deciduous forests (usually with oak as the dominant tree species) and in pine stands. These habitats are certainly still common in the European area of distribution and, unlike the beetle, have not declined. It therefore seems improbable that the drastic decline in populations of *C. marginalis* is based on the destruction of its habitats. With this species it seems more probable that climatic changes (e.g. increasing Atlanticism of the climate) are a decisive factor.

As these examples show, both anthropogenic and climatic factors (or a combination of both) may be responsible for the decline of some *Carabus* species in Europe. However, only species that are in decline because of anthropogenic influences will be considered in the following discussions.

In recent decades (since circa 1950) changes in land use have been rapid. In particular, the structural reforms of the European Union agricultural policies, have had far-reaching effects over extensive regions. This in particular affects the southern European countries, which are renowned for their species richness.

◀ ***C. italicus rostagnoi*** Luigioni Italy, Latium (Rome). Photo by A. Vigna Taglianti

C. auratus can be taken as an example of a species that has strongly declined in recent decades. The beetle was prevalent over much of Europe in the 20th century (Chapter 5), and was particularly common in Central Europe. Impressive descriptions of 'mass reproduction' can be found in Barner (1937): 'in 1891 *C. auratus* was ... so common that one could not walk on a field path without treading on an animal at each step' (translated). Basedow (1987) was able to demonstrate that in Schleswig-Holstein, the impact of insecticides resulted in the complete extinction of the populations within just ten years, whilst the species continued to survive in organically farmed areas. Heydemann (1983) also reports on the drastic decline in the species. Similar losses are also known from other regions of Central Europe (cf. Desender & Turin, 1989). *C. auratus* has not only survived in 'ecologically' farmed fields, but also in extensively used grasslands (e.g. Holste, 1974) and, particularly in south-west Europe, in montane and subalpine pastures (Assmann, *own observ.*).

The decline in numerous animal and plant species in Europe has led to the introduction of Red Data Books and Red Lists, which have to be taken into consideration when landscape plans are being considered, in order to prevent further decline of a species. In the past ten years carabid beetles have increasingly been taken into consideration in these lists (e.g. Marggi, 1992; Trautner *et al.*, 1997; Luff, 1998). In addition, laws have been enacted in several countries which forbid all members of the genus *Carabus* or certain species from being caught and collected (e.g. in Spain and Germany). Species such as the widely distributed *C. clatratus* are listed, as well as pronounced locally distributed endemic species, such as *C. olympiae* or *C. auriculatus* (see Chapter 5).

Such procedures, however, do not seem to be particularly efficient. The crucial factors causing the decline seem to continue to affect populations, because increases in species that have become rare are only seldom reported (e.g. *C. nitens*, see below). In this chapter aspects of conservation biology will be introduced in order to convey an overview of the problems and possibilities of the preservation of this diverse group of ground beetles.

9.2. WHAT SHALL WE PROTECT? A POPULATION-BIOLOGICAL APPROACH

The objective of conservation biology is the preservation of biodiversity, which is usually subdivided into three levels: (1) diversity below the level of species, (2) diversity of the species, and (3) diversity of species communities (Primack, 1993). Conservation strategies usually concentrate on the latter two levels. With the genus *Carabus*, however, it seems important to turn to the variability and differentiation within and between conspecific populations. The intraspecific diversity of their members is particularly pronounced, showing itself not only in morphological characteristics, but also in ecological and physiological differences. Besides the species, the more strongly differentiated populations should also be included for protection in expert considerations on conservation. The 'evolutionarily significant unit' (ESU) concept, which has been introduced by Ryder (1986) to describe unique groups of organisms that should be managed separately, corresponds best to such considerations. While this concept is accepted among conservationists, there is no consensus of how it should be applied in practical conservation situations (cf. Cracraft, 1997).

Based on the phylogenetic species concept (cf. Claridge *et al.*, 1997), Vogler & DeSalle (1994) favour a definition for ESU based on patterns of variation. In the theoretical framework of the phylogenetic species concept, conservation units are delimited by genetical characters that diagnose clusters of individuals or populations (e.g. by synapomorphies) to the exclusion of other such units. This concept is explained using two examples from the genus *Cicindela*. The authors emphasise that besides genetic characteristics, morphological, ecological and ethological characteristics should also be considered. The main thing is that the ESUs are genetically related, and not the result of an environmental induced reaction of a given genotype. One advantage of this concept is definitely based on the objectivity and the ability of other researchers to test results. One of the disadvantages, however, is the large expenditure involved in the genetic analysis of numerous populations.

With the help of microsatellite DNA, Rasplus *et al.* (2000) were able to examine the genetic population structure of *C. solieri* from its relatively restricted range in France and Italy. They showed that two populations belonging to the subspecies *C. s. bonnetianus* differ from all other populations in numerous synapomorphies. These two populations therefore represent an ESU. Populations of *C. s. curtii* cannot be classified with good confidence. The results confirm the hybrid origin of this subspecies and therefore such populations are not an ESU.

Using allozyme electrophoresis Assmann & Weber (1997) found several alleles with a discontinuous spatial change of frequency in *C. punctatoauratus* from the Pyrenees. Several alleles were found only in one population (e.g. Gpi-0.81: 46 % in the Forêt des Hares) or a group of populations (e.g. Est-x-0.84 in the populations between the rivers Ariège and Aude). Such characteristics are a feature of ESUs. On the other hand, there are populations that do not have 'private' alleles, such as, for example, both populations of the Massif de Bigorre, for which only widespread allozymes could be detected. According to these characteristics, these populations do not form an ESU.

The potential significance of genetic differentiation to a populations' capacity to survive is discussed in Chapter 9.3.

9.3. REASONS FOR THE DECLINE OF CARABID POPULATIONS

9.3.1. Habitat destruction

Changes to and destruction of habitats are seen as the most common cause for the decline in numerous *Carabus* species. These changes can, however, arise from natural causes. In Austria *C. hungaricus* is very locally restricted to steppe habitats in the vicinity of the Neusiedler Lake. The decline of traditional farming practices in this area has led to the loss of pasture habitats and their replacement by woodland and this can be linked to a decline in the species in question (cf. Chapter 5). Due to the afforestation of previously extensively used open habitats, numerous other species have also declined (e.g. *C. nitens* in heathlands and peat bogs; *C. convexus* in regions where it colonises poor or limestone grasslands, cf. Desender & Turin, 1989).

Most semiaquatic *Carabus* species have probably declined because of the destruction of their habitats. *C. clatratus, C. nodulosus*, and *C. variolosus*, species populating light and shaded moors, have declined over large parts of their distribution, due to peat digging and drainage. *C. clatratus*, which occurs in oligotrophic moors in some parts of its distribution, is also threatened by eutrophication: Grossecappenberg *et al.* (1978) caught considerably more individuals on oligotrophic banks than at comparable observation points in mesotrophic aquatic environments. The change of habitats in intensively used agricultural landscapes, due to changes in the groundwater level and to moist deposits (greatly increased NHx-depositions), has a negative effect on these beetles. *C. galicianus*, an endemic species of north-west Spain which settles on the banks of running waters, is endangered by the increased construction of bank reinforcements and the ensuing loss of stream banks, as well as an increase in water pollution (Zaballos & Jeanne, 1994; Assmann, *own observ.*). *C. alysidotus*, an endemic species of Italy and south-east France, has lost numerous populations due to the drainage of bogs and destruction of habitats caused by increasing urbanisation (Casale *et al.*, 1982). The only semiaquatic European *Carabus* species that does not seem to be endangered is *C. melancholicus.*

The decline in forest species is puzzling, since the woodlands and forests in Europe are not declining, at least in Central Europe (cf. Desender & Turin, 1989; Assmann, 1999). The increase in some forest species (e.g. *C. problematicus*: Desender & Turin, 1989) can easily be explained by increases in the relevant habitats. *C. glabratus* and *C. irregularis,* however, belong to the species that demonstrated a conspicuous downward trend (Desender & Turin, 1989; Assmann, 1999). *C. convexus* probably also has to be partially included in this group, since the species lives in woodlands in some regions of Central Europe (cf. Desender & Turin, 1989). This is a good example of the necessity to include ESUs as well as species, when considering the conservation aspects of the genus *Carabus*. The reasons for the decline in these species have not been clarified. Indications of climatic reasons for decline do not exist, as far as known to us. Possibly agricultural intensification has had a negative effect on these species (cf. the paragraph 'Conservation' of the *C. intricatus* species' text in Chapter 5). With *C. glabratus* there could be additional problems with the (re)colonisation of unsettled wood plots ('empty patches'). In the north-west German lowlands (Lower Saxony and perhaps also in the Westphalian Lowlands and at the Lower Rhine), *C. glabratus* is to a large extent restricted to woodlands that are over 200 years old. In this region at least, the potential for dispersal seems to be low (Assmann, 1998; 1999). If local populations are extinguished by clear-cutting or other forest measures, the probability of resettlement after regeneration of the wood is low. The three forest species discussed here show a population decline in parts of their distribution. In northern Italy (*C. convexus* and *C. glabratus*: Casale *et al.*, 1982) and in Austria (*C. irregularis*: Paill, *pers. comm.*) they are still common and prevalent. These contrary tendencies within their distribution regions make it impossible to classify the species in a common European scale (Tab. 9.1).

In some cases changes to carabid habitats are far-reaching, but not immediately recognisable. In recent decades many extensive heathland areas of north-west Europe (England, the Netherlands, Belgium, north-west Germany) were transformed to pasture, whilst other traditional agricultural practices ceased. Simultaneously, *C. nitens* declined in the remaining heathlands (Turin & den Boer, 1988). However, the beetles were able to profit from the reintroduction of traditional agricultural practice in the Netherlands. At Kralo Heath (Netherlands) where den Boer & van Dijk (1994) carried out a long-term study over twelve years, the species became more common again four years after the complete heather vegetation had been mown (0, 7, 23 and 36 individuals per year in 10 traps) (see also van Essen, 1993). In the nature reserve 'Lüneburger Heide' (eastern Lower Saxony) a link to low-growing heath (e.g. *Calluna* heath in the building phase) could be ascertained (Assmann & Janssen, 1999). For *C. nitens* not the heath itself, but its phases of development are important. Den Boer & van Dijk (1994) were also able to demonstrate that *C. arvensis*, which is in decline in the Netherlands, Belgium and Denmark (Desender & Turin, 1989), reacts positively upon 'habitat management': after a fire the numbers of individuals observed rose from 0 to 478 in the second year back to 299 in the third year. In other regions of its distribution *C. arvensis* has probably not declined at all, or at least not as strongly; it has even succeeded in occupying some previously uncolonised woodlands (western Lower Saxony, *own observ.*).

The importance of taking the different habitat preferences of conspecific populations (see section 9.2) into consideration is made clear by population groups of *C. solieri*. In the most southern extent of its distribution in the Western Alps, the ssp. *bonnetianus* is found in the meso-Mediterranean zone (below the holm oak (*Quercus ilex*) timberline, cf. Ozenda, 1988). In woodlands, which are often dominated by *Pinus*, the subspecies populate the peripheral zones of small (and relatively moist, cool) valleys (often with stands of *Alnus*). Devastating forest fires, frequently caused by arson, are repeatedly reported in this region. Areas destroyed by fire that are close to the coast are then often used for building activities. This development (habitat destruction and urbanisation) has already led to the extinction of individual populations (e.g. in the Massif du Tanneron; Bonadona, 1971; Korell, *pers. comm.*). On the other hand, populations occurring in mountainous areas (e.g. ssp. *solieri*) inhabit much larger areas and do not appear to be threatened. In the Ligurian Alps and Apennines ssp. *liguranus* locally forms the most common species of the genus (Casale, *pers. comm.*). Such populations even survive in forests which are intensively commercially forested (e.g. in the vicinity of the Col de Turini, *pers. observ.*).

9.3.2. Fragmentation

In recent years the metapopulation concept has been increasingly accepted in conservation biology (e.g. Hanski & Gilpin, 1997). The concept is based on local populations that occur in separate sites, and which are in contact with one another through migrating individuals. This exchange of individuals facilitates recolonisation within a metapopulation if local populations die out through population-dynamic processes. If the rates of extinction and recolonisation are equal, a metapopulation remains stable. If, however, the recolonisation rate falls in comparison to the rate of extinction, the

Table 9.1. Examples of endangered European *Carabus* species (after Korell, 1975; Lindroth, 1985; 1986; Desender & Turin, 1989; Balletto & Casale, 1991; Zaballos & Jeanne, 1994; Marggi 1992; Mahler *et al.*, 1996; Trautner *et al.*, 1997; Luff, 1998; Turin, 2000; Assmann *et al.*, 2002; Paill, *pers. comm.*; Assmann, *own observ.*).

Species declining in their whole distribution area	Species declining in parts of their distribution area	Subspecies declining[1]	Endemic species with small distribution areas
C. clatratus	*C. scabriusculus*	*C. menetriesi pacholei*[2]	*C. olympiae*[3]
C. italicus	*C. arvensis*	*C. solieri bonnetianus*	*C. cychroides*[4]
C. alysidotus	*C. auratus*	*C. faminii faminii*	*C. auriculatus*[5]
C. nitens	*C. cancellatus*		*C. planatus*[6]
C. galicianus	*C. vagans*		
C. nodulosus	*C. glabratus*		
C. variolosus	*C. bessarabicus*		
	C. convexus		
	C. marginalis		
	C. hungaricus		
	C. intricatus		
	C. creutzeri		
	C. irregularis		
	C. caelatus		
	C. rugosus		
	C. coriaceus		
	C. gigas		

[1] At least one subspecies of these given species seems not endangered.

[2] Regarded as a protected subspecies of the FFH Directive of the European Union.

[3] Regarded as a protected species of the FFH Directive of the European Union.

[4] Protected species in Parco Naturale Orsiera-Rocciavré (Italy).

[5] Protected species in National Park of the Picos d'Europa (Spain).

[6] Protected species in Parco Naturale dei Nebrodi (Italy, Sicily).

number of local populations within a metapopulation continues to decline. Such a long-lasting trend then leads to the extinction of the metapopulation. Den Boer (1981, 1990) and den Boer & van Dijk (1994) were able to show for a number of carabid beetle species (incl. *Carabus* species) that the extent of natural fluctuations of local populations can exceed a factor ten square, so that extinction processes are probable at the local level. Many species of carabid beetles possess efficient mechanisms (e.g. the ability to fly) to colonise vacant habitats. Population fluctuations are therefore a probable cause of local extinctions for many species of carabid beetles, although this is not widely proven. Extinctions and recolonisations need to be verified to prove the model.

Data on the population dynamics and population genetics of some *Carabus* species seem to confirm the concept of metapopulations (e.g. Niehues *et al.*, 1996; Assmann & Weber, 1997). However, the magnitude of variation in the populations of many local *Carabus* populations is probably not as large as those described for many other insects. The low fluctuations in the population size of the well-investigated *C. auronitens* in an enclosure in Westphalia substantiate this observation (e.g. in comparison to *Poecilus versicolor* and *Calathus melanocephalus*) (Althoff *et al.*, 1992). Moreover, the potential for recolonisation is lower, due to the (almost exclusive) brachyptery of the species. Some *Carabus* species may not show metapopulation dynamics. This could particularly apply to species that occur as stable relict populations in isolated refugia (e.g. *C. glabratus* in northwest Germany, cf. Chapter 5).

If the distance between the habitat patches of a *Carabus* species increases, or if the habitats between the patches change so much that they are more rarely crossed by the beetles, the rate of recolonisation should decrease. Even if the habitats are suitable for the particular species, changes to the landscape would in such a case lead to a changed (or initial) fragmentation, which would then, according to the metapopulation concept, lead to a decline.

According to this concept, vacant areas can be predicted to occur within the ranges of relatively weakly dispersing species. Translocation experiments have indicated that these empty habitat areas are likely for some species such as *Poecilus lepidus* (de Vries, 1996) and *Carabus auronitens* (Schwöppe *et al.*, 1998). At the same time, large habitats, which are able to house several local populations, ought to demonstrate on average a greater probability of settlement than smaller sites. For one ground beetle species it has indeed be shown that larger sites were more likely to house one or more populations than small ones (*Agonum ericeti*: de Vries & den Boer, 1990). Furthermore, it was shown that for several ground beetle assemblages a positive correlation exists between the area and the number of stenotopic species occurring (e.g. heathlands in the Netherlands: de Vries, 1994; sand dunes in Germany: Assmann & Falke, 1997; woodlands in Germany and Belgium: Gruttke, 1997; Desender *et al.*, 1999). This result is in agreement with assumptions arising from the metapopulation concept. However, such species-area relationships do not exist in other habitats or regions (e.g. woodlands in Finland, England, and Germany: Niemelä *et al.,* 1988; Terrell-Nield, 1990; Assmann, 1999). This could be related to the hypothesis that at least some of the species taken into consideration do not show distinct metapopulation dynamics (see above), or that the areas under investigation are so large that even the smaller ones house several local populations, such that the probability of local extinction is low (Assmann, 1999).

The results introduced above on species-area relationships enable us to conclude that population effects of the fragmentation of habitats for stenotopic *Carabus* species cannot be ruled out. It therefore seems sensible to carry out investigations on the 'minimum viable population size' concept (MVP) elucidated in the next section, at least for endangered species or ESUs.

9.3.3. Insecticides

The impact of insecticides was briefly mentioned in section 9.1 using the example of *C. auratus.* Basedow (1987) was able to show clearly that the species has disappeared from fields of Schleswig-Holstein where the use of insecticides is common. In a long-term study he was also able to prove that over the same period the beetles were common in fields which were farmed without the intensive use of insecticides (Basedow, 1998). Other species that inhabit fields are also decreasing in parts of their distribution, such as, for example, *C. cancellatus* in Belgium, the Netherlands, Denmark, Slovakia, and Germany (Desender & Turin, 1989; Kleinert, 1987; Trautner *et al.*, 1997). The decline of the populations may be linked to the considerably increased use of insecticides in recent decades. However, other factors also may need to be considered. Thus den Boer & van Dijk (1994) point out that the species has declined considerably in the heathlands of the province of Drenthe where insecticides are not used.

Laboratory experiments undertaken by Scherney (1958) show that *C. granulatus*, which is not endangered in Europe and is prevalent in fields, is less sensitive to several insecticides than *C. cancellatus* and *C. auratus*, which have declined considerably in large parts of their distribution. The results of Basedow *et al.* (1976, 1981) demonstrated a 100% degree of effectiveness of oxydemeton-methyl and parathion on *C. auratus.* According to several other experiments, synthetic pyrethroids and pirimicarb seem to be largely harmless to carabid beetles (cf. literature cited in Basedow, 1998).

Whilst the use of insecticides on farmland is generally known, that forests are also treated with such poisons is often overlooked. They are employed to prevent the mass reproduction of Lepidoptera, since their larvae eat the leaves or needles of the trees. In 1987 and 1988 some oak woodlands in the Westphalian Lowlands were sprayed by helicopter with dimilin (diflubenzuron, 75 g/ha) to control larvae of the winter moth (*Operophthera brumata*) and the green oak moth (*Tortrix viridana*). In a post-treatment comparison of 8 sprayed and 6 control stands, Klenner (1994) found that in all dimilin-treated plots the total number of captured spring breeders (e.g. *C. auronitens*, *Pterostichus oblongopunctatus*) is lower than in the control areas. The author explained this result as an effect of the insecticide which interferes with moulting during metamorphosis. Dimilin was applied during summer, the development season of the larvae of the spring breeders. *Carabus* species with winter larvae (e.g. *C. violaceus*, *C. problematicus*) did not show reduced catch rates in the sprayed stands. Population drops clearly can be caused by insecticide applications in forests. Repeated applications of pesticides may be the reason for the extinction of a population.

The ability of numerous insects to acquire resistance to chemical toxins is the subject of intensive research. Low concentrations of insecticide preferentially select for polygenic responses and high concentrations for monogenic ones (McKenzie & Batterham, 1994). It could be shown for several substance groups, to which strong resistance has been acquired, that genes which code for proteins of ion channels (GABA/chloride, sodium) and enzymes (e.g. esterases like acetylcholinesterases, carboxylesteases, oxidases or transferases like glutathione-S-transferases) are strongly amplified (McKenzie & Batterham, 1994). The acquisition of resistance therefore has an expressly conservative genetic basis. New proteins which are better adapted to the conditions of insecticides generally do not seem to be evolved. Hence it can be assumed that *Carabus* species can also acquire such resistance. Direct indications from field investigations of such phenomena do not exist (e.g. increase of population density of *C. auratus* on intensively managed fields). In view of the significance of the potential role of these beetles as predators of pests (e.g. Scherney, 1957a), appropriate investigations are not only important to conservation biology, but also to agriculture.

9.3.4. Small population size

Several factors affecting small populations are recognised in current literature on conservation biology (e.g. Shaffer, 1981; Soulé, 1987; Samway, 1994; Stewart & Hutchings, 1996): (1) Demographic stochasticity can doom a population (e.g. if a generation only consists of individuals of one sex). (2) All populations are subject to the effects of stochastic environmental factors (incl. catastrophes), which refers to chance fluctuations (mostly in the weather) and can result in a low reproduction rate. In small populations such events may result in the complete disappearance of the population. (3) Loss of genetic variability (number of alleles and heterozygosity: genetic erosion) and inbreeding occur in small populations (inbreeding depression). This population-genetic factor is of great importance, because it can influence the fitness of the whole population, especially when the population is (normally) large, but temporarily consists of few individuals (see below).

Alleles are different forms of a gene at a given locus. The relative proportions of alleles at a given gene in a population are referred to as the allele frequencies or gene frequencies (e.g. Li, 1997). Allele frequency changes can be caused by selection, mutation, gene flow, and chance (= random genetic drift) (e.g. Wright, 1931; Hartl & Clark, 1989). The latter case, in which the changes are not directional but random, is of special importance in conservation biology. Genetic drift occurs rapidly, when a population passes through a bottleneck situation (a low number of reproducing individuals). The smaller a population and the longer it remains small, the more genetic variation it loses. The best indicator of the intensity of a bottleneck seems to be the number of alleles of (pre-bottleneck) polymorphic loci (Nei *et al.*, 1975; Leberg, 1992).

In the absence of migration the number of alleles in a population decreases when bottlenecks occur. In populations, which for a long time live in such a situation, genetic variability continuously declines (genetic erosion). Results of many laboratory and field studies suggest that heterozygous individuals are often fitter than those of the same cohort with lower heterozygosity (e.g. Futuyma, 1986; Mitton, 1997).[7] The reduction of the overall fitness of the given population is a consequence of declining (within-population) genetic variability. Additionally the smaller the genetic variability of the population, the less able it is to adapt to a changing environment (e.g. Lynch, 1996).

The effects of genetic drift depend more on the effective population size (N_e) than on the real population size (N). N_e is a measure of how many individuals contribute their genes (respectively alleles) to the next generation (Nunney & Campbell, 1993); N_e is less than N (for example, a 3:1 sex ratio means that N_e is 0.75N). The most important factors influencing N_e are unequal numbers of males and females, overlapping generations, Non-Poisson distribution of fecundity, dispersion of individuals within the occupied habitat and fluctuations in population size (Hartl & Clark, 1986, see this book for further explanations). It is obvious that numerous population-ecological and genetical parameters are required (but are generally unknown!) in order to establish the N_e-value for a real population.

If the dangers to which small populations are exposed are recognised (for additional intrinsic factors see Stewart & Hutchings, 1996), the critical minimum population (MVP) below which it is threatened to extinction must be investigated. The MVP concept tries to give answers with the help of demographic models (most of which include some form of population regulation). In this context it should be

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[7] All the same it is very difficult to demonstrate that monomorphism leads to disease and ultimately to a higher rate of extinction in natural populations. See Nunney & Campbell (1993) for a more detailed discussion.

noted (following Stewart & Hutchings, 1996): (1) An MVP can only be defined in the context of the probability of survival over a defined period for a given population (e.g. x % chance of surviving over a minimum of y years). (2) The information differs for every species and for many conspecific populations. An MVP which applies to all species does not exist. (3) A comprehensive concept should take both the genetic risks of small populations and the demographic stochasticity and stochastic environmental factors (incl. catastrophes) into account.

For practically orientated nature conservation (especially for the protection of insect populations), such a model has to provide information on the minimum size of a habitat, which will be colonised with the respective probability for the considered period ('minimum viable area': MVA; Stewart & Hutchings, 1996). Such a model can only supply approximate information because in most cases insufficient population-biological data is available.

Two values are discussed again and again in the literature on the MVP concept: Ne = 50 is the minimum value to avoid inbreeding depression (Franklin, 1980). This value is taken from animal breeding. As explained by Nunney & Campbell (1993) this value is problematic. When the effective population size is 50, the rate of inbreeding is 1%, meaning a significant chance of deleterious alleles becoming fixed. 'For example, the chance that a recessive allele with 5% fitness disadvantage will spread to fixation is about 0.007. This small chance, integrated over only 100 loci, translated into a 50% chance of at least one deleterious allele becoming fixed' (Nunney & Campbell, 1993: 236). This probability decreases strongly with increasing N_c. Even if inbreeding effects are unlikely for this population size, the danger of a loss of alleles still exists. Franklin (1980) recommends Ne > 500 for a long-term persistence of populations. Mace & Lande (1991) define a population size of 50 or 500 as 'critical' or 'endangered', respectively.

Tests on the effect of smaller population sizes on the probability of survival, fitness or genetic variability of *Carabus* populations have not yet been carried out. Thus definitive data relating to inbreeding depression are lacking (for a review from the insect conservation biology viewpoint see Brakefield, 1991). Nevertheless, it is probable that small *Carabus* populations are exposed to an increased risk of extinction.

Indications of reduced genetic variability, which were presumably lost during one or more bottlenecks, can be found in the literature on populations. This concerns *C. auronitens* in the Münsterland (Westphalian Lowlands: Terlutter, 1990; Niehues *et al.*, 1996; see for further explanation section 9.4). The feature of most *C. punctatoauratus* populations is a high number of alleles for four gene coding enzymes (Assmann & Weber, 1997). However, only two respective variants of these enzymes could be determined for two local populations from the Massif de Bigorre (exception: only 1 AAT-1 allozyme at sampling site 2). Indications that these populations were suffering simultaneously from reduced fitness, however, were not apparent. On the contrary, *C. auronitens* populations have probably spread across a large area over a very short period of time (cf. Niehues *et al.*, 1996).

Malausa & Drescher (1991) established that *C. olympiae*, even with two 13-generation lines based on around ten individuals each, showed neither morphological malformations, reduced body sizes nor any other indications of 'degeneration'. The translocation experiments that were carried out seem, however, to have failed (see section 9.4).

9.3.5. Collecting

Carabus species have been popular collectors' items since at least the XIXth century. The (scientifically doubtful) description of numerous taxa beneath the species level, as practised mainly by Breuning (1932-37), probably also had a positive influence on this. The demand for large and colourful animals has furthermore led to a lively trade. Unit price may be very high: some endemic species from Asian mountains have been advertised at up to US $ 1,000/specimen. In Europe the collective pressure on endemic species which are only locally distributed (e.g. *C. olympiae*, *C. cychroides*, *C. auriculatus*) are valued so highly by some environmental protection agencies that some species are protected by state law (cf. Chapter 3). *C. olympiae* is listed in Annex II of the EU Habitats Directive, which means that strict protection is necessary (The Council of the European Communities, 1992). In the amendment *C. menetriesi* ssp. *pacholei* was also incorporated (Ssymank *et al.*, 1998).

Carabus species demonstrate different population densities which can also fluctuate from year to year. Althoff *et al.* (1994) obtained measurements of 0.13 to 0.27 beetles per m^2 for a *C. auronitens* population in the Münsterland. According to this, between 13,000 and 27,000 individuals of this species live in a 10 hectare forest. When the specimens were caught in pitfall traps over a period of one year, captures of just a few hundred individuals are possible (cf. the results of pitfall trapping in woodlands of the Westphalian Lowlands; Klenner, 1994). The number of captured individuals is therefore far below the natural amplitude established for population fluctuations of this species. This simple observation also seems to be applicable to other *Carabus* species. The Forêt de Belesta (Pyrenees) is visited by numerous collectors looking for beetles of the *C. punctatoauratus* subspecies with the longest body length. The consequence of this is that the fallen tree trunks in the vicinity of roads, which serve as their winter location, have been completely 'hacked off' over a length of several kilometres (Assmann, *own observ.*). Large numbers of beetles are taken, and at the same time the places of hibernation in the decaying wood are repeatedly destroyed (presumably several hundreds or thousands of beetles, perhaps every year). Pitfall-trap catches show, however, that the beetles remain common in this area. A threat to the population can therefore not be perceived. Even the long-term use of pitfall traps (e.g. for a period of 10 years or longer) has not indicated a reduction in numbers (cf. den Boer & van Dijk, 1994).

For this reason it seems improbable that *Carabus* populations in larger habitats are endangered by collectors. However, the situation in small habitat remnants which have been fragmented by (usually anthropogenic) environmental degradation could be affected differently (e.g. *C. alysidotus*, *C. nodulosus*). These populations may contain just a few hundred individuals. Intensive collecting in these remaining populations could possibly lead to a critical reduction of their population sizes (see the paragraph 'small population size').

Knisly & Schultz (1997) made a very similar assessment for representatives of tiger beetles in North America (South Atlantic states of the USA), which are also popular collectors' items. Certain natural history characteristics of the members of this family may provide them with some protection against overcollecting. Indications that population sizes are actually reduced by collectors only exist for a handful of species.

General protection prohibiting the capture of *Carabus* species is advantageous to neither scientific nor environmental protection activities. The example of *C. auriculatus*, for which a new subspecies outside the previously known area was described in 1998 (Peña Orniz: Forel & Leplat, 1998), demonstrates clearly how little is known about some protected species. A considerable amount of information about the occurrence and biology of species and populations is provided by amateur collectors and is necessary for their effective protection. It therefore seems important to encourage the activities of entomologists. Moreover, the collections put together by amateur entomologists are often of considerable scientific value, which can exceed their purely faunal significance. Nowadays not only 'classic' morphometric investigations (morphometric differentiation and fluctuating asymmetry, see section 9.4) and DNA sequencing, but also the determination of the heavy metal content can be carried out on such collection material. Hence *Carabus* collections also represent significant archives for both the present and the future.

9.4. STOPPING THE LOSS – PRESERVATION AND SUSTAINABLE CONSERVATION

How can *Carabus* populations be kept from extinction? The most important prerequisite is the preservation of their habitats. The habitat preferences of most species are relatively well known (cf. Chapter 5); however, that conspecific *Carabus* populations can occur regionally in different habitats must be taken into consideration. An example of this is the endangered *C. clatratus*, which occurs in various different regions in the north of Germany in both raised bogs and fens, riverine meadows and coastal flooded moors (Huk, 1998, see also Gries *et al.*, 1973; Assmann, 1981; Schultz & Müller-Motzfeld, 1995; Müller-Motzfeld *et al.*, 1996). The maintenance of water level dynamics with their seasonal fluctuations (especially flooding during the winter, but not in summer) is necessary for the preservation of the populations concerned (Huk, 1997; 1998). However, the habitats vary considerably. Thus 'habitat management' must vary according to the relative habitat.

Habitat management must furthermore take into consideration that several species only inhabit habitats temporarily. The example of *C. nitens*, which occurs in particular during the first development phase of *Calluna* heath, has already been mentioned (section 7.3).

It is more difficult to preserve habitats which are changed by processes affecting whole landscapes. Progressive eutrophication is just one of these problems. But conservation concepts even exist for oligotrophic habitats such as heathlands, which seem to enable their long-term preservation (e.g. Bakker & Berendse, 1999).

Besides the preservation of habitats, further problems arise for the species in question which are to be discussed in this chapter:

(1) The area of many habitats is shrinking due to the changing socio-economic conditions in Europe. At the same time the question arises as to whether some *Carabus* populations are approaching critical threshold values. Therefore in the following discussion recommendations are indicated which can be incorporated into the practices of modern conservation biology (e.g. MVP, genetic monitoring).

(2) Many new conservation concepts are directed towards the restoration of habitats which previously occurred in the respective areas (e.g. Bakker & Berendse, 1999). However, difficult problems probably arise here for numerous *Carabus* species, since the power of dispersal of these flightless and often stenotopic species is insufficient in a fragmented landscape to reach the new habitats on a large scale. With such considerations (and the metapopulation concept) in mind, habitat corridors to aid dispersal are repeatedly suggested. In the following, the opportunity which such landscape structures can offer to *Carabus* species will therefore be discussed.

(3) If habitat corridors are not possible (or too costly), but suitable habitats are available, reintroductions can be considered. The aspects to be taken into consideration with such a process for the genus *Carabus* will be briefly introduced.

(4) As described in section 9.3, numerous *Carabus* populations in agricultural fields have declined as a consequence of the use of insecticides. Do programmes of field edges (set aside) and agricultural reserves where pesticides are not used have a positive influence on *Carabus* species?

(5) Finally, the possibilities of enforcable species protection programmes for the genus *Carabus* and the signif-

icance of good publicity in their presentation will be dealt with.

9.4.1. MVP, genetic monitoring

Information about endangered *Carabus* populations in small habitats can be gained from capture and recapture experiments with individually marked beetles. Such experiments (mostly in enclosures, e.g. Althoff *et al.*, 1994; de Vries, 1996) have already been carried out for *Carabus* species (and other ground beetles), providing a great deal of information about the relevant populations and species, as well as their protection (e.g. on reproduction rates and their dependence on abiotic parameters: Schwöppe *et al.*, 1998). The data gained (at least after a relatively long period of investigation) facilitate an assessment of important parameters for a 'population viability analysis' (PVA), which is an integral part of the MVP concept.

In combination with capture and recapture experiments, investigations of the genetic variability of smaller populations can be carried out. Not only small populations are suitable for this; small groups of conspecific individuals can be artificially excluded within a larger population via enclosures, in order to investigate how genetic variability parameters change. The fitness of a population can simultaneously be gained from the reproduction rate. Representatives of the genus *Carabus* are particularly suitable for such investigations, since they can be marked relatively easily, and genetic parameters can be obtained individually without having to kill the beetles. Terlutter (1990) removed hemolymph with a sharpened 5 µl glass capillary which was cautiously inserted between two abdominal sternites. The survival rates of beetles so treated, was not or only slightly reduced (Terlutter, *pers. comm.*; Assmann, *own observ.*). It is possible to stain several enzymes after electrophoresis of the hemolymph samples (e.g. esterases, glucose-6-phosphate isomerase, cf. section 6.2). By the removal of a tarsus from a *Carabus* individual it is also possible to examine the microsatellite DNA and to obtain knowledge about the precise genetic structure within a population (cf. Rasplus *et al.*, 2000).

Apart from single locus markers (allozymes, haplotypes) morphometric features can be used as expressions for polygenic systems, e.g. the fluctuating asymmetry (FA). Three types of bilateral asymmetry can be distinguished by differences in the spreading of left-minus-right values of a character among individuals (Leary & Allendorf, 1989): (1) Directional asymmetry (DA) occurs if a character on one side of the body is normally larger than its counterpart (e.g. the gonads of humans are usually larger on the right side than on the left). (2) Antisymmetry is meant if asymmetry is the norm, but the side with the larger character varies (e.g. the large signalling claw of male fiddler crabs occurs left and right with the same frequency). (3) FA is realised if symmetry is the normal state and there is no tendency under normal conditions for one side to have a larger value than the other.

The amount of FA depends on the genetic variability of the genes, which influences the developmental stability, as well as the environment, in which the observed organism developed. When the variability of the genes is low, the FA value is high, which has been shown by many animal breeding experiments in the laboratory (Leary & Allendorf, 1989). Under unfavourable environmental conditions the FA also increases. Therefore the FA is a suitable indicator of both genetic impoverishment and environmental stress, that is hardly detectable in the field (New, 1995). Several authors pointed out that the other forms of asymmetry (shortly outlined above) could indicate genetic or environmental stress. Within a biomonitoring context repeated measurements in the same population are recommended for its own internal control (Møller & Swaddle, 1997) (a comparison with other genetic markers, e.g. single gene markers, seems furthermore useful). An important advantage of FA investigations is the comparatively low personal and non-personal costs. Some examples of this bioassay technique for monitoring habitat quality are discussed by Møller & Swaddle (1997).

9.4.2. Habitat corridors

Habitat corridors are designed to counteract the fragmentation of habitats by enabling movement between isolated patches. *Carabus* species are apparently able to orientate themselves by such linear structures. Riecken & Raths (1996) could demonstrate with the use of radio telemetry that *C. coriaceus* lives in 'ecotone habitats' and is capable of directed movement in forest strips. So these strips can serve as guidelines for dispersal or for orientation within the habitat. *C. auronitens* probably has also used hedges connecting woodlands, the typical habitat of this species, where it dispersed within a few decades in the Westphalian Lowlands near Münster (Niehues 1995; Niehues *et al.*, 1996). Additional investigations of hedgerow habitats have been conducted by Thiele (1964a; 1977).

On the other hand there are indications that certain species in fragmented habitats do not use corridors. In a long-term research project, the colonisation of a newly created habitat strip by carabids has been investigated (Gruttke *et al.*, 1998). The proportion of new colonisers was low among the vagrant ground beetles, the development towards a typical hedge fauna was progressing slowly, and the 9-year-old woodlots did not function as a corridor for the dispersal of woodland species.

It is possible to distinguish between ancient and recent woodlands in north-west Germany. Ancient woodlands are woodlands occupying sites which have been wooded continuously, at least since the end of the 18th century. However, most of them are older, because at the end of the 18th century (when the first detailed maps were produced) north-west German woodlands were at the lowest. Recent woodlands are those which have become established since the end of the 18th century. Assmann (1999) demonstrated that *C. violaceus* occurs more frequently in recent woodlands which are linked (hedgerows or woodlots) to ancient ones compared to isolated ones. *C. glabratus* was mainly found in ancient woodlands (7 records within 16 ancient woodlands) whereas there is only one record from 30 recent woodlands. *C. problematicus* is widespread and is present in nearly all woodlands throughout the investigation area. In this case the importance of the habitat network in one particular area is different for the three species.

Vermeulen (1994) investigated a roadside covered with a sandy dry lawn and an adjacent large area with the same vegetation in order to gain information about the use of the roadside as a corridor. He was able to show that stenotopic carabids (*Poecilus lepidus*, *Harpalus servus*, *Cymindis macularis*) enter the corridor from the larger habitat, but rarely reproduce there. It may be concluded from these results that corridors function as a sink for some stenotopic species and Mader *et al.* (1990) are right in thinking that corridors can increase the probability of the extinction of local populations. Comparable investigations for species of the genus *Carabus* have not yet been carried out but, similar effects may be expected.

These results show that, besides the positive effects, negative effects may also exist. Furthermore, corridors can only connect certain habitats in Europe's present cultural landscape. These certainly include forests, which can (partly) be integrated via hedges and forest strips. However, landscape developments in recent decades have effectively and irreversibly led to fragmentation of many habitats. Frequently it is no longer possible to restore the landscape, especially when the necessary financial investment is not forthcoming. Examples are coastal brackish waters which have partly been destroyed by tourism and urbanisation, the remnants of which are now left without connections between them; and *Calluna* dominated heathlands in northern Central Europe. Therefore, habitat corridors are not applicable in the case of many endangered *Carabus* species and populations.

9.4.3. Reintroduction projects

In the interests of active conservation it seems reasonable to re-establish populations by releasing specimens into isolated vacant habitats. Similar introductions have inadvertently been carried out (probably several times) by humans in the case of *C. morbillosus* in the Mediterranean region (see Chapter 3). The populations of *C. granulatus* and *C. nemoralis* in North America probably also (first) became established by anthropogenic means (Lindroth, 1957). It may therefore be possible to establish new *Carabus* populations. However, the experiments carried out on endangered species to date were more complex. *C. olympiae*, an endemic species limited to just one valley in the Western Alps, was released in two other locations in the Western Alps. Despite the large number of individuals released in the experiments (4195 larvae and 1813 imagines), only a few young were found in the ensuing years. The released beetles (and larvae) originated from two lineages which had been propagated for over 13 generations (Malausa & Drescher, 1991). It is possible that the beetles had therefore adapted to captive breeding conditions (cf. Samways, 1994), and at the same time, might have lost their ability to adapt to a natural habitat.

Mathyl (1990) reported on a reintroduction experiment of *C. nitens* in north-east Germany in which five, three, one and one animals were found in four subsequent years after release. However, data on the age structure in the Lüneburg Heath (Assmann & Janssen, 1999) suggested that the data obtained by Mathyl (1990) may also reflect the gradual extinction of an iteroparous population instead of a successful (re)establishment of the species. For other ground beetle species, older individuals have been found in the natural habitat with the help of individual markings (recapturing the same animals over five and eight years; Rusdea, 1994 and *pers. comm.*; Baumgartner *et al.*, 1997). In order to determine during the first years after a reintroduction whether the *Carabus* population has reproduced, it would therefore be necessary to mark all beetles before releasing them.

Schwöppe *et al.* (1998) carried out a successful settlement experiment with *C. auronitens* in a forest in the vicinity of Münster ('Warterhorster Sundern', north-west Germany). He employed six circular enclosures with a diameter of 20 m, into which 47-51 beetles were released. After four years, two of the enclosed populations were shown to be stable.

This result and that of de Vries's (1996) equally successful translocations of *Poecilus lepidus* in enclosures, suggest the use of enclosures in release experiments could contribute in a positive way to the establishment of new populations. The simple release of the beetles into a habitat can lead to a 'thinning out' of the species, which could making them fall below their critical minimum population density. Furthermore, the advantage of enclosure experiments is that numerous population-biological parameters, and those which are important for the survival of a population, can be controlled (Schwöppe *et al.*, 1998). These parameters may be equally important to the management of introduced populations. Moreover, it guarantees that monitoring the results of success or failure of each translocation will largely contribute to the understanding of requirements for successful reintroductions.

9.4.4. Programmes of crop edges and field enhancement

Conservation programmes using crop edges (conservation programmes in which strips a few metres wide along the edges of fields are not treated with pesticides) are relatively common, at least in Germany (although they are in decline).

These relatively narrow areas cannot be investigated with the use of pitfall traps alone, since the locomotory activity (which may be affected by the application of insecticides by causing a gradient in the numbers of prey items available, cf. Chiverton, 1984), can fluctuate greatly and movement between sprayed and unsprayed parts of the crop are possible. For this reason, Raskin (1995) used 4m^2 enclosures in addition to pitfall traps. The author came to the conclusion that the density of *Carabus* species can be so low that the relatively small strips do not enable populations to survive. It seems that the enhancement of whole fields is necessary.

Basedow (1998) was able to show in a long-term study on an intensively farmed field in Schleswig-Holstein that *C. auratus* had become extinct there in 1981. The first evidence of recolonisation after field enhancement (reduced use of insecticides) was observed in 1994. Dispersal probably took place from an organically farmed field approx. five km away. This result shows that *C. auratus*, which is an efficient coloniser (see Chapter 3), has the potential to spread under the conditions of modern-day agriculture. At the same time, recolonisation shows that the living conditions in the area under investigation have improved for the species (changed use of insecticides). For a large-scale recolonisation of *C. auratus* or an increase in number of other species that were previously common to fields, however, a large scale enhancement of farming needs to take place.

9.4.5. Action plans for conservation

Programmes for the preservation of endangered species have been in use for a long time. Mammals in particular have enjoyed and still enjoy protection, at high costs. In Anglo-Saxon countries, population ecology and genetics have been incorporated more generally in conservation strategies than in Central Europe, where conservation is dominated by an aesthetically-oriented protection of the countryside. In many cases biological investigations have been carried out to achieve efficient conservation. Generally, whole ecological assemblages gain from such programmes, not just the targeted species.

In the last ten years more insects have been included in these action projects, e.g. the tiger beetle *Cicindela dorsalis dorsalis* in the USA (U.S. Endangered Species List, Federal Register, Vol. 55, pp. 32089-32094, 7 August 1990). Now numerous publications on the biology and ecology of this species exist, which facilitate their effective protection. The first reintroductions are on the way and developing positively (Knisley & Schultz, 1997).

The longhorn beetle *Dorcadion fuliginator* only occurs at two localities in Switzerland, one of them situated on the embankment of the river Rhine in the centre of Basle. Since 1990, only 0.28 ha of suitable habitat has been available to the beetles. Baur *et al.* (1997) described translocation experiments and the urgent need for a special management concept for the highly endangered population.

The Council of the European Communities (1992) asked for protection programmes directed towards *C. olympiae* and *C. menetriesi pacholei.* Intensive investigations on the habitat preferences of other priority protected species, such as *Osmoderma eremita*, are currently being carried out (Ranius & Nilsson, 1997), as well as an EU-sponsored 'Life Project'.

The examples mentioned above, show that protection programmes for endangered species of beetles can be carried out successfully and presented well to the public (*Cicindela dorsalis*: several homepages (such as http://vims.edu/cbnerr/species/tiger_beetle.html); *Dorcadion fuliginator*: acceptance of the action plan). Similar projects also seem to be viable for the genus *Carabus*. Special attention should be paid to species or ESUs which are in decline in the whole of their area of distribution (Table 9.1). The hygrophilous species *C. nodulosus* in Central Europe and *C. alysidotus* in Italy and France are prime examples. Besides an accurate analysis of their habitat preferences, genetic parameters should also be established. If vacant habitats are found, reintroductions should also be considered.

9.5. CONCLUSIONS

Many European *Carabus* species have been declining in recent decades. The causes of this vary from habitat destruction and fragmentation to the use of insecticides and fertilisers. In most cases, collecting by man has not caused the decline of any species. In formulating promising conservation policies, several features of the genus have to be taken into account, such as the strongly differentiated populations and the reduced power of dispersal due to winglessness, for the preservation and/or restoration of the habitats is not the only factor necessary for species conservation. Additional options, such as the potential of habitat corridors and reintroductions (especially using extensive enclosures), as well as plans involving the participation of the public should also be examined. A programme of monitoring that includes evaluation of the population-biological parameters will be essential for assessing the effectiveness of the projects.

Such programmes and measures may enable us to halt the decline in populations of endangered species. This objective cannot be attained by simply adding species to the Red Data Books (including Red Lists) or by granting them the status of legal protection.

Chapter 10 Carabus evaluations

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INTRODUCTION

In this chapter, the content of the previous chapters is briefly summarised and evaluated. Current scientific data of European Carabidae are reviewed, and gaps in our knowledge are identified with proposals for further research provided.

Carabidae are one of the most studied groups of insects, with the genus *Carabus* being most comprehensively investigated. One of the early milestones was the research by Stephan Breuning (1932-1937) who provided a 1600 page monograph that included distribution maps for all species and most subspecies known at that time. This work, together with the earlier pioneering monographic treatment of the Carabidae by Vacher de Lapouge (1929-1932), demonstrated that these insects provide a model group for biogeographical studies. It is therefore surprising that in the years following Breuning's *opus magnum* few further studies were published (see Chapter 8. *Biogeography*), although eventually a major study of the *Carabus* of Middle Asia (Kryzhanovskij, 1953) provided important insight of the origin of this fauna.

During the second half of the 20th century the number of publications greatly increased. In Europe in particular, several national contributions have been published on *Carabus* faunas, often with detailed maps for species and subspecies. Furthermore, many papers have been dedicated to taxonomy, including catalogues at a world scale, phylogeny (also based on new characters such as the endophallus structures and molecular data), biology, ecology, biogeography and larval morphology of species, species groups, subgenera and phyletic lineages.

The idea for this book was developed in Bulgaria, during the summer of 1989. In the period 1990 to 1992 the initiators, Lyubomir Penev (Bulgaria) and Hans Turin (Netherlands), held discussions during several meetings in Bulgaria, the Netherlands and Russia. They succeeded in persuading Oleg Kryzhanovskij (Russia) and Achille Casale (Italy) to prepare a key to the adults. When Erik Arndt (Germany) and Kirill Makarov (Russia) agreed to construct a key to the larvae, a solid taxonomic basis was secured. In 1991, a first draft of a key to the adults was finished by Kryzhanovskij, comprising about 80 species from C. and E. Europe. Casale added a further 55 species from the Alps and the Mediterranean area to the key, as well as the majority of the subspecies. It soon became obvious that a European checklist was required that could serve as a basis for all cooperators in the project. Based on a first 'complete' version of the key, this checklist (including preliminary distribution maps) was published in 1993 (Turin *et al.,* 1993). At that time the taxonomy of the genus was mostly in agreement with the system proposed by Breuning (1932-37). Exceptions were the new proposals introduced by Deuve (1991), following Ishikawa's researches. These works *in toto* signalled a new epoch in Carabidae research and during the last decade, many new species-group taxa have been discovered and described, mostly from East Asia, new subgenera have been proposed, and many papers have been published on the genus as a whole.

The first, restricted, idea of making a simple study with keys, brief species accounts and a biogeographical chapter with special attention to the 'local-fauna concept' (see Chapter 8) was soon overruled by revolutionary research in the field of *Carabus*. Highly stimulated by these events, the number of ideas as well as the number of cooperators increased rapidly, which resulted in adding thematic chapters on phylogeny, biology, ecology and conservation. However, the main problem was that of time. It appeared that most cooperators could only work on the project in their spare time and the project generally progressed slowly. The authors also were continuously faced with the necessity to include important publications after the receipt of a manuscript from co-authors and editors. The 'Addendum' reveals that this process continued until the deadline for the printing of the book. Therefore, the book reflects the limitations of a 'work in progress'. In several instances it was difficult or even impossible to evaluate the huge amount of *Carabus* literature. An additional problem were the many, sometimes inadequate, often poorly documented short (taxonomic) notes, such as descriptions of 'new names'. Therefore, it should be stressed that the present work is not a new thorough revision of the European taxa of the genus, but rather it is a compendium of knowledge on different topics related to this group of ground beetles.

◀ ***C. morbillosus alternans*** Kraatz. Italy. Sicily. San Vito Lo Capo. Photo by A. Vigna Taglianti.

Chapter 2 – Checklist

Studies in faunistics, biogeography and ecology require a clear taxonomic basis. The taxonomy of the genus *Carabus* is chaotic, with thousands of superfluous names. It reflects a long history of the work of professional and amateur researchers coming from different schools, often with different opinions. However, for the European *Carabus* species there are no major gaps in the basic taxonomic knowledge. Despite different opinions on supra-specific classification, questions about 'species or subspecies' can mostly be answered by the extensive checklists of Deuve (1994), Březina (1999), and the recent 'Nomina Carabidarum' of Lorenz (1998a,b). These important works served as a basis for the present checklist. Also, many recent catalogues and checklists of local faunas (such as that of Vigna Taglianti, 1993) have been evaluated and used. The final result, which is not a true systematic revision, is a compromise between different opinions, with all the limitations, imposed by such an approach.

The checklist is not always in agreement with the above mentioned authors, but rather it is in several aspects original and is based on the examination of a very extensive amount of material. The choice of some names is explained, in particular the conservation of those accepted by long tradition, for instance *C. depressus* instead of *C. bonellii* or *C. lucens*, respecting the principle of stability of zoological nomenclature. In most other cases the basic principles of priority, of primary homonymy, and of original spelling of names have been respected, so that some readers will find well-known taxa treated with unfamiliar, or modified names. Only the modification of some names in the subgenus *Orinocarabus* published recently by Deuve (2002), could not be processed in our checklist. The paper appeared when this book was at an advanced stage of production. Therefore, the changes proposed by Deuve have been summarised in the 'Addendum'. This also holds for the far-reaching 'last-minute' proposals of Imura (2002a,b) and Osawa *et al.* (2002).

Finally, the decision of ranks (specific, subspecific, or synonyms) has been the most difficult question, and the proposals presented will undoubtedly generate criticisms and discussions by colleagues. The authors welcome all criticism, when supported by valid arguments, contributing to clarify the many unsolved questions. As examples, the reader will note that some allopatric or parapatric, very close taxa, such as *variolosus* and *nodulosus*, some representatives of the subgenera *Morphocarabus, Orinocarabus* and *Procerus*, and others, have been here treated as distinct species. Conversely, taxa traditionally treated as distinct species (e.g. *auronitens* and *punctatoauratus*) have been listed here at a subspecific rank. Many of these choices have been dictated by recent contributions of reliable specialists; some others are based mostly on personal opinions of the authors.

The challenge to discover new morphological characters, both for adults and larvae, the use of molecular methods, breeding experiments (and hybridisation) in the laboratory, as well as field work, will be the instruments for a new look at the European *Carabus* fauna. The recent proof of specific separation of *C. concolor* and *C. lepontinus* by sympatry is a good example of such innovation.

Chapter 3 – Key to the adults

Like many lepidopterists, *Carabus* amateurs are not very familiar with identification keys. Many (but not all!) *Carabus* species are easily recognisable by a skilled eye, as they are large and characteristically coloured. Most species are illustrated in excellent iconographic books, both at a local and a global scale. Unfortunately, many *Carabus* collectors forgot that the systematics on which the names and classification of ground beetles depend, are not based on size, colour or attractiveness, but on reliable morphological characters instead. It is regrettable that many amateurs are not able to use identification keys, through not being familiar with the basic terminology used for the anatomy and morphology of insects.

For these reasons we include the present key, which is the first complete key for identification of all European subgenera and species to be published since Breuning's (1932-1937) monograph.

The present key is pragmatic and does not reflect the phylogeny of the genus. In particular, the authors used the primary, traditional dichotomy between 'brevimandibulares' and 'longimandibulares' for the key to the subgenera (as in the classic Breuning's monograph). This character has been demonstrated as not phylogenetically reliable. Also, other easy to recognise morphological features have been used and sometimes illustrated. We hope to have provided a key that can be used by any worker in entomology, and is useful for non-specialist workers utilizing *Carabus* in ecology or other branches of biological sciences. The key is mainly based on features of the male genitalia, the only available diagnostic characters, for some difficult species groups (e.g. *Orinocarabus*, and some *Megodontus* species).

Finally, we recommend that the key be used in combination with the excellent iconographic papers on the European *Carabus* fauna.

Chapter 4 – Key to the larvae

Chapter 4 presents a description of the larval morphology of the genus *Carabus* and a key to second and third larval instars of all European subgenera (except *Heterocarabus* Morawitz, of which the larva of the only species *C. marietti* is still unknown). Keys to the known larvae of the subgenera *Morphocarabus*, *Trachycarabus*, *Eucarabus*, *Tomocarabus*, *Platycarabus*, *Chrysocarabus*, and *Megodontus* have been included, allowing the determination of about 75% of European species. The larval morphology of two species from the European fauna contradicts the present taxonomy. *Carabus ermaki* differs markedly from *Pachycranion* in the larval stage. Therefore, we suggest that the subgenus *Carabulus* Lutshnik should be maintained for this species. *Carabus truncaticollis* should be transferred to *Aulonocarabus* because of its larval (and also genital) characters.

Chapter 5 – Species accounts

The availability of faunistic, ecological and biological data is of importance for any future work. In Table 10.1, we have attempted to summarise the most important both available and missing information in Chapter 5. In this chapter, distribution, habitat preferences and information on reproduction period, development, larvae, food, hibernation etc. have been treated in a systematic way. However, even for this well-known genus, there is a severe lack of basic data, especially from the eastern part of Europe. In Chapter 4. *Key to the larvae*, table 4.1 demonstrates that, partly by allopatric distribution (41 species), the larvae of 98 European species can be identified. Consequently, the larvae of 33 species (25.2%) are indistinguishable, and thus crucial biological information is missing.

Table 10.1 indicates that in some instances even basic information on habitat preference or periodicity is completely absent, especially for species that only occur in parts of Europe where the scientific interest was restricted mainly to taxonomy and biogeography. Part of these gaps can easily be filled by building good databases from collections. In this way the phenology of some species can be traced back, by gathering a sufficient amount of dates from collection labels. From adequately labeled specimens one can also get a basic insight of the ecological preferences of the species. However, the most effective information can be obtained from the results of pitfall trapping, especially in transects as described in Chapter 8 (see below: Biogeography and Synthesis), and additionally by sampling by hand and from rearing.

Table 10.1. Species for which biological and ecological information is scarce or absent.

SG Sp	name	ecol	activ	per	hiber	food adult	larva descr	food larva	cons
02 001	aeruginosus		x	min	x	x	x	x	x
002	besseri	min	x	x	x	x	x	x	x
003	bosphoranus		x	min	x	x	x	x	x
004	comptus	min	x	x	x	x	x	x	x
005	errans	min	x	x	x	x	x	x	x
006	estreicheri		x	min	x	min	x	x	x
007	excellens		x	min	x	x	x	x	x
008	haeres	min	x	min	x	min	x	x	x
009	hampei		x	min	x	x		x	x
010	henningi		x			x		x	x
011	hummeli		x	x	x	x	x	x	x
012	karpinskii	min	x	x	x	x	x	x	x
013	kollari		x	x	x	x	x	x	min
015	odoratus		x			x		x	
016	perrini	min	x	x	x	x		x	min
017	regalis		x	min	x	x	x	x	
018	rothi		x	x	x	x	x	x	x
019	rybinskii		x	x	x	x	x	x	x
020	scabriusculus		x						min
021b	versicolor		x	x	x	x	x	x	x
022	sibiricus		x	x	x	x	x	x	x

SG Sp	name	ecol	activ	per	hiber	food adult	larva descr	food larva	cons
023a	zawadzkii	min	x	x	x	x		x	x
023b	zherichini	x	x	x	x	x	x	x	x
04 003	deyrollei					x	x		
005	obsoletus		x						
006	parreyssii	min							
007	stscheglowi	min	x	min	x	x		x	x
05 004	vagans		x					x	
06 002	monticola		x						
005	pseudomonticola	min	x				x	x	
007	steuartii		x	min	x	x	x	x	x
008	wiedemanni	min	x	x	x				x
08 001	loschnikovii	min	x	x	x	x	x	x	x
002	truncaticollis		x			x			x
09 001	canaliculatus		x	min	x	x		x	
10 001	dufourii				x	min		x	min
002	lusitanicus		x					x	min
003	macrocephalus							x	min
11 001	adamellicola		min	x	x	min	x	x	
004	carinthiacus			min				x	
005	castanopterus	min	x	min	x	x	x	x	
006	cenisius		x						
007a	concolor		x						
007b	lepontinus	min	x	min	x				
008	fairmairei						x		
009	heteromorphus	min	x	min	x	x		x	
010	latreilleanus					x		x	
12 001+007	amplipennis					x		x	
002	ghilianii	min	x	min	x	x	x	x	
004	guadarramus		x	min	x	x	x	x	
005	hortensis								x
006	preslii		x	x	x	min		x	x
13 002	bessarabicus		x						
004	marginalis		x	min	x	x	x	x	min
14 001	faminii		x						
002	genei		x					x	

SG Sp	name	ecol	activ	per	hiber	food adult	larva descr	food larva	cons
15 001	cavernosus		min	min	x				
002	cribellatus		x					x	x
003	graecus		x	min	x		x	min	
004	hungaricus		x					x	
005	trojanus		x	min	x				x
16 001	galicianus			min	x				
19 001	arcadicus	min	x	min	x	x		x	
003	krueperi	min	min	min	x	min			
004	lefebvrei	min	x	min	x			x	
005	merlini	min	min	min	x	x		x	
20 004	fabricii	min	x			x			
21 001	marietti	min	x	min	x	x	x	x	
22 001	varians (janthinus)	min	x	x	x	x	x	x	x
23 001	aurolimbatus	min	min	min	x	x	x	x	
002	caelatus		x					x	
003	croaticus		x	min	x			x	
004	exaratus		x	min	x			x	x
005	germarii		min	min	x	min		x	
006	gyllenhali	min	x	x	x	x	x	x	x
007	planicollis	min	x	x	x	x	x	x	x
009	septemcarinatus	min	x	x	x			x	x
24 001	ermaki	min	x	x	x	x	x	x	x
002	schoenherri		x	min	x			x	x
25 001	auriculatus			min	x		x	x	min
002	pyrenaeus			min	x			x	
28 002	planatus	min	x						min
29 001	torosus	min	x	x	x			mim	x
30 001	banoni	min		min	x				
31 001	duponchelii	min		min	x				
003	scabrosus	min	x	x	x				x
004	sommeri			x	x	min		min	x

Columns: SG = subgenus number, **Sp** = species number, **name** = species name, **ecol** = ecology, **activ** = day/night activity, **per** = periodicity, **hiber** = stage of hibernation, **food adult** = diet of adult animals, **larva descr** = description of larva, **food larva** = diet of larva, **cons** = conservation biology.

Contents of the cells: min = only minimal information available, **x** = (almost) no information available (compare information in Chapter 5. *Species accounts*), or larva unknown. A **blank cell** means that the information is sufficient or that the larva has been described.

Chapter 6 – Biology and ecology

In this chapter, the author was faced with a major problem of selecting and choosing from the enormous amount of literature available. The ecology and biology of carabids are described in thousands of published papers. Mostly papers dealing with *Carabus* were used, but frequently publications on non-*Carabus* taxa were helpful in providing supplementary information.

After treating the reproductive system and reproduction, some information on breeding is provided. A brief review of daily and annual rhythms is followed by the treatment of locomotory activity, the kind of movement to which most *Carabus*-species are restricted because they are unwinged. Most species are excellent runners and several species climb shrubs and trees. The influence of ecological parameters has been divided in abiotic and biotic factors. As for many carabids, moisture, temperature and soil type are very important abiotic factors, which are more or less under influence of vegetation cover. For surface dwellers like carabids, the most important structural and spatial parameters are vegetation and its derivatives (litter, bark, rotten trunks etc.). Vegetation strongly influences the degree of temporal ecological stability. Examples of stable biotopes are bogs, forests and heathland. More dynamic environmental factors can be found in wastelands, arable fields and shores. This is an important factor with respect to the founding and survival of populations. In a forest the microclimate is much more stable than in the open field. In general, *Carabus*-species and especially the larvae favour stable environmental conditions. Another biotic factor of major importance is the availability of food. Several species are specialised predators, for instance of certain snail species, but many have a wide diet, which also includes plants. The chapter concludes with the treatment of various aspects of population biology and (long-term) dispersal power in *Carabus*. Some remarks are made on the glaciation and the postglacial history, which is one of the most important events in the history of the European fauna.

A general note is made on the widespread use of pitfall traps. It is well-known that pitfalls can be very useful in biological, ecological and population studies. However, the present compilation illustrates that these are not the only parameters for investigating ground-beetles. The usefulness of pitfalls is sometimes over-estimated, because they measure densities for different species in different ways. Under different circumstances the catches may lead to deviant estimations of densities within a species. Moreover, some species can hardly, or not at all, be sampled by pitfalls. In many cases e.g. observations in the field, analysing labelled specimens, sampling by hand and breeding experiments will be indispensable to obtain the desired information.

Chapter 7 – Phylogeny

An analysis of 37 characters of larval morphology and male genitalia, as well as an analysis of molecular data of the mitochondrial NADH dehydrogenase subunit 5 gene, reveals that the present classifications of the genus *Carabus* do not reflect the phylogenetic relationships adequately, in spite of the recent increase in knowledge (coming from the examination of new morphological features, both for the adults and the larvae, and the discovery of new, highly informative taxa, particularly in Eastern Asia). It is questionable whether the three larval groups (see Bengtsson, 1927; Lapouge, 1929-32), the five supra-specific taxa based on characters of the endophallus (Ishikawa, 1978; Deuve, 1994), and the eight or nine taxa based on molecular data (Imura, 1996; Imura *et al.*, 1998) represent monophyletic taxa. The phylogenetic analysis implies a much more differentiated relationship between species and subgroups. Generally, the following conclusions could be made: the genus *Carabus* (*s.l.*) is monophyletic with *Calosoma* (in the widest sense) as its sistergroup. The first split-offs at the basis of *Carabus* are the subgenera *Tachypus* (in part), and *Limnocarabus*. Metacarabi (excl. *Hygrocarabus*) and Neocarabi *sensu* Bengtsson (1927) are possibly monophyletic. The Neocarabi probably evolved most recently and represent the largest monophylum in the genus.

Chapter 8 – Biogeography

This chapter is one of the most complicated in the book. The authors were faced with the ambitious task to write down what was supposed to reflect the main approaches and methods used in biogeography during the last century. The chapter is divided in two parts, following De Lattin's main stages of biogeographical research, the *descriptive* and *causal*. The first, descriptive, part aims to describe both the global and European distribution of *Carabus* in detail, to define the range limits of the genus and to reveal the main patterns of geographical variation. Special attention was paid to the classification of species ranges into chorotypes and range characteristics, two independent systems of chorological classification. The chorological structure of the European *Carabus* fauna, together with other features (e.g. taxonomic structure, specificity, endemism, characteristic species absences etc.) were used in an attempt to construct a zoogeographical division of Europe.

The second, *causal*, part of the chapter aims at hypothesizing and explaining the origin and formation of the present-day European *Carabus* fauna in the light of the historical development of the European continent. The possible origins and routes of colonisation are discussed on the basis of present-day distribution patterns of *Carabus,* paleontological evidence and related phenomena obtained from the fields of palaeo-geography, palaeo-climatology, glaciology, palae-ecology and others. Of special interest is the section describing historical connections between the *Carabus* faunas of Eurasia and North America, offering the hypothesis that North America must have been colonised by two Eurasian lineages of *Carabus*, different in origin and age. As a result, a scenario of the origin for the European *Carabus* fauna is proposed.

Besides the abovementioned two 'traditional' approaches to the biogeography, we applied a new method, named 'locality-based biogeography', developed from the concept of 'local faunas'. The local fauna is understood here as an assemblage of species occurring in all habitats around a geographical location. The rationale of the concept lies in the understanding that the species composition at a geographical location is the result of a local selection of species from the regional species pool. Therefore, the local species composition reflects the history of the region, the local habitat conditions and possible biotic interactions. To illustrate the possibilities of the method we constructed a dataset of 100 local faunas of *Carabus* spread throughout the European continent and analysed them with multivariate methods. They are presented graphically as habitat (ecological) transects, giving simple and clear pictures of the local distributions of *Carabus* in different regions of Europe. The results convinced us that the 'local faunas' can be regarded as an anastomosis between biogeography and ecology and allow an unprejudiced approach in analysing the spatial distribution of a group of taxa.

In general, it can be concluded that the genus *Carabus* is one of the best models for biogeographical research. The recently accumulated molecular data (see Chapter 6) on postglacial history and colonisation of *Carabus* shed new light on the 'old' biogeographical phenomena studied during the last 150 years. We hope that such analyses will be carried out soon in Eastern Europe as well, especially in the huge territory of the Russian Plain, Carpathians and the Balkan Peninsula. The perspectives in the biogeography of *Carabus* are undoubtedly connected with the necessity to map the species distributions at the European scale more precisely, using the modern method of GIS-mapping, a procedure started already for many other groups of plants and animals.

Chapter 9 – Conservation

Carabus is an excellent group for environmental studies and monitoring of changes in the faunal composition. The genus *Carabus* is rather well-represented in most parts of Europe, much is already known about the biology and ecology, for insects they are quite large and attractive, and they can be studied easily with standardised methods. This makes them ideal objects for amateurs and professional entomologists as well as collectors. Also, the fact that many species have various well-defined subspecies increases the value of the group. On a larger scale, the species richness generally matches the diversity in habitat types. In many cases, there is a good relationship between the richness of *Carabus*-species and the richness of the entire surface-dwelling fauna, such as the number of snails and slugs, myriapods, isopods, earth worms, insect larvae etc. Furthermore, most species are unwinged and thus sensitive to isolation and habitat fragmentation.

Our knowledge about *Carabus* faunistics in different parts of Europe is generally good. We can summarise the present state of our knowledge on *Carabus* as follows: 1) very good in N. and NW. Europe (many atlases and critical checklists), 2) good in Central Europe and the Alps, 3) rather good in Mediterranean Europe: Iberia, Italy, Balkans and, 4) good to insufficient in CE. and NE. Europe: Carpathians, Russian Plain and Urals. Especially in NW. and in Central Europe a number of Red Lists have been published, listing vulnerable and endangered species. From these and other studies, we may conclude that species that live in oligotrophic biotopes, in ancient forests and in places with very special and balanced hydrological conditions, are especially endangered. In general, more eurytopic species, inhabiting ruderal or disturbed places, are less endangered. The same holds also for montane species, with the exception of large-scale habitat destruction in regions with intensive (winter) tourism. We conclude that Red Lists are useless if they do not result in stopping the endangering and destruction of habitats. Moreover, it is difficult to determine time trends in the occurrence of rare species and draw significant conclusions from the often scarce faunistic information. In many cases the assumptions for correcting sampling intensities in the past, are not adequate and are highly disputable.

A good alternative can be the building of a European database of 'local faunas' from as many localities as possible. Such a database (see Chapter 8) could constantly be updated by a network of *Carabus*-students, both amateurs and professionals. The investigations could be carried out, using a combination of pitfall trapping and sampling by hand (not all species can easily be caught by pitfalls, see above). We believe that, if well-organised, it will be possible to create a reference set of local faunas in a relatively short time. This might become a fantastic instrument for the evaluation of the state of the invertebrate surface-dwelling faunal throughout Europe, of which these predators are the indicators. Moreover, such a database may be suitable for increasing our knowledge on the 'evolution' of faunal communities, dynamics in distribution patterns, as well as on climatic changes. Of course, there will be more groups of surface-dwelling arthropods that are as suitable for such purposes. However, which groups will have the same advantages of being as well-investigated, having a suitable number of species (and subspecies) covering most terrestrial and some (semi) aquatic biotopes, and being relatively easy to identify? The only condition is that professional entomologists, who have the ability to start and maintain the organisation of such a database, will be able to work together with a (large) number of amateurs.

CONCLUSIONS

1. Molecular work will undoubtedly have a major impact on clarifying questions on phylogeny, systematics and biogeography in future.

2. The genus *Carabus* illustrates that, considering the results of our work, it is worthwhile to compile all available knowledge from various disciplines for certain groups of invertebrates, no matter how heterogeneous the approaches and the opinions of the different contributors are. From a study as presented here, one may expect that stimuli for new ideas will be generated, and that improvements of our existing knowledge will be realised.

3. The genus *Carabus,* despite the gaps in information, has proven to be a suitable and useful model group for studying biogeography, faunistics and conservation biology.

4. The results from ecological transects, strongly corroborate the approach of building a comprehensive database of local faunas of *Carabus*, based on a mixture of pitfall-trapping and sampling by hand, as useful and strong instrument for further biogeographical and environmental research.

Glossary

In the list below, we mainly restricted to terms and issues that are sometimes confusing and might be interpreted in different ways (e.g. *habitat* and *biotope*; *broad-leafed* and *deciduous* forests). Also the terminology for describing the elytral structure, although widely used in the taxonomy of *Carabus*, might be confusing to some biologists, especially specialists in genetics, for example the terms *diploid*, *tetraploid* etc. Other concepts, more or less common to biologists, educated in Eastern Europe, may be quite new for readers from western countries, such as *concrete-* or *local flora/fauna*. A smaller group are terms only used in carabidology, such as *abacisation, cychrisation* and *procerisation*. The other terms have been explained in order to make it easier, for a broader public, to read some specialised chapters, especially the Chapters **6** (*Biology & Ecology*), **7** (*Phylogeny*) and **8** (*Biogeography*).

In agreement with the rules used in the list of references, **[2,3,5...etc.]** means that the term especially has been used in the respective chapters and **[t]** refers to the ecological transects in Chapter 8.

Abacisation – morphology resembling species of the carabid genus *Abax* Bonelli, 1810. These species have often flat and broad forebodies in order to be able to enter corpses and carrion. **[3,5,6,7]**

Abiotic factors – factors created by non-living elements in the environment (soil, water, temperature etc.). **[5,6]**

Activity density – density of species in the field as measured by pitfall traps, often the number of individuals caught during the period that the animals are surface active. This measure is not necessarily a realistic estimate of the real population densities, but is primarily usefull for intraspecific comparison and determining (frequencies of) species occurrences. **[1,6,8,t]**

Adelphotaxon – closely related (sister) taxon. **[3,5,8]**

Aestivation – see *diapause*. **[5,6]**

Allopatric – not living in the same area; no overlap of ranges. **[3,4,5,6,8]**

Alpine (belt) – belt with open alpine vegetation (above timber line), generally at altitudes from 1500-1750 m and higher. **[5,8]**

Alpine (distribution) – distribution restricted to the chain of the Alps in Central Europe. **[5]**

Alpine steppe or **alpine meadows** – high altitude, grasslands above the timber line. **[3,5,6,8,9,t]**

Alps (mountain chain) – mostly used for the Central-European mountains. Sometimes also for very high (alpine) mountains outside this particular chain. **[5,6,8,9]**

Arctic – a region around the Northern Pole, often used as a synonym of polar environments (see *tundra*). **[5,8]**

Atlantic – regions under influence of the atlantic climate (soft winters and relatively cool summers), most typical for Western European coasts.

Biome – the largest recognised units in the ecological biogeography of the Globe, defined by macroclimate. See: *tundra, taiga, forest zone, steppe and desert.*

Biotic factors – factors created by living elements in the environment (vegetation, prey, predators etc.). **[5,6]**

Biotope – a more or less easy to recognise unit in a landscape, such as a forest, moor, heathland, grassland (pasture, meadow), agricultural field, road verge, shore, swamp etc. (compare *habitat*). **[5,6,8,t]**

Bootstrap analysis – a statistical method based on a repeated random sampling with replacement from the original sample to provide a collection of new pseudoreplicate samples, from which sampling variance can be estimated. **[7]**

Boreal – biogeographical term describing a biome type, floras or faunas occurring in the northern regions of the Northern hemisphere, dominated by coniferous forests (see *taiga*). **[5,6,8]**

Boreo-alpine (distribution) – distributed in N. regions with one or more occurrences in the higher altitudes of S. mountains. The 'alpine' populations (which are mainly glacial relicts) are geographically and genetically separated from the N. populations. **[5,8]**

Boreo-montane (distribution) – distributed in N. lowlands and towards the S., in the middle and upper montane belts, sometimes without a clear disjuction between the N. lowland and the S. upland populations. **[5,8]**

Brachypterous – unwinged. **[3,5,6,9]**

Broad-leafed (forest) – see *deciduous* forests. **[5,8]**

Chaetotaxy – position of the fixed sensorial setae on the body of either adult or larva. **[3,4]**

CANOCO – a software for providing ordination analyses of ecological data, see *ordination*. **[8]**

Character – a morphological or molecular structure. **[7]**

Character state – Condition of a certain character, e.g. derived, ancestral. **[7]**

Chorotypes – types of species ranges, resulting into a classification of species' distributions, here according to the system that has been proposed for the Western Palearctic Region by Vigna Taglianti *et. al.* (1999) (see p. 152 and p. 370). **[5,8]**

Circumpolar – distributed in all the north of the Holarctic region, both N. Eurasia and N. America. **[5,8]**

Cladogramm – a tree indicating phylogenetic relationships. **[7]**

Classification – systematic order, not in each case based on phylogenetic relationships. **[7]**

Clustering – statistical (multivariate) method(s) used to divide a dataset into more or less logical units. The samples of species can be classified into groups of similarity, called *clusters*, by either a *divisive clustering procedure* (for instance TWINSPAN; see Chapter 8 and Hill, 1979a), or an *agglomerative clustering procedure* (for instance UPGMA, see Chapter 8 and Baev & Penev, 1995).

Concrete flora/fauna – see *local flora/fauna.* **[8]**

Coniferous forest – forest dominated by coniferous tree species (e.g. *Pinus*, *Abies*).

Continental – area with a land climate, less influenced by sea or ocean. Continentality often means cold winters and hot summers. **[5,8]**

Convergence – parallel evolution: results in corresponding character states which evolved independently in (at least two) different lines. **[7]**

Corpora lutea – dark rings that remain visible in the ovary after the first reproductive season of a female. **[5,6]**

Cychrisation – morphology resembling species of the carabid genus *Cychrus* Fabricius, characterized by very narrow head and mandibles, able to prey on small sized snails. **[5,6]**

Decay index – number of additional steps required to collapse a particular branch in the strict consensus tree. **[7]**

Deciduous forest – forest composed of deciduous (broadleafed) trees, such as *Quercus*, *Tilia*, *Carpinus*, *Fagus* etc.

DECORANA – a software for providing ordination analyses of ecological data, see *ordination.* **[8]**

Desert – landscape with sparse vegetation usually existing in areas of subtropical hot and very dry climate, characterised by large 'sterile' areas of sand or rocks. **[5]**

Diapause – an obligatory or facultative dormancy during the development of larva or adult, during which the physiological processes in the organism slow down to a minimum. A diapause can take place during a very cold period (winter: hibernation) or a very hot and/or dry period (summer: aestivation). **[5,6]**

Diploid – see *elytral sculpture.* **[3]**

Disjunct (distribution) – mostly concerning remnants of a formerly coherent distribution area, but now separated in two or more sub-areas of distribution, for instance in case of *boreo-alpine* species. **[5,8]**

Dispersal power – ability of getting from one place to another and to cross eventual barriers. In general, species capable of flight (having well-developped wings and functional flight muscles) have a better power of dispersal. Species of the genus *Carabus* are mostly unwinged (for some exceptions see Chapters 5, 6 and 9) and are thus restricted to walking. Because of their moderately large sizes, most *Carabus* species have on average good dispersal abilities on not too long distances. **[5,6,8,9]**

Dynamic (habitat, biotope) – places with a lot of short-term variation with respect to environmental variables, e.g. shores, agricultural fields or ruderal places (compare *stable*). **[5,9]**

Dystrophic – Humin acid water with low both nutrient contents and primary production. **[5,6,9]**

Ecological transect – a concept used in this book to present the species' distributions across habitats at certain geographical location. **[1,5,8,t]**

Elytral intervalls – see *elytral sculpture.* **[3]**

Elytral sculpture – The classification of elytral sculpture of the genus *Carabus* uses some terms that are also frequently used in genetics. The basic structure is an elytron with 3 primary ribs (e.g. *C. granulatus*) which can be reduced to *grains* or even can be completely vanished (e.g. *C. glabratus*, *C. violaceus violaceus*). In between them, secondary intervals occur sometimes among striae, or chains of *grains*: this sculpture is indicated by the term *diploid.* Between the primary and secondary, tertiairy or more intervals may exist, and the sculptures are subsequently indicated as *triploid*, *tetraploid, pentaploid, heptaploid.* See also Chapter 3. **[3,5]**

Endemic (endemism) – species or taxon restricted to a certain geographical unit: region, part of a region, island, mountain chain or even a single mountain. **[3,5,6,8,9]**

Extensive – agricultural use of land by man in a more natural way with low amounts of fertilisers or low densities of caddle, common before the fifties/sixties of last century. Nowadays in W. Europe extensive agriculture is also applied as a kind of nature management. **[5,6,8,9,t]**

Eurytopic – wide ecological amplitude; occurring in many types of biotopes.

Eutrophic – biotopes rich in nutrition. **[5,6,9]**

Fennoscandia – Norway, Sweden, Finland and a small area of adjacent Russia (Karelia); Denmark is usually not included (see Lindroth, 1945, 1949, 1985). **[5,8]**

Foot hills – hilly landscapes at the foot of larger mountain chains. **[5]**

Forb-grass steppe – biotope type, type of steppe, characterised by grassland, rich in species and abundance **[8,t]**

Forest-steppe zone – transitional zone (some authors call it subzone), situated between the forest and steppe zones. Geographically extends from Southeastern Europe (Hungary, NE Bulgaria), through the middle regions of European Russia to Central Siberia. **[5,8]**

Forest zone – including several biomes dominated by forests as climax-type vegetation. Extends from the *tundra* in the north to the *steppes* in the south and can be divided into three major subzones, namely those of *coniferous*, *mixed* and *deciduous* forests. **[5,8]**

Gene flow – the spread of particular alleles within a population, or between populations, resulting from outbreeding and subsequent intercrossing. **[5,6]**

Gene tree – relationship of genes which may but must not reflect the relationship of the species. **[7]**

Gradient – spatial unit (compare *transect*) of different size or extensison along which one or more environmental variables gradually change their values. **[1,5,6,8,t]**

Grasslands – major group of biotopes. Grasslands may vary from poor grasslands on sandy soils (dune grasslands, poor heath-grasslands, (alpine) steppes) to natural grasslands on heavy soils with luxurious vegetation, as well as intesively fertilised pastures and meadows. In some classifications, also heathlands have been classified under grasslands **[5,8,t]**

Habitat – indication for the environment, necessary for a population of a certain species to settle, reproduce and survive. In English, this term has also been used for groups of plants that produce similar habitats, e.g. deciduous forests, or *Calluna* heathlands. In the present work, we tried to restrict to the first definition and used the term biotope for the second. Thus a habitat of an eurytopic species may comprise more than one biotope. **[5,6,8]**

Heathlands – group of moist to dry biotopes, mostly in temperate or montane regions, mainly built of dwarf-scrub vegetations with *Calluna*, *Empetrum* or *Erica*. **[5,8,t]**

Heliophilic – species adapted to direct sunshine. **[5]**

Heptaploid – see *elytral sculpture*. **[3]**

Hills – landscape element with altitudes between 200 and 500 m. **[5,8,t]**

Holarctic (distribution, region) – a biogeographical term, uniting *Palaearctic* and *Nearctic*. Extended over the polar, temperate, and subtropic areas of the Northern Hemisphere both in Eurasia and N. America. **[5,6,8]**

Homodynamous – sculpture of elytron characterized by intervals all of the same relevance. **[3]**

Homoplasy – identical character state in two or more taxa because of parallel evolution or reversal development. **[7]**

Hygrophilic – with a preference for moist to wet places. **[5,6]**

Intensive – agricultural use of land by man by using high amounts of fertilisers or high densities of caddle, common in western Europe after the Second World War.

Left bank – the left-hand bank when looking in the direction of the river flow. **[5,8]**

Licinisation – morphology resembling species of the carabid genus *Licinus*, characterised by a broad head and strong mandibles for cutting resistant preys, for instance for cutting snail shells. **[3,5]**

Local flora/fauna – a list of species of plants or animals, respectivelly, occurring around a geographical location (see also p. 3, 345 and 445). **[1,8,10]**

Lowlands – country of low altitude, normally not over 200 m, mostly flat. **[5,8,t]**

Maghrebian (area, distribution) – comprises Marocco, Algeria and Tunisia (Maghreb). Maghrebian species can also occur in S. Spain and/or S. Italy (Sicily) (see *Siculo-Maghrebian*). **[8]**

Mediterranean (region, distribution, climate) – existing around the Mediterranean Sea in close sense or in the Mediterranean-like climatic regions in wider sense (besides Mediterranean Sea, also California, Central Chile, Cape Region in South Africa and southeastern part of Australia), characterised by mainly one peak of rain in winter and dry (not always hot) summer. Climates with one peak of rain in the autumn and one in sping are often called Sub-Mediterranean. **[5,6,8,9]**

Mesophilic – species, often with a wide range of tolerance to moisture conditions, but mostly not occurring in very wet or very dry places. **[5,6,t]**

Mixed-forest zone – biome type, indicating the zone (some authors call it subzone) existing between the coniferous and deciduous forests. This zone comprises most of Central Europe and the middle regions of European Russia and has the highest diversity of *Carabus* species. **[5,8]**

Monophyletic (in Hennig's sense) – a group of related taxa including an ancestor and all of its descendants. **[7]**

Monotypic – taxon (subgenus, genus), represented by only one species. **[2,3,4,5,6,7,8]**

Montane (belt) – middle altitudes of a mountain, approximately between 500 and 1500/1750 m. **[5,8,t]**

Morphometric – based on external, morphological metric characters and proportions. **[3,4,7]**

MyBP (mybp) – million years before present. **[8]**

Nasale – anterior central part of larval head. **[4]**

Nearctic (distribution, region) – a biogeographical unit, consisting of the N. American continent including the N. part of Mexico and Greenland. **[8]**

Oligotrophic – biotopes poor in nutrition. **[5,6,9]**

Ombrotrophic – the only influx of material comes from rain. **[5]**

Ordered – Used in computer programs to calculate phylogenetic trees. Character states change in following way: 0=>1=>2=>3 etc. (compare *Unordered*). **[7]**

Ordination – statistical (multivariate) method of grouping data (sites or species) in a multi-dimensional (hypothetical) environmental space or along an environmental gradient. The method searches, for instance, for species that react in a similar way to (depending of the method) real or hypothetical environmental gradients and the results are graphically visualised on axes in two or more dimensions. Well-known software packages are DECORANA (Hill, 1979b; a method which does not incorporate environmental data directly), and CANOCO (Ter Braak *et al.*, 1988; a group of methods which can relate measured environmental data for each species or site directly to the ordination results). **[8]**

Oriental (distribution, region) – biogeographical unit, including SE Asia and S. of the Himalayas. **[5,8]**

Outgroup – one or more taxa assumed to be phylogenetically outside the regarded taxon. **[7]**

Outgroup comparison – a method for determining the root of a topology, thus, assigning the direction of character state changes and establishing the relationships. **[7]**

Palaearctic (distribution, region) – biogeographical unit, including Europe, the northern, temperate and subtropic areas of Asia, and N. Africa. **[5,6,8]**

Pannonian – the lowlands of Hungaria, Romania and N. Serbia, mostly along the Danube basin, surrounded to the E. by the Carpathians. **[5,6,8]**

Parsimony method – Method to calculate phylogenetic trees. The strategy is to search a tree which requires the smallest number of character state changes under the assumption of parsimony (so called 'most parsimonious tree', MPT). **[7]**

Pentaploid – see *elytral sculpture*. **[3]**

Periodicity – description of the developmental time path of a species, from egg to larva, pupa and adult until the start of the reproduction period of the next generation. **[5,6]**

Pioneer – (biotope, species) – a term used to characterise the first stages of an ecological succession. **[5]**

Plesiomorphy – an ancestral character state. **[7]**

Pontic – In the narrow sense, type of distribution of species, occurring in the regions around the Black Sea. In wider sense referring to an area of SE Europe, the Western Caucasus and Northern Anatolia with a fauna and flora characterised by presence of pontic elements. **[5,8]**

Prealps – In the narrow sense, the series of hills and mountains that fringes the southern side of the Alps, N of the Padanian plain. **[3,5,8]**

Primary row – (see *elytral sculpture*). **[3]**

Procerisation – morphology resembling species of the *Carabus* subgenus *Procerus*, implying a very large size and narrow mandibles, to prey snails of large size. **[3,5,6,7]**

Range characteristics – a system for classification of species ranges, used here to define precisely the distribution of each species among geographical regions. **[5,8]**

Ravine forest – biotope type, occurring in ravines within the steppe zone. **[5,8.t]**

Red Lists – officially declared, national or regional lists of endangered species. **[5,9]**

Refugium – an area, unaffected or only slightly affected by historic environmental events, such as glaciations, where certain taxa succeeded to survive, for example areas not covered by ice during the Pleistocene. **[5,6,8]**

Relict – taxon that survived a historic environmental event (i.e. glaciation) in a certain part (refugium) of its former distribution area. **[5,6,8,9]**

Reversal – the change of a character to a former state (e.g. 0=>1=>0 or G=>A=>G). **[7]**

Right bank (river) – the right-hand bank of a river, when looking in the direction of the river flow. **[5,8]**

Ripicolous – living along the waterline, on shores and river banks.

Ruderal (habitat, biotope) – places highly disturbed by man activities, often used such as ground deposits, rubbish-dumps, sites prepared for building activities and so on. **[5,9]**

Salt marhes – dynamic biotope type, muddy flats (partly) vegetated with halophytes, under direct influence of the sea. This biotope occurs along the atlantic coasts; frequently occurring along the norhern German and the Dutch coasts (Frysian islands, Zeeland). **[5]**

Secondary row – see *elytral sculpture*. **[3]**

Siculo-Maghrebian – distributed in Maghreb (see *Maghreb*) and Sicily. **[5,8]**

Small-leafed (forest) – forest composed mainly of birch (*Betula* spp.) and poplar (*Populus* spp.). **[5]**

Stable (biotope) – sites where environmental variables show little or a very constant (taerly) cyclic variation, such as forests, moors, swamps and heathland, in contrast to dynamic places. **[5,9]**

Stenotopic – small ecological amplitude; species or race restricted to one or very few types of biotopes. **[5,6,8,9]**

Strict consensus tree – abstracted phylogenetic tree which (a) combines the information of all MPTs and (b) only present nodes which appear identically in the combined trees, see also *Parsimony method*, *MPT*. **[7]**

Sub-alpine – Sub-alpine is in our understanding the altitudinal zone between montane forest belt and alpine steppes or meadows. **[3,5,6,8,9,t]**

Sub-arctic – close to, or near to the Arctic. **[3,5,6,8]**

Sub-endemic – species distributed mainly in one region, however slightly extending in one or more adjacent region(s). **[8]**

Sub-Mediterranean – a type of distribution of Mediterranean species which extend their ranges in regions surrounding the Mediterranean area *s. str.* Also used to indicate regions adjascent to the Mediterranean basin *s.str.*, Mediterranean-like climates or biotopes **[3,5,6,8,9,t]**

Sympatric – species living in the same geographical area. **[3,4,5,6,8]**

Synanthropic – species occurring only or mostly in biotopes created by human activities, in first line villages and towns (but not agricultural fields!). **[5,8,9,t]**

Synapomorphy – derived character state shared by two or more taxa. It is used to define monophyletic groups. **[7]**

Syntopic – species living together, in the same area and in the same biotope. **[7]**

Taiga – biome, the zone between the tundra and the mixed-forest zone. This biome is characterised by cool climate with vast areas of coniferous forests. **[5,8,t]**

Taxon – natural entity used in the systematics (e.g. species, genus, family). **[7]**

Taxonomy – systematics, the science of classification of the plants and animals. **[2,3,4,5,6,7,8,10]**

Tetraploid – see *elytral sculpture.* **[3]**

Thermophilic – preferening (relatively) warm places.

Transect – see *ecological transect.* **[1,5,8,t]**

Triploid – see *elytral sculpture.* **[3]**

Tundra – biome, treeless zone, existing in the northernmost regions of Eurasia and N. America, characterised by permanently frozen subsoil (permaforst), covered by hygrophilous vegetations, mostly mosses, lichens, herbs and dwarf shrubs. **[5,8,t]**

Ubiquist – species, often eurytopic, well adapted to human activities, often to be found in a broad range of biotopes. **[5,6.9]**

Unordered – Used in computer programs to calculate phylogenetic trees. Any character state can change directly to any other state (compare *Ordered*). **[7]**

Urogomphi – appendices on the 9th abdominal segment of the larva. **[4]**

Vicariance – geographically separated occurrence of (closely related) species that occupy contiguous areas or similar habitats and niches (for example reindeer and caribou), often separated by environmental barriers. **[8]**

Xerophilic – species with a preference to dry environmental conditions. **[5,6,9]**

Xerothermic – species with a preference for warm and dry places, for instance found on south-facing slopes, or limestome soils in more northern areas. **[5,6,8,t]**

Zeitgeber – environmental factor that synchronises the endogenous rhythm. **[6]**

Zone – Climatical and vegetational regions of the earth, changing each other mainly in North-Southern direction. From the N. to the S., the main zones in Eurasia are *tundra*, *forest* (*taiga*, *mixed*, *deciduous*), *steppe* and subtropical *desert.* **[5,6,8]**

Addendum

We present below a list of works that are significant to studies on *Carabus* and/or carabidology in general, but which were not – or only partly – taken into account in this book. The main reason for this is, that we had access to these works only when the preparation for printing was at an advanced stage. In some cases, brief notes or summaries have been added. Several contributions of less significance have been omitted. The works have been arranged by year of publication and then in alphabetical order, by author.

1997

Valemberg, J. 1997a Catalogue descriptif, biologique et synonymique de la faune Paléarctique des Coléoptères Carabidae Latreille 1806. De la nomenclature taxonomique mondiale, spécifique et subspécifique des Carabinae Horn 1881 et d'une cartographie commentée des formes Françaises. Tome 1 Corpus. – Mem. Soc. ent. du Nord de la France: 1-659.

Valemberg, J. 1997b Catalogue descriptif, biologique et synonymique de la faune Paléarctique des Coléoptères Carabidae Latreille 1806. De la nomenclature taxonomique mondiale, spécifique et subspécifique des Carabinae Horn 1881 et d'une cartographie descriptive des formes Françaises. Tome 2 Cartographie. – Mem. Soc. ent. du Nord de la France: 660-1119.

Note: Part 1 has a general section with the themes: I. Taxonomie, II. Mélanisme-Nigrisme, III. Chromatisme-Chromatogénèse and IV. Eléments de génétique. The very extensive systematic section deals with proposals for world classification, a table for the supra-specific taxa in the Palaearctic region and a worldwide taxonomic nomenclature of the Carabinae. The voluminous 'Corpus' contains a taxonomic catalogue with 12.299 taxa. There are several indices, among which is a list with 1554 bibliographical references. Part 2 deals in detail with the faunistics of the French Carabinae. It contains over 150 large-size and very detailed maps and notes on habitat preference. Both works have not been taken into account, because, although published several years ago, they seem to be very rare even in large libraries and came to our attention at a too late stage.

1999

Mollard A. 1999 Monographie de *C. (Chrysocarabus) rutilans* Dejean, 1826. – Rutilans, suppl. 1: 1-22.

Note: Morphology and distribution of *C. (Chrysocarabus) rutilans*, with citations of new localities, and descriptions of the following taxa referred to the species, the validity of which has to be verified: *basetaensis* Mollard, 1999, *capdellensis* Mollard, 1999, *benensis* Mollard, 1999, *perversensis* Mollard, 1999, *juberriensis* Mollard, 1999, *turbonensis* Mollard, 1999, *cotiellensis* Mollard, 1999, *alinsis* Mollard, 1999, *merangensis* Mollard, 1999, *casteilensis* Mollard, 1999, *urgelensis* Mollard, 1999, *frontanyaensis* Mollard, 1999, *soredensis* Mollard, 1999, *alberensis* Mollard, 1999, *quillansis* Mollard, 1999, *romaricus* Mollard, 1999.

2000

Bosquet, J.C., A. Mollard & P. Meyer 2000 Monographie du sous-genre *Iniopachys* Solier, 1848. – Rutilans, suppl. 1: 1-20.

2001

Caubet, F. 2001 Monographie de *Carabus (Chrysocarabus) punctatoauratus* Germar, 1824. – Rutilans, suppl. 2: 1-47.

Düring, A., A. Brückner & D. Mossakowski 2001 Differenzen zwischen gene tree und organismal tree? Mitochondriale Gene und die Verwandtschaftsbeziehungen der *Chrysocarabus*-Arten. – Ent. Basil. 23: 93-98.

Note: *C. olympiae* forms an independent branch from the other *Chrysocarabus* species. This supports a close relationship between *C. olympiae* and *C. solieri* with respect to the remaining species of *Chrysocarabus*. In Imura's opinion (2002, see below), this should support a re-evaluation of the subgenus *Sellaecarabus* Sturani.

Mossakowski, D. & S. Braun 2001 Glacial refuges in *Carabus splendens*: reconstructed using population differences in enzyme variability. – Mitt. Dtsch. Ges. allg. angew. Ent. 13: 105-110

Note: Enzyme data supports the hypothesis that there existed two refuges: one in the Pyrenees near the Mediterranean Sea and another one near the Biskaya.

Pearson, D.L. & A.P. Vogler 2001 Tiger Beetles. The evolution, Ecology and Diversity of the Cicindelids. – Cornell University Press, Ithaca & London: 1-333.

Note: A thorough study of tiger beetles on world scale. In some respects comparable to the present work. It treats many aspects of diversity, from taxonomic as well as from an ecological point of view. Classification, speciation, biogeography, biology, ecology and conservation have been treated extensively. It has interesting appendices on observation and collecting, and on the natural history of the major genera in this subfamily worldwide. It is interesting that there are some (flightless) *Carabus*-like forms of tiger beetles in the genera *Picnochile* Mostchulsky and *Omus* Eschscholtz.

Rasplus J.Y. 2001 De l'origine et de la diversité génétique de *Carabus (Chrysocarabus) punctatoauratus* Germar, 1824. – Rutilans, suppl. 2: 48-56.

Schütze, H. & F. Kleinfeld 2001 Die Caraben Kaukasiens mit einem besonders ausfürlichen Fundortverzeichniss. – Eigenverlag: 1-178.

Note: Of interest to the distribution of *Carabus* species in an important adjacent region.

2002

Bousquet, Y. 2002 Additions and corrections to the world catalogue of genus-group names of Geadephaga (Coleoptera) published by Lorenz (1998) – Folia Heyrovskyana, suppl. 9: 1-78.

Brouat, C., G. Mondor, P. Audiot, F. Sennedot, L. Lesobre, & J. Y. Rasplus 2002 Isolation and characterization of microsatellite loci in the ground beetle *Carabus nemoralis* (Coleoptera, Carabidae). – Molecular Ecology Notes 2: 119-120.

Deuve, T. 2002 Sur l'identité de *Carabus (Oreocarabus) fairmairei* Thomson, 1875, et de *C. (O.) putzeysianus* Géhin, 1876, et note sur la variation géographique de *C. (O.) pedemontanus* Ganglbauer, 1892, bona species (Coleoptera, Carabidae). – Rev. fr. Entomol. (N.S.) 24 (1): 1-17.

Note: This paper introduces important changes in the nomenclature of some taxa in *Orinocarabus* (treated as *Oreocarabus*, as in the worldlist of Deuve, 1994), based on a careful study of type specimens.

Summary (by A. Casale):

The taxonomic status of two taxa described by C. G. Thomson has been revised after examination of their respective type-specimens, which are preserved in the Museum of Lund (Sweden). The first taxon, *Carabus fairmairei* Thomson, 1875, corresponds to the populations distributed in the Alps around the Mont Cenis. Consequently, the taxon *cenisius* Kraatz, 1878, becomes a new junior synonym of *fairmairei* Thomson, 1875, and *baudii* Kraatz, 1878, from the Mount Viso area, has been established as a valid taxon. The second taxon, *Carabus putzeysi* Thomson, 1875, described from the 'Alps of Switzerland' is a new junior synonym of *Carabus castanopterus* Villa et Villa, 1833. Consequently, its substitute name, *Carabus putzeysianus* Géhin, 1876, is also a synonym of *castanopterus* Villa et Villa, 1833, and the populations of *Carabus pedemontanus* Ganglbauer, 1892, bona species, from the Haut-Vésubie Valley, in French Southern Alps, require a new subspecific name. Some lectotypes have been designated, a taxonomic revision has been given for the polytypic species *C. pedemontanus* (valid species, in the new sense) and two new taxa are named: *C. (O.) pedemontanus vesubianus* nom nov. (for *maritimus* Schaum, 1860, nec Motschulsky, 1850), and *C. pedemontanus maurinensis* subsp. n. The taxa have been treated as members of the subgenus *Oreocarabus* in the widest sense of Deuve (1994) (*Orinocarabus* in the sense of the present book), and some, which are treated as valid species in the present paper, have been treated by Deuve at subspecific rank. The changes introduced in the nomenclature of the genus are the following (the numbers refer to the checklist in Chapter 2):

11.005 ***castanopterus*** Villa & Villa, 1833
(*alpestris castanopterus* s. Deuve, 2002)
= *putzeysi* Thomson, 1875 (**nov. syn.**)
= *putzeysianus* Géhin, 1876 (**nov. syn.**)

11.006 a. ***cenisius cenisius*** Kraatz, 1878
(*fairmairei cenisius* s. Deuve, 2002)
= *fairmairei fairmairei* Thomson, 1875 (**nov. syn.**)
[valid name: ***fairmairei fairmairei*** Thomson, 1875]

11. 008 a. ***fairmairei fairmairei*** Thomson, 1875
[valid name: ***baudii baudii*** Kraatz, 1875]
(*fairmairei baudii* s. Deuve, 2002)

11. 012 a. ***putzeysianus putzeysianus*** Géhin, 1876
= *putzeysi* Thomson, 1875
[valid name: ***pedemontanus pedemontanus*** Ganglbauer, 1892]

Addenda:

g. ***pedemontanus tendanus*** Born, 1898 (**nov. comb.**) (valid ssp. s. Deuve, 2002)
h. ***pedemontanus vesubianus*** Deuve, 2002 (nom. nov. pro *maritimus* Schaum, 1856, nec Motschulsky, 1850) (valid ssp. s. Deuve, 2002)
i. ***pedemontanus maurinensis*** Deuve, 2002 «Alpes-de-Haute-Provence, Maurin»

Ghiretti, D. 2002 Photographic catalogue of the genus *Carabus*, Supplement III. – Conte Editore, Lecce: sticker pages.

Note: Additional iconographic stickers to Ghiretti (1996, 1997).

Holland, J.M. 2002 (ed.) The agroecology of carabid beetles. – Intercept, Andover: 1-450.

Note: A collection of comprehensive review papers on agroecological research on carabids.

Imura Y. 2002a Proposal of Eighteen New Genera and Subgenera of the Subtribe Carabina (Coleoptera, Carabidae). – Spec. Bull. Jpn. Soc. Coleopterol. 5: 129-147.

Note: The author, following his opinion that an independent clade of the molecular genealogical trees 'should be regarded as a full genus' (Osawa *et al.*, 2002: see title and classification below), proposes new genera and subgenera – many monotypical – for species that are currently treated in the genus *Carabus* (in the widest sense of authors), and/or are attributed to different, previously named subgenera. Most of the proposed genera and subgenera concern Asiatic species, extraneous to the fauna that is the object of the present book. The following, however, concern European taxa, or taxa that are treated or cited at least in one of the Chapters (*Phylogeny* and/or *Biogeography*):

Baptaulonocarabus Imura, subgen nov. of the genus *Aulonocarabus* (Monotypical. Type species: *Carabus truncaticollis* Eschscholtz).

Durangocarabus Imura, gen. nov. (Monotypical. Type species: *Carabus forreri* Bates).

Protomegodontus Imura, gen. nov. (Monotypical. Type species: *Carabus germarii* Sturm). In the author's opinion, the close resemblance between *violaceus* (note: attributed to the monotypical subgenus *Proteocarabus* Imura of the genus *Pachycranion* Solier: Imura, 2002, see below) may be regarded as the result of 'parallel evolution that occurred in two different phyletic lines'; *germarii* 'constitutes a completely isolated branch, at least concerning the analysed population from Northeast Italy'. Further comments see below.

Imura Y. 2002b Classification of the Subtribe Carabina (Coleoptera, Carabidae) Based on Molecular Phylogeny. – Elytra, Tokyo 30 (1): 1-28.

Note: The author proposes a new system for the higher classification of the subtribe Carabina (*Carabus* in the broad sense of the present contribution). The genealogical trees on which the present study is based, have been constructed by the NJ method or UPGMA, analysing 1,069 base-pairs of the mithochondrial gene encoding NADH dehydrogenase subunit 5 (ND5). The author gives a synthesis and a discussion of previous classifications of the subtribe Carabina (see Table 1) ('divisions', 'subdivisions', 'sections' or 'groups', not regulated by ICZN), as follows:

Summary (by A. Casale):

Terms proposed by LAPOUGE and ISHIKAWA were settled between the subtribe Carabina and its component

Table 1. Higher names of the subtribe Carabina either not regulated by ICZN or to be synonymyzed.

Author	Higher names
REITTER (1896)	Carabi angustocephali, C. procerogenici, C. procrustogenici, C. macrocephali, C. cechenogenici, C. multisetosi, C. tribacogenici, C. glabriventri, C. latipalpi, C. crenolimbi, C. emarginati, C. morphogenici, C. multistriati, C. costiferi, C. glabripenni
BENGTSSON (1927)	Archaeocarabus*, Metacarabus*, Neocarabus*
LAPOUGE (1929)	Carabes Rostrilabres* (Fissirostres, Obtusirostres, Conirostres, Ténuirostres, Lamellirostres), C. Quadricuspides* (Macrocerques, Brachycerques), C. Serrilabres* (Holodontes, Synodontes, Tétrodontes, Pentodontes); Psilogoniens, Pliochètes, Tribacogéniens, Multistriés, Carabogéniens
BREUNING (1932)	Carabi Brevimandibulares, C. Carabogenici, C. Multistriati, C. Longimandibulares
ISHIKAWA (1978)	Carabogenici, Spinulati, Multistriati
DEUVE (1991)	Spinulati, Digitulati, Lipastrornorphi, Archicarabomorphi, Multistriati
DEUVE (1994)	Spinulati, Digitulati, Lipastrormorphi, Archicarabormorphi, Lobifera
IMURA (1996)	Carabogenici (Digitulati, Lipastromorphi, Archicarabomorphi), Multistrati (Spinulati, Crenolimbi, Latitarsi, Arciferi, Procrustimorphi)
DEUVE (1997)	Spinulati, Digitulati, Lipastromorphi, Archicarabomorphi, Lobifera (Crenolimbi, Multistriati, M. Tomocaraboides, M. Oreocaraboides, Longimandibulares, Neocarabi)

genera, and those proposed by other authors were settled between the genus *Carabus* (*s. lato*) and its component subgenera. Terms denoted by asterisks indicate that they were proposed on the basis of the larval morphology.

The proposal of the new classification is summarised as follows. In the new system, the subtribe Carabina is classified into 29 divisions and 137 genera (sic!).

Note: Only the European species cited by Imura have been listed below. We corrected for the spelling accepted in our checklist (for instance, *clatratus* instead of *clathratus*, and *zawadzkii* instead of *zawadszkii*). Additions ('**add.**') have been indicated for taxa which in our list have been treated at specific rank, as well as for some main synonyms.

CLASSIFICATION

Subtribe Carabina (all divisions *sedis mutabilis*)

1. **Division Limnocarabigenici**
Genus *Limnocarabus* GEHIN, 1876
Subgenus *Limnocarabus* GEHIN, 1876
clatratus L.
Subgenus *Euleptocarabus* NAKANE, 1956
(Asiatic)
2. **Division Chaetocarabigenici**
Genus *Heterocarabus* MORAWITZ, 1886
marietti CRS. et JAN
Genus *Chaetocarabus* THOMSON, 1875
intricatus L., ***arcadicus*** GISTL (**add.**: ***krueperi*** REITTER, ***lefebvrei*** DJ., ***merlini*** SCHAUM)
Genus *Platycarabus* MORAWITZ, 1886
(=*Pseudocechenus* MORAWITZ, 1886; *Baudiicarabus* GANGLBAUER, 1909)
depressus BONELLI, ***irregularis*** FBR., ***creutzeri*** FBR., ***cychroides*** BAUDI, ***fabricii*** PANZER
3. **Division Hemicarabigenici**
Genus *Hemicarabus* GÈHIN, 1885
nitens L. (plus Asiatic and Nearctic species)
Genus *Homoeocarabus* REITTER, 1896
(Siberian-Nearctic)
4. **Division Ischnocarabigenici**
Genus *Archicarabus* SEIDLITZ, 1887
(=*Aptocarabus* REITTER, 1896; *Deuterocarabus* REITTER, 1896; *Nemoralus SCHULER*, 1976)
monticola *DJ.*, ***nemoralis*** MULLER, ***montivagus*** PALLIARDI, ***pseudomonticola*** LP., ***rossii*** DJ. (**add.: *steuartii*** DEYR.) (plus Anatolian species)
Genus *Ischnocarabus* KRAATZ, 1877
(Asiatic)
Genus *Gnathocarabus* DEUVE, 1991
(Asiatic)
5. **Division Rhipocarabigenici**
Genus *Rhipocarabus* REITTER, 1896
alysidotus ILLIGER
6. **Division Apotomopterigenici**
Genus *Apotomopterus* HOPE, 1838
Subgenus *Apotomopterus* HOPE, 1838
(Asiatic)
Subgenus *Dolichocarabus* LAPOUGE, 1927
(=*Siamocarabus* IMURA, 1989)
(Asiatic)
Subgenus *Taiwanocarabus* IMURA et M. SATO, 1989
(Asiatic)
7. **Division Lipastrigenici**
7.1. **Subdivision A** (group *of Cyclocarabus*)
Genus *Cyclocarabus* REITTER, 1896
(Asiatic)
Genus *Ophiocarabus* REITTER, 1896
(=*Cryptocarabus* REITTER, 1896; *Haplocarabus* SEMENOV, 1898; *Microcarabus* ISHIKAWA, 1979*)*
(Asiatic)
7.2. **Subdivision B** (group *of Lipaster)*
Genus *Lipaster* MOTSCHULSKY, 1865
(=*Lamprocarabus* THOMSON, 1875; *Titanocechenus* BR. et RUSPOLI, 1970)
(Ponto-Caucasian)
Genus *Mimocarabus* GEHIN, 1885
maurus ADAMS (plus Asiatic species)
Genus *Lyperocarabus* LAPOUGE, 1930
estreicheri FS., ***sibiricus*** FS., ***besseri*** FS., ***perrini*** DJ. (**add.**: ***bosphoranus*** FS, ***errans*** FS. [= ***sibiricus errans,*** nec GORY], ***haeres*** FS., ***rybinskii*** REITTER (plus Asiatic species)
Genus *Trachycarabus* GEHIN, 1885
scabriusculus OLIVIER
Genus *Morphocarabus* GEHIN, 1885
(=*Sajanocarabus* LUTSHNIK, 1924; *Amorphocarabus* LAPOUGE, 1930; *Basilicocarabus* LAPOUGE,1930)
henningi FS., ***monilis*** FBR., ***regalis*** FS., ***rothi*** DJ., ***scheidleri*** PANZER, ***excellens*** FBR., ***zherichini*** SHL (**add.** : ***comptus*** DJ., ***hampei*** KST., ***kollari*** PLLDI ., ***versicolor*** FRIV., ***zawadzkii*** KR.) (plus Asiatic species)
Genus *Apostocarabus* REITTER, 1896
odoratus MTS*.,* ***karpinskii*** KRY. et MATVEEV (plus Asiatic species)
Genus *Pancarabus* REITTER, 1896
aeruginosus FS. (plus Asiatic species)
Genus *Ancylocarabus* REITTER, 1896*)*
(=*Promorphocarabus* REITTER, 1896; *Gigantocarabus* SEMENOV, 1898)

    - (Asiatic)
  - Genus *Leptinocarabus* REITTER, 1896
    - (=*Rhigoidocarabus* DEUVE, 1997)
    - ***hummeli*** FS. (plus Asiatic species)
8. **Division Tachypigenici**
  - Genus *Tachypus* WEBER, 1801
    - (=*Autocarabus* SEIDLITZ, 1887)
    - ***auratus*** L.
  - Genus *Cancellocarabus* LUTSHNIK, 1924
    - ***cancellatus*** ILLIGER, ***vagans*** OLIVIER
9. **Division Mesocarabigenici**
  - Genus *Mesocarabus* THOMSON, 1875
    - (=*Hadrocarabus* THOMSON, 1875)
    - ***problematicus*** HERBST, ***dufourii*** DJ., ***lusitanicus*** FBR. (**add.**: ***macrocephalus*** DJ.)
  - Genus *Eupachycechenus* SEMENOV, 1898
    - (North-African)
10. **Division Ortocarabigenici**
  - Genus *Oreocarabus* GÉHIN, 1876
    - ***errans*** GORY (=***amplipennis*** Auct.), ***ghilianii*** LA FERTÉ-SÉNECTERE, ***guadarramus*** LA FERTÉ-SÉNECTERE]
11. **Division Orinocarabigenici**
  - Genus *Orinocarabus* KRAATZ, 1878
    - ***concolor*** FBR., ***fairmairei*** TMS., ***heteromorphus*** DANIEL, ***maritimus*** SCHAUM (=***putzeysianus*** Auct.=***pedemontanus*** GNLB.), ***sylvestris*** PANZER, ***adamellicola*** GGL., ***alpestris*** STURM, ***bertolinii*** KRT., ***carinthiacus*** STURM, ***castanopterus*** A. & G. B. VILLA, ***cenisius*** KRT. (**add.**: ***lepontinus*** BORN)
12. **Division Cavazzutiocarabigenici**
  - Genus *Cavazzutiocarabus* IMURA, 1998
    - ***latreillei*** DJ. (=***latreilleanus*** Auct.)
13. **Division Tmesicarabigenici**
  - Genus *Tmesicarabus* REITTER, 1896
    - ***cristoforii*** SPENCE
14. **Division Eurycarabigenici**
  - Genus *Eurycarabus* GÉHIN, 1885
    - (=*Apatocarabus* SEMENOV, 1898)
    - ***faminii*** DJ., ***genei*** GENÉ
15. **Division Nesaeocarabigenici**
  - Genus *Nesaeocarabus* BEDEL, *1895*
    - (=*Liocarabus* REITTER, 1896)
    - (Canary Islands)
16. **Division Cytilocarabigenici**
  - Genus *Cytilocarabus* REITTER, 1896
    - (Anatolian-Caucasian)
17. **Division Pentacarabigenici**
  - Genus *Pentacarabus* ISHIKAWA, 1972
    - (Asiatic)
18. **Division Pachycarabigenici**
  - Genus *Pachycarabus* GEHIN, 1876
    - (= *Caucasocarabus* LAPOUGE, 1930)
    - (Caucasian)
19. **Division Pachystigenici**
  - Genus *Pachystus* MOTSCHULSKY, 1865
    - Subgenus *Euporocarabus* REITTER, 1896
      - ***hortensis*** L. (**add.**: ***preslii*** DJ.)
    - Subgenus *Pachystus* MOTSCHULSKY, 1865
      - (=*Melancarabus* THOMSON, 1875; *Phricocarabus* REITTER, 1896) ***cavernosus*** FRIVALDSKY, ***glabratus*** PAYKULL, ***graecus*** DJ., ***hungaricus*** FBR. (**add.** : ***cribellatus*** ADAMS, ***trojanus*** DJ.) (plus Anatolian species)
20. **Division Meganebriigenici**
  - Genus *Meganebrius* KRAATZ, 1895
    - (Asiatic)
21. **Division Piocarabigenici**
  - Genus *Titanocarabus* BREUNING, 1933
    - (Asiatic)
  - Genus *Piocarabus* REITTER, 1896
    - Subgenus *Piocarabus* REITTER, 1896
      - (Asiatic)
    - Subgenus *Qinlingocarabus* IMURA, 1998
      - (Asiatic)
22. **Division Leptocarabigenici**
  - Genus *Aulonocarabus* REITTER, 1896
    - Subgenus *Weolseocarabus* KWON et LEE, 1984
      - (Asiatic)
    - Subgenus *Adelocarabus* REITTER, 1896
      - (Asiatic)
    - Subgenus *Aulonocarabus* REITTER, 1896
      - ***canaliculatus*** ADAMS (plus Asiatic species)
    - Subgenus *Baptaulonocarabus* IMURA, 2002
      - ***truncaticollis*** ESCHSCHOLTZ (**add.**: ***loschnikovii*** FS.) (plus Asiatic species)
  - Genus *Leptocarabus* GEHIN, 1885
    - (Asiatic)
23. **Division Rhigocarabigenici**
  - Genus *Zhongdianocarabus* IMURA, 2002
    - (Asiatic)
  - Genus *Batangocarabus* IMURA, 2002
    - (Asiatic)
  - Genus *Araeocarabus* REITTER, 1896
    - (Asiatic)
  - Genus *Litangocarabus* IMURA, 2002
    - (Asiatic)
  - Genus *Deqenocarabus* IMURA, 2002
    - (Asiatic)
  - Genus *Zheduocarabus* IMURA, 2002
    - (Asiatic)
  - Genus *Sinoleptocarabus* IMURA, 2002
    - (Asiatic)
  - Genus *Tibetorinocarabus* IMURA, 2002
    - (Asiatic)

Genus *Syzygocarabus* SEMENOV, 1898
(Asiatic)
Genus *Mianningocarabus* IMURA, 2002
(Asiatic)
Genus *Rhigocarabus* REITTER, 1896
(Asiatic)
Genus *Tachycarabus* SEMENOV, 1898
(Asiatic)
Genus *Sangocarabus* IMURA, 2002
(Asiatic)
Genus *Hypsocarabus* SEMENOV, 1898
(Asiatic)

24. **Division Tomocarabigenici**
Genus *Rhytidocarabus* IMURA, 2002
(Asiatic)
Genus *Glossocarabus* IMURA, 2002
(Caucasian)
Genus *Coreocarabus* IMURA, 2002
(Asiatic)
Genus *Tomocarabus* REITTER, 1896
(=*Procrustides* SEMENOV, 1905)
convexus FBR., **bessarabicus** FS.
Genus *Asthenocarabus* LAPOUGE, 1930
(Asiatic)
Genus *Callistocarabus* REITTER, 1896
marginalis FBR.
Genus *Scambocarabus* REITTER, 1896
(=*Eremocarabus* LAPOUGE, 1930)
(Asiatic)
Genus *Stephanocarabus* IMURA, 1995
(Asiatic)
Genus *Tanaocarabus* REITTER, 1896
(Nearctic)
Genus *Diocarabus* REITTER, 1896
(=*Allocarabus* LAPOUGE, 1921)
(Asiatic)
Genus *Watanabeocarabus* IMURA, 2002
slovtzovi MNH.
Genus *Cryocarabus* LAPOUGE, 1930
(Nearctic)
Genus *Neocarabus* LAPOUGE, 1931
(Nearctic)
Genus *Durangocarabus* IMURA, 2002
(Nearctic)
Genus *Zoocarabus* REITTER, 1896
(Asiatic)
Genus *Ulocarabus* REITTER, 1896
(=*Bactrocarabus* SEMENOV, 1927)
(Asiatic)
Genus *Coccocarabus* IMURA, 2002
(Asiatic)
Genus *Carpathophilus* REITTER, 1896
linnaei PANZER
Genus *Semnocarabus* REITTER, 1896
(=*Anthracocarabus* LAPOUGE, 1930)
(Asiatic)

25. **Division Carabigenici**
Genus *Carabus* LINNÉ, 1758
(=*Eutelocarabus* REITTER, 1896; *Apocarabus* LAPOUGE, 1930; *Nippocarabus* LAPOUGE, 1930)
arvensis HERBST, **deyrollei** GORY, **granulatus L.**, **menetriesi** HUMMEL., **stscheglowi** MNH. (plus Asiatic species)
Genus *Eucarabus* GEHIN, 1885
Subgenus *Eucarabus* GEHIN, 1885
(=*Loxocarabus* REITTER, 1896; *Xystrocarabus* REITTER, 1896)
catenulatus SCOPOLI, **italicus** DJ., **obsoletus** STURM, **parreyssii** PALLIARDI, **ulrichii** GERMAR]
Subgenus *Tylocarabus* REITTER, 1896
(Caucasian)
Subgenus *Parhomopterus* LAPOUGE, 1931
(=*Orientocarabus* KWON *et* LEE, 1984)
(Asiatic)
Genus *Lichnocarabus* REITTER, 1896
(Nearctic)
Genus *Archaeocarabus* SEMENOV, 1898
(=*Acoptopterus* LAPOUGE, 1927)
(Asiatic)
Genus *Ohomopterus* REITTER, 1896
(Asiatic)

26. **Division Ctenocarabigenici**
Genus *Ctenocarabus* THOMSON, 1875
galicianus GORY
Genus *Rhabdotocarabus* SEIDLITZ, 1887
melancholicus FBR.

27. **Division Hygrocarabigenici**
Genus *Hygrocarabus* THOMSON, 1875
nodulosus CREUTZER, **variolosus** FBR.

28. **Division Cathopliigenici**
Genus *Cathoplius* THOMSON, 1875
(=*Cychrocephalus* GEHIN, 1875)
(North-African)

29. **Division Procrustigenici**

29.1. **Subdivision A** (group of *Macrothorax*)
Genus *Chrysocarabus* THOMSON, 1875
Subgenus Chrysocarabus THOMSON, 1875
auronitens FBR., **lineatus** DJ., **splendens** OLIVIER
Subgenus *Chrysotribax* REITTER, 1896
hispanus FB., **rutilans** DJ.
Genus *Iniopachys* SOLIER, 1848
auriculatus PTZ., **pyrenaeus** AUDINET-SERVILLE
Genus *Macrothorax* DESMAREST, 1850
(=*Dichocarabus* REITTER. 1896; *Dorcarabus* REITTER, 1896; *Paracarabus* REITTER, 1896)

morbillosus FBR. , **planatus** CHD., **rugosus** FBR.
Genus *Sellaecarabus* STURANI, 1947 38)
(=*Dysmictocarabus* PUISSEGUR, 1964)
olympiae SELLA, **solieri** DJ.
Genus *Sphodristocarabus* GEHIN, 1885
(=*Sphodristus* THOMSON, 1875)
varians FS.(plus Ponto-Caucasian species)
Genus *Relictocarabus* LEDOUX, 1984
(North-African)
Genus *Apoplesius* DEUVE, 1990
(Anatolian)
Genus *Imaibius* BATES, 1889
(=*Tropidocarabus* KRAATZ. 1895; *Parimaibius* BREUNING, 1958; *Lithariophorus* MANDL, 1985)
(Asiatic)

29.2. **Subdivision B** (group of *Tribax*)
Genus *Tribax* FISCHER, 1817
(=*Playchrus* KOLENATI, 1845; *Neoplectes* REITTER, 1885; *Archiplectes* GOTTWALD, 1982; *Microtribax* GOTTWALD. 1982)
(Ponto-Caucasian)
Genus *Microplectes* REITTER, 1896
(Caucasian)
Genus *Cechenochilus* MOTSCHULSKY, 1850
Subgenus *Cechenochilus* MOTSCHULSKY, 1850
(Caucasian)
Subgenus *Procechenochilus* IMURA et BELOUSOV, 2002
(Caucasian)

29.3. **Subdivision C** (group *of Procrustes*)
Genus *Pachycranion* SOLIER, 1848
Subgenus *Aulacocarabus* GEHIN, 1876
exaratus QUENSEL, **carinatus** MTS. (=**septemcarinatus** Auct.), **dejeani** FS. (=**gyllenhali** Auct.), **planicollis** KUSTER
Subgenus *Proteocarabus* GEHIN, 1876
violaceus L.
Subgenus *Pachycranion* SOLIER, 1848
(=*Carabulus* LUTSHNIK, 1924;*Ainocarabus* MANDL., 1973; *Nabicarabus* KWON et LEE,1984)
amoenus CHD. (=**ermaki** Auct.), **schoenherri** FS.(**add.**: **aurolimbatus** DJ.) (plus Asiatic species)
Genus *Protomegodontus* IMURA, 2002
germarii STURM
Genus *Procerus* DEJEAN, 1828
Subgenus *Procerus* DEJEAN, 1828
gigas CREUTZER, **scabrosus** OLIVIER (**add.**: **duponchelii** DJ., **sommeri** MNN.) (plus Caucasian-Anatolian species)
Subgenus *Megodontus* SOLIER, 1848
caelatus FBR., **croaticus** DJ. (plus Irano-Anatolian species)
Genus *Procrustes* BONELLI, 1809
Subgenus *Procrustes* BONELLI, 1809
(=*Procrusticus* WHITE, 1845; *Macrogenus* MOTSCHULSKY, 1846; *Sphodristus* MOTSCHULSKY, 1865; *Pseudoprocrustes* MORAWITZ, 1886)
coriaceus L., **banoni** DJ. (plus Anatolian species)
Subgenus *Creprostus* IMURA, 2002
(Asiatic)
Subgenus *Lamprostus* MOTSCHULSKY, 1865
(*Chaetogaster* LAPOUGE. 1930)
torosus FRIVALDSKY (plus Caucasian-Anatolian species)
Subgenus *Oxycarabus* SEMENOV, 1898
(Anatolian)
Subgenus *Chaetomelas* THOMSON, 1875
(=*Procrustocarabus* GEHIN, 1876; *Chaetoprostus* REITTER, 1896)
(Asiatic)

29.4. **Subdivision D** (group of *Cratocephalus)*
Genus *Cratophyrtus* REITTER, 1896
(Asiatic)
Genus *Pseudotribax* KRAATZ, 1884
(Asiatic)
Genus *Pantophyrtus* THIEME, 1881
(Asiatic)
Genus *Goniocarabus* GEHIN, 1885
(=*Alagocarabus* MORAWITZ, 1886; *Acarabus* SEMENOV, 1890)
(Asiatic)
Genus *Cratocarabus* REITTER, 1896
(Asiatic)
Genus *Cratocechenus* REITTER, 1896
(Asiatic)
Genus *Cratocephalus* KIRSCH, 1857
(Asiatic)
Genus *Eotribax* SEMENOV, 1898
(Asiatic)
Genus *Deroplectes* REITTER, 1895
(=*Plesius* SEMENOV, 1905)
(Asiatic)
Genus *Axinocarabus* MORAWITZ, 1886
(Asiatic)
Genus *Cechenotribax* SEMENOV-TIAN-SHANSKIJ et ZNOJKO, 1932
(Asiatic)
Genus *Pachycechenus* SEMENOV, 1898
(Asiatic)
Genus *Alipaster* REITTER, 1896
(Asiatic)
Genus *Leptoplesius* REITTER, 1898

(Asiatic)
29.5. **Subdivision E** (group of *Damaster*)
Genus *Pseudocoptolabrus* REITTER, 1896
(=*Protodamaster* IMURA et KEZUKA, 1989; *Nigracoptolabrus* DEUVE, 1991)
(Asiatic)
Genus *Megodontoides* DEUVE, 1991
(Asiatic)
Genus *Acathaicus* REITTER, 1896
(=*Cathaicodes* REITTER, *1896)*
(Asiatic)
Genus *Coptolabrodes* BREZINA et IMURA, 1997
(Asiatic)
Genus *Imaibiodes* DEUVE, 1991
(Asiatic)
Genus *Lasiocoptolabrus* IMURA, 1993
(Asiatic)
Genus *Aristocarabus* SEMENOV, 1896
(Asiatic)
Genus *Pagocarabus* MORAWITZ, 1886
Subgenus *Shunichiocarabus* IMURA, 1995
(Asiatic)
Subgenus *Pagocarabus* MORAWITZ, 1886
(Asiatic)
Genus *Sigenacarabus* KLEINFELD, 2000
(Asiatic)
Genus *Eccoptolabrus* SEMENOV, 1898
(Asiatic)
Genus *Calocarabus* SEMENOV, 1887
(*Calocechenus* REITTER, 1896*; Cryptocechenus* SEMENOV, 1898)
(Asiatic)
Genus *Neoplesius* REITTER, 1896
(=*Indocarabus* LAPOUGE, *1930; Eocechenus* SEMENOV-TIAN-SHANSKIJ et ZNOJKO, 1932; *Cupreocarabus* DEUVE, 1997)
(Asiatic)
Genus *Pseudocranion* REITTER, 1896
(=*Cratocranion* SEMENOV, 1898)
(Asiatic)
Genus *Damaster* KOLLAR, 1836
(=*Adamaster* REITTER, 1896)
(Asiatic)
Genus *Cephalornis* SEMENOV, 1889
(=*Cychrocarabus* MORAWITZ, 1889)
(Asiatic)
Genus *Cychrostomus* REITTER, 1896
(Asiatic)
Genus *Teratocarabus* SEMENOV-TIAN-SHANSKIJ et ZNOJKO, 1932
(Asiatic)
Genus *Fulgenticarabus* DEUVE et LI, 1998
(Asiatic)
Genus *Acoptolabrus* MORAWITZ, 1886
Subgenuis *Yezacoptolabnis* IMURA, 2002
(Asiatic)
Subgenus *Acoptolabrits* MORAWITZ, 1886
(=*Koreacoptolabrus* KWON et LEE, 1984)
(Asiatic)
Genus *Eupachys* CHAUDOIR, 1857
(Asiatic)
Genus *Shenocoptolabrus* IMURA, ZHOU et SU, 1999
(Asiatic)
Genus *Cathaicus* BATES, 1870
(Asiatic)
Genus *Coptolabrus* SOLIER, 1848
(=*Coptolabrinus* REITTER, 1897; *Eocarabus* SEMENOV, 1898; *Eucoptolabrus* SEMENOV, 1898; *Nesocoptolabrus* LAPOUGE, 1930)
(Asiatic)

General remarks

by A. Casale & D. Mossakowski

It is evident that accepting this proposal would introduce an enormous amount of changes to the classification adopted in the present volume. This would affect both nomenclature and taxonomy, i.e. in case of re-evaluation of old names, no more homonyms (this is, however, not in agreement with the ICZN, 1999, see Chapter 12. *Homonymy*, such as *latreillei* in place of *latreilleanus*, for instance). Well-known species would be attributed to other 'genera' or subgenera, some of which have been proposed as new, such as, for instance, *glabratus* to *Pachystus*. The species *germarii* and *violaceus* even would be attributed to distinct genera!

Moreover, any comment on this paper, greatly exceeds the purpose of our work, which is mostly devoted to the knowledge of the faunistics, ecology and biogeography of the European *Carabus* (*sensu lato*) species, more than to the phylogeny and classification of the higher taxa. Therefore, this is not the best place to discuss a freshly published proposal for a new, molecular classification. The following main points may be recalled as the most critical and disputable:

1. The opportunity to propose new names for higher 'divisions' or 'subdivisions', rejecting those previously existing (for instance, Apotomopterigenici in place of Spinulati, Ischnocarabigenici in place of Archicarabomorphi, etc.).

2. The consistency of a phylogeny based on ND5. In fact, it is currently accepted that not necessarily the variation of a single mitochondrial, encoding gene is significant for phylogenetic analysis at higher ranks. But, more important, the fact that the bootstrap values, that is the support of the data for many of the groups now established as 'genera' or subgenera, are very low. Too low to establish substantiated relationships, despite the relationships should be the basis of taxonomy. The ND5 gene, as other mitochondrial genes, is evolving too fast to be suited to resolve such deep splits as the subgenera of *Carabus*.

3. Finally, the opportunity to propose distinct, often monobasic taxa, at generic or subgeneric ranks, for species forming an 'independent clade on the molecular genealogical trees', when these trees are based on a single, although molecular, character (a mitochondrial gene). It is to be stressed, in fact, that each line in a tree, also a species, is an independent clade in a tree. Above species level it is only the decision of the author to assign a categorial rank to a taxon.

Therefore we think that much time and research will be needed to test the value of the phylogeny and classification proposed by the Japanese author. In other words, for a modern systematic of *Carabus* (always in the old, widest sense), it is a must to connect morphological data of the imagines, the larva and molecular data. A system based only on insufficent molecular data is beyond the state of the art.

Obydov, D. 2002 Revision du genre *Callisthenes*. – Association Magellanes: 1-128.

Note: *Callisthenes* in the widest sense, including, in the opinion of some authors, *Callisthenes* also, is the adelphotaxon of *Carabus* (see Chapters 7 and 8).

Osawa, S., Z.-H. Su & Y. Imura 2002 Molecular Phylogeny and Evolution of the Carabid Ground Beetles of the World. – Tetsugakushobo, Tokyo: 1-264. [In Japanese, with English book title].

Note: Paper not yet examined. The 6th chapter of this publication, mainly contributed by the third author, proposes a new molecular classification system of the subtribe Carabina (genus *Carabus* of authors), with the necessity of 'establishing at least nineteen new genera and subgenera' (Imura, 2002a: see above).

Rasplus, J. Y., S. Garnier, S. Meusnier, S. Piry, P. Audiot, & J. M. Cornuet 2002 Setting conservation priorities: The case study of *Carabus solieri* (Col. Carabidae). – Genetic, Selection and Evolution 33: 141-175.

Reimann T., T. Assmann, O. Nolte, H. Reuter, C. Huber & F. Weber 2002 Palaeogeography and palaeoecology of *Carabus auronitens* (Coleoptera): characterization and localization of glacial refugia in southern France and reconstruction of postglacial expansion routes by means of allozyme polymorphismus. – Abhandlungen des Naturwissenschaftlichen Vereins in Hamburg (NF) 35: 1-155.

Note: Largely in agreement with the biogeographical analysis in the present work.

References

[n] = number(s) of the chapter(s) in which the reference has been cited or used as a source of general information.
[t] = reference used for transects (Chapter 8).
[maps] = reference used for construction of distribution maps.
[A] = mostly not mentioned in the text; see Addendum.

Aa. Vv. 1981 Principi e metodi nell'analisi biogeografica. – Biogeographia (N.S.) XI (1985), 296 pp. **[8]**

Adashkevich, B.P., A.A. Petrusenko & O.N. Perekrest 1973 Ekologo-faunisticheskii obzor zhuzhelits (Coleoptera, Carabidae) Moldavii (Soobshchenie pervoe). (Eco-faunistic review of the ground-beetles (Coleoptera, Carabidae) of Moldavia) – In: Fauna i biologiya nasekomykh Moldavii. Kishinev: Shtiintsa: 62-71. [In Russian]. **[5]**

Aguinaldo, A.M.A., J.M. Turbeville, L.S. Linford, M.C. Rivera, J.R. Garey, R.A. Raff & J.A. Lake 1997 Evidence for a clade of nematodes, arthropods and other moulting animals. – Nature 387: 489-493. **[8]**

Alexandrovitch, O.R., I.K. Lopatin, A.D. Pisanenko, V.A. Tsinkevitch & S.M. Snitko 1996 A catalogue of Coleoptera (Insecta) of Belarus. – Minsk, FFR RB: 1-103. **[5,maps]**

Alfieri, A. 1976 Carabidae In: The Coleoptera of Egypt. – Mémoires de la Société entomologique d'Egypte 5: 1-30. **[5,8]**

Allemand, R. & J. P. Malausa 1984 Compatibilité génétique et distances phylétiques entre les espèces du genre *Chrysocarabus* Thomson (Col., Carabidae). – Annls. Soc. ent. Fr. (N.S.) 20: 347-363. **[6]**

Alonso M., F. Novoa F. & E. Eiroa 1987 Los Carabidae (Col. Adephaga) de Sierra Segundera y Peña Trevinca (Noroeste de Espana). I. Estudio faunistico. – Bol. Real Soc. Esp. Hist. Nat. Biologia 83: 19-34. **[5]**

Alonso M., F. Novoa F. & E. Eiroa 1988 Los Carabidae (Col. Adephaga) de Sierra Segundera y Peña Trevinca (Noroeste de Espana). II. Estudio de los taxocenosis de carabidos de los distintos tipos de vegetation – Bol. Real Soc. Esp. Hist. Nat. Biologia 84: 5-13. **[5]**

Althoff G.-H., M. Ewig, J. Hemmer, P. Hockmann, M. Klenner, F.-J. Niehues, R. Schulte & F. Weber 1992 Ergebnisse eines Zehn-Jahres-Zensus an einer *Carabus auronitens*-Subpopulation im Münsterland. – Abh. Westf. Mus. Naturkde 54: 3-64. **[5,6,9]**

Althoff, G.-H., P. Hockmann, M. Klenner, F.-J. Niehues & F. Weber 1994 Dependence of running activity and net reproduction in *Carabus auronitens* on temperature. – In: Desender, K., M. Dufrêne, M. Loreau, M. Luff & J.-P. Maelfait (eds.): Carabid beetles: ecology and evolution. Dordrecht: Kluwer Academic Publishers: 95-100. **[9]**

Anderson, R. 1993 Rufinism in Irish *Pterostichus nigrita* (Paykull) (Coleoptera, Carabidae). – Entomologists' Monthly Magazine 129: 122. **[5]**

Anderson, R., D. McFerran & A. Cameron 2000 The ground beetles of Northern Ireland (Coleoptera: Carabidae). – Belfast: 1-246 **[5,maps]**

Andrade Malde, J. 1977 *Ctenocarabus galicianus* Gory (Coléoptère Carabidae). Estados larvarios (Ex societate imaginis) – Nouvelle Revue d'Entomologie 7: 257-260. **[4]**

Andreeva, T.R. & P.K. Eremin 1989 Ekologo-faunisticheskaya kharakteristika zhuzhelits (Coleoptera, Carabidae) Yuzhnogo Yamala. (Eco-faunistic characteristics of ground-beetles (Coleoptera, Carabidae) of the South Yamal) – In: Nasekomye v biogeotsebozakh Urala: Inform. mater. Sverdlovsk: 4-5. [In Russian]. **[5,8]**

Andrewartha, H.G. & L.C. Birch 1954 The distribution and abundance of animals. – Chicago: Chicago Univ. Press. **[6]**

Antoine, M. 1955-1962 Coléoptères carabiques du Maroc 1-5. – Mémoires de la Société des Sciences naturelles et phys. du Maroc, Zoologie (N.S.). Rabat: 1-692. **[5,maps]**

Anufriev, G.A. & G.A. Sharygin 1989 Fauna i naselenie zhuzhelits (Coleoptera, Carabidae) v lesnykh ekosistemakh Gor'kovskoi oblasti. (Fauna and population of ground-beetles (Coleoptera, Carabidae) in forest ecosystems of the Gorky Province) – In: Nazemnye i vodnye ekosistemy 12. Gorky: 38-51. [In Russian]. **[5]**

Anyushin, V.V. 1982 Vidovoi sostav i osobennosti prostranstvennogo raspredeleniya zhuzhelits i chernotelok (Coleoptera, Carabidae, Tenebrionidae) v Krasnoturanskom boru Idrinskogo leskhoza. (Species composition and spatial distribution of ground-beetles and tenebrionids (Coleoptera, Carabidae, Tenebrionidae) in the Krasnoturansk pine forest of the Idrinsk forestry.) – In: Nasekomye lesostepnykh borov Sibiri. Novosibirsk: Nauka: 76-98. [In Russian]. **[5]**

Apfelbeck, V. 1904 Die Käferfauna der Balkanhalbinsel I, Caraboidea. – Berlin: 1-422. **[5,maps]**

Apfelbeck, V. 1918 Koleopteren aus dem nordalbanisch-montenegrinischen Grenzgebiete. – Sitzungsber. Akad. Wiss. Wien, math.-nat. Kl., Abt. 1, 127: 4-18. **[8]**

Arndt, E. 1985 Larvenbestimmungsschlüssel der *Carabus*-Arten Europas (Col., Carabidae). – Entomol. Nachr. Ber. 29: 49-62. **[3,4,5,6]**

Arndt, E. 1989 Beiträge zur Insektenfauna der DDR: Gattung *Carabus* Linné (Coleoptera: Carabidae). – Beitr. Ent. 39: 63-103. **[5,6,8,9,maps]**

Arndt, E. 1991a Beitrag zur Kenntnis der Licinini-Larven (Coleoptera, Carabidae). – Entomol. Nachr. Ber. 35: 117-121. **[3,6]**

Arndt, E. 1991b Carabidae. – In: B. Klausnitzer: Die Larven der Käfer Mitteleuropas 1. Krefeld: 45-141. **[4,5]**

Arndt, E. 1993 Phylogenetische Untersuchung der Carabidae (Insecta, Coleoptera) unter besonderer Berücksichtigung larvalmorphologischer Merkmale. – Stuttgarter Beiträge zur Naturkunde, Ser. A, 488: 1-56. **[7]**

Arndt, E., Mossakowski, D. & F. Prüser 1994 Description of the larvae of the subgenus *Cathoplius* Thomson of *Carabus* L., with a key to North African *Carabus* larvae (Coleoptera: Carabidae) – Koleopterologische Rundschau 64: 21-25. **[4,7]**

Arndt, E. & J. Trautner (in prep.) Tribus Carabini. Revision of Band 2, Freude, Harde & Lohse (1976). – Die Käfer Mitteleuropas. Goecke & Evers Verlag. **[A]**

Arnett, R. H. Jr. & M.C. Thomas (eds.) 2001 American Beetles, 1. – Boca Raton-London-New York-Washington D.C.: CRC Press. **[8]**

Arnol'di, L.V. 1952 Obshchii obzor zhukov oblasti srednego i nizhnego techeniya r. Ural, ikh ekologicheskoe raspredelenie i khozyaistvennoe znachenie. (A general review of the beetles in the middle and low flow of Ural river, their ecological distribution and economic importance) – Tr. Zool. inst. Akad. nauk SSSR 11: 44-65. [In Russian]. **[5]**

Arnol'di, K.V. 1956 Ocherk entomofauny i kharakteristika entomokompleksov lesnoi podstilki v raione Derkula. (A review of the insect fauna and characteristics of soil and litter insect complexes in the Derkul flow) – Tr. Inst. lesa Akad. nauk SSSR 30: 279-342. [In Russian]. **[5]**

Arnol'di, K.V., T.S. Perel' & I.Ch. Sharova 1971 Vliyanie iskustvennykh lesnykh nasazhdenii na pochvennykh bespozvonochnykh glinistoi polupustyni. (Influence of artificial forest plantations upon soil invertebrates in the loamy semi-desert) – In: Zhivotnye iskustvennykh lesnykh nasazhdenii v glinistoi polupustyne. Moscow: Nauka: 34-54. [In Russian]. **[5]**

Arnol'di, K.V., I.Ch. Sharova, T.N. Klyukanova & N.N. Butrina 1972 Zhuzhelitsy (Carabidae, Coleoptera) Streletskoi stepi pod Kurskom i ikh sezonnaya dinamika aktivnosti. (Ground-beetles (Coleoptera, Carabidae) of Strelets steppe near Kursk and their seasonal abundance dynamics) – In: Fauna i ekologiya zhivotnykh. Moscow: 215-230. [In Russian]. **[5,t]**

Arzamasau, I.C. 1966 Drapezhn'ya zhuzhali rodu *Carabus* L. na ter'torii Belavezhskoi pushty. (The genus *Carabus* L. in the territory of Belovezha forest) – Vesci Akad. navuk BCCR, ser. biyal. 4: 114-118. [In Russian]. **[5,t]**

Assmann, T. 1981 Ein Beitrag zur Kenntnis der Carabidenfauna des Oppenweher Moores. – Osnabrücker naturwiss. Mitt. 8: 161-171. **[9]**

Assmann, T. 1983 Über die Bodenkäferfauna des Naturschutzgebietes "Lenger Meer" im Kreis Leer (Ostfriesland) (Coleoptera: Carabidae et Silphidae). – Drosera 83: 5-12. **[5]**

Assmann, T. 1990 Multiallelic genes in the carabid beetle *Carabus punctatoauratus* Germar from the Pyrenees. – In: Stork, N. E. (ed.): The role of ground beetles in ecological and environmental studies. – Hampshire: Intercept: 319-324. **[6]**

Assmann, T. 1994 Epigäische Coleopteren als Indikatoren für historisch alte Wälder der Nordwestdeutschen Tiefebene. – NNA-Berichte 3/94: 142-151. **[5,8]**

Assmann, T. 1995 Zur Populationsgeschichte der Laufkäfer *Carabus punctatoauratus* Germar und *Carabus auronitens* Fabricius (Coleoptera, Carabidae). Über Endemismus in eiszeitlichen Refugialräumen und postglaziale Arealausweitung. – Osnabrücker Naturwiss. Mitt. 20/21: 225-273. **[5,6,8]**

Assmann, T. 1998 Bedeutung der Kontinuität von Lebensräumen für den Naturschutz – Untersuchungen an waldbewohnenden Laufkäfern (Coleoptera, Carabidae) mit Beispielen für methodische Ergänzungen zur Langzeitforschung. – Schr.-R. f. Landschaftspfl. u. Natursch. 58: 191-214. **[6,8,9]**

Assmann, T. 1999 The ground beetle fauna of ancient and recent woodlands in north-west Germany (Coleoptera, Carabidae). – Biodiv. Cons. 8: 1499-1517. **[5,8,9]**

Assmann, T., M. Balkenohl, H. Dafner, J. Gebert, F. Hieke, G.A. Lohse, A Lompe, G. Müller Motzfeld, J. Schmidt, J. Trautner & D. Wrase 1998 Ergänzungen und Berichtigungen zu "Die Käfer Mitteleuropas". 1. Familie: Carabidae. – In: W. Lucht & B. Klausnitzer (eds.): Die Käfer Mitteleuropas 15: 5-76. **[5]**

Assmann, T., W. Dormann, H. Främbs, S. Gürlich, K. Handke, T. Huk, P. Sprick & H. Terlutter 2002 Rote Liste der in Niedersachsen und Bremen gefährdeten Laufkäferarten. – Inform. d. Natursch. Nieders. (accepted) **[9]**

Assmann, T. & B. Falke 1997 Bedeutung von Hudelandschaften aus tierökologischer und naturschutzfachlicher Sicht. – Schr.-R. f. Landschaftspfl. u. Natursch. 54: 129-144. **[9]**

Assmann, T. & J. Günther 2000 Relict populations in ancient woodlands: genetic differentiation, variability, and power of dispersal of *Carabus glabratus* (Coleoptera, Carabidae) in north-western Germany. – In: Brandmayr, P., G. L. Lövei, T. Z. Brandmayr, A. Casale & A. Vigna Taglianti (eds.): Natural history and applied ecology of carabid beetles. Sofia-Moscow: Pensoft Publishers: 197-206. **[6,8,t]**

Assmann, T. & J. Janssen 1999 Effects of habitat changes on the endangered ground beetle *Carabus nitens* (Coleoptera: Carabidae). – J. Ins. Conserv. 3: 107-116. **[5,6,8,9]**

Assmann, T., O. Nolte & H. Reuter 1994 Postglacial colonization of middle Europe by *Carabus auronitens* as revealed by population genetics (Coleoptera, Carabidae). – In: Desender, K., M. Dufrêne, M. Loreau, M. Luff & J.-P. Maelfait (eds.): Carabid beetles: ecology and evolution. – Dordrecht: Kluwer Academic Publishers: 3-9. **[5,6,8]**

Assmann, T. & C. Schnauder 1998 Morphometrische Untersuchungen an einer Kontaktzone zwischen *Carabus* (*Megodontus*) *violaceus* und *purpurascens* in Südwest-Niedersachsen (Coleoptera: Carabidae). – Osnabrücker Naturwiss. Mitt. 24: 111-138. **[5,6,maps,t]**

Assmann, T., E. Schröder & H. Terlutter 2000 Morphometric differentiation of *Carabus pyrenaeus* populations specialised in eating shell-bearing snails (Coleoptera, Carabidae). – In: Brandmayr, P., G. L. Lövei, T. Z. Brandmayr, A. Casale & A. Vigna Taglianti (eds.): Natural history and applied ecology of carabid beetles. Sofia-Moscow: Pensoft Publishers: 171-178. **[6]**

Assmann, T. & F. Weber 1997 On the allozyme differentiation of *Carabus punctatoauratus* Germar (Coleoptera, Carabidae). – J. Zool. Syst. Evol. Research 34: 33-43. **[5,6,9]**

Averin, V.G. 1938 Khishchnye zhuzhelitsy UkrSSR i vopros ob uspol'zovanii ikh dlya borby s vreditelyami (Predvaritelnoe soobshtenie). (Predatory ground-beetles in Ukrainian SSR and the problem of their use for pest control (Preliminary report)) – Zap. Khar'k. s.-kh. inst. 1: 3-37. [In Russian]. **[5]**

Azzaroli, A. 1983 Biogeografia dei Mammiferi della Sardegna. – Lav. Soc. ital. Biogeogr. (n.s.) 8 (1980) : 35-52. **[8]**

Baars, M.A. 1979 Patterns of movement of radioactive carabid beetles. – Oecologia (Berl.) 44: 125-140. **[6]**

Baev, P. & L. Penev 1995 BIODIV – a program for calculating biological diversity parameters, similarity, niche overlap and cluster analysis. – New York: Exeter Software: 1-57. **[8]**

Bakker, J.P. & F. Berendse 1999 Constraints in the restoration of ecological diversity in grassland and heathland communities. – Trends Ecol. Evol.: 63-68. **[9]**

Balkenohl, M. 1981 Die Carabidenfauna einer Hoch- und Wacholderheide des Sauerlandes. – Natur und Heimat 41: 51-55. **[5]**

Balkenohl, M. 1988 Coleoptera Westfalica: Familia Carabidae, Subfamilia Scaritinae et Broscinae. – Abhandlungen aus dem Landesmuseum für Naturkunde zu Münster 50: 1-28. **[5]**

Balkenohl, M. & H. Grosseschallau 1985 Höhenbedingte Veränderungen der Habitatbindung bei Carabiden. – Mitt. dtsch. Ges. allg. angew. Entomol. 4: 219-222. **[5,8,t]**

Balkenohl, M. & F. Weber 1981 Sind auch bei holometabolen Insekten circadiane Schrittmacher der Aktivität in den optischen Loben lokalisiert? – Mitt. dtsch. Ges. allg. angew. Ent. 3: 223-227. **[5,6]**

Ball, G.E. 1960 Carabidae (Latreille, 1810). – In: E. Arnett, The Beetles of the United States: 55-181. **[5,8]**

Ball, G.E. 1979 Conspectus of carabid classification: history, holomorphology and higher taxa. – In: T.L. Erwin, G. E. Ball, D.R. Whitehead & A.L. Halpern (eds.): Carabid beetles, their evolution, natural history, and classification. The Hague-Boston-London: Dr. W. Junk Publ.: 63-111. **[5]**

Ball G.E. & Y. Bousquet 2001 Family 6. Carabidae Latreille, 1802. – In: R.H. Arnett, Jr. & M.C. Thomas (eds.). American Beetles 1. Boca Raton-London-New York-Washington D.C.: CRC Press: 32-132. **[8]**

Balletto, E. & A. Casale 1991 Mediterranean insect conservation. – In: Collins, M. & J. Thomas (eds.): The conservation of insects and their habitats. London: Academic Press: 121-142. **[8,9]**

Ball, G.E., A. Casale, A. Vigna Taglianti (eds.) 1998 Phylogeny and classification of Caraboidea (Coleoptera: Adephaga). – Proceedings of a Symposium (28 August 1996, Florence, Italy). XX International Congress of Entomology. Atti Mus. reg. Sci. nat. Torino. **[8]**

Bangsholt, F. 1983 Sandspringernes og løbebillernes udbredelse og forekomst i Danmark ca. 1830-1981. (Coleoptera: Cicindelidae and Carabidae). – Dansk faunistisk Bibliotek 4: 1-271. **[5,maps,t]**

Barndt, D., S. Brase, M. Glauche, H. Gruttke, B. Kegel, R. Platen & H. Winkelmann 1991 Die Laufkäfer von Berlin (West)- mit Kennzeichnung und Auswertung der verschollenen und gefährdeten Arten (Rote Liste, 3. Fassung). – In: A. Auhagen *et al.* Rote Listen der gefährdeten Pflanzen und Tiere in Berlin. Landschaftsentwicklung und Umweltforschung S6: 243-275. **[5]**

Barner, K. 1937 Die Cicindeliden und Carabiden der Umgebung von Minden und Bielefeld I. – Abh. Landesmus. Naturk. Münster L8: 1-34. **[5]**

Barron, E.J., C.G.A. Harrison, J.L. Sloan & W.W. Hay 1981 Paleogeography, 180 million years ago to the present. – Eclogae Geol. Helv. 74: 443-470. **[8]**

Barsevskis, A. 1993 The Beetles of Eastern Latvia. – Saule: 1-90. **[5]**

Barsevskis, A. 1997 Carabidae. In: D. Telnov *et al.* Checklist of Latvian Beetles (Insecta: Coleoptera). – Mitteilungen der Internationaler Entomologischer Verein, Frankfurt am Main, suppl. 5: 9-20. **[5]**

Barsevskis, A. 2002 A check-list of Latvian Carabidae (Coleoptera: Adephaga). – Baltic J. Coleopterol. 2(2): 127-136. **[5]**

Basedow, T. 1987 Der Einfluß gesteigerter Bewirtschaftungsintensität im Getreidebau auf die Laufkäfer (Coleoptera, Carabidae). – Postdoctoral thesis required for qualification as a university lecturer, University of Gießen. **[9]**

Basedow, T. 1998 Langfristige Bestandsverändeungen von Arthropoden in der Feldflur, ihre Ursachen und deren Bedeutung für den Naturschutz, gezeigt an Laufkäfern (Carabidae) in Schleswig-Holstein, 1971-96. – Schr.-R. f. Landschaftspfl. u. Natursch. 58: 215-227. **[9]**

Basedow, T., Å. Borg & F. Scherney 1976 Auswirkungen von Insektizidbehandlungen auf die epigäischen Raubarthropoden in Getreidefeldern, insbesondere die Laufkäfer (Col., Carabidae). – Entomol. exp. appl. 19: 37-51. **[5,9]**

Basedow, T., Å. Borg & F. Scherney 1981 Auswirkungen von Insektizidbehandlungen auf die epigäischen Raubarthropoden in Getreidefeldern, insbesondere die Laufkäfer (Col., Carabidae). II. – Acta Agric. Scand. 31: 153-164. **[9]**

Battoni, S., A. Casale, P. Cavazzuti & P. Ratti 1995 Carabini 3. *Morphocarabus* (2), *Lipaster*. – Les coléoptères du monde 22. Venette: Sciences Nat. **[5,maps]**

Bauer, T. 1975 Stridulation bei *Carabus irregularis* Fabr. (Col., Carabidae). – Zool. Anz. 194: 1-5. **[5,6]**

Bauer, K.M. & U.N. Blutz von Blotzheim 1966 Handbuch der Vögel Mitteleuropas. – Frankfurt am Main: Akademische Verlagsgesellschaft. **[6]**

Baumgartner, R. 2000 Sexual attraction in *Carabus auronitens* F.: males lured by females. – In: Brandmayr, P., G. L. Lövei, T. Z. Brandmayr, A. Casale & A. Vigna Taglianti (eds.): Natural history and applied ecology of carabid beetles. Sofia-Moscow: Pensoft Publishers: 139-145. **[5,6]**

Baumgartner, R. 2002 Individual constancy of behavioural and developmental characters in *Carabus auronitens* F. (Coleoptera, Carabidae). – Szyszko *et al.* (eds.): Proceedings of the 10th European Carabidologist's Meeting, Tuczno (2001): *in prep.* **[5]**

Baumgartner, R., A. Bechtel, A. van den Boom, P. Hockmann, B. Horstmann, V. Kliewe, M. Landwehr and F. Weber 1997 Age pyramid of a local population and viability fitness of phenotypical fractions in *Carabus auronitens* (Coleoptera, Carabidae). – Ital. J. Zool. 64: 319-40. **[5,6,9]**

Baumgartner, R., P. Brandmayr & B.F.J. Manly 1998 Population and community ecology for insect management and conservation. – Proceedings of the ecology and population dynamics section of the 20th Int. Congr. of Entomology, Florence (1998). Rotterdam: Brookfield. **[5]**

Baur, B., D. Burckhardt, A. Coray, A. Erhardt, R. Heinertz, M. Ritter & M. Zemp 1997 Der Erdbockkäfer, *Dorcadion fuliginator* (L., 1758) (Coleoptera: Cerambycidae), in Basel. – Mitt. ent Ges. 47: 59-124. **[9]**

Bengtsson, S. 1927 Die Larven der nordischen Arten von *Carabus* L. – Lunds. Univ. Arsskript N.F. Adv. 24: 1-89. **[4,5,6,7,10]**

Berlov, O.E. 1989 Breeding of ground-beetles in the Baikal region. – In: Nasekomye paukoobraznye Sibiri. Irkutsk: 71-76. [In Russian] **[5]**

Berlov, O.E. 1990 *Carabus ermaki* Lutshnik: ekologiya, biologiya i razvedenie. (*Carabus ermaki* Lutshnik: ecology, biology and breeding) – Fauna i ekologiya zhuzhelits, Tez. dokl. III Vses. karabidol. sov. Kishinev: 7-8. [In Russian]. **[5]**

Berlov, O.E. & E.Ya. Berlov 1984 K biologii pribaikal'skich zhuzhelits roda *Carabus* L. (Coleoptera, Carabidae). (On the biology of ground-beetles of the genus *Carabus* (Coleoptera, Carabidae) in the territories surrounding the Lake Baikal) – In: Zhestkokrylye Sibiri. Irkutsk: 67-77. [In Russian]. **[5]**

Berlov, E.Ya. & O.E. Berlov 1997a Biologiya zhuzhelits podroda *Morphocarabus* (Coleoptera, Carabidae) Pribaikal'ya. (Biology of the ground beetles of the genus *Morphocarabus* (Coleoptera, Carabidae) of the Baikal Region) – Vestn. Irkut. Gos. Sel'khoz. Akad. 9: 39-41. [In Russian]. **[5]**

Berlov, E.Ya. & O.E. Berlov 1997b Zhiznennyi tsikl trekh sibirskikh populyatsii zhuzhelitsy *Carabus granulatus* (Coleoptera, Carabidae). (The life cicle of three Siberian populations of the ground beetle *Carabus granulatus* (Coleoptera, Carabidae)) – Vestn. Irkut. Gos. Sel'khoz. Akad. 7: 34-36. [In Russian]. **[5]**

Berlov, E.Ya. & O.E. Berlov 1997c Zametki o krymskoi zhuhelitse *Carabus (Procerus) scabrosus tauricus* (Coleoptera, Carabidae). (Notes on the Crimean ground beetle *Carabus (Procerus) scabrosus tauricus* (Coleoptera, Carabidae)) – Vestn. Irkut. Gos. Sel'khoz. Akad. 7: 37-40. [In Russian]. **[5]**

Berlov, E.Ya. & O.E. Berlov 1998 Osobennosti biologii dal'nevostochnykh populyatsii *Carabus granulatus* (Coleoptera, Carabidae). (Peculiarities in bionomy of the Fareastern populations of *Carabus granulatus* (Coleoptera, Carabidae)) – Vestn. Irkut. Gos. Sel'khoz. Akad. 10: 40-41. [In Russian]. **[5]**

Bertoldi, R., R. Domenico & R. Thunell 1989 Pliocene-Pleistocene vegetational and climatic evolution of the South-central Mediterranean. – Palaeogeogr. Palaeoclimatol. Palaeoecol. 72 : 263-275. **[8]**

Betz, J.O. 1992 Studies on winter-active larvae of the ground beetle *Carabus problematicus* (Coleoptera, Carabidae). – Pedobiologia 36: 159-167. **[5,6]**

Biondi, E., J.C. Koeniguer & C. Privé-Gill 1985 Bois fossils et vegetations arborescentes des régions méditerranéennes durant le Tertiaire. – G. bot. ital. 119: 167-196. **[8]**

Bisio, L. 1999 Contributo alla conoscenza di *Carabus* del subg. *Orinocarabus* del Piemonte: *Carabus latreilleanus* Csiki, 1927 (Coleoptera, Carabidae). – Riv. Piem. St. Nat. 20: 193-208. **[3,5,8]**

Bisio, L. 2000 Secondo contributo alla conoscenza di *Carabus* del subg. *Orinocarabus* del Piemonte: *Carabus putzeysianus*, e il gruppo *fairmairei-cenisius-heteromorphus* (Coleoptera, Carabidae). – Riv. Piem. St. Nat. 21: 115-152. **[3,5,8]**

Bisio, L. 2002 Terzo contributo alla conoscenza di *Carabus* del subg. *Orinocarabus* del Piemonte: *Carabus concolor* Fabricius, 1792 (Coleoptera, Carabidae). – Riv. Piem. St. Nat. 23: 155-166. **[3,5,8]**

Birks, H.J.B. & J.M. Line 1993 Glacial refugia of European trees – a matter of change? – Diss. Bot. 196: 283-291. **[6]**

Blumenthal, C.L. 1981 Einheimische *Carabus*-Arten als Bioindikatoren. – Jahresbericht der naturwissenschaftligen Verein Wuppertal 34: 70-77. **[5]**

Blumenthal, C.L. , C. Neudecker & U. Neumann 1977 *Carabus violaceus* L. in der Rheinprovinz. Zur Verbreitung in der Eiffel. – Decheniana, Beihefte 20: 10-21. **[5]**

Boettger, C.R. 1921: *Carabus morbillosus* Fabr. and *Otala tigri* Gerv., eine Studie gegenseitiger Anpassung. – Abh. Senckenb. Naturf. Ges. 37: 321-329. **[5,6]**

Bonadona, P. 1971 Catalogue des coléoptères carabiques de France. – Nouv. Rev. Entomol., suppl.: 1-177. **[5,9]**

Bonadona, P. 1973 Nouvelle contribution à la connaissance des races françaises de *Chrysocarabus solieri* (Col., Carabidae). – Ann. Soc. ent. Fr. (N.S.) 9: 759-812. **[3,6]**

Bosquet, J.C., A. Mollard & P. Meyer 2000 Monographie du sous-genre *Iniopachys* Solier, 1848. – Rutilans, suppl. 1: 1-20. **[A]**

Bousquet, Y. 1985 Morphologie comparée des larves de Pterostichini (Coleoptera: Carabidae). Descriptions et tables de détermination des espèces du nord-est de l'Amérique du nord. – Naturaliste canadien (Revue d'écologie et de systématique) 112: 191-251. **[4,7]**

Bousquet, Y. 2002 Additions and corrections to the catalogue of genus-group names of Geadephaga (Coleoptera) published by Lorenz (1998) – Folia Heyrovskyana, suppl. 9: 1-78. **[A]**

Bousquet, Y. & H. Goulet 1984 Notation of primary setae and pores on larvae of Carabidae (Coleoptera: Adephaga). – Canadian Journal of Zoology 62: 573-588. **[4,7]**

Bousquet, Y. & A. Larochelle 1993 Catalogue of the Geadephaga (Coleoptera: Trachypachidae, Rhysodidae, Carabidae including Cicindelini) of America North of Mexico. – Mem. Entomol. Soc. Canada 167: 1-397. **[7,8]**

Brakefield, P.M. 1991 Genetics and conservation of invertebrates. – In: Spellerberg, I.F., F.B. Goldsmith & M.G. Morris (eds.): The scientific management of temperate communities for conservation. Oxford: Blackwell: 45-79. **[9]**

Brandmayr, P. 1972 Studio ecologico sui Coleotteri Carabidi di due formazioni vegetali dell' Istria montana. – Bollettino di zoologia 39: 523-529. **[5]**

Brandmayr, P. 1983 The main axis of the coenoclinal continuum from macroptery to brachyptery in carabid communities of the temperate zone. – Report 4th Symp. Carab. 1981: 147-169. **[6]**

Brandmayr, P., G. Colombetta & S. Polli 1983 Waldcarabiden des Triester Karstes als Bioindikatoren des macroklimatischen Überganges vom kontinentalen Europa zur Mediterraneis (Coleoptera, Carabidae). – Zool. Jb.. Syst. 110: 201- 220. **[5,t]**

Brandmayr, P. & R. Pizzolotto 1988 Indicatori "storici" ed ecologici nella coleotterofauna terricola delle foreste dell'Appennino. – Atti XV Congr. naz. ital. L'Aquila: 589-608. **[5,t]**

Brandmayr, P. & T. Zetto-Brandmayr 1979 Contribution to ecology of an europhysic ground-beetle of Eastern Alps and Dinaric Karst, *Carabus creutzeri* Fabr. – Zool. Jb. Syst. 106: 50-64. **[6]**

Brandmayr, P. & T. Zetto-Brandmayr 1986a Food and feeding behaviour of some *Licinus* species (Coleoptera Carabidae Licinini). – Monitore zool. ital. (N.S.) 20: 171-181. **[6]**

Brandmayr, P. & T. Zetto-Brandmayr 1986b Phenology of ground beetles and its ecological significance in some of the main habitat types of southern Europe. – In: Den Boer *et al.* (eds.): Carabid beetles, their adaptations and dynamics. – Stuttgart: Gustav Fischer: 195-220. **[5]**

Brandmayr, P. & T. Zetto-Brandmayr 1988 Coleotteri Carabidi delle Dolomiti sudorientali e delle Prealpi Carniche. – Studi Trentini Sci. nat., Acta Biologica 64, suppl.: 125-250. **[8]**

Braun, S. 1988 Verwandtschaftsanalyse bei nahverwandten *Carabus*-Arten (Coleoptera, Carabidae) mittels elektrophoretischer Untersuchungen. – Mitt. dtsch. Ges. allg. angew. Ent. 6: 548-559. **[6]**

Braun, S., J.-C. Malausa & D. Mossakowski 1991 Genetic control of Chymotrypsin- and Trypsin-like enzymes in carabid beetles (Coleoptera, Carabidae). – Journal of Heredity 82: 164-167. **[5]**

Bremer, K. 1994 Branch support and tree stability. – Cladistics 10: 295-304. **[7]**

Breuning, S. 1926 Über *Carabus variolosus* Fabr. – Koleopterologische Rundschau 12: 19-25. **[5]**

Breuning, S. 1932-37 Monographie der Gattung *Carabus* L. – Bestimmungstabellen europäischer Coleopteren. Troppau: Reitter Edit. **[1,2,3,5,6,7,8,9,10]**

Březina, B. 1994 The check-list of the genus *Carabus* (Coleoptera, Carabidae). – Klapalekiana 30: 1-164. **[3,5]**

Březina, B. 1999 World catalogue of the genus *Carabus* L. – Sofia-Moscow: Pensoft Publishers: **[3,5,6,7,8,10]**

Briggs J.C. 2000 Centrifugal speciation and centres of origin. – J. Biogeogr. 27 (5): 1183-1188. **[8]**

Bro Larsen, G. 1936 Vergleichende Untersuchungen über die tunnelgrabenden Käfer von Skallingen. – Vidensk. Medd. Dansk Naturh. Foren. 100: 1-231. **[6]**

Broen, B. von 1965 Vergleichende Untersuchungen über die Laufkäferbesiedlung einiger norddeutschen Waldbestände und angrenzender Kalkschlagflächen. – Dt. ent. Z. N.F. 12: 67-82. **[5]**

Brouat, C., G. Mondor, P. Audiot, F. Sennedot, L. Lesobre, and J. Y. Rasplus 2002 Isolation and characterization of microsatellite loci in the ground beetle *Carabus nemoralis* (Coleoptera, Carabidae). – Molecular Ecology Notes 2: 119-120. **[A]**

Bruno, S. 1968 Distribuzione morphologia ed ecologia del *Carabus* (*Macrothorax*) *planatus* Chaudoir, 1843 (Coleoptera, Carabidae). – Boll. Acc. Gioenia Sc. Nat. Catania 9: 382-394. **[5]**

Brunsting, A.M.H. & H.J.L. Heessen 1984 Density regulation in the carabid beetle *Pterostichus oblongopunctatus*. – J. Animal Ecology 53: 751-760. **[6]**

Budarin, A.M. & E.G. Matis 1981 Zhuzhelitsy (Coleoptera, Carabidae) yuga Magadanskoi oblasti (The ground-beetles of the south of Magadan Province) – In: Fauna i ekologiya chlenistonogikh Sibiri. Irkutsk: Irkutsk University Press: 3-20. [In Russian]. **[5]**

Burakowski, B., M. Mroczkowski & J. Stefanska 1973 Chrzaszze Coleoptera Biegaczowate – Carabidae, czesc 1. – Katalog Fauny Polski 23: 1-233. **[5,6,maps]**

Buresch, I. & S. Kantardzhieva 1928 Vidovete ot podsem. Carabinae (sem. Carabidae, Coleoptera) v Balgaria, tyakhnoto razpoznavane i rasprostranenie. (The species of subfamily Carabinae (Carabidae, Coleoptera) in Bulgaria, their indentification and distribution) – Izv. Tcar. prir. inst. Sofia, 1: 45-107. [In Bulgarian]. **[8]**

Burmeister, F. 1939 Biologie, Ökologie und Verbreitung der europäischen Käfer 1, Adephaga-Caraboidea. – Krefeld. **[5]**

Busato E. & P.M. Giachino 1994 Contributo alla conoscenza della morfologia larvale del genere *Carabus*. La larva di *Carabus (Orinocarabus) latreilleanus* Csiki, 1927 (Coleoptera, Carabidae). – Riv. piem. St. nat. 14 (1993): 185-193. **[5]**

Butterweck, M. 1997 Metapopulationsstudien an Waldlaufkäfern (Coleoptera: Carabidae): Einfluß von Korridoren und Trittsteinbiotopen. – Berlin: Wissenschaft und Technik Verlag. **[6]**

Callot, H.-J. & C. Schott 1993 Catalogue et Atlas des Coléoptères d'Alsace, Tome 5: Carabidae. – Societé Alsacienne d'Entomologie: 1-168. **[5]**

Calow, P. (ed.) 1998 The encyclopedia of ecology and environmental management. – Oxford: Blackwell Science. **[6]**

Cárdenas, A. M. 1994 On the life history of *Calathus granatensis* (Coleoptera, Carabidae) in southwest Iberian Peninsula. – In: Desender, K., M. Dufrêne, M. Loreau, M. Luff & J.-P. Maelfait (eds.): Carabid beetles: ecology and evolution. – Dordrecht: Kluwer Academic Publishers: 109-116. **[6]**

Cárdenas, A.M. & C. Bach 1992 Primeras datos sobre la biologia de reproduccion y desarrollo larvario de *Macrothorax rugosus baeticus* Fabricius 1792 (Col. Carabidae). – Zool. Bat. 3: 139-146. **[5]**

Cárdenas, A.M. & J.M. Hidalgo 1995 Datos sobre la biologia de reproduccion y desarrollo larvario de *Carabus (Hadrocarabus) lusitanicus* (Fabricius 1802) (Coleoptera, Carabidae). – Elytron 9: 139-145. **[5]**

Cárdenas, A.M. & J.M. Hidalgo 2000 Seasonal activity and reproductive biology of the ground beetle *Carabus dufouri* (Coleoptera: Carabidae). – European J. Entomol. 97: 329-338. **[5,6]**

Casale A. 1988 Revisione degli Sphodrina (Coleoptera, Carabidae, Sphodrini). – Mus. reg. Sci. nat. Torino, Monografie 5: 1-1024. **[8]**

Casale, A., M. Bastianini & M. Minniti 1987 Sulla presenza in Toscana di *C. (Macrothorax) morbillosus* Fabricius (Coleoptera, Carabidae, Carabini) e sul suo significato zoogeografico. – Frust. entomol. (N.S.) 10: 67-72. **[8]**

Casale, A. & P. Cavazzuti 1975 Sul *Carabus (Chrysocarabus) solieri* Dejean in Italia (Col. Carabidae): sistematica, corologia, ecologia. – Boll. Ist. Entomol. Univ. Bologna 32: 231-255. **[3,8]**

Casale, A., F. Prüser, E. Arndt & D. Mossakowski 1998 Phylogenetic relationships in the subgenus *Platycarabus* Morawitz, 1886 (Coleoptera: Carabidae: Carabini). – In: Ball *et al.* (eds.): Phylogeny and classification of Caraboidea (XX I.C.E. 1996, Firenze, Italy). – Atti mus. reg. Sci. nat. Torino: 429-448. **[3,6,7,8]**

Casale, A., M. Sturani & A. Vigna Taglianti 1982 Coleoptera, Carabidae. I. Introduzione, Paussinae, Carabinae. – Fauna d'Italia 18: 1-499. **[2,3,4,5,6,8,9,maps,t]**

Casale, A. & A. Vigna Taglianti 1992 I Coleotteri Carabidi delle Alpi occidentali e centro-occidentali (Coleoptera, Carabidae). – Biogeographia (n.s.) 16: 331-339. **[8]**

Casale, A. & A. Vigna Taglianti 1996. Coleotteri Carabidi di Sardegna e delle piccole isole circumsarde, e loro significato biogeografico (Coleoptera, Carabidae). – Biogeographia (n.s.) 18 (1995): 391-427. **[5,8]**

Casale, A. & A. Vigna Taglianti 1999 Caraboid beetles (excl. Cicindelidae) of Anatolia, and their biogeographical significance (Coleoptera, Caraboidea). – Biogeographia 20: 277-406. **[5,8,maps]**

Caubet, F. 2001 Monographie de *Carabus (Chrysocarabus) punctatoauratus* Germar, 1824. – Rutilans, suppl. 2 : 1-47. **[A]**

Cavazzuti, P. 1989 Monografia del Genere *Procerus* (Coleoptera, Carabidae, Carabini). – Edizione L'Artistica Savigliano, Mem. Ass. Natur. Piem. I: 1-200. **[3,4,5,6,maps]**

Cavazzuti, P. & D. Ghiretti 1992 Schedario iconografico del genere *Carabus* L. Vol. I. *Lamprostus* Mostchulsky. Colombo & C.: 1-8 + 69 pl. **[5]**

Cavazzuti, P. & M. Meli 1999. *Carabus* (*Orinocarabus*) *putzeysianus bisioi* n. ssp. delle Alpi occidentali italiane (Coleoptera, Carabidae). – Boll. Soc. entomol. ital. 131: 111-118. **[8]**

Chatenet, G. du 1986 Généralités, Carabidae. In: Guide des coléoptères d'Europe. – Paris: 1-189. **[5]**

Chernov, Yu.I. 1975 Prirodnaya zonal'nost' i zhivotnyi mir sushi. (The nature zonation and the terrestrial animals) – Moscow: Mysl': 1-222. [In Russian]. **[8]**

Chernov, Yu.I. 1984 Flora i fauna, rastitel'nost' i zhivotnoe naselenie (Flora and fauna, vegetation and animal communities) – Zhurn. Obshch. Biol. 45 (6): 732-748 [In Russian]. **[8]**

Chiverton, P.A. 1984 Pitfall-trap catches of the carabid beetle *Pterostichus melanarius*, in relation to gut contents and prey densities, in insecticide treated and untreated spring barley. – Entomol. exp. appl. 36: 23-30. **[9]**

Chumakov, L.C. 1986 Zhuzhelitsy lesnykh biotsenozov v usloviyakh vozdeistviya promyshelennykh vybrosov (The ground-beetles of forest biocoenoses in the conditions of industrial pollution). – Izv. Akad. nauk BSSR 22: 1-33. [In Russian]. **[5]**

Chumakov, L.S. 1987 Sezonnaya aktivnost' zhuzhelits melkolistvennykh lesov v usloviyakh vozdeistviya promyshlennykh vybrosov. (Seasonal activity of ground-beetles in small-leaved forests under impact of industrial pollution) – Izv. Akad. nauk BSSR, Ser. biol. Nauk: 1-12 (Depoz. VINITI 19.02.87, N 1829-B87). [In Russian]. **[5]**

Chumakov, L.S. 1990 Zhuzhelitsy v lesakh Pripyatskogo zapovednika BSSR. (The ground-beetles in forests of the Pripyat Reserve in Byelorussia) – Fauna i ekologiya zhuzhelits, Tez. dokl. III Vses. karabidol. sov. Kishinev: 69. [In Russian]. **[5]**

Claridge, M.F., H.A. Dawah & M.R. Wilson 1997 Practical approach to species concepts for living organisms. – In: M.F. Claridge, H.A. Dawah & M.R. Wilson (eds.): Species: the units of biodiversity. London: Chapman and Hall: 1-16. **[9]**

Cleu, H. 1965 Les variations evolutives des carabes du groupe de *Megodontus violaceus* L. en Europe occidentale et centrale (Col.Carabidae). – Annales de la Société Entomologique de France (N.S.) 1: 29-56. **[3]**

Cleu, H. 1966 Les variations evolutives des carabes du groupe de *Megodontus violaceus* L. en Europe occidentale et centrale (Col.Carabidae). – Annales de la Société Entomologique de France (N.S.) 2: 951-966. **[3]**

Cleu, H. 1969 Revision des formes du phylum de *Megodontus violaceus* L. dans la peuplement de l'Europe, leur determination et leur classification (Col. Carabidae). – Bulletin de la Société Entomologique de France 74: 162-175. **[3]**

Clutton-Brock, T. H. 1991 The evolution of parental care. – Princeton University Press, Princeton: New Jersey: 1-352. **[6]**

Conradi-Larsen, E.M. & L. Sømme, 1973a Anaerobiosis in the overwintering beetle *Pelophila borealis* (Coleoptera, Carabidae). – Nature 245: 388-390. **[6]**

Conradi-Larsen, E.M. & L. Sømme, 1973b The overwintering of *Pelophila borealis* Payk. (Coleoptera, Carabidae), II. Aerobic and anaerobic metabolism. – Norsk. Entomol. Tidsskr. 20: 325-332. **[6]**

Coope, G.R. 1977 Fossil Coleopteran assemblages as sensitive indicators of climatic changes during the Devensian (Last) cold stage. – Phil. Trans. Royal Soc. London Series B 280: 313-340. **[6]**

Coope G.R. 1979a. Late cenozoic fossil Coleoptera: Evolution, Biogeography, and Ecology. – Ann. Rev. Ecol. Syst. 10: 247-267. **[8]**

Coope G.R. 1979b. The Carabidae of the Glacial Refuge in the British Isles and their Contribution to the Post Glacial Colonization of Scandinavia and North Atlantic Islands. – In: T.L. Erwin, G.E. Ball, D.R. Whitehead & A.L. Halpern (eds.): Carabid beetles, their evolution, natural history, and classification. The Hague-Boston-London: Dr. W Junk Publ.: 407-424. **[8]**

Coulon, J., P. Marchal, R. Pupier, P. Richoux, R. Allemand, L.-C. Genest & J. Clary, 2000 Coléoptères de Rhône-Alpes. Carabiques et Cicindèles. – Muséum d'Histoire naturelle de Lyon; Société linnéenne de Lyon: 1-193, planches (549 maps): 1-183. **[5]**

Coyne, J.A., A.A. Felton & R.C. Lewontin 1978 Extent of genetic variation at a highly polymorphic esterase locus in *Drosophila pseudoobscura*. – Proc. Nat. Acad. Sci. USA 75: 5090-5093. **[6]**

Cracraft, J. 1997 Species concepts in systematics and conservation biology – an ornithological viewpoint. – In: M.F. Claridge, H.A. Dawah & M.R. Wilson (eds.): Species: the units of biodiversity. London: Chapman and Hall: 325-339. **[9]**

Crisci J.V. 2001. The voice of historical biogeography. – J. Biogeogr. 28(2): 157-168. **[8]**

Croizat L., G. Nelson & D.E. Rosen 1974 Centers of origin and related concepts. – Syst. Zool. 23: 265-287. **[8]**

Csiki, E. 1906 Adatok a magyarországi *Morphocarabus* ok ismeretéhez. (Beiträge zur Kenntniss der ungarischen Morphocaraben.) – Annales Musei Nationalis Hungarici 4: 244-262. **[5]**

Csiki, E. 1927-1932 Coleopterorum Catalogus: Pars 91, 92, 97, 98, 104, 115, 121, 124, 126, 127 – Berlin. **[5]**

Csiki, E. 1941 Adatok Kőszeg és vidéke bogárfaunájának ismeretéhez. (Beiträge zur Kenntnis der Käferfauna in Kőszeg und Umgebung.) – Dunántúli Szemle 8: 158-168; 283-288; 332-338. **[5]**

Csiki, E. 1946 Die Käferfauna des Karpaten-Beckens 1, Alg. Teil und Caraboidae. – Budapest: 1-546, 707-722. **[5,maps]**

Dahl, E. 1987 The nunatak theory reconsidered. – Ecol. Bull. 38: 77-94. **[6]**

Daly, H.V., J.T. Doyen & A.H. Purcell 1998 Introduction to insect biology and diversity. – Oxford-New York: Oxford University Press: 1-680. **[6]**

Darge, Ph. 1991 Introduction au genre *Carabus* en Turquie. – Clenay: France: 1-83. **[5,maps]**

Darlington Ph.J., Jr. 1957 Zoogeography : the Geographical Distribution of Animals. – New York-London: John Wiley & Sons and Chapman & Hall: xiv + 1-675. **[8]**

Darlington, P.J. 1979 Some events and trends in study of Carabidae in North America. – In: Erwin, T.L., G.E. Ball & D.R. Whitehead (eds.): Carabid beetles, their evolution, natural history, and classification. The

Hague-Boston-London: Dr W. Junk Publishers: 17-20. [8]

Darnaud, J. 1977 *Chrysocarabus auronitens* F. 1792. – Iconographie Entomologique Coléoptères, planche 1. **[5,maps]**

Darnaud, J., M. Lecumberry & R. Blanc 1978a *Chrysocarabus rutilans* Dejean 1826. Iconographie Entomologique Coléoptères, planche 2. **[5,maps]**

Darnaud, J., M. Lecumberry & R. Blanc 1978b *Chrysocarabus auronitens* F. 1792 (suite 1). – Iconographie Entomologique Coléoptères, planche 3. **[5,maps]**

Darnaud, J., M. Lecumberry & R. Blanc 1978c *Chrysocarabus solieri* Dejean 1826. – Iconographie Entomologique Coléoptères, planche 4. **[5,maps]**

Darnaud, J., M. Lecumberry & R. Blanc 1979a *Chrysocarabus lineatus* Dejean 1826. – Iconographie Entomologique Coléoptères, planche 6. **[5,maps]**

Darnaud, J., M. Lecumberry & R. Blanc 1979b *Megodontus purpurascens* F. 1787. – Iconographie Entomologique Coléoptères, planche 8. **[5,maps]**

Darnaud, J., M. Lecumberry & R. Blanc 1980a *Eucarabus monilis* F. 1792. – Iconographie Entomologique Coléoptères, planche 10. **[5,maps]**

Darnaud, J., M. Lecumberry & R. Blanc 1980b *Chrysocarabus punctatoauratus* Germar 1824. – Iconographie Entomologique Coléoptères, planche 11. **[5,maps]**

Darnaud, J., M. Lecumberry & R. Blanc 1981a *Chrysocarabus punctatoauratus* Germar 1824 (suite). – Iconographie Entomologique Coléoptères, planche 12. **[5]**

Darnaud, J., M. Lecumberry & R. Blanc 1981b Genre *Macrothorax* Desmarest 1850. – Iconographie Entomologique Coléoptères, planche 13. **[5,maps]**

Darnaud, J., M. Lecumberry & R. Blanc 1983a *Chrysocarabus hispanus* F. 1792. – Iconographie Entomologique Coléoptères, planche 14. **[5,maps]**

Darnaud, J., M. Lecumberry & R. Blanc 1983b *Autocarabus auratus* L. 1761. – Iconographie Entomologique Coléoptères, planche 15. **[5,maps]**

Darnaud, J., M. Lecumberry & R. Blanc 1984a Le genre *Procerus* Dejean 1825. – Iconographie Entomologique Coléoptères, planche 16 . **[5,maps]**

Darnaud, J., M. Lecumberry & R. Blanc 1984b Genre *Megodontus* Solier, *caelatus/croaticus*. – Iconographie Entomologique Coléoptères, planche 17 . **[5,maps]**

De Felice, S. 2000 Biolit, a literature database system with CarLit2000. – In: Turin, H. 2000: De Nederlandse Loopkevers, cd-rom **[5]**

De Lattin, G. 1967 Grundriss der Zoogeographie – Jena: Gustav Fischer Verlag: 1-602. **[8,10]**

Delkeskamp, K. 1930 Biologische Studien über *Carabus nemoralis* Müll. – Z. Morph. Ökol. Tiere 19: 1-58. **[6]**

Den Boer, P.J. 1968 Spreading of risk and stabilization of animal numbers. – Acta Biotheor. 18: 165-194. **[6]**

Den Boer, P.J. (ed.) 1971 Dispersal and dispersal power of Carabid beetles. – Misc. Papers Wageningen 8: 1-151. **[8]**

Den Boer, P.J. 1977 Dispersal power and survival. Carabids in a cultivated countryside (with a mathematical appendix by J.Reddingius). – Misc. Papers Wageningen 14: 1-190. **[5]**

Den Boer, P.J. 1981 On the survival of populations in a heterogeneous and variable environment. – Oecologia 50: 39-53. **[6,9]**

Den Boer, P.J. 1990 Density limits and survival of local populations in 64 carabid species with different powers of dispersal. – J. evol. Biol. 3: 19-48. **[6,9]**

Den Boer, P.J. & W. den Boer-Daanje 1990 On life history tactics in carabid beetles: are there only spring and autumn breeders? – In: Stork, N.E. (editor): The role of ground beetles in ecological and environmental studies. – Andover: Intercept: 247-258. **[6]**

Den Boer, P. J. & Th. S. van Dijk 1994 Carabid beetles in a changing environment. – Wageningen Agricultural University Papers 94-6: 1-30. **[5,6,9]**

Den Boer, P.J., T.H.P. van Huizen, W. den Boer-Daanje, B. Aukema & C.F.M. den Bieman 1980 Wing Polymorphism and Dimorphism as Stages in an Evolutionary Process (Coleoptera, Carabidae). – Entomologia Generalis 6: 107-134. **[5]**

Dercourt, J., L.P. Zonenshein, L.E. Ricou, V.G. Kazmin, X. Le Pichon, A.L. Knipper, C.Grandjacquet, J.M. Sbortshikov, J. Geyssant, C. Lepvrier, D.H. Pechersky, J.C. Boulin, L.A. Savostin, O. Sorokhtin, M. Wesphal, M.L. Bazhenov, J.P. Laver & B. Biju-Duval 1986 Geological evolution of the Tethys Belt from the Atlantic to the Pamirs since the Lias. – Tectonophysics 123: 241-315. **[8]**

Desender, K. 1986 Distribution and ecology of carabid beetles in Belgium (Coleoptera, Carabidae). Part 1–4. – Studiedocumenten van het Koninklijk Belgisch Instituut voor Natuurwetenschappen 26, 27, 30, 34. **[5,maps]**

Desender, K., R. Bosmans & K. de Smet 1987 Nouvelle données sur le genre *Carabus* (Coleoptera, Carabidae) de l'Afrique du Nord. – Annales de l'institute national agronomique (el - harrach) Alger 2: 46-57. **[5]**

Desender, K., A. Ervynck & G. Tack 1999 Beetle diversity and historical ecology of woodlands in Flanders. – Belg. J. Zool. 129 (1): 137-154. **[6,9]**

Desender, K., D. Maes, J.-P. Maelfait & M. van Kerckvoorde 1995 Een gedocumenteerde Rode lijst van de zandloopkevers en loopkevers van Vlaanderen. – Brussel: 1-208. **[5,maps]**

Desender, K. & H. Turin 1989 Loss of habitats and changes in the composition of the ground and tiger beetle fauna in four West European countries since 1950 (Coleoptera: Carabidae, Cicindelidae). – Biol. Conser. 48: 277-294. **[5,9]**

Deuve, T. 1991 La nomenclature taxonomique du genre *Carabus*. – Bibliothèque entomologique, vol. 4. Paris-Venette: Sciences Nat: 1-198. **[3,5,7,10]**

Deuve, T. 1993 L'abdomen et les genitalia des femelles de Coléoptères Adephaga. – Mémoires du Muséum National d'Histoire Naturelle, Zoologie 155: 1-184. **[5,6]**

Deuve, T. 1994 Une classification du genre *Carabus*. – Venette: Sciences Nat. **[3,5,6,7,8,10]**

Deuve, T. 1997a Etude d'un hybride exceptionnel entre deux *Carabus* des sous-genres *Chrysocarabus* et *Iniopachys* (Coleoptera, Carabidae). – Bull. Soc. entomol. France 102: 255-263. **[5,6]**

Deuve, T. 1997b Catalogue des Carabini et Cychrini de Chine. – Mém. Soc. entomol. Fr. 1-236. **[8]**

Deuve, T. 1998a L'origine des Hexapodes. Les Insectes sont-ils des Crustacés adaptés à la vie terrestre ? – Bull. Soc. entomol. Fr. 103 (4): 319-326. **[8]**

Deuve, T. 1998b Trois fossiles remarquablement conservés du Miocène de France, appartenant aux genres *Carabus* L. et *Ledouxnebria* nov. (Coleoptera, Carabidae et Nebriidae). – Bull. Soc. entomol. Fr. 103 (3): 229-236. **[8]**

Deuve, T. 2002 Sur l'identité de *Carabus (Oreocarabus) fairmairei* Thomson, 1875, et de *C. (O.) putzeysianus* Géhin, 1876, et note sur la variation géographique de *C. (O.) pedemontanus* Ganglbauer, 1892, *bona species* (Coleoptera, Carabidae). – Rev. fr. Entomol. (N.S.) 24 (1): 1-17. **[10,A]**

De Vries, H.H. 1994 Size of habitat and presence of ground beetle species. – In: K. Desender, M. Dufrêne, M. Loreau, M. Luff and J.-P. Maelfait (eds.): Carabid beetles: ecology and evolution. Dordrecht: Kluwer Academic Publishers: 253-259. **[9]**

De Vries, H.H. 1996 Metapopulation structure of *Poecilus lepidus* and *Olisthopus rotundatus* on heathland in the Netherlands: the results from transplant experiments. – Ann. Zool. Fennici 33: 77-84. **[9]**

De Vries, H.H. 2000 Multiple paternity of ground beetles. – Mitt. Dtsch. Ges. Allg. Angew. Ent. 12: 441-448. **[6]**

De Vries, H.H. & P.J. den Boer 1990 Survival of populations of *Agonum ericeti* Panz. (Col., Carabidae) in relation to fragmentation of habitats. – Neth. J. Zool. 40: 484-498. **[9]**

Dewey, I.F., W.C. Pitman, W.B.F. Ryan & J. Bonnin 1973 Plate Tectonics and the Evolution of the Alpine System. – Geol. Soc. Amer. Bull. 84: 3137-3180. **[8]**

Drees, C. & T. Huk 2000 Sexual differences in locomotory activity of the ground beetle *Carabus granulatus* L. – In: Brandmayr, P., G. L. Lövei, T. Z. Brandmayr, A. Casale & A. Vigna Taglianti (eds.): Natural History and applied ecology of carabid beetles. Sofia-Moscow: Pensoft Publishers: 133-138. **[5]**.

Drovenik, B. 1972 Rod *Carabus* L. (Coleoptera) v Sloveniji. – Acta Entomol. Jugoslavica 8 (1-2): 23-31. **[8,t]**

Drovenik, B. 1995 Carabiden der Balkanländer. – Coleoptera. Schwanfelder Coleopterologische Mitteilungen: 3-103. **[5,maps]**

Du Chatenet, G. 1986 Généralités, Carabidae. – In: Guide des coléoptères d'Europe. Paris: 1-189. **[5,maps]**

Düring, A. & M. Brückner 2000 The evolutionary history of the tribus Molopini: a first molecular approach. – In: Brandmayr, P., G. L. Lövei, T. Z. Brandmayr, A. Casale & A. Vigna Taglianti (eds.): Natural History and applied ecology of carabid beetles. Sofia-Moscow: Pensoft Publishers: 1-4. **[7]**

Düring, A., A. Brückner & D. Mossakowski 2001 Differenzen zwischen gene tree und organismal tree? Mitochondriale Gene und die Verwandtschaftsbeziehungen der *Chrysocarabus*-Arten. – Ent. Basil. 23: 93-98. **[A]**

Düring, A., M. Brückner, M. Zimmermann, I. Bobenhausen, N. Eicke & D. Mossakowski 2000 Geographic distribution of two highly different mtDNA haplotypes in *Carabus (Chrysocarabus) splendens* Olivier. – In: Brandmayr, P., G. L. Lövei, T. Z. Brandmayr, A. Casale & A. Vigna Taglianti (eds.): Natural History and applied ecology of carabid beetles. Sofia-Moscow: Pensoft Publishers: 5-9. **[5,8]**

Easteal, E. 1988 Range expansion and its genetic consequences in populations of the Giant Toad, *Bufo marinus*. – Evolutionary Biology 23: 49-84. **[6]**

Eberhard, W.G. 1985 Sexual selection and animal genitalia. – Cambridge (Massasuchetts): Harvard University Press. **[6]**

Ehrendorfer, F 1999 Übersicht des Pflanzenreichs. – In: Sitte, P., H. Ziegler, F. Ehrendorfer & A. Bresinsky (eds.): Strasburger: Lehrbuch der Botanik für Hochschulen. – Stuttgart: Gustav Fischer Verlag: 517-819. **[6]**

Eidam, P. 1941a *Carabus violaceus* L. und *purpurascens* L. – Entomologische Blätter für Biologie und Systematik der Käfer 37: 45-46. **[5]**

Eidam, P. 1941b Berichtungen und Ergänzungen zu Breunings Monographie des *Carabus cancellatus* Ill. – Entomologische Blätter für Biologie und Systematik der Käfer 37: 194-207. **[5]**

Eidelberg, M.M., I.V. Mal'tsev & V.P. Pervakov 1988 Vidovoi sostav zhuzhelits (Coleoptera, Carabidae) Kryma. (Species composition of the ground-beetles (Coleoptera, Carabidae) of the Crimea) – In: Ekologiya i taksonomiya nasekomykh Ukrainy. Kiev: Naukova dumka: 61-68. [In Russian]. **[5]**

Elias, S.A. 1994 Quaternary insects and their environments. – Washington and London: Smithsonian Institution Press. **[6]**

Eremin, P.K. 1986 Dinamika naseleniya zhuzhelits (Coleoptera, Carabidae) v estestvennykh biotsenozakh Privetluzh'ya. (Dynamics of ground-beetle population (Coleoptera, Carabidae) in natural biocenoses of the territory near Vetluga) – Dokl. Mosk. obshch. ispyt. prir., Zool. i botan. Novye aspekty issledov. biol. flory i fauny SSSR. Moscow: 19-21. [In Russian]. **[5]**

Erwin T.L. 1979 Thoughts on the Evolutionary History of Ground Beetles: Hypotheses Generated from Comparative Faunal Analyses of Lowland Forest Sites in Temperate and Tropical Regions. – In: T.L. Erwin, G.E. Ball, D.R. Whitehead (eds.): Carabid beetles, their evolution, natural history, and classification. The Hague-Boston-London: Dr W. Junk Publ.: 539-592. **[8]**

Erwin T.L. 1981 Taxon Pulses, Vicariance, and Dispersal: An Evolutionary Synthesis Illustrated by Carabid Beetles. In: G. Nelson, D.E. Rosen (eds.): Vicariance Biogeography: A Critique. New York: Columbia University Press: 159-183. **[8]**

Erwin T.L. 1982 Tropical forests: their richness in Coleoptera and other species. – Coleopterists Bulletin 36: 74-75. **[1]**

Erwin T.L. 1988 The tropical forest canopy. The hearth of biotic diversity. – In: E.O. Wilson (ed.): Biodiversity. Washington D.C.: Nat. Academy Press: 123-129. **[1]**

Erwin, T.L., D.R. Whitehead & G.E. Ball 1977 North American Beetle Fauna Project, Family 4. Carabidae, The Ground Beetles, Checklist (Yellow version). – NY: Kinderhook: 4.1-4.68. **[5]**

Estabrook, G.F. 2001. Vicariance or dispersal: the use of natural historical data to test competing hypotheses of disjunction on the Thyrrhenian coast. – J. Biogeogr. 28: 95-103. **[8]**

Esterberg, L.K. 1935 Nasekomye Gor'kovskogo i Kirovskogo kraev. (The insects of the Gorky and Kirov provinces) – In: Priroda Gor'kovskogo i Kirovskogo kraev. Gor'kii: 196-210. [In Russian]. **[5]**

Esjunin, S.I., S.I. Golovatch & L.D. Penev 1993 The fauna and zoogeography of spiders inhabiting oak forests of the East European Plain. – Ber. Nat.-med. Verein Innsbruck 80: 175-249. **[5,8]**

Esjunin, S.L., V.O. Koz'minykh & A.V. Kozyrev 1995 Zhestkokrylye Permskoi oblasti. 10. Materialy k faune zhestkokrylykh zapovedinka "Basegi": spisok vidov po semeistvam. (The beetles (Insecta, Coleoptera) of the Perm province. 10. Materials on the beetle fauna of Basegi reserve: a list of species by families) – Depozited in the Scientific Laboratory "Denast" [In Russian]. **[5]**

Evans, M.E.G. 1977 Locomotion in the Coleoptera Adephaga, especially Carabidae. – J. Zool. London 181: 189-222. **[6]**

Evans, M.E.G. 1986 Carabid locomotor habits and adaptations. – In: den Boer, P.J., M.L. Luff, D. Mossakowski & F. Weber 1986 (eds.): Carabid beetles: their adaptations and dynamics. Stuttgart-New York: Gustav Fischer: 59-77. **[6]**

Evans, W.G. 1982 *Oscillatoria* sp. (Cyanophyta) mat metabolites implicated in habitat selection in *Bembidion obtusidens* (Coleoptera: Carabidae). – J. Chem. Ecol. 8: 671-678. **[6]**

Evans, W.G. 1983 Habitat selection in the Carabidae. – Coleopt. Bull. 37: 164-167. **[6]**

Falke, B., S. Oevermann & T. Assmann 2000 Ground beetle diversity of a medieval wood-pasture reserve in north-west Germany (Coleoptera, Carabidae). – In: Brandmayr, P., G. L. Lövei, T. Z. Brandmayr, A. Casale & A. Vigna Taglianti (eds.): Natural History and applied ecology of carabid beetles. Sofia-Moscow: Pensoft Publishers: 265-275. **[9]**

Fedorenko, D.N. 1988 Fauna zhuzhelits (Coleoptera, Carabidae) Moskovskoi oblasti. (The fauna of ground-beetles (Coleoptera, Carabidae) of Moscow Province) – In: Nasekomye Moskovskoi oblasti: Problemy kadastra i okhrany. Moscow: Nauka: 20-46. [In Russian]. **[5]**

Feoktistov, V.F. 1979 Kompleksy zhuzhelits v fitotsenoticheskikh ryadakh Mordovskogo zapovednika. (Ground-beetle complexes of phytocenotic series in the Mordov Reserve) – In: Fauna i ekologiya bespozvonochnykh zhivotnykh. Moscow: 26-40. [In Russian]. **[5]**

Ferenz, H.-J. 1977 Two-step photoperiodic and hormonal control of reproduction in the female beetle, *Pterostichus nigrita*. – J. Insect. Physiol. 23: 671-676. **[6]**

Ferenz, H.-J. 1986 Photoperiodic regulation of juvenile hormone and reproduction in the carabid beetle *Pterostichus nigrita*. – In: den Boer, P.J., M.L. Luff, D. Mossakowski & F. Weber (eds.): Carabid beetles: their adaptations and dynamics. Gustav Fischer: Stuttgart-New York: 113-123. **[6]**

Filippov, B.Yu. 2000 Naselenie i dinamika demograficheskoi struktury populyatsii zhuzhelits (Coleoptera, Carabidae) v lesakh severnoi taigi (Communities and dynamics of demographic structure of the ground beetle populations in the northern taiga forests) – Avtoref. Kand. Diss. Moscow: 1-16. **[5]**

Focarile, A. 1987 Écologie et biogéographie des coléoptères de haute altitude en Région Autonome de la Vallée d'Aoste. – Récherches sur la faune entomologique de la Vallée d'Aoste. – Reg. Valle d'Aosta, Ass. Agric., For. e Amb. natur 16: 1-167 (incl. 77 maps; 4 Pl.). **[5,maps]**

Focarile, A. & A. Casale 1978 Primi rilevamenti sulla coleotterofauna alticola del vallone di Clavalité (Fenis, Aosta). – Rev. Valdôtaine d'Hist. Naturelle 32: 67-92. **[maps]**

Fomichev, A.I. 1982 Predvaritel'nyi ocherk koleopterofauny Kalmykii. (A provisional review of the beetle fauna of Kalmykia) – In: Zhivotnyi mir Kalmykii, ego okhrana i ratsional'noe ispol'zovanie. Elista: 117-123. [In Russian]. **[5]**

Fomichev, A.I. 1983 Spisok vidov zhestkokrylykh Kalmykii i sopredel'nykh rayonov. (A list of species of Coleoptera of Kalmykiya and the adjacent territories) – Kalm. gos. univ. Elista: 1-60 (Rukopis' depoz. VINITI, 12.04.1983, N 1921-83 (Dep.)). [In Russian]. **[5]**

Forel, J. & J. Leplat 1995 Les Carabes de France. – Venette: Sciences Nat. **[5,6,maps]**

Forel, J. & J. Leplat 1998 Faune des *Carabus* de la Péninsule Ibérique. – Andrésy: Magellanes. **[5,6,9,maps]**

Forsythe, T.G. 1981 Running and pushing in relationship to hind leg structure in some Carabidae (Coleoptera). – Coleopt. Bull. 35: 353-378. **[6]**

Forsythe, T.G. 1983 Locomotion in ground beetles (Coleoptera Carabidae): an interpretation of leg structure in functional terms. – J. Zool. Lond. 200: 493-507. **[6]**

Franklin, I.R. 1980 Evolutionary change in small populations. In: Soulé, M.E. & B.A. Wilcox (eds.): Conservation biology: an evolutionary-ecological perspective. – Sunderland, Massachusetts: Sinauer: 135-150. **[9]**

Franz, H. 1929 Morphologische und phylogenetische Studien an *Carabus* L. und den nächstverwandten Gattungen. – Z. wiss. Zool. 135: 163-213. **[6]**

Franz, H. 1943 Die Landtierwelt in der mittleren hohen Tauern. Ein Beitrag zur tiergeographischen und soziologischen Erforschung der Alpen. – Denkschriften der Akademie der Wissenschaften in Wien. Mathematisch-naturwissenschaftenliche Klasse, 107. **[5,8,maps]**

Franz, H. 1970 Die Nordost-Alpen im Spiegel ihrer Landtierwelt, III. – Innsbruck-München: Universitätsverlag Wagner. **[5,8,maps,t]**

Franz, H. 1971 Beiträge zur Zoogeographie der Bergamasker Alpen und der Berninagruppe. – Zeitschrift für Arbeitsgem. Oesterr. Entomol. 23: 2-10. **[5,8]**

Franz, H. 1983 Rote Liste der in Österreich gefährdeten Käferarten (Coleoptera) – Hauptteil. In: Gepp, J. (ed.): Rote Listen gefärdeter Tiere Österreichs. – Bundesministeriums fur Gesundheit und Umweltschutz. Wien: 9-92. **[5]**

Franz, H. 1984 Beitrag zur Kenntnis der Coleopterenfauna Mazedoniens. – Zeitschrift für Arbeitsgem. Oesterr. Entomol. 36: 57-62. **[5]**

Franzen, M. 1995 Nachweise von *Carabus irregularis* Fabricius, 1792 aus Rheinland-Pfalz (Coleoptera: Carabidae). – Fauna Flora Rheinland-Pfalz 8: 5-15. **[6]**

Franzke, A. 1999 Molekulare Phylogeographie des *Cardamine pratensis*-Komplexes (Brassicaceae). – Doctoral Thesis, University of Osnabrück. **[6]**

Freude, H., K.W. Harde & G.A. Lohse 1965 Die Käfer Mitteleuropas, Band 1, Einfürung. – Krefeld: Goecke & Evers. **[5]**

Freude, H., K.W. Harde & G.A. Lohse 1976 Die Käfer Mitteleuropas, Band 2, Adephaga 1: Carabidae. – Krefeld: Goecke & Evers. **[5]**

Fuellhaas, U. 1997 Der Einfluß von Vernässung und Überstaumaßnahmen in degeneriertem Niedermoorgrünland auf ausgewählte Laufkäferarten (Coleoptera, Carabidae). – Arbeitsberichte Landschaftsökologie Münster 18: 133-146. **[5,6]**

Furon R. 1950 Les grandes lignes de la paléogeographie de la Méditerranée (Tertiaire et Quaternaire). – Vie et Milieu I : 131-162. **[8]**

Futuyma, D.J. 1986 Evolutionary biology. – Sunderland, Massachusetts: Sinauer. **[9]**

Gabrielsen, T.M., K. Bachmann, K.S. Jakobsen & C. Brochmann 1997 Glacial survival does not matter: RAPD phylogeography of Nordic *Saxifraga oppositifolia*. – Mol. Ecol. 6: 831-842. **[6]**

Ganglbauer, L. 1892 Die Käfer von Mitteleuropa 1, Carabidae. – Wien. **[5]**

Ganglbauer, L. 1931 Revision der Gattung *Zabrus* Clairv. (mit einem Bildnis). – Koleopterologische Rundschau 17: 1-55 **[5]**

Gardner, S.M. 1991 Ground Beetle (Coleoptera Carabidae) communities on upland heath and their association with heatland flora. – J. Biogeogr. 18: 281-289. **[5]**

Géhin, J.B. 1876 Catalogue des Coléoptères carabiques de la Tribu des Carabides. – Nancy: 1-72. **[3]**

Géhin, J.B. 1885 Catalogue synonymique et systematique des Coléoptères de la Tribu des Carabides. – Remirout et Prague: 1-104. **[3]**

Geiler, H. 1980 Freilanddaten zur autoekölogischen Charakteristik des Gartenlaufkäfers *Carabus hortensis* (Coleoptera: Carabidae). – Entomol. Gener. 6: 181-191. **[5]**

Gerasimov, I.P. 1964 Fiziko-geograficheskii atlas mira (A physiogeographical atlas of the world). – Moscow: USSR Acad. Sci. & Head Dept. of Geodesy & Cartography: 1-298. [In Russian]. **[5,8]**

Gersdorf, E. 1937 Ökologisch-faunistische Untersuchungen über die Carabiden der mecklenburgischen Landschaft. – Zool. Jb. Syst. 70: 17-86. **[6]**

Gersdorf, E. & K. Kuntze 1957 Zur Faunistik der Carabiden Niedersachsens. – Ber. Naturhist. Ges. Hannover 103: 101-136. **[5,6,9]**

Gersdorf, E. & K. Kuntze 1959 Zur Faunistik der Carabiden Niedersachsens II. – Ber. Naturhist. Ges. Hannover 105: 101-103. **[5]**

Geus, A. 1969 Sporentierchen, Sporozoa: Die Gregarinida der land- und süßwasserbewohnenden Arthropoden Mitteleuropas. – Die Tierwelt Deutschlands 57: 1-765. **[6]**

Ghiretti, D. 1996 Photographic catalogue of the genus *Carabus*. – Lecce: Conte Editore. **[5]**

Ghiretti, D. 1997 Photographic catalogue of the genus *Carabus*. Supplement I & II. – Lecce: Conte Editore: 12 & 17 sticker pages. **[5]**

Ghiretti, D. 2002 Photographic catalogue of the genus *Carabus*. Supplement III. – Lecce: Conte Editore: sticker pages. **[A]**

Giers, E. 1973 Habitatgrenzen der Carabiden (Coleoptera, Insecta) im *Melico-Fagetum* des Teutoburger Waldes. – Abhandl. Westf. Museum Naturkunde 35: 1-36. **[8,t]**

Giers-Tiedtke, E., W. Schiller, P. Hockmann, F.-J. Niehues & F. Weber 1998 Hinweise auf die Wirksamkeit abiotischer Schlüsselfaktoren in Carabiden-Populationen – Erkenntnisse aus mehr- und vieljährigen Untersuchungen. – Schr.-R. f. Landschaftspflege u. Natursch. 58: 229-242. **[6,8,t]**

Goldschmidt, H. & S. Todt 1997 Variable degrees of granivory and phytophagy in insectivorous carabid beetles. – Pedobiologia 41: 521-525. **[6]**

Golovatch, S.I. 1984 Razprostranenie i faunogenezis diplopod evropeiskoi chasti SSSR (The distribution and faunogenesis of millipedes of the USSR European part) – In: Chernov Yu.I. (Ed.). Faunogenesis I filotsenogenesis. Moscow: Nauka: 92-138. [In Russian]. **[8]**

Golovatch, S.I. 1992 Some patterns in the distribution and origin of the millipede fauna of the Russian Plain

(Diplopoda) – Ber. Nat.-med. Verein Innsbruck, suppl. 10: 373-383. **[8]**

Goulson, D. 1993 Variation in the genitalia of the butterfly *Maniola jurtina* (Lepidoptera: Satyridae). – Zool. J. Linn. Soc. 107: 65-71. **[6]**

Grangeon, P. 1958 Contribution à l'étude de la paléontologie végétale du Massif du Coiron (Ardèche) (Sud-Est du Massif Central Français). – Mém. Soc. Hist. nat. Auvergne 6: 1-299. **[8]**

Greenslade, P.J.M. 1963 Daily rhythm of locomotor activity in some Carabidae (Coleoptera). – Entomol. Exptl. Appl. 6: 171-180. **[6]**

Grechanichenko, T.E. 2000 Izmenenie biotopicheskogo raspredeleniya zhuzhelits roda *Carabus* L. v usloviyakh lesostepi za poslednie desetiletiya. (Changes in the habitat preferences of the ground beetles of the genus *Carabus* in the forest steppe for the last decades) – In: Chteniya pamyati prof. V.V. Stanchinskogo, Smolensk 3: 42-45. [In Russian]. **[5]**

Grichuk, V.P. 1989 Istoriya flory i rastitel'nosti Russkoi ravniny v Pleistotsene (History of flora and vegetation of the Russian Plain in the Pleistocene) – Moscow: Nauka: 1-184. [In Russian]. **[8]**

Gridelli, E. 1950 Il problema delle specie a diffusione transadriatica con particolare riguardo ai Coleotteri. – Mem. Biogeogr. Adriatica 1: 7-299. **[8]**

Gries, B., D. Mossakowski & F. Weber 1973 Coleoptera Westfalica: Familia Carabidae, Genera *Cychrus*, *Carabus* und *Calosoma*. – Abh. Landesmus. Naturk. Münster 33: 1-79. **[5,6,8,9,t]**

Grimm, R. & W. Jans 1984 Tageszeitliche Aktivität von Waldcarabiden. – Jber. naturwiss. Ver. Wuppertal 37: 51-55. **[6]**

Grinfel'd, E.K. 1948 Nablyudeniya nad raspredeleniem zhuzhelits (Carabidae), mertvoedov (Silphidae) i nekotorykh drugich nazemnykh hasekomykh po biotopam. (Observations on habitat distribution of carabids, silphids and some other terrestrial insects) – Entomol. obozr. 30 (1/2): 154-156. [In Russian]. **[5,t]**

Grossecappenberg, W., D. Mossakowski & F. Weber 1978 Beiträge zur Kenntnis der terrestrischen Fauna des Gildehauser Venns bei Bentheim. – Abh. Westf. Museum Naturkunde 40: 12-34. **[5,9]**

Grosseschallau, H. 1981 Ökologische Valenzen der Carabiden (Ins., Coleoptera) in hochmontanen, naturnahen Habitaten des Sauerlandes (Westfalen). – Abh. Westf. Museum Naturkunde 43: 3-33. **[8,t]**

Grüm, L. 1966 Diurnal activity rhythm of starved Carabidae. – Bull. Pol. Acad. Sci. 14: 405-411. **[5,6]**

Grüm, L. 1975a Growth rate of the *Carabus* L. larvae (Col. Carabidae). – Wiad. Ekol. 23: 667-671. **[6]**

Grüm, L. 1975b Mortality patterns in carabid populations. – Wiad. Ekol. 23: 649-665. **[6]**

Grüm, L. 1984 Carabid fecundity as affected by extrinsic and intrinsic factors. – Oecologia 65: 114-121. **[6]**

Grüm, L. 1986 Density fluctuations in a carabid guild. – In den Boer, P.J., M.L. Luff, D. Mossakowski & F. Weber (eds.): Carabid beetles: their adaptations and dynamics. Stuttgart: Fischer: 465-487. **[6]**

Gruttke, H. 1997 Impact of landscape changes on the ground beetle fauna (Carabidae) of an agricultural countryside. In: K. Canters (ed.): Habitat fragmentation and infrastructure. Delft: NIVO Drukkerij: 149-159. **[9]**

Gruttke, H., P.M. Kornacker & S. Willecke 1998 Effizienz eines neu angelegten Biotopstreifens als Ausbreitungskorridor in der Agrarlandschaft – Ergebnisse einer Langzeitstudie. – Schr.-R. f. Landschaftspfl. u. Natursch. 58: 243-290. **[9]**

Gryuntal, S.Y. 1993 Segregation of ecological niches by the *Carabus* dominant species (Coleoptera, Carabidae) in forest biocoenoses of the broad-leaved-spruce forest subzone. – Izv. Akad. Nauk. Biol. 5: 732-748. **[5,6]**

Guéorguiev, V.B. & B.V. Guéorguiev 1995 Catalogue of the ground-beetles of Bulgaria (Coleoptera, Carabidae). – Sofia-Moscow: Pensoft Publishers: 1-279. **[5,maps]**

Gullan, P.J. & P.S. Cranston 1994 The insects: an outline of entomology. – London: Chapman & Hall. **[6]**

Günther, J. & T. Assmann 2000 Competition in the woodland? Phenology, weight, and body size of cohabiting *Carabus* species: preliminary results (Coleoptera, Carabidae). – In: Brandmayr, P., G. L. Lövei, T. Z. Brandmayr, A. Casale & A. Vigna Taglianti (eds.): Natural History and applied ecology of carabid beetles. Sofia-Moscow: Pensoft Publishers: 185-195. **[5,6]**

Gusev, A.A. & N.A. Guseva 1987 Naselenie pochvoobitayushchikh nasekomykh v dinamike zapovednykh ekosistem. (Soil-dwelling insect population in relation to the dynamics of protected ecosystems) – Probl. pochv. zool., Mater. dokl. 9 Vses. sov. Tbilisi: 77-78. [In Russian]. **[5]**

Haberman, H. 1965 Eesti jooksiklastefauna oekologilis-zoogeograafiline analuus. (Ecological and zoogeographical analysis of the ground-beetle fauna of Estonia) – ENSV TA Toimetised, biol. seeria 1. [In Estonian]. **[5,maps]**

Hammond, P.M. 1974 Changes in the British coleoptera fauna. – In: D.L. Hawksworth, The changing flora and fauna of Britain. London: 323-369. **[5]**

Hanning, K. & J. Drewnskus 1995 Erstnachweiss von *Carabus glabratus* in der Westfälischen Bucht (Nordrhein-Westfalen) (Coleoptera: Carabidae) – Entomologische Zeitschrift mit Insektenbörse 22: 455-456. **[5]**

Hanski, I.A. & M.E. Gilpin 1997 Metapopulation biology: ecology, genetics, and evolution. – San Diego: Academic Press. **[9]**

Hansen, V. 1968 Danmarks Fauna, 76; Biller XXIV, Sandspringere og Lolebiller. – Kobenhavn: 1-451. **[5]**

Hartl, D.L. & A.G. Clark 1989 Principles of population genetics. – Sunderland (Massachusetts): Sinauer. **[9]**

Harrison, R.G. 1990 Hybrid zones: windows on evolutionary process. – Oxford Surv. Evol. Biol. 7: 69-128. **[6]**

Hausmann, K. & N. Hülsmann 1996 „Einzellige Eukaryota". – In Westheide, W. & R. Rieger (eds.): Spezielle Zoologie, Teil 1: Einzeller und Wirbellose Tiere. – Fischer Verlag: Stuttgart: 3-72. **[6]**

Heijerman, Th. & H. Turin 1989 The Carabid fauna of some types of forests in the Netherlands; a numerical comparative analysis. – Tijdschrift voor Entomologie 132: 241-250. **[5]**

Heinz, W. & H.Korge. 1967 Über die *Carabus*-Arten Anatoliens. – Ent. Bl. Biol. Syst. Käfer 63: 87-105. **[8]**

Hemmer, J. & H. Terlutter 1987 Die Carabidenfauna der hochmontanen Lagen des Rothaargebirges: Untersuchungen zur Habitatbindung und Jahresperiodizität. – Decheniana 140: 87-93. **[5,6,8,t]**

Hengeveld, R. 1980 Qualitative and quantitative aspects of the food of ground beetles (Coleoptera, Carabidae): a review. – Neth. J. Zool. 30: 555-563. **[6]**

Hengeveld, R. 1989 Dynamics of biological invasions. – London-New York: Chapman and Hall: 1-160. **[5]**

Hengeveld, R. 1990 Dynamic Biogeography. – Cambridge University Press: 1-249. **[5]**

Henseler, C. 1938 Die deutschen *Carabus*-Arten. – Dechenniana 97B: 21-61. **[5]**

Henseler, C. 1940 *Carabus violaceus* L. und *purpurascens* F. in Deutschland (Altreich). – Ent. Bl. Biol. Syst. Käfer 36: 152-157. **[5]**

Henseler, C. 1941 *Carabus violaceus* L. und *purpurascens* F. – Ent. Bl. Biol. Syst. Käfer 37: 117-118. **[5]**

Herrera, L. & F.J. Arricibita 1990 Los Carabidos de Navarra Espana (Coleoptera, Carabidae). – Entomonograph 12. Leiden. **[5,maps]**

Hewitt, G.M. 1988 Hybrid zones – natural laboratories for evolutionary studies. – Trends Ecol. Evol. 3: 158-167. **[6]**

Hewitt, G.M. 1996 Some genetic consequences of ice age, and their role in divergence and speciation. – Biol. J. Linn. Soc. 58: 247-276. **[6]**

Heydemann, B. 1957 Die Biotopstruktur als Raumwiderstand und Raumfülle für die Tierwelt. – Verh. Deut. Zool. Ges. Hamburg 1956: 332-347. **[5,6]**

Heydemann, B. 1983 Aufbau von Ökosystemen im Agrarbereich und ihre langfristigen Veränderungen. – In: Daten und Dokumente zum Umweltschutz: Sonderreihe Umwelttagung 35: 53-83. **[9]**

Hieke, F. 1966 Vergleichende funktionelle Anatomie der Abdominalmuskulatur einiger männlicher Coleopteren unter besonderer Berücksichtigung des Genitalkomplexes. – Dt. ent. Z. N.F. 13: 1-168. **[6]**

Hieke, F. & D.W. Wrase 1988 Faunistik der Laufkäfer Bulgariens (Coleoptera, Carabidae). – Dt. ent. Z. N.F. 35: 1-171. **[5,maps]**

Highton, R. & T.P. Webster 1976 Geographic protein variation and divergence in populations of the salamander *Plethodon cinereus*. – Evolution 30: 33-45. **[6]**

Hill, M.O. 1979a TWINSPAN: A Fortran program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes. – Ithaca: New York. **[5,8]**

Hill, M.O. 1979b DECORANA: A Fortran program for detrended correspondence analysis and reciprocal averaging. – Ithaca: New York. **[5]**

Hillis, D.M., C. Moritz & B.K. Mable 1996 (eds.): Molecular systematics. Second edition. – Sunderland (Massachusetts): Sinauer. **[7]**

Hiura, I. 1971 Discovery of *Apotomopterus* from the Japanese Neogene (Coleoptera, Carabidae). – Occ. Pap. Osaka Mus. nat. Hist. 1: 49-50. **[8]**

Hochhardt, W. & R. Ostermann 1998 Die Laufkäferbesiedlung eines Edelkastanien-Niederwaldes im Mittleren Schwarzwald (Ödsbach/Oberkirch). – Mitt. bad. Landesver. Naturkunde u. Naturschutz N.F. 17 (1): 137-153. **[9]**

Hockmann, P., B. Horstmann, A. van den Boom, M. Landwehr, A. Bechtel, V. Kliewe, R. Baumgartner, S. Mond, U. Fennemann, D. Kurz & F. Weber 1998 The age structure in a local population of *Carabus auronitens* under the influence of an abiotic key factor for reproduction. – In: Baumgartner *et al.* (eds.): Population and community ecology for insect management and conservation. Proceedings of The 20th Int. Congr. of Entomology Florence (1998): 145-156. **[5,8]**

Hockmann, P., K. Menke, P. Schlomberg & F. Weber 1992 Untersuchungen zum individuellen Verhalten (Orientierung und Aktivität) des Laufkäfers *Carabus nemoralis* im natürlichen Habitat. – Abh. Westf. Mus. Naturkunde 54: 65-98. **[6]**

Hockmann, P., P. Schlomberg, H. Wallin & F. Weber 1989 Bewegungsmuster und Orientierung des Laufkäfers *Carabus auronitens* in einem westfälischen Eichen-Hainbuchen-Wald (Radarbeobachtungen und Rückfangexperimente). – Abh. Westf. Mus. Naturkunde 51: 1-71. **[5,6,8]**

Hoffmann, A. 1907 Verticale Verbreitung der Caraben. – Entomologische Blätter 4: 49-51. **[5]**

Holder, K., R. Montgomerie & V.L. Friesen 1999 A test of the glacial refugium hypothesis using patterns of mitochondrial and nuclear DNA sequence variation in rock ptarmigan (*Lagopus mutus*). – Evolution 53: 1936-1950. **[6]**

Holdhaus, K. 1911 Über die Abhängigkeit der Fauna vom Gestein. – Verh. VIII Int. Zool. Kongr. Graz: 726-745. **[6]**

Holdhaus, K. 1954 Die Spuren der Eiszeit in der Tierwelt Europas. – Abh. Zool.-Bot. Ges. Wien 18: 1-493. **[6]**

Holdhaus, K. & C.H. Lindroth 1939 Die europäischen Koleopteren mit boreoalpiner Verbreitung. – Ann. Naturh. Mus. Wien 50: 123-293. **[8]**

Holland, J.M. (ed.) 2002 The agroecology of carabid beetles. Intercept: Andover: 1-450. **[10,A]**

Holste, U. 1974 Faunistisch-ökologische Untersuchungen zur Carabiden- und Chrysomelidenfauna (Coleoptera, Insecta) xerothermer Standorte im Oberen Weserbergland. – Abh. Landesmus. Naturkde. Münster Westf. 36: 28-53. **[9]**

Hölzel, 1942 Über den Fang von Caraben aus ihrem Winterbett in der Sattniz und in den Karakanken. Hege und Beobachtungen im Terrarium. – Carinthia 2: 89-108. **[5]**

Horion, A. 1935 Nachtrag zu 'Fauna Germanica' von E. Reitter (Nachtrag zu Band I). – Krefeld: I-VIII, 1-59. **[5]**

Horion, A. 1941 Faunistik der deutschen Käfer. Band I: Adephaga-Caraboidea. – Krefeld: Goecke & Evers. **[5,9,maps]**

Horvatovich, S. 1992 Liste der Carabiden-Arten (Coleoptera, Carabidae) Ungarns (Stand 1991). – Janus Pannonius Múzeum 37: 5-12. **[5]**

Houston, W.W.K. 1981 The life cycle and age of *Carabus glabratus* Paykull and *C. problematicus* Herbst (Col., Carabidae) on moorland in northern England. – Ecol. Entomol. 6: 263-271. **[5,6]**

Hristovski, S. 1997 Preliminary catalogue of the ground beetles of Macedonia, list of species and subspecies of the family Carabidae in Macedonia. **[5]**

Hsu, K.J. 1983 The Mediterranean was a desert. – Princeton (NJ): Princeton University Press. **[8]**

Hsu, K.J., L. Montadert, D. Bernoulli, M.B. Cita, A. Ericson, R.E. Garrison, R.B. Kidd, F. Melieres, C. Muller & R. Wright 1977 History of the Mediterranean Salinity Crisis. – Nature 267: 399-403. **[8]**

Huk, T. 1997 Auswirkungen eines langfristigen Überstaus auf die Laufkäferfauna einer extensiv genutzten Niedermoorwiese. – Arbeitsberichte Landschaftsökol. Münster 17: 147-160. **[9]**

Huk, T. 1998 Ausbreitungsvermögen, Lebenszyklus, Larvalökologie und Habitatwahl von *Carabus clatratus* L. 1761. – Angewandte Carabidologie 1: 41-50. **[6,9]**

Huk, T. & B. Kühne 1999 Substrate selection by *Carabus clatratus* (Coleoptera, Carabidae) and consequences for offspring development. – Oecologia 121: 348-354. **[5,6]**

Huk, T. & B. Kühne 2000 Egg laying strategy and aspects of larval biology of two *Carabus* species. – In: Brandmayr, P., G. L. Lövei, T. Z. Brandmayr, A. Casale & A. Vigna Taglianti (eds.): Natural History and applied ecology of carabid beetles. Sofia-Moscow: Pensoft Publishers: 161-168. **[5,6]**

Hůrka, K. 1958 Versuch einer Zusammenfassung der montanen Carabidenfauna von Krkonoše (Riesengebirge). – Acta Fauna Ent. Mus. Nat. Pragae, 3: 31-52. **[5]**

Hůrka, K. 1970 Die unbekannten oder wenig bekannten Larven der mitteleuropäischen *Carabus-* und *Procerus-*Arten (Col., Carabidae). – Acta ent. bohemslov. 67: 254-276. **[6]**

Hůrka, K. 1971a Die Larven der mitteleuropäischen *Carabus-* und *Procerus-*Arten. – Rozpravy CSAV, Rada mat. prir. ved. 81: 1-136. **[4,6,7]**

Hůrka, K. 1971b Entwicklungstypen der Mitteleuropaischen *Carabus-*Arten in Ihrer beziehung zu den endogenen und exogenen faktoren. – Proceedings of the XIII International Congres of Entomology Moscow 1: 501-502. **[3,5]**

Hůrka, K. 1972 Über Ergebnisse der Aufzucht von mitteleuropäischen Laufkäfern der Gattung *Carabus* (Coleoptera). – Pedobiologia 12: 244-253. **[6]**

Hůrka, K. 1973 Fortpflanzung und Entwicklung der mitteleuropäischen *Carabus-* und *Procerus-*Arten. – Studie CSAV 9: 1-80. **[5,6,maps]**

Hůrka, K. 1996 Carabidae of the Czech and Slovak Republics. Zlin: Kabourek: 1-565. **[5,6,maps]**

Hůrka, K., P. Vesely & J. Farkac 1996 Die Nutzung der Laufkäfer (Coleoptera: Carabidae) zur Indikation der Umweltqualität. – Klapalekiana 32: 15-26. **[5]**

Hyman, P.S. 1992 A review of the scarse and threatened Coleoptera of Great Britain, part 1 (updated and revised by M.S. Parsons). – UK Nature Conservation: Petersboorough. **[5,maps]**

Imura, Y. 1996 A Revised Classification of the Major Divisions and Subdivisions of *Carabus* (*s. lat.*) (Coleoptera, Carabidae). – Elytra, Tokyo 24: 5-12. **[7,10]**

Imura, Y. 1998 Proposal of a new subgenus for the unique alpine species *Carabus latreilleanus* (Coleoptera, Carabidae). – Elytra, Tokyo 26: 8. **[3,10]**

Imura Y. 2002a Proposal of Eighteen New Genera and Subgenera of the Subtribe Carabina (Coleoptera, Carabidae). – Spec. Bull. Jpn. Soc. Coleopterol. Tokyo 5: 129-147. **[A]**

Imura Y. 2002b Classification of the Subtribe Carabina (Coleoptera, Carabidae) Based on Molecular Phylogeny. – Elytra, Tokyo 30 (1): 1-28. **[A]**

Imura, Y., C.-G. Kim, Z.-H. Su & S. Osawa 1998 An Attempt at the Higher Classification of the Carabina (Coleoptera, Carabidae) Based on Morphology and Molecular Phylogeny, with Special Reference to *Apotomopterus*, *Limnocarabus* and *Euleptocarabus*. – Elytra, Tokyo 26: 17-35. **[3,5,7]**

Imura, Y. & K. Mizusawa 1996 The *Carabus* of the World. – Mushi-Sha's Iconographic Series of Insects 2, Tokyo. **[3,5]**

Ishikawa, R. 1973 Notes on some basic problems in the taxonomy and the phylogeny of the subtribe Carabina. – Bull. Natn. Sci. Mus. Tokyo 16: 191-215. **[3,6,7]**

Ishikawa, R. 1978 A revision of the higher taxa of the subtribe Carabina (Coleoptera, Carabidae). – Bull. Natn. Sci. Mus. Ser. A (Zool.) 4: 15-68. **[3,6,7]**

Ishikawa, R. 1979 A preliminary Revision of the Carabogenici of the Subtribe Carabina (Coleoptera, Carabidae). – Bull. Natn. Sci. Mus. Ser. A (Zool.) 5: 95-114. **[7]**

Ishikawa, R. 1984 Phylogeney and subgeneric classification of the genus *Chaetocarabus* Thomson (Coleoptera, Carabidae). – Kontuyu, Tokyo 53: 94-109. **[7]**

Ishikawa, R. 1985 Carabidae (Carabinae). The Coleoptera of Japan in color. – Hoikusha Publ. 2: 54-88. **[3]**

Jakobson, G.G. 1905-16 Zhuki Rossii, Zapadnoi Evropy i sopredel'nykh stran. (The beetles of Russia, West Europe and adjacent countries) – Sanct Petersburg: Devrien: 1-1024. [In Russian]. **[5,maps]**

Jarmer, G. 1973 Vergleich der Carabidenfauna des 'Grieterbuschs' und des 'Schwarzen Wassers' am Niederrhein (eutrophe und dystrophe Standorte). – Jahresbericht Universität Köln: 290. **[5]**

Jeanne, C. 1974 Carabiques nouveaux (5e note). – Bulletin de la Société Entomologique de France 79: 66-71. **[3]**

Jeanne, C. & J.P. Zaballos 1986 Catalogue des Coléoptères Carabiques de la Peninsule Iberique. – Supplement au Bulletin mensuel Société Linnéene de Bordeaux: 1-186. **[5]**

Jeannel, R. 1940 Les Calosomes (Coleoptera, Carabidae). – Mém. Mus. natn. Hist. nat. Paris (n.s.) 13: 1-240. **[8]**

Jeannel, R. 1941 Coléoptères Carabiques 1. – Faune de France 39: 1-571. **[3,5,6,maps]**

Jeannel, R. 1942 La génèse des faunes terrestres. Eléments de Biogéographie. – Paris: Presses Universitaires de France: 1-514. **[8]**

Jeannel, R. 1949 Faune de France 51, Coléoptères Carabiques (Supplement). – Paris. **[5]**

Jelínek, J. 1993 Checklist of Czechoslovak Insects IV (Coleoptera). – Folia Heyrovskyana, suppl. 1: 9-22. **[5]**

Jiroux, E. 1996 Révision du genre *Ceroglossus*. – Verneuil sur Seine: Magellanes. **[5]**

Jordan, H. 1910 Über extraintestinale Verdauung im allgemeinen und bei *Carabus auratus* im besonderen. – Biol. Zbl. 30: 85-96. **[6]**

Jørum, P. 1985 Life cycle and phenology of *Carabus problematicus* Herbst. in Denmark (Coleoptera, Carabidae). – Entomologiske Meddelelser 53: 27-30. **[5]**

Jørum, P. 1989 Bogekovsløberen (*Carabus intricatus* Linnaeus, 1761) – en løbebille der et truet i Skandinavien. – Flora og Fauna 95: 6-19. **[5]**

Jørum, P. 1991 Rødliste '90, Særligt beskyttelsesjrævende planter og dyr i Denmark, Løbebiller: 14-14; 99-101, 220-221. **[5]**

Jørum, P. 1995 Løbebiller (Carabidae) Rødlistede arter (manuscript). **[5]**

Jørum, P. & T. Pind Jorim 1996 En sikker dansk forekomst af stor guldløber *Carabus auratus* Linnaeus, 1761 (Coleoptera, Carabidae). – Entomologiske Meddelelser 64: 273-276. **[5]**

Josifow, M. 1981 Über den zoogeographischen Charakter der Südeuropäischen Insektenfauna unter besonderer Berücksichtigung der Heteropteren. – Berichte Nat. Med. Vereins Innsbruck 75: 177-184. **[8]**

Jung, W. 1940 Ernährungsversuche an *Carabus*-Arten. – Entomol. Bl. 36: 117-124. **[6]**

Junk, W. & S. Schenkling 1910, 1926-1933 Coleopterorum Catalogus. auctt.: **E. Csiki** – Pars 91-92 (1927), 97-98 (1928), 104 (1929), 112 (1930), 115 (1931), 121, 124 (1932), 126-127 (1933) – Berlin. **[5]**

Karpova, V.E. 1983/84 Vidovoi sostav i osobennosti raspredeleniya zhuzhelits v agrotsenosakh yuga Moldavii. (Species composition and distribution patterns of ground-beetles in agrocenoses of South Moldavia) – In: Fauna i ekologiya bespozvonochnykh zhivotnykh. Moscow: MGPI: 82-87. [In Russian]. **[5]**

Karpova, V.E. & A.V. Matalin 1992 Annotirovannyi spisk zhuzhelitz (Coleoptera, Carabidae) Moldovy. (An annotated checklist of Carabidae of Moldova). – Entom. Obozr. 72 (2): 570-585. [In Russian]. **[t]**

Kashevarov, B.N. 1986 Osobennosti naseleniya zhuzhelits v gorno-taezhnoi zone Yuzhnogo Urala. (Peculiarities of ground-beetle communities in the mountain taiga zone of South Urals) – In: Fauna i ekologiya bespozvonochnykh zhivotnykh v zapovednikakh RSFSR. Moscow: 56-67. [In Russian]. **[5,t]**

Keith, T.P. 1983 Frequency distribution of esterase-5 alleles in two populations of *Drosophila pseudoobscura*. – Genetics 105: 135-155. **[6]**

Kennedy, P.J. 1994 The distribution and movement of ground beetles in relation to set-aside arable land. – In: Desender, K., M. Dufrene, M. Loreau, M.L. Luff & J.-P. Maelfait (eds.): Carabid beetles: ecology and evolution. Dordrecht: Kluwer Academic Publishers: 439-444. **[6]**

Kern, P. 1912 Über die Fortpflanzung und Eibildung die einigen Caraben. – Zool. Anz. 40: 345-351. **[6]**

Kern, P. 1921 Beiträge zur Biologie der Caraben. – Entomologische Blätter für Biologie und Systematik der Käfer 17: 10-12, 162-172. **[5,6]**

Kern, P. 1925 Beiträge zur Biologie der Caraben II. – Entomologische Blätter für Biologie und Systematik der Käfer 21: 114-119. **[5,8]**

Khot'ko, E.I., N.K. Lavrova, S.V. Saluk, L.S. Chumakov, M.V. Maksimenkov, A.K. Tishechkin & S.V. Buga 1989 Otryad Zhestkokrylye – Coleoptera. (Order Beetles – Coleoptera) – In: Nasekomye Berezinskogo zapovednika. Flora i fauna zapovednikov SSSR. Moscow: 19-57. [In Russian]. **[5,t]**

Kieseritzky, V.A. 1912 K faune zhukov Oblasti Voiska Donskogo. (Contribution a la faune des Coléoptères de la Province des Cosaques du Don) – Russk. entomol. obozr. 12 (1): 82-94. [In Russian]. **[5]**

Kieseritzky, V.A. 1915 K faune zhukov Poltavskoi gubernii. (Contribution a la faune des Coléoptères du gouvernement de Poltava) – Russk. entomol. obozr. 15: 167-184. [In Russian]. **[5]**

Kinnunen, H. 1999 In search of spatial scale. Carabid beetle communities in agricultural landscapes. – Thesis, Helsinki. **[8,t]**

Kirchner, H. 1927 Biologische Studien über *Carabus cancellatus* Illig. – Zeitschrift für Morphologie und Ökologie der Tiere 7: 489-534. **[5]**

Kirchner, H. 1960 Untersuchungen zur Ökologie feldbewohnender Carabiden. – Thesis, Universität Köln. **[5]**

Kirchner, H. 1964 Tageszeitliche Aktivitätsperiodik bei Carabiden. – Z. vergl. Physiol. 48: 385-399. **[6]**

Kleinert, J. 1987 Changes in the distribution of *Carabus cancellatus* in Slovakia. – Acta Phytopath. Entom. Hung 22: 161-163. **[5,9]**

Kleinfeld, F. & H. Schütze 1999 Systematische Liste der Gattung *Carabus* mit zahlreichen taxonomischen Anmerkungen. 5/e – Schwanfeld: Delta-Druck und Verlag Reks: 1-62. **[2,5]**

Klenner, M.F. 1989 Überlebensstrategien einer stenotopen Waldart: Untersuchungen zur Dynamik einer westfälischen *Carabus auronitens*-Population (Coleoptera, Carabidae). – Verh. Ges. Ökologie 18: 781-791. **[6]**

Klenner, M. 1994 The carabid fauna of diflubenzuron-sprayed and unsprayed plots in Westphalian oak forests – a post-treatment comparison. – In: Desender, K., M. Dufrêne, M. Loreau, M. Luff & J.-P. Maelfait (eds.): Carabid beetles: ecology and evolution. – Dordrecht: Kluwer Academic Publishers: 445-449. **[9]**

Knisley, C.B. & T.D. Schultz 1997 The biology of tiger beetles and a guide to the species of the South Atlantic states. – Martinsville, Virginia: Virginia Museum of Natural History. **[9]**

Koch, K. 1989 Ökologie. Band 1. – In: Freude, Harde & Lohse. Die Käfer Mitteleuropas E1. Krefeld. **[5]**

Ködóbócz, V. & T. Magura 1999 Biogeographical connections of the carabid fauna (Coleoptera: Carabidae) of the Beregi-síkság to the Carpathians. – Folia Entomologica Hungarica 60: 195-203. **[8,t]**

Kolbe, W. 1968 Der Einfluß der Waldameise auf die Verbreitung von Käfern in der Bodenstreu eines Eichen-Birken-Waldes. – Natur und Heimat 3: 120-124. **[6]**

Kolbe, W. 1969 Käfer im Wirkungsbereich der Roten Waldameise. – Entomol. Z. 79: 269-280. **[6]**

Komarov, E.V. 1986 Kompleks zhuzhelits (Coleoptera, Carabidae) pshenichnogo polya i ego izmenenie pod vliyaniem orosheniya v popupustynnoi zone Nizhnego Povolzh'ya. (The ground-beetle complex (Coleoptera, Carabidae) in a wheat field and its changes under influence of irrigation in the semi-desert zone of Lower Volga) – In: Biotsenoz pshenichnogo polya. Moscow: Nauka: 88-93. [In Russian]. **[5]**

Komarov, E.V. 1990 Dopolneniya k spisku zhuzhelits Volgogradskoi oblasti. (Additions to the list of ground-beetles of the Volgograd Province) – Fauna i ekologiya zhuzhelits. Tez. dokl. III Vses. karabidol. sov. Kishinev: 36-37. [In Russian]. **[5]**

Korell, A. 1975 Über die *Carabus*-Arten Siziliens (Coleoptera, Carabidae). – Nachrichtenblatt der Bayerischen Entomologen 24: 92-95. **[6]**

Korobeinikov, Yu.I. 1979 Zhuzhelitsy Il'menskogo zapovednika i ikh sezonnaya dinamika aktivnosti. (The ground-beetles of the Ilmen Reserve and their seasonal activity dynamics) – In: Strukturno-funktsional'nye vzaimosvyazi v biogeotsenosakh Yuzhnogo Urala. Tr. Inst. ekol. rast. zhivotn. Sverdlovsk 130: 44-62. [In Russian]. **[5,t]**

Korobeinikov, Yu.I. 1987 Ekologo-faunisticheskaya kharakteristika zhuzhelits Yuzhnogo Yamala. (Eco-faunistic characteristics of ground-beetles of the South Yamal peninsula) – In: Fauna i ekologiya nasekomykh Urala. Sverdlovsk: 33-44. [In Russian]. **[5,t]**

Korobeinikov, Yu.I. 1988 K faune zhuzhelits (Coleoptera, Carabidae) vysokogorii Yuzhnogo Urala. (On the fauna of carabids (Coleoptera, Carabidae) of the alpine regions of South Ural) – Entomol. obozr. 67: 738-740. [In Russian]. **[5]**

Korobeinikov, Yu.I. 1990 O vertikal'nom raspredelenii zhuzhelits na Pripolyarnom Urale. (On the altitudinal distribution of ground-beetles in the Subarctic Urals) – Fauna i ekologiya zhuzhelits. Tez. dokl. III Vses. karabidol. sov. Kishinev: 37-38. [In Russian]. **[5,8]**

Koth, W. 1974 Vergesellschaftungen von Carabiden (Col., Ins.) bodennasser Habitate des Arnsberger Waldes verglichen mit Hilfe der Renkonenzahl. – Abhandl. Westf. Museum Naturkunde 36: 1-43. **[8,t]**

Koval', A.G. 1983 Vliyanie khimicheskikh obrabotok kartofel'nykh polei na khishchnykh zhuzhelits. (Influence of chemical treatments on potato fields upon predatory ground-beetles) – Okhrana zhivoi prirody. Tez. dokl. Vses. konf. molod. uchenykh. Moscow: 92-97. [In Russian]. **[5]**

Koval', A.G. 1989 K izucheniyu biologicheskikh osobennostei *Carabus (Morphocarabus) hampei* iz Zakarpat'ya. (To a study on the biological peculiarities of *Carabus (Morphocarabus) hampei* Kuest. from the Transcarpathia) – Ekol. i takcon. nasekom. Ukrainy. Sborn. nauchn. trud. 3: 29-36. [In Russian]. **[5]**

Koval', A.G. 1990 Novye dlya Kryma zhuzhelitsy roda *Carabus*. (Species of the genus *Carabus* new to the fauna of Crimea) – Fauna i ekologiya zhuzhelits. Tez. dokl. III Vses. karabidol. sov. Kishinev: 31-32. [In Russian]. **[5]**

Kozlov, A.E. 1990 Fauna i biotopicheskoe raspredelenie zhuzhelits (Coleoptera, Carabidae) goroda Novosibirska i ego okrestnostei. (Fauna and habitat distribution of ground-beetles (Coleoptera, Carabidae) of Novosibirsk and its vicinity) – In: Vrednye organizmy kul'turnykh rastenii. Novosibirsk: 72-87. [In Russian]. **[5]**

Kozlova, E.A. 1964 O faune zhuzhelits Udmurtskoi ASSR. (On the ground-beetle fauna of the Udmurtian ASSR) – II nauchn. konf. zoologov pedagog. institutov RSFSR. Tez. dokl. Krasnodar: 49-51. [In Russian]. **[5]**

Koz'minykh, V.O. & S.L. Esyunin 1991a Ekologicheskie gruppirovki zhuzhelits (Coleoptera, Carabidae) zapovednogo urochishta "Spasskaya gora" (Permskaya oblast') (Ecological groupings of ground-beetles (Coleoptera, Carabidae) of Spasskaya Gora Reserve in Perm Province) – In: Ekologicheskie gruppirovki zhuzhelits (Coleoptera, Carabidae) v estestvennylh i antropogennykh landshaftakh Urala. Izd-vo UrO AN SSSR: 39-50. [In Russian]. **[5,t]**

Koz'minykh, V.O. & S.L. Esyunin 1991b Izuchenie zhuzhelits (Coleoptera, Carabidae) Urala. Podsemeistva Cicindelinae, Omophroninae, Carabinae (triby Carabini, Cychrini). (Studies on the ground beetles (Coleoptera, Carabidae) of the Ural. Subfamilies Cicindelinae, Omophroninae, Carabinae (tribes Carabini, Cychrini)) – Depozited in VINITI 2709-B91: 1-12. [In Russian]. **[5]**

Koz'minykh, V.O., S.L. Esyunin, T.I. Gridina & P.V. Durmanov 1991a Zhestkokrylye Permskoi oblasti. II. Materialy k faune zhestkokrylykh semeistv Trachypachidae, Carabidae (Coleoptera). (The beetles of the Perm Province. II. Materials on the fauna of the families Trachypachidae and Carabidae) – Depozited in VINITI 1722-B91: 1-12. [In Russian]. **[5]**

Koz'minykh, V.O., T.I. Gridina & S.L. Esyunin 1991b Zhestkokrylye Permskoi oblasti. III. Fauna zhuzhelits roda *Carabus* (Coleoptera, Carabidae). (The Coleoptera of the Perm Province. III. Fauna of the ground-beetles of the genus *Carabus* (Coleoptera, Carabidae)) – Depozited in VINITI 1928-B91: 1-11. [In Russian]. **[5]**

Koz'minykh, V.O., A.V. Kozyrev, S.L. Esyunin & T.I. Gridina 1994 Zhestkokrylye Permskoi oblasti. V. Bibliografiya i annotorivannyi spisok vidov zhuzhelits (Trachypachidae, Carabidae). Zametki po otdel'nym vidam zhizhelits. (The beetles of the Perm Province. V. A checklist of the ground beetles (Trachypachidae and Carabidae). Notes on particular species) – Depozited in ONP NPEZ "Veras-Eko" and Insitute of zoology of Byelorussian Academy of Sciences: 1-20. [In Russian]. **[5]**

Kozyrev, A.V. 1989 Razmnozhenie i sezonnaya aktivnost' zhuzhelits (Coleoptera, Carabidae) Srednego Urala. (Reproduction and seasonal activity of the ground-beetles (Coleoptera, Carabidae) of the Middle Urals) – In: Nasekomye v biogeotsebozakh Urala: Inform. mater. Sverdlovsk: 27-28. [In Russian]. **[5]**

Kozyrev, A.V. 1990 Zhuzhelitsy goroda Sverdlovska. (The ground-beetles of Sverdlovsk) – Fauna i ekologiya zhuzhelits. Tez. dokl. III Vses. karabidol. sov. Kishinev: 35-36. [In Russian]. **[5]**

Kozyrev, A.V. & V.O. Koz'minykh 1997 Sravnitel'nyi sostav polevykh kompleksov zhuzhelits (Coleoptera, Carabidae) v agrotsenozakh zapadnykh i vostochnykh sklonov Srednego Urala (A comparative study of the composition of the ground-beetle assemblages of the agrocoenoses on the western and eastern slopes of the Middle Ural) – In: Muzei i nauka. Mater. nauchn. konf. 28-20.04.1997, Syktyvkar. Izd-vo Syktyvkarskogo gos. unta: 61-63. [In Russian]. **[5,t]**

Kozyrev, A.V., V.O. Koz'minykh & S.L. Esyunin 1995 Antropogennye statsii okrestnostei g. Permi– rezervaty redkih zhukov-zhuzhelits (Coleoptera, Carabidae) (Anthropogenic habitats in the environs of Perm City as reserves of rare ground-beetles (Coleoptera, Carabidae)) – In: Ekologiya i okhrana okruzhayuschei sredy. Tez. dokl. 2-oi mezhdunar. nauch.-prakt. konf. 12-15.09.1995, IV. Perm: 25-27. [In Russian]. **[5,t]**

Krehan, I. 1970 Die Steuerung von Jahresrhythmik und Diapause bei Larval- und Imagoüberwinterern der Gattung *Pterostichus*. – Oecologia 6: 58-105. **[6]**

Krishtal, O.P. 1956 Entomofauna gruntu ta podstilki v dolini seredn'oi techii r. Dnipra. (The soil and litter entomofauna in the valley of Middle Dnepr flow) – Kiev: Kiev. Derz. Univ.: 1-423. [In Russian]. **[5,t]**

Krogerus, H. 1932 Über die Ökologie und Verbreitung der Arthropoden der Triebsandgebiete an den Küsten Finnlands. – Acta Zool. Fenn. 12: 1-308. **[6]**

Krogerus, H. 1948 Ökologische Untersuchungen über Uferinsekten. – Acta Zool. Fenn. 53: 1-157. **[6]**

Krogerus, H. 1960 Ökologische Studien über nordische Moorarthropoden. – Commentat. Biol. 21: 1-238. **[6]**

Krumbiegel, I. 1932 Untersuchungen über physiologische Rassenbildung (Ein Beitrag zum Problem der Artbildung und der geographischen Variation). – Zoologische Jahrbücher, Abteilung Systematik, Oekologie und Geographie der Tiere 63: 183-280. **[5]**

Krumbiegel, I. 1936 Morphologische Untersuchungen über Rassenbildung (Ein Beitrag zum Problem der Artbildung und der geographischen Variation). – Zoologische Jahrbücher, Abteilung Systematik, Oekologie und Geographie der Tiere 68: 105-178. **[5,6]**

Krumbiegel, I. 1960 Die Rudimentation. – Stuttgart: Fischer. **[6]**

Krusteva, I., V. Popov & V. Sakalian 1995 Indirect gradient analysis of carabid (Coleoptera, Carabidae) spatial pattern on Vitosha Mountain (West Bulgaria) – In: Treta natsion. nauchn konf. po entomologiya. Sofia: 55-59. **[5,t]**

Kryzhanovskij, O.L. 1953 Zhuki-zhuzhelitsy roda *Carabus* Srednei Azii (The ground-beetles of the genus *Carabus* of Middle Asia). – Opredeliteli po faune SSSR, Moscow-Leningrad: Zool. inst. Akad. nauk SSSR 52: 1-134. [In Russian]. **[3,5,8,10]**

Kryzhanovskij, O.L. 1965a Carabidae – In: Opredelitel nasekomych ewropejskoj tsachsti SSSR. T. 2. Leningrad: 29-77. [In Russian]. **[5,8,maps]**

Kryzhanovskij, O.L. 1965b The components and the origin of the terrestrial fauna of Central Asia. – Moscow-Leningrad: 1-419. [In Russian]. **[5,8]**

Kryzhanovskij, O.L. 1980-1982 *Carabus glabratus* Paykull, *C. nitens* Linnaeus, *C. coriaceus* Linnaeus, *C. cancellatus* Illiger and *C. nemoralis* O.F. Müller. – Distribution of insects in the USSR: maps 33-35 1980), 75-77 1981), 135-136 1982). [In Russian]. **[5]**

Kryzhanovskij, O.L. 1983 Zhuki podotryada Adephaga: semeistva Rhysodidae, Trachypachidae, semeistvo Carabidae (vvodnaya chast' i obzor fauny SSSR). (The ground beetles of the suborder Adephaga: Families Rhysodidae, Trachypachidae, family Carabidae) (introduction and a review of the USSR fauna) – Fauna SSSR, Leningrad: Nauka: 1 (2): 1-343. [In Russian]. **[2,3,5,8]**

Kryzhanovskij, O.L., I.A. Belousov, I.I. Kabak, B.M. Kataev, K.V. Makarov & V.G. Shilenkov 1995 A Check-list of the Ground-Beetles of Russia and Adjacent Lands (Insecta, Coleoptera, Carabidae). – Sofia-Moscow: Pensoft: 1-271. **[4,7]**

Kryzhanovskij, O.L. & A.B. Matveev 1993 A new species of *Carabus* from the South Urals (Coleoptera: Carabidae). – Zoostistematica Rossica 2: 143. **[5]**

Kult, K. 1947 Klic k urcovani brouku celedi Carabidae Ceskoslovenske republiky (Key for identification of Carabidae of Czechoslovakia). – Praha. **[5]**

Kurosa, K. 1959 Illustrated insect larvae of Japan. – The Hokuryukan, Tokyo: 396-415. **[7]**

Kutasi, Cs. 1997 A Bakony-hegység területére új bogárfajok (Carabidae) Veszprémvarsány környékéről. (New ground beetle species (Carabidae) to the Bakony Mountains from the surroundings of Veszprémvarsány. – Folia Musei Historico-Naturalis Bakonyiensis 12 (1993): 99-103. **[5]**

Kutasi, Cs., J. Muskovits & I. Rozner 2000 Adatok Torockó (Erdély) és környékének bogárfaunájához (Insecta: Coleoptera). (Data to the Beetle fauna of the Village Torockó (Rimetea, Alba County) and its environs (Insecta: Coleoptera).) – Acta 1999/I. Csíki Székely Múzeum. Székely Nemzeti Múzeum. Muzeul National Secuiesc. Muzeul Secuiesc al Ciucului: 75-82. **[5]**

Lafer, G.Sh. 1989 Family Carabidae; the ground beetles. – In: Opredelitel nasekomykh Dalnego Vostoka SSSR. III Zhestkokrylye ili zhuki 1. Leningrad: 70-222 [In Russian]. **[3]**

Lagar, A. 1965 Los *Carabus* de las Islas Canarias. – Graellsia 23: 79-84. **[8]**

La Greca, M. 1964 Le categorie corologiche degli elementi faunistici italiani. – Atti Accad. naz. ital. Entomol. Rendiconti 11 (1963): 231-253. **[8]**

Lagunov, A.V. & Yu.I. Novozhenov 1996 Fauna zhestkokrylykh Il'menskogo zapovednika. (The beetle fauna of the Ilmen Reserve) – Izd-vo Uralsk. Otd. RAN: 1-104. [In Russian]. **[5,8,t]**

Lamprecht, G. & F. Weber 1971 Die Synchronisation der Laufperiodik von *Carabus*-Arten (Ins. Coleoptera) durch Zeitgeber unterschiedlicher Frequenz. – Z. vergl. Physiol. 72: 226-259. **[6]**

Lamprecht, G. & F. Weber 1973 Mitnahme, Frequenzdemultiplikation und Markierung der Laufaktivität von *Carabus*-Arten (Coleoptera) durch Lichtzyklen. – J. Insect Physiol. 19: 1579-1590. **[6]**

Lang, G. 1994 Quartäre Vegetationsgeschichte Europas. – Jena: Fischer. **[6]**

Lapouge, G. 1902 Phylogénie des *Carabus*. – Bulletin de la Société des Scientifique et Médicales de l'Ouest 10: 325-344; 11: 306-317. **[2,3,5]**

Lapouge, G. 1905 Descriptions des larves de *Carabus* et de *Calosoma*. – Bulletin de la Société des Scientifique et Médicales de l'Ouest 14: 273-293. **[3]**

Lapouge, G. 1908 Descriptions des larves de *Carabus* et de *Calosoma*. – Bulletin de la Société des Scientifique et Médicales de l'Ouest 17: 150-177. **[3]**

Lapouge, G. 1929-1932 Coleoptera Adephaga, Fam. Carabidae. – Genera Insectorum. Tervuren: Quatre bras. Edit. **[4,6,7,8]**

Lapshin, L.V. 1969 Vidovoi sostav i sezonnaya dinamika chislennosti zhuzhelits (Carabidae) v lesnykh kolkakh Orenburgskoi lesostepi. (Species composition and seasonal abundance dynamics of ground-beetles (Carabidae) in insular woods of the Orenburg forest-steppe) – Probl. pochv. zool. Tez. dokl. III Vses. sov. Moscow: Nauka: 102-103. [In Russian]. **[5]**

Lapshin, L.V. 1972 Zhuzhelitsy v Orenburgskoi lesostepi. (The ground-beetles in the Orenburg forest-steppe) – Probl. pochv. zool. Tez. dokl. IV Vses. sov. Baku. Moscow: Nauka: 90-91. [In Russian]. **[5]**

Larochelle, A. 1975 Notes sur l'activité diurne de quelques Carabidae du Québec. – Ann. Soc. Ent. Québec. 20: 3-6. **[5]**

Larochelle, A. 1990 The food of carabid beetles (Coleoptera: Carabidae, including Cicindelinae. – Fabreries Supplement 5. **[5]**

Larsson, S.G. 1939 Entwicklungstypen und Entwicklungszeiten der daenischen Carabiden. – Entomologiske Meddelelser. 20: 273-562. **[5,6]**

Larsson, S.G. & G. Gigja 1959 Coleoptera 1. Synopsis of species – Zoology of Iceland III, 46a. – København. **[5]**

Lassalle, B. & Y. Delaporte 1989 Un foyer basque d'hybridation entre *C. (Mesocarabus) problematicus* et *C. (M.) macrocephalus*. – L'Entomologiste 45 (1): 45-52. **[2]**

Lauterbach, A.W. 1964 Verbreitungs- und aktivitätsbestimmende Faktoren bei Carabiden in sauerländischen Wäldern. – Abh. Landesmus. Naturkde Münster Westf. 26: 1-100. **[6]**

Lavrenko, E.M. 1938 Istoriya flory i rastitel'nosti SSSR na osnove dannykh o sovremennom rasprostranenii rastenii (History of the flora and the vegetation of USSR according to data on the recent distribution of plants) – Moscow-Leningrad: Izd-vo AN SSSR: 235-396. [In Russian]. **[8]**

Lawrence, J. F. 1991 Order Coleoptera. – In: Stehr, F. W. Immature Insects. Vol. 2. Dubuque: 144-658. **[7]**

Leary, R.F. & F.W. Allendorf 1989 Fluctuating asymmetry as an indicator of stress: implications for conservation biology. – Trends Ecol. Evol. 4: 214-217. **[9]**

Leberg, P.L. 1992 Effects of population bottlenecks on genetic diversity as measured by allozyme electrophoresis. – Evolution 46: 477-494. **[9]**

Lehman, H. 1965 Ökologische Untersuchungen über die Carabidenfauna des Rheinufers in der Umgebung von Köln. – Zeitschrift für Morphologie Ökologie der Tiere 55: 597-630. **[5]**

Lenski, R.E. 1982a Effects of forest cutting on two *Carabus* species: evidence for competition for food. – Ecology 63: 1211-1217. **[6]**

Lenski, R.E. 1982b The impact of forest cutting on the diversity of ground beetles (Coleoptera: Carabidae) in the southern Appalachians. – Ecol. Entomol. 7: 385-390. **[6]**

Lenski, R.E. 1984 Food limitation and competition: a field experiment with two *Carabus* species. – J. Anim. Ecol. 53: 203-216. **[6]**

Lequet, A. 1982 Nouvelle contribution a la connaissance phylogénétique de nos Chrysotribax Reitt. (Coléoptères Carabidae). - Nouvelle Revue Ent. 12: 129-133. **[5]**

Li, W.-H. 1997 Molecular evolution. – Sunderland (Massachusetts): Sinauer. **[9]**

Lie, P. 1987 Betrachtungen über das Vorkommen der *Carabus*-Arten (Coleoptera) im Domogledgebied bei Baile Herculane (Herkulesbad), Banat, Rumänien. – Galathea. Berichte des Kreises Nürnberger Entomologen 3/4: 11-122. **[8,t]**

Lie, P. 1989 Neue Angaben über *Carabus comptus* Dejean (Coleoptera: Carabidae) im rumänischen Banat. – Folia Entomologica Hungarica 50: 41-46. **[5]**

Lie, P. 1990 Considerabii asupra răspândirii speciei *Carabus* (*Eucarabus ulrichii*) Germ. (Coleoptera) în Banat, cu prezentarea unor forme noi. – Analele Banatului 2: 42-47. **[8]**

Lie, P. 1994 Neue Beiträge zur Kenntnis der Carabofauna des Rumänischen Banates für das Jahr 1993 (Coleoptera, Carabidae). – Folia Entomologica Hungarica 55: 225-232. **[5,t]**

Lie, P. 1998 Allgemeine Betrachtungen über die Carabofauna (Coleoptera, Carabidae) des Cernatales (Rumänien, Banat). – Galathea. Berichte des Kreises Nürnberger Entomologen 14: 86-101. **[8,t]**

Lie, P. 1999 Das rätselhafte Vorkommen von *Carabus* (*Morphocarabus*) *alutensis* Svulescu 1972 in der Carabofauna Rumäniens. – Galathea. Berichte des Kreises Nürnberger Entomologen 15 (3): 120-130. **[5]**

Lie, P. 2001 Betrachtungen über *Carabus (Morphocarabus) hampei* Küster, 1846 und seine Rassen in Transsylvanien, Rumänien (Coleoptera: Carabidae). – Galathea. Berichte des Kreises Nürnberger Entomologen 17 (2): 75-94. **[5]**

Lie, P. & I. Máthé 2000 *Carabus (Callistocarabus) marginalis decorus* Seidlitz 1891 wurde in Transsilvania (Siebenbürgen) – Rumänien – nach fast hundert Jahren wieder aufgefunden. – Galathea. Berichte des Kreises Nürnberger Entomologen 16 (1): 18-30. **[5]**

Lindemann, K. 1871 Obzor geograficheskogo rasprostraneniya zhukov v Rossiiskoi imperii. (Überblick über die geographische Verbreitung der Käfer des russischen Reiches) – Tr. Russk. Entomol. obshch. 6: 41-366. [In Russian]. **[5]**

Lindroth, C.H. 1939 Die Insektenfauna Islands und ihre Probleme. – Zoologiska Bidrag fran Uppsala 13: 105-599. **[5]**

Lindroth, C.H. 1945 Die Fennoskandischen Carabiden I. Spezieller Teil II. Die Karten. – Göteborg. **[5,8,maps,t]**

Lindroth, C.H. 1946 Inheritance of wing dimorphism in *Pterostichus anthracinus* Ill. – Hereditas 32. Lund: 37-40. **[5]**

Lindroth, C. H. 1949 Die Fennoskandischen Carabidae III. Allgemeiner Teil. – Kungl. Vetensk. Vitterhh. Samh. Handling. Ser. B 4: 1-911. **[5,6,8]**

Lindroth, C.H. 1957 The faunal connections between Europe and North America. – Uppsala: Alquist & Wiksells. **[6,9]**

Lindroth, C.H. (ed.) 1960 Catalogus Coleopterorum Fennoscandiae et Daniae. – Entomologiska Sällskapet Lund. **[5]**

Lindroth, C.H. 1961-69 The ground-beetles (Carabidae, excl. Cicindelidae) of Canada and Alaska. Parts I-VI – Opuscula Entomologica, suppl. 20, 24, 29, 33, 34, 35: 1-1192, and 48p. **[5,6]**

Lindroth, C.H. 1968 The Icelandic form of *Carabus problematicus* Hbst. (Col. Carabidae): a statistical treatment of subspecies. – Opusc. Ent. 33: 157-182. **[6]**

Lindroth, C.H. 1970 Survival of animals and plants on ice-free refugia during the Pleistocene glaciations. – Endeavour 29 (108): 129-134. **[6]**

Lindroth, C.H. 1974 Handbooks for the identification of British insects. Coleoptera – Carabidae. Vol. IV. Part 2. – London. **[5]**

Lindroth, C.H. 1979 The Theory of Glacial Refugia. – In: T.L. Erwin, G. E. Ball, D.R. Whitehead & A.L. Halpern (eds.): Carabid beetles, their evolution, natural history, and classification. The Hague-Boston-London: Dr. W. Junk Publ.: 385-394. **[8]**

Lindroth, C.H. 1985 The Carabidae (Coleoptera) of Fennoscandia and Denmark I. – Fauna Entomologica Scandinavica 15 (1): 1-226. **[5,6,maps]**

Lindroth, C.H. 1986 The Carabidae (Coleoptera) of Fennoscandia and Denmark II. – Fauna Entomologica Scandinavica 15: 227-497. **[5,6,maps]**

Lo Pinto, G. 1998 Descrizione della larva di *Carabus (Chaetocarabus) arcadicus* (Coleoptera, Carabidae). – Boll. Soc. entomol. It. 130: 105-110. **[5]**

Lohse, G.-A. 1954 Die Laufkäfer des Niederelbegebietes und Schleswig-Holsteins. – Verh. Ver. naturwiss. Heimatforsch. Hamburg 31: 1-39. **[9]**

Loreau, M. 1986 Niche differentiation and community organization in forest carabid beetles. – In: Den Boer, P.J., M.L. Luff, D. Mossakowski & F. Weber (eds.): Carabid beetles: their adaptations and dynamics. – Stuttgart: Fischer: 465-487. **[6]**

Lorenz, W. 1998a Systematic list of extant ground beetles of the world (Insecta Coleoptera "Geadephaga": Trachypachydae and Carabidae incl. Paussinae, Cicindelinae, Rhysodinae). – Tutzing, Germany: 1-502. **[2,3,5,10]**

Lorenz, W. 1998b Nomina Carabidarum. A directory of the scientific names of ground beetles (Insecta Coleoptera "Geadephaga": Trachypachydae and Carabidae incl. Paussinae, Cicindelinae, Rhysodinae). – Tutzing, Germany: 1-937. **[2,3,5,10]**

Lorenzen, S. 1996a Nematoda, Fadenwürmer. – In: Westheide, W. & R. Rieger (eds.): Spezielle Zoologie, Teil 1: Einzeller und Wirbellose Tiere. – Stuttgart: Fischer Verlag: 692-710. **[6]**

Lorenzen, S. 1996b Nematomorpha, Saitenwürmer. – In: Westheide, W. & R. Rieger (eds.): Spezielle Zoologie, Teil 1: Einzeller und Wirbellose Tiere. – Stuttgart: Fischer Verlag: 711-713. **[6]**

Lövei, G.L., I.A.N. Stringer, C.D. Devine & M. Cartellieri 1997 Harmonic radar – a method using inexpensive tags to study invertebrate movement on land. – New Zealand J. Ecol. 21: 187-193. **[6]**

Lövei, G.L. & K.D. Sunderland 1996 Ecology and behaviour of ground beetles (Coleoptera: Carabidae). – Annu. Rev. Entomol. 41: 231-256. **[6,8]**

Lucht, W. 1988 Die Käfer Mitteleuropas, Katalog. – In: Freude, Harde & Lohse. Band K. Krefeld. **[5]**

Lucht, W. 1989 Die Käfer Mitteleuropas. Katalogteil zum 1. Supplementband. – In: Freude, Harde & Lohse. Band 12. Krefeld: 249-260. **[5]**

Lucht, W. & B. Klausnitzer (eds.) 1998 Die Käfer Mitteleuropas. Band 15. Supplement 4. Jena: 58-72. **[5]**

Luff, M.L. 1969 The Larvae of the British Carabidae (Coleoptera), I. Carabidae and Cychrini. – The Entomologist 102: 245-263. **[5]**

Luff, M.L. 1982 Preliminary Atlas of British Carabidae (Coleoptera). – Monkswood: Biological Records Centre: 1-8. Maps: 1-101. **[5,maps]**

Luff, M.L. 1986 Aggregation of some Carabidae in pitfall traps. – In: den Boer, P.J., M.L. Luff, D. Mossakowski & F. Weber (eds.): Carabid beetles: their adaptations and dynamics. Stuttgart: Fischer: 385-390. **[6,9]**

Luff, M.L. 1993 The Carabidae larvae of Fennoscandia and Denmark. – Fauna Entomologica Scandinavica (Leiden) 27: 1-186. **[5,6]**

Luff, M.L. 1994 Starvation capacity of some carabid larvae. – In: Desender, K., M. Dufrêne, M. Loreau, M. Luff & J.-P. Maelfait (eds.): Carabid beetles: ecology and evolution. Dordrecht: Kluwer Academic Publishers: 171-175. **[6]**

Luff, M.L. 1998 Provisional atlas of the ground beetles (Coleoptera, Carabidae) of Britain. – Huntingdon: Biological Records Centre. **[5,9,maps]**

Lukasiewicz, J. 1996 Predation by the beetle *Carabus granulatus* L. (Coleoptera, Carabidae) on soil macrofauna in grassland on drained peats. – Pedobiologia 40: 364-376. **[5,6]**

Lynch, M. 1996 A quantitative-genetic perspective on conservation issues. – In: Avise, J.C. & J.L. Hamrick (eds.): Conservation genetics: case histories from nature. New York: Chapman & Hall: 471-501. **[9]**

Mace, G.M. & R. Lande 1991 Assessing extinction threats: towards a reevaluation of IUCN threatened species categories. – Conserv. Biol. 5: 148-157. **[9]**

Machado, A. 1992 Monografía de los carábidos de las islas Canarias (Insecta, Coleoptera) – Instituto de estudios Canarios. La Laguna: 1-734 **[5,8]**

Mader, H.-J., C. Schell & P. Kornacker 1990 Linear barriers to arthropod movements in the landscape. – Biol. Conserv. 54: 209-222. **[9]**

Magistretti, M. 1965 Coleoptera, Cicindelidae, Carabidae, Catalogo topografico. – Fauna d'Italia VIII. Bologna: Calderini: 1-512. **[5]**

Magura, T., V. Ködöböcz, B. Tóthmérész, T. Molnár, Z. Elek, G. Szilágyi & G. Hegyessy 1997 Carabid fauna of the Beregis'kság and its biogeographical relations. – Folia Entomologica Hungarica 58: 73-82. **[8,t]**

Magura, T. & T. Molnár 1996 Comparison of the carabid fauna of the Ménes-valley and a higher karst plateau (Coleoptera: Carabidae). – In: Tóth & Horváth (eds.): Research in Aggtelek National Park. Proceedings of the Research, Conservation, Management Conference Vol II: 117-122. **[8,t]**

Magura, T., B. Tóthmérész & T. Molnár 2000 Spatial distribution of carabids along grass-forest transects. – Acta Zoologica Academiae Scientarum Hungaricae 46: 1-17. **[8,t]**

Mahler, V., R. Suikat & T. Assmann 1996 Red List of beetles of the wadden sea area. – Helgoländer Meeresunters 50, suppl.: 83-96. **[5,9]**

Makarov, K.V. 1992 Larvae of the carabids of the genus *Carabus* L. (Coleoptera, Carabidae) of the fauna of Russia and neighbouring countries. 1. Morphology of larvae and key to the subgenera. – Entom. Obozr. 71: 752-774 [in Russian]. **[3,4,7]**

Makarov, K.V. 1994 A key to the genera of ground-beetle larvae (Coleoptera, Carabidae) of the fauna of Russia and neighboring countries. I. Morphology of the larvae. A key to the subgenera. – Ent. Rev. 72: 94-117. **[4]**

Makarov, K.V. & K. I. Atamuradov 1994 Biology and Premature Stages of *Carabus (Mimocarabus) roseni* (Coleoptera, Carabidae). – Vestnik Zoologii 3: 57-65 [In Russian]. **[4,7]**

Makarov, K.V. & O.E. Berlov 1993 Larvae of the Carabids of the genus *Carabus* L. (Coleoptera, Carabidae). II. Larvae of the Subgenus *Cryptocarabus* Reitt. – Entom. Obozr. 72: 345-350 [in Russian]. **[4]**

Makarov, K.V. & V.G. Shilenkov 1991 Beschreibung der Larve von *Carabus* (*Eupachys*) *glyptopterus* Fischer von Waldheim (Coleoptera: Carabidae) – Koleopterologische Rundschau 61: 11-18. **[4]**

Malausa, J.-C. 1977 L'élevage des coléoptères Carabidae dans la perspective d'une multiplication de masse. – Annales de Zoologie et d'Écologie Animale 9: 487-505. **[5]**

Malausa, J.-C. 1978a L'élevage d'une espèce en voie d'extinction en vue d'assurer sa protection: *Sellaecarabus olympiae* (Sella) (Col. Carabidae). – Bull. Soc. ent. France 83: 153-159. **[5]**

Malausa, J.-C. 1978b Étude des dormances intervenant dans le cycle de developpement de *Procrustes coriaceus* L. (Coleoptera, Carabidae). – Annales de Zoologie et d'Écologie Animale 10: 77-83. **[5]**

Malausa, J.C. & J. Drescher 1991 The project to rescue the Italian ground beetle *Chrysocarabus olympiae*. – International Zoological Yearbook 30: 75-79. **[9]**

Malausa, J.-C., Y. Pujante, J. Drescher & J. Amand 1984 Preuves génétiques de la synonymie de *Chrysocarabus punctatoauratus* Germar avec *Chrysocarabus auronitens* Fabricius (Coleoptera, Carabidae). – Nouvelle revue d'Ecologie (N.S.) 1: 359-363. **[5]**

Malausa, J.-C., M. Raviglione & F. Boggio 1983 Il *Carabus olympiae* dell' alta Valle Sessera. – Pro Natura Biellese: Tip. Gariazzo: 108. **[5]**

Mal'tsev I.V., A.A. Petrusenko & S.V. Petrusenko 1971 K izucheniyu zhuzhelits (Coleoptera, Carabidae) Krymskoi Yaily. (On studying tiger and ground beetles (Coleoptera, Carabidae) from the Crimean Yaila) – Vestn. zool. 5: 25-29. [In Russian]. **[5]**

Mandl, K. 1955 *Carabus alpestris* Strm. und seine Rassen. – Entomologische Nachrichten Oesterr. und Schweizer. Entomologen 7: 13-20. **[3,8]**

Mandl, K. 1956-1958 Die Käfer Österreichs. III Die Carabiden Österreichs, Tribus Carabini, Genus *Carabus* L. – Koleopterologische Rundschau 34: 4-49; 34: 50-104; 36: 1-13 + 28 maps. **[5,8,maps]**

Mandl, K. 1960 Ergebnisse der vom Dr. O .Pagel und Dr. E. Kritscher auf Rhodos durchgeführten zoologischen Exkursionen. III. Coleoptera. – Annalen des Naturhistorischen Museums in Wien. Serie B. Botanik und Zoologie 64: 127-134. **[3]**

Mandl, K. 1962 Die fennoskandischen Formen des *Carabus violaceus* L. (Carabidae, Col.). – Opuscula entomologica 27: 193-209. **[3,8]**

Mandl, K. 1965 *Carabus scheidleri* Panzer und sein Formenkreis. – Ent. Abhandl. Staatl. Mus. Tierk. Dresden 32: 415-457. **[8]**

Mandl, K. 1967 Der Rassenkreis *Carabus creutzeri* Fabricius, ein taxonomisches und tiergeographisches Problem. – Ent. Abhandl. Staatl. Mus. Tierk. Dresden 34: 201-217. **[3,8]**

Mandl, K. 1972 Catalogus Faunae Austriae XVa, Cicindelidae und Carabidae: Carabinae. – Wien. **[5,maps]**

Mandl, K. 1978 Catalogus Faunae Austriae XVa, Cicindelidae und Carabidae II. – Wien. **[5,maps]**

Mandl, K. 1984 *Carabus*-Formen als Praeglazialrelikte in den niederen Tauern. – Koleopt. Rdsch. 57: 35-51. **[8]**

Mandl, K. 1985 *Cychrus caraboides* L. – Mitteilungen Entomologischer Gesellschaft. Basel 35: 17-26. **[3]**

Marggi, W.A. 1992 Faunistik der Sandlaufkäfer und Laufkäfer der Schweiz (Cicindelidae & Carabidae, Coleoptera), Teil 1 / Text. – Centre Suisse de cartographie de la faune Neuchatel: 1-477; Teil 2 / Verbreitungskarten. – Centre Suisse de cartographie de la faune Neuchatel: 1-243 **[5,9,maps]**

Martius, C. 1986 Die Laufkäferfauna (Coleoptera: Carabidae) eines Kalkbuchenwaldes. – Drosera 86: 1-11. **[5,6]**

Mascanzoni, D. & H. Wallin 1986 The harmonic radar: a new method of tracing insects in the field. – Ecol. Entomol. 11: 387-390. **[6]**

Matthews, J. V. 1979 Late Tertiary Carabid Fossils from Alaska and Canadian Archipelago. – In: T.L. Erwin, G.E. Ball, D.R. Whitehead & A.L. Halpern (eds.): Carabid beetles, their evolution, natural history, and classification. The Hague-Boston-London: Dr W. Junk Publ.: 425-445. **[8]**

Matalin, A.V. 1993 Ekologicheskie osobennosti migratsii zhuzhelitz (Coleoptera, Carabidae) stepnoi zony (Ecological features of flight migrations of the ground beetles in the steppe zone). – Avtoref. diss. kand. biol. nauk. MGPU: Moscow: 1-16. [In Russian]

Mathyl, E. 1990 Maßnahmen zum Schutz des Heidelaufkäfers (*Carabus nitens*) (Coleoptera, Carabidae). – Entomol. Nachr. Ber. 34: 73-75. **[9]**

Matveev, A.B. 1988 Carabid beetles of the genus *Carabus* of the Southern Ural and Urals foothills. – XII Internat. Sypm. Entomofaun. Mitteleur., Kurzfass. d. Vortraege. Kiev: 105. [In Russian]. **[5]**

Matveev, A.B. 1990 Zhuzhelitsy (Coleoptera, Carabidae) Yuzhnogo Urala i Predural'ya (fauna, biotopicheskoe raspredelenie, zoogeograficheskii analiz, vozmozhnosti ispol'zovaniya v monitoringe). (The ground-beetles (Coleoptera, Carabidae) of the South Urals and Cisural region (fauna, habitat distribution, zoogeographical analysis, possibilities for use in monitoring)) – Avtoref. kand. diss. Leningrad: 1-19. [In Russian]. **[5]**

Matveeva, V.G., T.S. Man'kova & V.S. Pisanov 1983/84 Pochvennye bespozvonochnye (mezofauna) v gidrologicheskom ryadu sosnyakov Darvinskogo zapovednika. (Soil invertebrates (macrofauna) in a hydrological sery of pine forests in the Darwin Reserve) – In: Fauna i ekologiya bespozvonochnykh zhivotnykh. Moscow: 171-182. [In Russian]. **[5]**

Maynard-Smith, J. 1998 Evolutionary Genetics. – Oxford: Oxford University Press. **[6]**

Mayr, E. 1976 What is a fauna?. – In: Mayr E. (ed.): Evolution and diversity of life. Cambridge: Harvard University Press: 552-564. **[8]**

McKenzie, J.A. & P. Batterham 1994 The genetic, molecular and phenotypic consequences of selection for insecticide resistance. – Trends Ecol. Evol. 9: 166-169. **[9]**

Medvedev, S.I. 1928(30) O rasprostranenii nasekomykh v Yuzhnom Zadneprov'e. (On the distribution of insects in the South Transdneprovia region (Zadneprovye)) – Visti Derzh. stepn. zapov. "Chapli" 7: 5-27. [In Russian]. **[5]**

Medvedev, S.I. 1950 Coleoptera. – In: Zhivotnyi mir SSSR, T. III. Zona stepei. Moscow-Leningrad: Izd-vo AN SSSR: 294-347. [In Russian]. **[5]**

Medvedev, S.I. & D.S. Shapiro 1957 K poznaniyu fauny zhukov (Coleoptera) Moldavskoi SSR i sopredel'nykh raionov Ukrainy. (A contribution to the knowledge of beetles (Coleoptera) of the Moldavian SSR and adjacent areas of Ukraine) – Uch. zap. Khar'k. univ. 90. Trudy Nauchn.-issled. inst. biologii i biol. fak. 30: 173-206. [In Russian]. **[5]**

Men'shikov A. & P. Gorbunov 1997 Zhuzhelitsa Gummelya *Carabus hummeli* Fischer von Waldheim, 1823. (The ground beetle *Carabus hummeli* Fischer von Waldheim, 1823) – In: Krasnaya kniga Yamalo-Nenetskogo avtonomnogo okruga. Ekaterinburg: Izd-vo Uralsk. Univ.: 1-86. [In Russian]. **[5]**

Meurgues, G. & G. Ledoux 1966 Intérêt de l'étude du sac interne dévaginé et en extension. – Ann. Soc. ent. Fr. N.S. 2: 661-669. **[3,6,7]**

Metzenauer, P. 1981 Extraintestinale Verdauung bei *Carabus problematicus* Herbst im Vergleich mit *Pterostichus nigrita* (Paykull) (Col., Carabidae). – Zool. Anz. 206 (1/2): 57-61. **[6]**

Meyer-Peters, H. 1988 Die Dynamik verschiedener Parameter der tagesperiodischen Laufaktivität bei *Carabus auronitens* (Coleoptera, Carabidae). – Mitt. dtsch. Ges. allg. angew. Ent. 6: 560-567. **[6]**

Meyer-Peters, H. 1993a Seasonality of circadian locomotor activity in an insect. – J. Comp. Physiol. A 171: 713-724. **[5,6]**

Meyer-Peters, H. 1993b Feeding effects on daily locomotor activity in *Carabus auronitens*. – J. Comp. Physiol. A 173: 49-55. **[5,6]**

Mitton, J.B. 1997 Selection in natural populations. – Oxford: Oxford University Press. **[6,9]**

Mletzko, G. 1970 Beitrag zur Carabiden – Fauna des NSG Burgholz Halle/S. – Hercynia. (N.F.) 7: 92-110. **[5]**

Mollard A. 1999 Monographie de *C.* (*Chrysocarabus*) *rutilans* Dejean 1826. Rutilans, suppl. 1: 1-22. **[A]**

Molodova, L.P. 1990 O zhuzhelitsakh roda *Carabus* na territorii Gomel'skoi oblasti. (On ground-beetles of the genus *Carabus* in the Gomel Province) – Fauna i ekologiya zhuzhelits. Tez. dokl. III Vses. karabidol. sov. Kishinev: 49-50. [In Russian]. **[5]**

Molenda, R. 1996 Zoogeographische Bedeutung von Kaltluft erzeugender Blockhalden im außeralpinen Mitteleuropa: Untersuchungen an Arthropoda, insbesondere Coleoptera. – Verh. Naturwiss. Ver. Hamburg (N.F.) 35: 5-94. **[6]**

Møller, A.P. & J.P. Swaddle 1997 Asymmetry, developmental stability, and evolution. – Oxford: Oxford University Press. **[9]**

Morati, J. & M. Huet, 1995 Présence de *Carabus* (*Hygrocarabus*) *nodulosus* Creutzer, 1799, dans le Jura Français (Coleoptera, Carabidae). – Bulletin Soc. ent. Fr. 100: 144. **[5]**

Morawitz, A. 1886 Zur Kenntniss der Adephagen Coleopteren. – Acad. imp. Sci. St. Pétersbourg 34: 1-88 **[3]**

Mossakowski, D. 1970a Zur Besiedlung salzbeeinflusste Torfstandorte durch Coleopteren. – Mitteilungen der Deutschen Bodenkundl. Gesellschaft 10: 217-219. **[5]**

Mossakowski, D. 1970b Oekologische Untersuchungen an epigaeischen Coleopteren atlantischer Moor und Heidestandorte. – Zeitschrift für wissenschaftenliche Zoologie 181: 233-316. **[5]**

Mossakowski, D. 1971 Zur Variabilität isolierter Populationen von *Carabus arcensis* Hbst. (Coleoptera). – Z. zool. Syst. Evolutionsforsch. 9: 81-106. **[6]**

Mossakowski, D. 1979 Evolution of habitat preference illustrated by the phylogeny of *Chrysocarabus* (Coleoptera, Carabidae). – In: P.J. den Boer, H.U. Thiele & F. Weber (eds.): On the evolution of behaviour in carabid beetles. Wageningen: Landbouwhogeschool: 103-112. **[8]**

Mossakowski, D. 1991 Zur Verbreitung der Laufkäfer (Carabidae) im Lande Bremen. – Abhandlungen Naturwissenschaftlichen Verein Bremen 41: 543-639. **[maps]**

Mossakowski, D., S. Braun & A. Roschen 1990 Hybridization in natural populations of ground beetles (Coleoptera, Carabidae). – Can. J. Zool. 68: 1783-1789. **[5,6]**

Mossakowski, D. & S. Braun 1993 Zur Verbreitungsgeschichte der *Chrysocarabus*-Formen. – Mitt. Dtsch. Ges. allg. angew. Ent. 8: 473-478. **[6,8]**

Mossakowski, D. & S. Braun 2001 Glacial refuges in *Carabus splendens*: reconstructed using population differences in enzyme variability. – Mitt. Dtsch. Ges. allg. angew. Ent. 13: 105-110 **[A]**

Mossakowski, D., A. Roschen & S. Vaje 1986 Hybridisation in *Chrysocarabus*. – In: den Boer, P.J., M.L. Luff, D. Mossakowski & F. Weber 1986 Carabid beetles: their adaptations and dynamics. Stuttgart-New York: Gustav Fischer: 281-295. **[6,8]**

Mossakowski, D., C. Schnauder, W. Carius & B. Klein 1995 Differenzen in der Enzym-Variabilität von *Carabus*-Arten nahe des früheren Eisrandes. – Mitt. Dtsch. Ges. allg. angew. Ent. 9: 787-792. **[6]**

Mossakowski, D. & J. Stier 1983 Vergleichende Untersuchungen zur Laufgeschwindigkeit der Carabiden. – Report 4th Symp. Carab. '81: 19-34. **[6]**

Mossakowski, D. & F. Weber 1972 Korrelationen zwischen Heterochromatingehalt und morphologischen Merkmalen bei *Carabus auronitens* (Coleoptera). – Z. f. zool. Syst. Evol.forsch. 10: 291-300. **[6]**

Mossakowski, D. & F. Weber 1976 Chromosomale und morphometrische Divergenz bei *Carabus lineatus* und *C. splendens* (Carabidae) I. Ein Vergleich sympatrischer und allopatrischer Populationen. – Z. f. zool. Syst. Evol. forsch. 14: 280-291. **[6]**

Müller, G. 1926a Coleopterologische Notizen. IX. – Wiener Entomologische Zeitung 43: 167-171. **[5]**

Müller, G. 1926b Coleotteri della Venezia Giulia. I. Adephaga. – Studi Etomol. Trieste I(2): 306 pp. **[5]**

Müller-Motzfeld, G. 1982 Faunenveränderungen – Indikation und ökologische Ursachen. – Wissenschaftliche Zeitschrift Ernst Moriz-Arndt Universität Greifswald 31: 53-56. **[5]**

Müller-Motzfeld, G. 1983 Kritische Liste der Laufkäfer der Bezirke Rostock, Schwerin und Neubrandenburg (Col. Carab.). – Natur und Naturschutz in Mecklenburg. Greifswald-Waren 19: 5-48. **[5]**

Müller-Motzfeld, G., F. Hieke, D. Wrase & E. Arndt 1989 Liste der Carabiden-Arten der DDR (Stand 1987). – Entomologische Nachrichten und Berichten 33: 49-57. **[5,maps]**

Müller-Motzfeld, G., R. Schultz & K.-U. Pössel 1996 Die Laufkäferfauna der Karrendorfer Wiesen als Indikator für die Sukzession der epedaphischen Arthropodenfauna nach dem Deichrückbau. – Natur und Naturschutz in Mecklenburg-Vorpommern 32: 112-129. **[9]**

Neculiseanu, Z.Z. 1988 Novye dlya fauny Moldavii vidy zhuzhelits (Coleoptera, Carabidae). (Ground-beetle species (Coleoptera, Carabidae) new to the fauna of Moldavia) – Izv. Akad. nauk MoldSSR. Ser. biol. khim. nauk 4: 70-71. [In Russian]. **[5]**

Neculiseanu, Z.Z. & A.V. Matalin 2000 A catalogue of the ground-beetles of the republic of Moldova (Insecta, Coleoptera, Carabidae). – Sofia-Moscow: Pensoft: 1-164. **[5,maps]**

Nei, M., T. Maruyama & R. Chakraborty 1975 The bottleneck effect and genetic variability in populations. – Evolution 29: 1-10. **[9]**

Nelemans, M.N.E. 1987a On the life history of the carabid beetle *Nebria brevicollis* (F.). Egg production and larval growth under experimental conditions. – Neth. J. Zool. 37: 26-42. **[6]**

Nelemans, M.N.E. 1987b Possibilities for flight in the carabid beetle *Nebria brevicollis* (F.). The importance of food during larval growth. – Oecologia 72: 502-509. **[6]**

Nelemans, M.N.E. 1988 Surface activity and growth of larvae of *Nebria brevicollis* (F.) (Coleoptera, Carabidae). – Neth. J. Zool. 38: 74-95. **[6]**

Nettmann, H.-K. 1986 Carabid systematics and chromosome numbers. – In: den Boer, P.J., M.L. Luff, D. Mossakowski & F. Weber (eds.): Carabid beetles – their adaptations and dynamics. Stuttgart: Fischer: 235-254. **[6]**

Neudecker, C. 1971 Lokomotorische Aktivität von *Carabus glabratus* Payk. und *Carabus violaceus* L. am Polarkreis. – Oikos 22: 128-130. **[5,6]**

Neumann, U. 1971 Die Sukzession der Bodenfauna (Carabidae – Coleoptera, Diplopoda und Isopoda) in den forstlich rekultivierten Gebieten des Rheinischen Braunkohlenreviers. – Pedobiologia 11: 193-226. **[5,6]**

Nève, G. 1994 Influence of temperature and humidity on the activity of three *Carabus* species. – In: Desender, K., M. Dufrêne, M. Loreau, M. Luff & J.-P. Maelfait (eds.): Carabid beetles: ecology and evolution. – Dordrecht: Kluwer Academic Publishers: 189-192. **[6]**

New, T.R. 1995 An introduction to invertebrate conservation biology. – Oxford: Oxford University Press. **[9]**

Nickerl, O. 1889 *Carabus auronitens* Fab., Ein Beitrag zur Kenntnis vom Lebensalter der Insekten. – Stettiner Entomologische Zeitung 50: 155-163. **[5]**

Niedl, J. 1956-1958 Monographie ceskoslovenský druhu tribu Carabini I-III. Prír. sb. ostr. kraje 17: 305-329; 18: 209, 237; 19: 7-41. Opava. **[5,maps]**

Niehues, F.-J. 1995 Die Geschichte einer Carabidenpopulation im Spiegel ihrer Genetik und Dynamik: Untersuchungen an *Carabus auronitens* im Münsterland. – Doctoral Thesis at the University of Münster. **[9]**

Niehues, F.-J., P. Hockmann & F. Weber 1996 Genetics and dynamics of a *Carabus auronitens* metapopulation in the Westphalian Lowlands (Coleoptera, Carabidae). – Ann. Zool. Fennici 33: 85-96. **[5,6,8,9]**

Niemelä, J. 1988 Habitat occupancy of carabid beetles on small islands and the adjacent Åland mainland, SW Finland. – Ann. Zool. Fennici 25: 121-131. **[8,t]**

Niemelä, J. 1993 Interspecific competition in ground-beetle assemblages (Carabidae): what have we learned? – Oikos 66: 325-335. **[6]**

Niemelä, J. & E. Halme 1992 Habitat associations of carabid beetles in fields and forests on the Åland islands, SW Finland. – Ecography 3-11. **[8,t]**

Niemelä, J., Y. Haila, E. Halme, T. Lahti, T. Pajunen & P. Punttila 1988 The distribution of carabids in fragments of old coniferous taiga and adjacent managed forest. – Ann. Zool. Fennici 25: 107-119. **[8,9,t]**

Noonan, G.R. 1979 The Science of Biogeography with relation to Carabids. – In: T.L. Erwin, G.E. Ball, D.R. Whitehead & A.L. Halpern (eds.): Carabid beetles, their evolution, natural history, and classification. The Hague-Boston-London: Dr W. Junk Publ.: 295-317. **[8]**

Novak, B. 1971 Diurnale Aktivität der Carabiden in einem Feldbiotop (Coleoptera, Carabidae). – Acta Univ. Palackianae Olomucensis Fac. Rer. Nat. 34: 129-149. **[6]**

Novak, B. 1972 Saisondynamik der tageszeitlichen Aktivität bei Carabiden in einem Feldbiotop (Coleoptera, Carabidae). – Acta Univ. Palackianae Olomucensis Fac. Rer. Nat. 39: 59-97. **[6]**

Novak, B. 1973 Jahreszeitliche Dynamik der diurnalen Aktivität bei Carabiden in einem Waldbiotop (Coleoptera, Carabidae). – Acta Univ. Palackianae Olomucensis Fac. Rer. Nat. 43: 251-280. **[6]**

Novoa, F. 1979 Los Carabidae (Coleoptera)de la Sierra de Caurel (Lugo). – Bol. R. Soc. Esp. Hist. Nat. (Sec. Biol.) 77: 429-449. **[5]**

Novoa, F., M. Saez, E. Eiroa & J. González 1989 Los Carabidae (Coleoptera) de la Sierra de Ancares (Noroeste de la Península Ibéroca). – Bol. R. Soc. Esp. Hist. Nat. (Sec. Biol.) 84: 287-305. **[5]**

Nunney, L. & K.A. Campbell 1993 Assessing minimum viable population size: demography meets population genetics. – Trends Ecol. Evol. 8: 234-239. **[9]**

Nüssler, H. 1969 Zur Ökologie und Biologie von *Carabus menetriesi* Hummel (Coleoptera, Carabidae). – Entomol. Abh. Staatl. Mus. Tierkde Dresden 36: 281-302. **[5,6]**

Obydov, D. 2000 New taxa of the genus *Carabus* from Northern European Russia (Coleoptera: Carabidae). – Acta Enomologica Slovenica 8: 123-128. **[2,3]**

Obydov, D. 2002 Revision du genre *Callisthenes*. – Association Magellanes: 1-128. **[A]**

Oertel, R. 1924 Biologische Studien über *Carabus granulatus* L. – Zool. Jb. Abt. Syst. 48: 299-366. **[6]**

Oosterbroek, P. 1994 Biodiversity of the Mediterranean Region. – Systematic Association Special Volume 50: 289-307. **[8]**

Orlov, V.A. 1983 Zhuzhelitsy roda *Carabus* v Moskovskoi oblasti. (Ground-beetles of the genus *Carabus* in the Moscow Province) – In: Fauna i ekologiya pochvennykh bespozvonochnykh Moskovskoi oblasti. Moscow: 113-120. [In Russian]. **[5]**

Osawa, S., Z.-H. Su & Y. Imura 2002 Molecular Phylogeny and Evolution of the Carabid Ground Beetles of the World. Tokyo: Tetsugakushobo: 1-264. [In Japanese, with English book title]. **[A]**

Ozenda, P. 1988 Die Vegetation der Alpen im europäischen Gebirgsraum. – Stuttgart: Fischer. **[9]**

Paarmann, W. 1979 Ideas about the evolution of the various annual climate zones. – In: den Boer, P.J., H.-U. Thiele & F. Weber (eds.): On the evolution of behaviour in carabid beetles, Miscellaneous Papers (Agricultural University Wageningen) 18: 119-132. **[6]**

Paill, W. 2000 Slugs as prey for larvae and imagines of *Carabus violaceus* L. (Coleoptera: Carabidae). – In: Brandmayr, P., G. L. Lövei, T. Z. Brandmayr, A. Casale & A. Vigna Taglianti (eds.): Natural history and applied ecology of carabid beetles. Sofia-Moscow: Pensoft Publishers: 221-227. **[5,6]**

Paje, F. & D. Mossakowski 1984 pH-preferences and habitat selection in carabid beetles. – Oecologia 64: 41-46. **[6]**

Panin, S. 1941 Les *Carabus* de la faune roumaine (gen. *Carabus* L.). – Bulletin de la Section scientifique de l'Académie Roumaine 23: 326-337. **[5]**

Panin, S. 1942 *Carabus convexus* de la faune roumaine et *Carabus antipai* sp.n. – Bulletin de la Section scientifique de l'Académie Roumaine 25: 198-211. **[3,5]**

Panin, S. 1952 Fauna Republicii populare Romane, Coleoptera, Cicindelidae. – Bucuresti: 10 (1): 1-53. **[5,maps]**

Panin, S. 1955 Fauna Republicii populare Romane, Coleoptera – Carabidae (genus *Cychrus* F. si genus *Carabus* L.). – Bucuresti: 10 (2): 1-148. **[5,8,maps]**

Pankevitch, T.P. 1978 K kachestvennoi i kolichestvennoi otsenke pitaniya *Carabus arcensis* Hbst. (Coleoptera, Carabidae) (To the qualitative and quantitative estimation) – Probl. pochv. zool., Tez. dokl. VI Vses. sov. Minsk: 177-178. [In Russian]. **[5]**

Pavicevic, D. & G. Mesaros 1997 Carabini of Jugoslavia and adjecent regions (Coleoptera: Carabidae). Catalogus Faunae Jugoslaviae. Encyclopaedia. Belgrade: Ecolibri-Bionet. Release on cd-rom. **[5,maps,t]**

Pavlova, G.N. 1974 Izmenenie kompleksa zhuzhelits (Coleoptera, Carabidae) yuzhnoi tipchakovo-kovyl'noi stepi pri ee iskustvennym vosstanovlenii. (Changes in the complex of ground beetles (Coleoptera, Carabidae) in the steppe under its artificial restoration) – Zool. Zhurn 53 (7): 1023-1029. [In Russian]. **[5,t]**

Pawłowski, Y. 1967 The beetles of Babia Góra range in the years 1959-1964. – Acta zool. cracov. 12: 419-665. [In Polish]. **[t]**

Pawłowski, Y. 1972 The beetles of Babia Góra range in the years 1959-1964. – Smithsonian Institution and the National Science Foundation Washington D.C. by the Foreign Scientific Publications Department of the National Centre for Scientific, Technical and Economic Information. Warsaw: 19-267, 8 Pl. **[t]**

Pearson, D.L. & A.P. Vogler 2001 Tiger Beetles. The evolution, ecology and diversity of the cicindelids. – Ithaca-London: Cornell University Press: 1-333. **[A]**

Penev, L.D. 1989 Fauna i zonal'noe raspredelenie shchelkunov (Coleoptera, Elateridae) Russkoi Ravniny (Fauna and zonal distribution of the click beetles (Coleoptera, Elateridae) of the Russian Plain) – Zool. Zhurn. 68: 193-205. [In Russian]. **[8]**

Penev, L.D. 1991 CARRUS, a literature database for the European Carabidae (Coleoptera). – Release on diskettes and manual, Renkum/Sofia: 1-41 (see also Turin, 1988 and De Felice, 2000). **[5]**

Penev, L.D. 1996 Large-scale variation in carabid assemblages, with special reference to the local fauna concept. – Ann. Zool. Fennici 33: 49-64. **[6,8]**

Penev, L.D. 1997 Concrete biotas – A neglected concept in biogeography? – Global Ecology and Biogeography Letters 6: 91-96. **[8]**

Penev, L.D. & S.K. Alekseev 1996 The click-beetles of North Ossetia, Caucasus: fauna, habitat distribution, and biogeography (Coleoptera: Elateridae). – Stuttgarter Beitr. Naturk. Ser. A 549: 1-19. **[8]**

Penev, L.D. & H. Turin 1994 Distribution of the genus *Carabus* in Europe: approaches and preliminary results. – In: Desender *et al.*, (eds.). Carabid beetles, ecology and evolution. Dordrecht: Kluwer: 37-43. **[5,8]**

Penterman, E. 1988a Über die Aktivitätsdichte der Carabidenpopulationen einiger Feuchthabitate südöstlich von Villach (Kärnten). – Carinthia II 46: 125-139. **[8,t]**

Penterman, E. 1988b Über die Aktivitaetsdichte der Carabidenpopulationen verschiedener Habitate in Wäldern südöstlich von Villach (Kärnten). – Carinthia II 178: 113-123. **[8,t]**

Pesenko, Yu. A. 1982 Printsipy i metody kolichetvennoga analiza v faunisticheskikh issledovaniyakh (Principles and methods of quantitative analysis in faunistic investigations). – Moscow: Nauka: 1-287. [In Russian]. **[8]**

Petrusenko, A.A. 1971 Ekologo-zoogeograficheskii analiz zhuzhelits lesostepnoi i stepnoi zon Ukrainy. (Eco-zoogeographical analysis of ground-beetles of the forest-steppe and steppe zones of Ukraine) – Avtoref. kand. diss. Kiev: 1-25. [In Russian]. **[5]**

Petrusenko, A.A. & S.V. Petrusenko 1971 Zhuzhelitsy (Coleoptera, Carabidae) zabolochennykh uchastkov Kryma. (The ground-beetles (Coleoptera, Carabidae) in boggy areas of the Crimea) – Vestn. zool.: 30-33. [In Russian]. **[5]**

Petruska, F. 1967 Carabiden als Bestandteil der Entomofauna des Rübenfelder in der Unicov Ebene. – Acta Universitatis Palackianae Olomucensis Facultas Rerum Naturalium 25: 121-243. **[8,t]**

Peus, F. 1928 Beiträge zur Kenntnis der Tierwelt nordwestdeutscher Hochmoore. Eine ökologische Studie. – Diss. Univ. Münster. **[5]**

Pirazzoli, P. 1991 World Atlas of Holocene Sea Level Changes. – Amsterdam: Helsevier Ocean: 1-300. **[8]**

Pisó, K. 1885 Az aranyosfutrinka hazánkban. (The occurrence of *Carabus auratus* in Hungary). – Rovartani Lapok 2: 249. **[5]**

Platnick, N.J. & G. Nelson 1978 A method of analysis for historical biogeography. – Syst. Zool. 27: 1-16. **[8]**

Ponomarchuk, V.I. 1956 Raspredelenie zhuzhelits (Carabidae) Zakarpatskoi oblasti. (Distribution of ground-beetles (Carabidae) in the Transcarpathian Province) – Nauchn. zap. Uzhgorod. gos. univ. 16: 167-176. [In Russian]. **[5]**

Ponomarenko, A.G. 1977 Mesozoic Coleoptera. -Trudy Pal. Inst. Moscow: Nauka: 161: 1-204. [in Russian]. **[8]**

Popov, M.G. 1927 The main features in the historical development of the flora of Middle Asia. – Bull. Middle Asian State Univ. 15: 239-292. [In Russian]. **[5]**

Popov, V.V. & I.A. Krusteva 1999 Epigeobiont animal assemblages from two landscapes of the Bulgarian Black Sea Coast: relationship to environmental gradients, assemblage structure and biodiversity. I. Ground beetles (Coleoptera: Carabidae). – Acta Zoologica Bulgarica 51: 81-114.

Poppius, B. 1905 Beiträge zur Kenntnis der Coleopteren-Fauna der nordoestlichen europäeischen Russlands. – Ezheg. Zool. muz. Imp. Akad. nauk 10: 302-315. **[5]**

Poppius, B. 1908/09 Die Coleopteren-Fauna der Halbinsel Kanin. – Acta Soc. Fauna Flora Fenn. 31 (8): 1-58. **[5]**

Poppius, B. 1910 Die Coleopteren des arktischen Gebietes. – Fauna Arctica Jena 5: 291-447. **[5]**

Posinger, F. von, 1949-50 Beitrag zur kenntnis der Lage der Arealgrenzen der ssp. *violaceus* und der ssp. *purpurascens* des *Megodontes violaceus* L. und der Biotope des *Carpathophilus linnei* Panz. im Bayerischen Wald. – Ent. Bl. Biol. Syst. Käfer. Bd. 45/46 S: 105-108. **[5]**

Pravdin, F.N. & L.L. Mishchenko 1980 Proishokhdenie i ekologicheskaya evolyutsiya fauny nasekomykh Srednei Azii. (Origin and ecological evolution of insect fauna of Middle Asia). Moscow: Nauka: 1-156. [In Russian]. **[8]**

Prentice, C. I., D. Jolly & Biome 6000 participants 2000 Mid-Holocene and glacial-maximum vegetation geography of the northern continents and Africa. – J. Biogeogr. 27: 507-519. **[8]**

Primack, R.B. 1993 Essentials of Conservation Biology. – Sunderland (Massachusetts): Sinauer. **[9]**

Prishutova, Z.G., Yu.G. Arzanov & E.A. Eremenko 2000 Zhestkokrylye parkov Rostov-na-Donu. (The beetles of the city park of Rostov-na-Donu)– In: Chteniya pamyati prof. V.V. Stanchinskogo. Smolensk: Izd-vo Smolenskogo Univ.: 3: 39-41. [In Russian]. **[5]**

Prüser, F. 1996 Variabilität mitochondrialer DNA-Sequenzen und die Phylogenie der Gattung *Carabus* Linné 1758 (Coleoptera: Carabidae). – Doctoral Thesis at the University of Bremen. **[3,6,7]**

Prüser F. & E. Arndt 1995 Description of the larva of *Ceroglossus chilensis* Eschscholtz, 1829 (Coleoptera: Carabidae: Carabini). – Studies on Neotropical Fauna and Environment 30: 229-235. **[7]**

Prüser, F., M. Brückner & D. Mossakowski 2000 Colonization of Canary Islands by *Carabus* species: evidence from different character complexes. – In: Brandmayr, P., G. L. Lövei, T. Z. Brandmayr, A. Casale & A. Vigna Taglianti (eds.): Natural History and Applied Ecology of Carabid Beetles. Sofia-Moscow: Pensoft Publishers: 45-52. **[3,7,8]**

Prüser, F. & D. Mossakowski 1990 Isoelektrische Fokussierung als Methode zur Darminhaltsanalyse. – Mitt. Dtsch. Ges. allg. angew. Ent. 7: 677-680. **[6]**

Prüser, F. & D. Mossakowski 1998 Low substitution rates in mitochondrial DNA in Mediterranean carabid beetles. – Insect molec. Biol. 7: 121-128. **[8]**

Prüser, F. & D. Mossakowski 1999 Conflicts in phylogenetic relationships and dispersal history of the supertribe Carabitae (Coleoptera: Carabidae). – In: Casale, A. *et al.* (eds.): Phylogeny and Classification of Caraboidea. Mus. reg. Sci. nat Torino: 297-328. **[7,8]**

Puilliainen, E., J. Itämies, P. Jussila & P. Tunkkari 1993 Phenology and habitats of *Carabus glabratus* Paykull (Coleoptera, Carabidae). – Entomologica Fennica 4: 27-30. **[5]**

Puisségur, C. 1957 Hybrides experimentaux de Carabes. – Vie et Milieu 8: 173-199. **[5]**

Puisségur, C. 1964 Recherches sur la génétique des Carabes (*Chrysocarabus* et *Chrysotribax*). – Vie et Milieu 18, suppl.: 1-288. **[5,6]**

Puisségur, C. 1972 La kystogenèse de grégarines hémocoeliennes chez les carabes (Coleoptera, Carabidae) des Pyrénées et des Corbières. – Bull. Biol. Fr. Belg. 106: 101-122. **[6]**

Pulpán, J. & K. Hůrka 1983 Verzeichnis der tschechoslowakischen Laufkäfer (Coleoptera, Carabidae). – Zpravodaj 1: 1-28. **[5]**

Pulpán, J. & K. Hůrka 1993 Carabidae. – In: Jelínek (ed.): Check-list of Czechoslovak Insects IV (Coleoptera, Carabidae). – Folia Heyrovskyana, suppl. 1: 12-22. **[5,maps]**

Pulpán, J. & M. Reska 1971 Vertikale und geographische Ausbreitung der Carabiden (Coleoptera) in der Tschoslowakei. – Acta Musei Reginaehradensis, serie A: 85-104 . **[5]**

Rabeler, W. 1947 Die Tiergesellschaft der trockenen *Calluna*-Heiden in Nordrwestdeitschland. – Jrb. Naturh. Gesellschaft Hannover 94/98: 357-375. **[5]**

Rage, J.-C. 1995 La Tethys et les dispersions transtethysiennes par voie terrestre. – Biogeographica 71: 109-126. **[8]**

Ranius, T. & S.G. Nilsson 1997 Habitat of *Osmoderma eremita* Scop. (Coleoptera: Scarabaeidae), a beetle living in hollow trees. – J. Ins. Conserv. 1: 193-204. **[9]**

Raskin, R. 1995 Die Bedeutung des Ackerrandstreifenprogramms für den Insektenschutz. – Mitt. Dtsch. Ges. allg. angew. Ent. 10: 337- 341. **[9]**

Rasplus, J.-Y. 2001 De l'origine et de la diversité génétique de *Carabus (Chrysocarabus) punctatoauratus* Germar, 1824. Rutilans, suppl. 2 : 48-56. **[A]**

Rasplus, J.-Y., S. Garnier, S. Meusnier, S. Piry, P. Audiot & J.-M. Cornuet 2002 Setting conservation priorities : The case study of *Carabus solieri* (Col. Carabidae). – Genetic, Selection and Evolution 33: 141-175. **[A]**

Rasplus, J.-Y., S. Meusnier, G. Mondor, S. Piry & J.-M. Cornuet 2000 Microsatellite analysis of genetic population structure in the endangered beetle: *Carabus solieri* (Carabidae) – In: Brandmayr, P, G. L. Lövei, T. Z. Brandmayr, A. Casale & A. Vigna Taglianti (eds.): Natural history and applied ecology of carabid beetles. Sofia-Moscow: Pensoft Publishers: 11-24. **[3,5,6,8,9]**

Rathlef, von H. 1905 Coleoptera Baltica, Käferverzeignis der Ostsee-Provinzen. – Archiv für Naturkunde Liv-, Est- und Kurlands (II. Ser.) 12 Dorpat: 1-15, 1-16. **[5]**

Ratti, P., P. Cavazzuti, A. Casale & S. Battoni 1990 Carabini, 1. *Apotomopterus, Ohomopterus, Archaeocarabus, Isiocarabus, Morphocarabus* (1). – Les coléoptères du monde 8. Venette: Sciences Nat. **[5,maps]**

Rautenstrauch, A., E. Rautenstrauch & G. Rautenstrauch 1994 *Carabus* Europa und Nordafrika. – Augsburg. **[5]**

Raynaud, P. 1943 *Carabus* Linné. Dates de ponte. – Miscellanea Entomologica 49: 93-96. **[5]**

Raynaud, P. 1965 *Iniopachys* (Solier) *pyrenaeus* Audinet-Serville (Coleoptera Carabidae). – Bulletin Mensuel de la Société Linnéenne de Lyon 34: 139-144. **[4]**

Raynaud, P. 1969 Stades larvaires 14, Planche XII, *Archicarabus pascuorum* Lapouge. – Bulletin Mensuel de la Société Linnéenne de Lyon 38: 19-30. **[5]**

Raynaud, P. 1975-76 Synopsis morphologique des larves de *Carabus* Lin. (Coleopteres Carabidae), connues a ce jour – Bulletin Mensuel de la Société Linnéenne de Lyon 44: 210-225, 256-273, 297-351, 352-372; 45: 9-40, 61-84, 107-127. **[3,4,7]**

Refseth, D. 1984 The life cycles and growth of *Carabus glabratus* and *C. violaceus* in Budalen, central Norway. – Ecol. Entomol. 9: 449-455. **[6]**

Regenfuß, H. 1968 Untersuchungen zur Morphologie, Systematik und Ökologie der Podapolipidae (Acarina, Tarsonemini). – Z. wiss. Zool. 177 (314): 183-282. **[6]**

Reimann, T. 1996 Genetische Untersuchungen zur Struktur und Dynamik von Populationen des Laufkäfers *Carabus granulatus* L. (Coleoptera: Carabidae). – Verh. Westd. Entom. Tag 1995: 257-265. **[6]**

Reimann, T. 2000 Die glazialen Refugien und die postglaziale Ausbreitung von *Carabus auronitens* Fabr. – Mitt. Dtsch. Ges. Allg. Angew. Ent. 12: 621-624. **[8]**

Reimann, T., T. Assmann, O. Nolte, H. Reuter, C. Huber & F. Weber 2002 The paleoecology of *Carabus auronitens* Fabricius: characterization and localization of glacial refugia in southern France and reconstruction of postglacial expansion routes as revealed by allozyme polymorphisms. – Abh. naturwiss. Ver. Hamburg (N. F.) 35: 1-151. **[6,A]**

Reimann, T., T. Assmann, O. Nolte, H. Reuter, C. Huber & F. Weber 2002 Palaeogeography and palaeoecology of *Carabus auronitens* (Coleoptera): characterization and localization of glacial refugia in southern France and reconstruction of postglacial expansion routes by means of allozyme polymorphismus. – Abhandlungen des Naturwissenschaftlichen Vereins in Hamburg (N.F.) 35: 1-155. **[6,A]**

Reinhold, J.O. & A.H. Vermaat 1989 Onderzoek naar de veranderingen in soorten en aantallen loopkevers veroorzaakt door de beheersmaatregel "plaggen" op de Kraloërheide (Drenthe) in de zomer van 1988. – Doctoraalverslag. Landbouwuniversiteit Wageningen: Vakgroep Natuurbeheer: 1-55. **[5]**

Reinig, W. F. 1938 Elimination und Selektion. – Jena: Gustav Fischer. **[6]**

Reitter, E. 1896 Carabidae, Carabini. – Bestimmungstabellen europäischer Coleopteren. 34: 38-198. **[3,7]**

Reitter, E. 1908 Fauna Germanica, Die Käfer des Deutschen Reiches 1. – Stuttgart. **[5]**

Renner, K. 1980 Faunistisch-ökologische Untersuchungen der Käferfauna pflanzensoziologisch unterschiedlicher Biotope im Evessell-Bruch bei Bielefeld-Sennestadt. – Ber. Naturw. Ver. Bielefeld Sonderheft 2: 145-176. **[6]**

Rensch, B. 1943 Studien über Korrelation und klimatische Parallelität der Rassenmerkmale von *Carabus*-Formen. – Zool. Jb. Syst. 76: 103-170. **[6]**

Rensch, B. 1958 Die ideale Artbeschreibung. – Uppsala Universitets Arsskrift 6: 91-103. **[6]**

Richter, K. & J. Jacob 1980 Ergänzungen zum Vorkommen von *Carabus intricatus* L. auf dem Darß. – Ent. Nachr. Ber. 24: 24. **[9]**

Riddoch, B.J. 1993 The adaptive significance of electrophoretic mobility in phosphoglucose isomerase (PGI). – Biol. J. Linn. Soc. 50: 1-17. **[6]**

Riecken, U. & U. Raths 1996 Use of radio-telemetry for studying dispersal and habitat use of *Carabus coriaceus* L. – Ann. Zool. Fennici 33: 109-116. **[5,6,9]**

Rijnsdorp, A.D. 1975 Dispersie en mate van dispersie van *Carabus problematicus* Hbst (Coleoptera, Carabidae) in het Nuilerbos. – Doctoraal verslag. Biologisch Station Wijster: Landbouw Universiteit Wageningen: 1-27 . **[5]**

Rijnsdorp, A.D. 1980 Pattern of movement in and dispersal from a Dutch forest of *Carabus problematicus* Hbst. (Coleoptera, Carabidae). – Oecologia 45: 274-281. **[5,6]**

Rizun, V.B. 1987 Zhuzhelitsy (Coleoptera, Carabidae) lesov Rostoch'ya. (The ground-beetles (Coleoptera, Carabidae) in the forests of Rostochye) – 3 Syezd Ukr. entomol. obshch. Tez. dokl. Kiev: 166-167. [In Russian]. **[5]**

Rizun, V.B. 1991 Zhuzhelitsy (Coleoptera, Carabidae) rodov *Calosoma* Web., *Carabus* L., *Cychrus* F. (Ground-beetles of the genera *Calosoma* Web., *Carabus* L., *Cychrus* F.) – Katalog muzeinykh fondov L'viv: 137-166. [In Russian]. **[5]**

Robertson, A.H.F., P.D. Clift, P.J. Degan & G. Jones 1991 Palaeogeographic and paleotectonic evolution of the Eastern Mediterranean Neotethys. – Palaeogeogr. Palaeoclimatol. Palaeoecol. 87: 289-343. **[8]**

Rogl, F. & F.F. Steininger 1983 Von Zerfall der Tethys zu Mediterran und Paratethys, Die neogene Palaogeographie und Palinspastik des zirkum-mediterranen Raumes. – Ann. naturhist. Mus. Wien (A) 85: 135-163. **[8]**

Roschen, A. 1988 A morphological cline: adaptation to climate or result of gene exchange by hybridisation what limits the territory of *Carabus lineatus* (Coleoptera: Carabidae)?. – Proceedings of the of XVIII International Congress of Entomology: 187. **[5]**

Roschen, A. & D. Mossakowski 1986 Ecological differentiation in *Chrysocarabus* population: a study of two sympatric species and their hybrid. – In: den Boer, P.J., M.L. Luff, D. Mossakowski & F. Weber (eds.): Carabid beetles: their adaptations and dynamics. Stuttgart-New York: Gustav Fischer: 297-312. **[6]**

Roschen, A. & D. Mossakowski 1990 Die geografische variabilität der Elytren-Rippung im *Carabus lineatus-splendens*-Komplex (Coleoptera, Carabidae). – Mitt. Stsch. Ges. allemeine angew. Entomologie 7: 663-669 **[5]**

Roubal, J. 1925 Coleopterologisches aus Mitteldalmatien. – Wiener entomologische Zeitung 42: 48-51. **[5]**

Rusdea, E. 1994 Population dynamics of *Laemostenus schreibersi* (Carabidae) in a cave in Carinthia (Austria). – In: K. Desender, M. Dufrêne, M., Loreau, M., Luff and J.-P. Maelfait (eds.): Carabid beetles: ecology and evolution. Dordrecht: Kluwer: 207-212. **[6,9]**

Ryabitsev, A.V. 1995 Nekotorye rezul'taty individual'nogo mecheniya zhuzhelitsy *Carabus truncaticollis* na Severnom Yamale. (Some results of an individual marking of the ground-beetle *Carabus truncaticollis* on the Northern Yamal) – In: Mechanizmy podderzhaniya biologicheskogo raznoobraziya. Materialy konf. Ekaterinburg: 1-127. [In Russian]. **[5]**

Ryabitsev, A.V. 1998 Naselenie i ekologiya zhizhelits na severe Yamala. (Communities and ecology of the ground beetles on the Northern Yamal) – Avtoref. kand. diss.: 1-20. [In Russian]. **[5,t]**

Ryder, O.A. 1986 Species conservation and systematics: the dilemma of subspecies. – Trends Ecol. Evol. 1: 9-10. **[9]**

Sahlberg, J. 1898 Catalogus praecursorius Coleopterorum in valle fluminis Petschora collectorum. – Horae Soc. Ent. Ross. 32. **[5,8]**

Salomon, M. 2001. Evolutionary biogeography and speciation: essay on a synthesis. – J. Biogeogr. 28 (1): 13-27. **[8]**

Samsinak, K. 1971 Die auf *Carabus*-Arten (Coleoptera, Adephaga) der palaearktischen Region lebenden Milben der Unterordnung Acariformes (Acari); ihre Taxonomie und Bedeutung für die Lösung zoogegraphischer, entwicklungsgeschichtlicher und parasitologischer Fragen. – Entomol. Abh. Staatl. Mus. Tierkde Dresden 38: 145-233. **[6]**

Samways, M.J. 1994 Insect conservation biology. – London: Chapman and Hall. **[9]**

Scherney, F. 1957a Unsere Laufkäfer. – Wittenberg: Ziemsen. **[6,9]**

Scherney, F. 1957b Über Biologie und Zucht von *Carabus*-Arten. – Bericht über die Wanderversammlung Deutscher Entomologen 8: 120-126. **[5]**

Scherney, F. 1958 Über die Wirkung verschiedener Insektizide auf Laufkäfer (Coleoptera, Carabidae). – Pflanzenschutz 10: 87-92. **[9]**

Scherney, F. 1959 Der biologische Wirkungseffekt von Carabiden der Gattung *Carabus* auf Kartoffelkäferlarven. – Verh. IV. Intern. Pflanzenschutz Kongr. Hamburg 1957 1: 1035-1038. **[5]**

Scherney, F. 1960a Kartoffelkäferbekämpfung mit Laufkäfern (Gattung *Carabus*). – Pflanzenschutz 12: 34-35. **[5]**

Scherney, F. 1960b Über die Zu und Abwanderung von Laufkäfern (Carabidae) in Feldkulturen. – Pflanzenschutz 12: 169-171. **[5]**

Scherney, F. 1960c Beiträge zur Biologie und ökonomischen Bedeutung rauberisch lebender Käferarten (Untersuchungen über das Auftreten von Laufkäfern (Carabidae) in Feldkulturen (Teil II)). – Zeitschrift für angewandte Entomologie 47: 231-255. **[5]**

Schildknecht, H., H. Winkler & U. Maschwitz 1968 Vergleichend chemische Untersuchung der Inhaltsstoffe der Pygidialwehrdrüsen von Carabiden. – Z. Naturforsch. 23b: 637-644. **[6]**

Schiller, W. & F. Weber 1975 Die Zeitstruktur der ökologischen Nische bei Carabiden (Untersuchungen in Schatten- und Strahlungshabitaten des NSG "Heiliges Meer" bei Hopsten). – Abh. Landesmus. Naturkde Münster Westf. 37: 1-34. **[6]**

Schiödte, J.C. 1867 De metamorphosi eleutheratorum observationes: Bidrag til Insekternes Udviklingshistorie **[3]**. – Naturh. Tidssk. 4: 415-552. **[5]**

Schjøtz-Christensen, B. 1965 Biology and population studies of Carabidae of the Corynephoretum. – Natura Jutlandica 11: 1-173. **[5,6]**

Schjøtz-Christensen, B. 1968 Some notes on the biology and ecology of *Carabus hortensis* L. (Coleoptera, Carabidae). – Natura Jutlandica 14: 127-154. **[5,6]**

Schmidt, G. 1955 Physiologische Untersuchungen zur Transpiration und zum Wassergehalt der Gattung *Carabus* (Ins., Coleoptera). – Zool. Jb. Physiol. 65: 459-495. **[6]**

Schmidt. G. 1955/56 Der Stoffwechsel der Caraben (Ins., Coleoptera) und seine Beziehung zum Wasserhaushalt. – Zool. Jb. Physiol. 66: 273-294. **[6]**

Schmidt, G. 1956 Der Einfluß des Wassergehalts und Stoffwechsels auf die Vorzugstemperatur der Insekten. – Biol. Zb. 75: 178-205. **[6]**

Schmidt-Rhaesa, A. 1995 Zur Morphologie, Biologie und Phylogenie der Nematomorpha: Untersuchungen an *Nectonema munidae* und *Gordius aquaticus*. – Doctoral Thesis, University of Göttingen. **[6]**

Schmidt-Rhaesa, A. 1997 Nematomorpha. – In: Schwoerbel, J. & P. Zwick (eds.): Süßwasserfauna von Mitteleuropa 4/4. Stuttgart: Gustav Fischer: 1-35. **[6]**

Schultz, R. & G. Müller-Motzfeld 1995 Faunistisch-ökologische Untersuchungen auf Salzstandorten bei Greifswald. – Z. Ökologie u. Naturschutz 4: 9-20. **[9]**

Schütze, H. & F. Kleinfeld 2001 Die Caraben Kleinasiens, mit einem besonders ausfürlichen Fundortverzeichniss. Eigenverlag: 1-178. **[A]**

Schwöppe, M., M. Kreuels & F. Weber 1998 Zur Frage der historisch oder ökologisch bedingten Begrenzung des Vorkommens einer waldbewohnenden, ungeflügelten Carabidenart: Translokationsexperimente unter kontrollierten Bedingungen mit *Carabus auronitens* im Münsterland. – Abh. Westf. Mus. Naturkde 60: 1-77. **[6,8,9]**

Sedlmair, D., R. Gerstmeier & R. Einspanier 2000 Application of ubiquitin SSCP analysis in taxonomic studies within the subgenus *Orinocarabus* (Coleoptera: Carabidae: *Carabus*). – European Journal of Entomology 97: 387-394. **[5]**

Seidlitz, G. von 1887 Fauna Baltica. Die Käfer der Ostseeprovinzen Russlands. – Königsberg. **[3]**

Semenov-Tian-Shanskij, A. 1896 Symbolae ad cognitionem generis *Carabus* (L.) A.Mor. I. Formarum novarum decas I et II. – Horae Soc. Entomol. Ross. 30: 193-229. **[3]**

Semenov-Tian-Shanskij, A. 1898 Remarques sur les Coléoptères de la Russe européenne et du Caucase I-L. – Bull. Soc. Imp. Nat. Mosc. 12. **[3]**

Serrano, J. 1981 Chromosome numbers and karyotypic evolution of Caraboidea. – Genetica 57: 51-60. **[6]**

Serrano, J. & J. Galian 1998 A review of karyotypic evolution and phylogeny of carabid beetles (Coleoptera). – In: Ball *et al.* (eds.): Phylogeny and classification of Caraboidea (XX I.C.E. 1996, Firenze, Italy). Atti mus. reg. Sci. nat. Torino: 191-228. **[8]**

Shaffer, M.L. 1981 Minimum population sizes for species conservation. – Biosciences 31: 131-134. **[9]**

Shafigullina, L.S. 1990 Izmenenie ekologicheskoi struktury karabidofauny ostrovov Kuibyshevskogo vodokhranilishcha po sravneniyu s byvshei poimoi Volgi i Kamy. (Changes in ecological structure of ground-beetle fauna of the islands of the Kuibyshev water reservoir in comparison with the former floodland of Volga and Kama) – Fauna i ekologiya zhuzhelits. Tez. dokl. III Vses. karabidol. sov. Kishinev: 69-70. [In Russian]. **[5]**

Shapiro, A.M. & A.H. Porter 1989 The lock-and-key hypothesis: evolutionary and biosystematic interpretation of insect genitalia. – Annu. Rev. Entomol. 34: 231-245. **[6]**

Sharova, I.Ch. 1958 Lichinki zhukov zhuzhelits, poleznykh i vrednykh v sel'skom khozyaistve. (Ground-beetle larvae useful and injurious in agriculture) – Uch. zap. Mosk. gos. pedagog. inst. 124 (7): 4-164. [In Russian]. **[5]**

Sharova, I.Ch. 1981 Zhiznennye formy zhuzhelits (Coleoptera, Carabidae). (Life forms of Carabids (Coleoptera, Carabidae)) – Moscow: Nauka: 1-360. [In Russian]. **[5]**

Sharova, I.Ch. 1982 Zonal'nye zakonomernosti formirovaniya kompleksov zhukov zhuzhelits v agrotsenozakh. (Zonal regularities of formation of ground-beetle complexes in agrocenoses) – Formir. zhivotn. i mikrobn. naselen. agrotsenozov. Tez. dokl. Vses. sov. Pushchino (IX. 1982): 14-15. [In Russian]. **[5]**

Sharova, I.Ch. & V.M. Dushenkov 1979 Tipy razvitiya i tipy sezonnoi aktivnosti zhuzhelits. (Types of development and seasonal activity of ground-beetles) – In: Fauna i ekologiya bespozvonochnykh Moscow: MGPI: 15-25. [In Russian]. **[5]**

Sharova, I.Ch. & L.V. Lapshin 1971 Biotopicheskoe raspredelenie i chislennost' zhuzhelits (Carabidae) v vostochnoi Orenburgskoi lesostepi. (Habitat distribution and abundance of ground-beetles (Carabidae) in the eastern Orenburg forest-steppe) – Uch. zap. Mosk. gos. pedagog. inst. 465: 87-89. [In Russian]. **[5,t]**

Shelyag-Sosonko, Yu.R. 1980 O konkternoi flore i metode konkretnykh flor (On the concrete flora and the method of concrete floras) – Bot. Zhurn. 65: 791-774. [In Russian]. **[8]**

Shernin, A.I. 1974 Otryad Coleoptera – zhestkokrylye. (Order Coleoptera – coleopterous insects) – In: Zhivotnyi mir Kirovskoi oblasti 2: 111-227. [In Russian]. **[5]**

Shilenkov, V.G. 1990 Die taxonomische Stellung von *Carabus mestsherjakovi* Lutshn., nebst Beschreibung einer neuen *Carabus*-Art und einer neuen Unterart aus dem arktischen Siberien (Insecta, Coleoptera, Carabidae, Carabini). – Reichenbachia 27 (20): 109-114 **[2,3,5]**

Shilenkov, V.G. 1994 Catalogue of the *Carabus* species of Siberia with preliminary notes to the taxonomical revision (Coleoptera, Carabidae). – In: Desender, K. *et al.* (eds.): Carabid Beetles, Ecology and Evolution. – Dordrecht: Kluwer: 63-70. **[5,8]**

Shilenkov, V.G. & A.I. Averinskii 1990 Materialy po faune zhuzhelits (Coleoptera: Trachypachidae, Carabidae Yakutii. (A contribution to the ground-beetle fauna Coleoptera: Carabidae, Trachypachidae) of Yakutia) – In: Nasekomye i paukoobraznye Sibiri. Irkutsk. [In Russian]. **[5]**

Shilenkov, V.G. & E.Ya. Berlov 1987 Opisanie lichinki krasotela *Callistenus elegans* Kirsch. (Coleoptera, Carabidae) iz Kazakhstana. (A description of the larvae of the carabid *Callistenes elegans* Kirsch. (Coleoptera, Carabidae) from Kazakhstan) – Entomol. Obozr. 66 (3): 584-590. [In Russian]. **[5]**

Shilenkov, V.G. & G.A. Voronov 1973 Ekologo-faunisticheskaya charakteristika naseleniya zhuzhelits yuzhnoi taigi Kamskogo Priural'ya. (Eco-faunistic characteristics of ground-beetle population in the southern taiga of Kama flow (Cisuralia)) – Vopr. ekol. teriol. Izd. Perm': Perm. univ.: 109: 88-118. [In Russian]. **[5]**

Siebart, H. 1984. Die Käfer (Coleoptera) in Buchenwäldern bei Braunschweig. – Braunschw. Naturk. Schr. 2 (1): 131-143. **[5]**

Silfverberg, H. 1977 Nomenclatoric notes on Coleoptera Adephaga. – Not. Entomol. 57: 41-44. **[3,5]**

Silfverberg, H. 1992 Enumeratio Coleopterorum Fennoscandiae, Daniae et Baltiae. – Helsinki: Helsingfors Hyonteisvaihtoyhdistys. **[3,5,maps]**

Singh, T. 1958 Ovulation and corpus luteum formation in *Locusta migratoria* Reiche and Fairmaire and *Schistocerca gregaria* (Forskål). – Trans. R. Ent. Soc. Lond. 110: 1-20. **[6]**

Skuhravý, V. 1956 Fallenfang und Markierung zum Studium der Laufkäfer. – Beitr. Entomol. 6: 285-287. **[6]**

Skuhravý, V. 1959a Bionomie der Feldcarabiden. – Rozprravy Ceskoslovenske Akademie Ved 69: 3-64. **[5]**

Skuhravý, V. 1959b Die Nahrung der Feldcarabiden. – Acta Societatis Entomologicae Cechosloveniae 56: 1-18. **[5]**

Smetanin, A.I. 1981 Khishchnye zhuki-zhuzhelitsy i stafilinidy zapovednika "Trostyanets". (The predatory beetles (carabids and staphylinids) of the Trostyanets Reserve) – Kiev: Naukova dumka: 1-70. [In Russian]. **[5]**

Smith, A.G., A.M. Hurley & J.C. Briden 1981 Phanerozoic paleocontinental world maps. – Cambridge University Press: 1-102. **[8]**

Sota, T. 1994 Variation of carabid life cycles along climatic gradients: an adaptive perspective for life-history evolution under adverse conditions. – In: Danks, H.F. (ed.): Insect life-cycle polymorphism. Dordrecht: Kluwer Academic Press: 91-112. **[6]**

Sota, T. & K. Kubota 1998 Genital lock-and-key as a selective agent against hybridization. – Evolution 52: 1507-1513. **[6]**

Soulé, M.E. 1987 Viable populations for conservation. – Cambridge: Cambridge University Press. **[9]**

Sparks, T.H., A. Buse & R.J. Gardens 1995 Life strategies of *Carabus problematicus* (Coleoptera, Carabidae) at different altitudes on Snowdon, North Wales. – J. Zool. Lond. 236: 1-10. **[5,6]**

Speight, M.C.D., R. Anderson & M.L. Luff 1982 An annotated list of the Irish ground beetles (Col., Carabidae + Cicindelidae). – Bulletin of the Irish Biogeographical Society 6: 25-53. **[5]**

Spence, J.R. 1990 Success of European carabid species: preadaptation for synantropy. – In: Stork, N.E. (ed.): The role of ground beetles in ecological and environmental studies. Intercept, Andover, Hampshire: 129-139.

Spuris, Z. 1983 Catalogue of the insects of Latvia 4. Ground beetles (Carabidae). – Latv. Ent. 26: 5-67. (In Latvian). **[5]**

Ssymank, A., U. Hauke, Ch. Rückriehm & E. Schröder 1998 Das europäische Schutzgebietssystem NATURA 2000. – Schr.-R. f. Landschaftspfl. u. Natursch. 53: 1-560. **[9]**

Stark, N.K. 1926 Spisok zhukov Bryanskogo lesnogo massiva. (List of the beetles of the Bryansk forest) – Tr. Smolensk. obshch. estestvoisp. vrachei Smolensk. gos. univ. 1. [In Russian]. **[5]**

Stegemann, K.-D. 1981 Bemerkungen zum Vorkommen von *Carabus intricatus* L. (Col., Carabidae) in der Eichhofer Heide (Kreis Uckermünde). – Ent. Nachr. Ber. 25: 93-94. **[9]**

Stewart, A.J.A. & M.J. Hutchings 1996 Conservation of populations. – In: I.F. Spellerberg (ed.): Conservation biology. Harlow: Langman: 122-140. **[9]**

Stiprais, M.A. 1961 Vyrashchivanie zhuzhelits roda *Carabus* L. (Aufzucht von Laufkaefer der Gattung *Carabus* L.) – Fauna Latviiskoi SSR Riga 3: 147-162. [In Russian]. **[5]**

Stiprais, M.A. 1964 Vyrashchivanie shesti vidov zhuzhelits roda *Carabus* L. (Aufzucht von sechs Arten der Gattung *Carabus* L) – Fauna Latviiskoi SSR Riga 4: 97-108. [In Russian]. **[5]**

Stork, N.E. 1980 A scanning electron microscope study of tarsal adhesive setae in the Coleoptera. – Zool. J. Linn. Soc. 68: 173-306. **[6]**

Storre, I., T. Assmann & G.H. Schmidt 1996 Altersstruktur sich im Frühjahr reproduzierender Laufkäfer-Arten (Insecta: Coleoptera, Carabidae). Populationsbiologische Untersuchungen mit Hilfe des *Corpus luteum*. – Verh. Ges. Ökol. 26: 587-590. **[6]**

Strand, A. 1946 Nord-Norges Coleoptera – Trömsö Mus. Arsh. 67. **[5,t]**

Sturani, M. 1947 Notizie ecologiche ed etologiche sul *Carabus olympiae* Sella (Coleoptera, Carabidae). – Bollettino dell' Istituto di Entomologia dell' Università di Bologna 16: 23-84. **[3]**

Sturani, M. 1962 Osservazioni e ricerche biologiche sul genere *Carabus* Lin. (s.l.). (Coleoptera, Carabidae) – Memorie della Società Entomologica Italiana 41: 85-202. **[3,4,5,6]**

Sturani, M. 1963 Nuove ricerche biologiche e morfologiche sul *Carabus* (*Hygrocarabus*) *variolosus* Fabr. – Boll. Zool. agraria Bachicolt. S II: 25-34. **[3,5,6]**

Sturani, M. 1964a Aggiunte e correzioni alle osservazioni e ricerche biologiche sul genere *Carabus* Linnaeus (*sensu lato*) (Coleoptera Carabidae). – Memorie della Società Entomologica Italiana 43: 63-79. **[5]**

Sturani, M. 1964b Osservazioni biologiche e morfologiche sul *Carabus* (*Hygrocarabus*) *variolosus* Fabricius (Coleoptera, Carabidae). – Atti Accad. Nazionale Italiana Entomologia. Bologna: Rendiconti: 11 (1963): 182-184. **[5]**

Sturani, M. 1967 Ligula ed endofallo in alcune specie appartenenti ai generi *Carabus* Linnaeus (s.l.), *Calosoma* Weber e *Campalita* Motschoulsky. – Memorie della Società Entomologica Italiana 47 1-2 9-21. **[3,7]**

Sturani, M. 1969 Osservazioni sulla diapausa invernale di alcune specie appartenenti al genere *Carabus* Lin. (*s.l.*) (Coleoptera, Carabidae). – Memorie della Società Entomologica Italiana 48: 157-166 . **[5]**

Su, Z.-H., T. Ohama, T.S. Okada, K. Nakamura, R. Ishikawa & S. Osawa 1996a Phylogenetic relationships and evolution of the Japanese Carabinae ground beetles based on mitochondrial ND5 gene sequence. – J. Mol. Evol. 42: 124-129. **[6,7]**

Su, Z.-H., T. Ohama, T.S. Okada, K. Nakamura, R. Ishikawa & S. Osawa 1996b Geography-linked phylogeny of the *Damaster* ground beetles inferred from mitochondrial ND5 gene sequences. – J. Mol. Evol. 42: 130-134. **[6,7]**

Su, Z.-H., T.S. Okada, S. Osawa, B. David, J.-L. Dommergues & F. Magniez 1996c Radiation of several carabina groups (Coleopera, Carabidae) inferred from the mitochondrial ND5 gene sequence. – Elytra, Tokyo 24: 175-179. **[7]**

Suc, J.P. 1984. Origin and evolution of the Mediterranean vegetation and climate in Europe. – Nature 307: 429-432. **[8]**

Swofford, D. L. 1998 PAUP*4.0b2: Phylogenetic analysis using parsimony. Computer program and manual. – Illinois: Illinois Natural History Survey Champain. **[7]**

Szyszko, J. 1983 State of Carabidae (Col.) Fauna in fresh pine forest and tentative valorisation of this environment. – Warsaw Agricultural University Press: 1-80. **[5]**

Szyszko, J. 1986 Dynamics of population size and development of the carabid fauna of pine stands on poor sandy soils (facts and supposition). – In: P.J. den Boer *et al.* (ed.): Carabid beetles, their adaptations and dynamics. Stuttgart: Fischer: 331-341. **[5]**

Szyszko, J. 1987 How can the fauna of carabidae be protected in managed pine forest? – Acta Phytopath. Entom. Hung. 22: 193-203. **[9]**

Szyszko, J. & S. Gryuntal (eds.) (2002 in prep.) How to protect or what we know about carabid beetles. – Proceedings of the XECM (10th European Carabidologists Meeting), in Tuczno, Poland 2001. **[5,10,A]**

Tassi, F. 1969 Problemi di conservazione nel campo dell'Entomologia. – Mem. Soc. entomol. Ital. 48: 609-626. **[5]**

Ter Braak, C.J.F. 1988 CANOCO – a FORTRAN program for canonical community ordination by (partial) (detrended) (canonical) correspondence analysis, ptincipal component analysis and redundancy analysis (version 2.1.) – ITI-TNO, Wageningen. **[8]**

Ter Braak, C.J.F. & I.C. Prentice 1988 A theory of gradient analysis. – Adv. Ecol. Res. 18: 271-317. **[8]**

Terlutter, H. 1990 An allele gradient of an esterase gene locus as a result of recent gene flow. – Electrophoretic investigations on *Carabus auronitens* F (Col. Carabidae). – In: Stork, N.E. (editor): The role of ground beetles in ecological and environmental studies. Andover: Intercept: 359-364. **[5,9]**

Terlutter, H. 1991 Morphometrische und elektrophoretische Untersuchungen an westfälischen und südfranzösischen *Carabus auronitens*-Populationen (Col. Carabidae). Zum Problem der Eiszeitüberdauerung in Refugialgebieten und der nacheiszeitlichen Arealausweitung. – Abh. Westf. Mus. Naturkde 53: 3-111. **[6,8]**

Terrel-Nield, C. 1990 Is it possible to age woodlands on the basis of their carabid beetle diversity? – The Entomologist 109: 136-145. **[5,6,9]**

The Council of the European Communities 1992 Council directive 92/43/EEC of 21. May 1992 on the conservation of natural habitats and of wild fauna and flora. – Official Journal of the European Communities. Series L. 206: 7-49. **[9]**

Thiele, H.-U. 1964a Ökologische Untersuchungen an bodenbewohnenden Coleopteren einer Heckenlandschaft. – Z. Morph. Ökol. Tiere 53: 537-586. **[5,9]**

Thiele, H.-U. 1964b Experimentelle Untersuchungen über die Ursachen der Biotopbindung bei Carabiden. – Z. Morphol. Ökol. Tiere 53: 387-452. **[5,6]**

Thiele, H.-U. 1977 Carabid beetles in their environments. – Berlin: Springer-Verlag: 1-369. **[5,6,8,9,10]**

Thiele, H.-U. & F. Weber 1968 Tagesrhythmen der Aktivität bei Carabiden. – Oecologia 1: 315-355. **[5,6]**

Thompson, J.D., D.G. Higgins & T.J. Gibson 1994 CLUSTAL W: improving the sensitivity of progressive multiple sequence alignment through sequence weighting, positions-specific gap penalties and weight matrix choice. – Nucleic Acids Research 22: 4673-4680. **[7]**

Thomson, C.G. 1875 Nagra anmärkningar öfver arterna of slägtet *Carabus*. – Opuscula Entomol. 7: 613-729. **[3]**

Tietze, F. 1963 Untersuchungen über die Beziehungen zwischen Flügelreduktion und Ausbildung des Metathorax bei Carabiden unter besondere Berücksichtigung der Flugmuskulatur (Coleoptera, Carabidae). – Beiträge zur Entomologie 13: 87-163. **[5]**

Tolmachev, A.I. 1931 O metodakh sravnitel'nykh floristichekikh issledovaniyakh. 1. O ponyatii "konkretnoi flory" v sravnitel'noi floristike (On the methods of comparative floristic investigations. 1. On the term "concrete flora" in the comparative floristics) – Zhurn. Russ. Bot. Obshch. 16: 111-124. [In Russian]. **[8]**

Topchiev, A.G. 1970 Pochvennye bespozvonochnye i ikh raspredelenie v lesnykh polezashchitnykh polosakh v raione Gerbovetskogo lesa (The soil-dwelling invertebrates and their distribution in shelter-belts in the vicinity of Gerbovets forest) – In: Gerbovetskii les. Sborn. rabot lesn. khoz. Mold. 4. Kishinev: Kartya moldovenyaska: 255-260. [In Russian]. **[5]**

Torsvik, T.A. & M.A. Smethurst 1994 Geographic mapping and paleoreconstruction package (GMAP). – Software description and examples of paleoreconstructions. [vers. GMAP for Windows]. **[8]**

Tosevski, I. 2000 *Carabus, Morphocarabus* and *Eucarabus* in Serbia. – Published as Internet page: http://www.chem.bg.ac.yu/~mario?carabus/Carabus.htm. **[3]**

Trautner, J. 1992 Rote Liste der in Baden-Württemberg gefährdeten Laufkäfer (Col., Carabidae *s. lat.*). – Weikersheim: Margraf. **[5,6]**

Trautner, J. 1994a Zum Beutespektrum von *Gnaphosa lucifuga* (Araneae: Gnaphosidae). – Arachnol. Mitt. 7: 41-44. **[6]**

Trautner, J. 1994b Laufkäfer als Indikatoren/Deskriptoren in der Planung und Probleme der Ausgleigbarkeit von Eingriffen am Beispiel dieser Artengruppe. – In: Die Beurteilung von Landschaften für die Belange des Arten- un Biotopshutzes als Grundlage für die Bewertung von Engriffen durch den Bau von Strassen. Forschung Strassenbau und Strassenverkehrstechnik 636: 207-233. **[5]**

Trautner, J. 1996 Der Große Puppenräuber *Calosoma sycophanta* (Linné, 1758) in Südwestdeutschland. – Mitt. internat. entomol. Ver. 21: 81-104. **[9]**

Trautner, J. 2001 Hochmoor-Laufkäfer (*Carabus menetriesi* subsp. *pacholei*). – In: Fartmann, T, H. Gunnemann, P. Salm & E. Schröder (eds.): Berichtspflichten in Natura 2000-Gebieten: Empfehlungen zur Erfassung der Arten des Anhangs II und Charakterisierung der Lebensraumtypen des Anhangs I der FFH-Richtlinie; Angewandte Landschaftsökologie 25: 288-293.

Trautner, J. & G. Müller-Motzfeld 1995 Checkliste der Laufkäfer Deutschlands. – Naturschutz und Landschaftsplanung 27: 96-105. **[5,maps]**

Trautner, J., G. Müller-Motzfeld & M. Bräunicke 1997 Rote Liste der Sandlaufkäfer und Laufkäfer Deutschlands. – Naturschutz und Landschaftsplanung 29: 261-273. **[5,9,maps]**

Tselishcheva, L.G. 2000 Fenologiya razvitiya i struktura populyatsii *Carabus schoenherri* F.-W. (Coleoptera, Carabidae) v lesakh podzony yuzhnoi taigi Volgo-Vyatskogo regiona. (Phenology, development and population structure of *Carabus schoenherri* F.-W. (Coleoptera, Carabidae) in the forests of the southern taiga subzone of the Volga-Vyatka Region) – Vestn. Vyatsk. Goss. Univ. Kirov 2: 27-30. [In Russian]. **[5]**

Turin, H. 1981 Provisional checklist of the European ground-beetles. – Monographieen van de Nederlandse Entomologische Vereniging 9, Amsterdam. **[5]**

Turin, H. 1983 Invertebratenfauna van de Zuidlimburgse kalkgraslanden, Loopkevers (Coleoptera, Carabidae). – Natuurhistorisch Maandblad 72: 73-83. **[5,t]**

Turin, H. 1988 CARLIT, a literature database for the European Carabidae (Coleoptera). – Release on diskettes and manual, Renkum: 1-41 (see also Penev, 1991) **[3,5,8]**

Turin, H. 1991 De loopkevers van de Nederlandse Waddeneilanden (Coleoptera, Carabidae) I – Faunistiek. – Entomologische Berichten, Amsterdam 51 (6): 69-78. **[t]**

Turin, H. 2000 De Nederlandse loopkevers, verspreiding en oecologie (Coleoptera: Carabidae). – Nederlandse Fauna 3. Nationaal Natuurhistorisch Museum Naturalis, KNNV Uitgeverij & EIS-Nederland: 1-666. **[5,8,9,maps,t]**

Turin, H., K. Alders, P. J. den Boer, S. van Essen, Th. Heijerman, W. Laane & E. Penterman 1991 Ecological characterization of carabid species in the Netherlands from thirty years of pitfall sampling. – Tijdschrift voor Entomologie 138: 279-304. **[5]**

Turin, H. & P. J. den Boer 1988 Changes in the distribution of carabid beetles in the Netherlands since 1880. II. Isolation of habitats and long-term time trends in the occurrence of carabid species with different powers of dispersal (Coleoptera, Carabidae). – Biol. Conser. 44: 179-200. **[9]**

Turin, H., A. Casale, O.L. Kryzhanovskij, K.V. Makarov & L.D. Penev 1993 Checklist and atlas of the genus *Carabus* Linnaeus in Europe (Coleoptera, Carabidae). – Backhuys: Universal Book Services. **[2,3,5,6,7,8,10,maps]**

Turin, H., J. Haeck & R. Hengeveld 1977 Atlas of the Carabid Beetles of the Netherlands. – Verhandelingen van de Nederlandse Koninklijke Academie van de Wetenschappen 68, Amsterdam. **[5,maps]**

Turin, H. & Th. Heijerman 1988 Ecological classification of forest dwelling Carabidae (Coleoptera) in the Netherlands. – Tijdschrift voor entomologie 131: 65-71. **[5]**

Utrobina, N.M. 1964 Obzor zhuzhelits Srednego Povolzh'ya. (A review of ground-beetles of the Middle Volga Region) – In: Pochvennaya fauna Srednego Povolzh'ya, Kazan': 93-119. [In Russian]. **[5]**

Uzenbaev, S.D., T.K. Bobrovskikh & V.V. Shorochov 1986 Vidovoi sostav i rasprostranenie zhuzhelits (Coleoptera, Carabidae) Yuzhnoi Karelii. (Species composition and distribution of ground-beetles (Coleoptera, Carabidae) in South Karelia) – In: Fauna i ekologiya chlenistonogikh Karelii, Petrozavodsk: 74-83. [In Russian]. **[5]**

Vacher de Lapouge, G. 1929-1932. (see: Lapouge 1929-1932)

Vaje, S., D. Mossakowski & D. Gabel 1984 Temporal, intra- and interspecific variation of proteolytic enzymes in carabid beetles. – Insect Biochem. 14: 313-320. **[6]**

Valcárcel, J.P., F.P. Piloña, S. Devesa Regueiro, F. Rosende & J.F. Abelleira 1995 Citas nuevas o interesantes de Caraboidea (Coleoptera) para Galicia (Península Ibérica). – Zapateri Revta. Aragon. ent. 5: 154-155. **[8]**

Valcárcel, J.P., F. Prieto, C. Mujeto & S. Devesa 1997 Aportaciones al inventario de los Caraboidea de Galicia (NO de la Peninsula Ibérica). – Bol. SEA 17: 15-17. **[8]**

Valemberg, J. 1997a Catalogue descriptif, biologique et synonymique de la faune Paléarctique des Coléoptères Carabidae Latreille 1806. De la nomenclature taxonomique mondiale, spécifique et subspécifique des Carabinae Horn 1881 et d'une cartographie commentée des formes Françaises. Tome 1 Corpus. – Mem. Soc. ent. du Nord de la France: 1-659. **[A]**

Valemberg, J. 1997b Catalogue descriptif, biologique et synonymique de la faune Paléarctique des Coléoptères Carabidae Latreille 1806. De la nomenclature taxonomique mondiale, spécifique et subspécifique des

Carabinae Horn 1881 et d'une cartographie descriptive des formes Françaises. Tome 2 Cartographie. – Mem. Soc. ent. du Nord de la France: 660-1119. **[A]**

Van der Drift, J. 1951 Analysis of the animal community in a beech forest floor. – Tijdschrift voor Entomologie 94: 1-168. **[5]**

Van der Drift, J. 1958 Life cycle and phenology of *Carabus problematicus* Herbst. – In: Proceedings of the 10th International Congress of Entomology 2: 661. **[5,6]**

Van der Drift, J. 1959 Fieldstudies on the surface fauna of forests. – Bijdragen tot de dierkunde 29: 79-103. **[5]**

Van der Ent, L.J. 1990 De bepaling van looppatronen van een tweetal loopkeversoorten (*Carabus arvensis* en *Carabus problematicus*) met behulp van een radar-detectie methode en de relevantie hiervan voor de levensverwachting van de populaties van beide soorten in hun leefgebied. – Doctoraal verslag, Biologisch Station Wijster, Landbouw Universiteit Wageningen: 1-64 en bijlagen. **[5]**

Van Dyke, E.C. 1945 A review of the North American species of the genus *Carabus* Linnaeus. – Ent. Amer. (n.s.) 24: 87-129. **[8]**

Van Essen, S. 1993 Loopkeverinventarisatie Dwingelderveld 1991. – Grafisch Service Centrum, Wageningen. **[5,9]**

Van Zuijen, M. 1994 Verspreiding, habitatvoorkeur en dispersievermogen van *Carabus coriaceus* L. (Col: Carabidae) in twee gebieden in Noord-Nederland. – Doctoraalverslag Landbouwuniversiteit Wageningen, Biologisch Station Wijster: 1-45 + bijlagen en kaarten. **[5]**

Van Zuijen, M. & T.S. van Dijk 1997 Presence, habitat preference and mobility of *Carabus coriaceus* (Coleoptera, Carabidae) in the northern part of the Netherlands. – In: M.J. Sommeijer & P.J. Francke (eds.): Proceedings of the section Experimental and Applied Entomology of the Netherlands Entomological Society (N.E.V.), 8: 23-27. **[5]**

Verhoeff, K.W. 1917 Zur Kenntnis der *Carabus* Larven. – Biologisches Zentralblatt 37: 14-23. **[5,6]**

Vermeulen, H.J.W. 1994 Corridor function of a road verge for dispersal of stenotopic heathland ground beetles (Carabidae). – Biol. Conserv. 69: 39-349. **[9]**

Vigna Taglianti, A. 1993 Coleoptera Archostemata, Adephaga 1 (Carabidae). – Checklist delle specie della Fauna d'Italia 44. Bologna: Calderini: 1-51. **[5,10]**

Vigna Taglianti, A. 1998 I carabidi nella faunistica e nella biogeografia. – Atti dell'Accademia Nazionale Italiana di Entomologia, Rendiconti 46: 245-276 **[8]**

Vigna Taglianti, A., A.P. Audisio, C. Belfiore, M. Biondi, M.A. Bologna, G.M. Carpaneto, A. De Biase, S. De Felici, E. Piattella, T. Racheli, M. Zapparoli & S. Zoia 1993 Riflessioni di gruppo sui corotipi fondamentali della fauna W-paleartica ed in particolare italiana. – Biogeographia, Lav. Soc. ital. Biogeogr. (N.S.) 16 (1992): 159-179. **[5,8]**

Vigna Taglianti, A., A.P. Audisio, M. Biondi, M.A. Bologna, G.M. Carpaneto, A. De Biase, S. Fattorini, E. Piattella, R. Sindaco, A. Venchi & M. Zapparoli 1999 A proposal for chorotype classification of the Near East fauna, in the framework of the Western Palearctic region. – Biogeographia 20: 31-59. **[8]**

Vigna Taglianti, A., A.P. Audisio & S. De Felici 1998 I Coleotteri Carabidi del Parco Nazionale della Val Grande (Verbania, Piemonte). – Riv. Piem. St. nat. 19: 193-245 **[3,5]**

Vigna Taglianti, A., P. Bonavita, S. Bruschi, A. Casale, C. Chemini & S. De Felici 2000 *Carabus montivagus* (Coleoptera, Carabidae) in the Italian Central Alps: relict or introduced by man? – In: Brandmayr, P., G. L. Lövei, T. Z. Brandmayr, A. Casale & A. Vigna Taglianti (eds.): Natural History and Applied Ecology of Carabid Beetles. Sofia-Moscow: Pensoft Publishers: 61-70. **[3,5,8]**

Vigna Taglianti, A. & S. De Felici 1994 Ground beetle communities in Central Apennine beech woods. – In: Desender *et al.* (eds.). Carabid Beetles, Ecology and Evolution. Dordrecht: Kluwer: 71-78. **[5,8]**

Vigna Taglianti, A. & S. Forestiero 1994 Sistematica e biogeografia: riflessioni attuali su concetti, problemi e procedure. – Atti XVII Congr. Naz. Ital. Ent. Udine (13-18 . 06.1994): 49-60. **[8]**

Vigna Taglianti, A., R. Spettoli, P. Brandmayr & M.C. Algieri 2001 Note tassonomiche e corologiche su *Carabus granulatus* in Italia, con descrizione di una nuova sottospecie di Calabria (Coleoptera Carabidae). – Mem. Soc. entomol. ital. 80: 65-86. **[1,5,8,maps]**

Vogler, A.P. & R. DeSalle 1994 Diagnosing units of conservation management. – Conserv. Biol. 8: 354-363. **[9]**

Von der Trappen, A. 1929 Die Fauna von Württemberg. Die Käfer 1. (Carabidae 1.). – Jh. Ver. vaterl. Naturkde. Württ. 85: 242-257. **[6]**

Von Lengerken, H. 1921 *Carabus auratus* und seine Larve. – Arch. Naturgesch. 87: 31-113. **[6]**

Von Lengerken, H. 1924 Coleoptera, Käfer. – In: Schulze, P. (ed.): Biologie der Tiere Deutschlands 12, Teil 40. Berlin. **[6]**

Voronin, A.G. 1979 Fauna i statsial'noe raspredelenie zhuzhelits okrestnostei g. Permi. (Fauna and habitat distribution of the ground-beetles in the vicinity of Perm) – Perm. Un-t, Rukopis' depoz. VINITI 19.02.1979 N 633-79 Dep. [In Russian]. **[5]**

Voronin, A.G. 1987 Fauna i naselenie zhuzhelits osnovnykh biotopov podzony predlesostepnykh sosnovykh i berezovykh lesov taezhnoi zony yuzhnogo Zauralyua. (Fauna and population of ground-beetles in main habitats of the pine and birch forest subzone in the taiga zone of the South Transuralia) – In: Fauna i ekologiya nasekomykh Urala. Sverdlovsk: 45-56. [In Russian]. **[5]**

Voronin, A.G. 1999 Fauna i kompleksy zhuzhelits (Coleoptera, Trachypachidae, Carabidae) lesnoi zony Srednego Urala (ekologo-zoogeograficheskii analiz). (Fauna and assemblages of the ground beetles (Coleoptera, Trachypachidae, Carabidae) of the forest zone of the Middle Ural (ecological and geographical analysis)) – Perm': Izd-vo Permskogo Universiteta: 1-244. [In Russian]. **[5,t]**

Voronin, A.G. 2000 K faune zhuzhelits zakaznika "Preduralye" (A contribution to the ground-beetle fauna of Preduralye reserve) – In: Sostoyanie i dinamika prirodnykh kompleksov osobo okhranyaemykh territorii Urala. Tez. dokl. nauchno-prakt. konf. posv. 70-letiyu Pechoro-Ilychskogo gos. prirodnogo zapovednika, 29.05-1.06.2000. Syktyvkar: 38-40. [In Russian]. **[5,t]**

Voronova, L.D. 1973 Pochvoobitayushchie bespozvonochnye bezlesnykh uchastkov Il'menskogo zapovednika i khrebta Taganai (Yuzhny Ural) (Soil-dwelling invertebrates in non-forested habitats of the Ilmen Reserve and Taganai range (South Urals)) – In: Ekologiya pochvoobitayushchikh bespozvonochnykh. Moscow: 84-93. [In Russian]. **[5,8,t]**

Voronova, L.D. 1987 Pochvennaya fauna yuzhnoi taigi Permskoi oblasti (Soil fauna of south taiga in Perm' region) – In: Pochvennaya fauna Severnoi Evropy. Moscow: Nauka: 59-65. [In Russian]. **[5,8,t]**

Wachmann, E., R. Platen & D. Barndt 1995 Laufkäfer, Beobachtung, Lebensweise. – Augsburg: Naturbuch-Verlag: 1-295. **[5]**

Wautier, V. 1971 Un phénomèn social chez les Coléoptères: le grégarisme de *Brachinus* (Caraboidea, Brachinidae). – Insectes Soc. 18 : 1-84. **[6]**

Wayne, M.L., J.B. Hackett & T.F.C. Mackay 1997 Quantitative genetics of ovariole number in *Drosophila melanogaster* I. Segregating variation and fitness. – Evolution 51: 1156-1163. **[6]**

Weber, F. 1965a Zur Tagaktivität von *Carabus*-Arten. – Zool. Anz. 175: 354-360. **[6]**

Weber, F. 1965b Vergleichende Untersuchungen über das Verhalten von *Carabus*-Arten in Luftfeuchtigkeitsgefällen. – Z. Morph. Ökol. Tiere 54: 551-565. **[6]**

Weber, F. 1966a Die tageszeitliche Aktivitätsverteilung von *Carabus cancellatus* Ill. und *nitens* L. unter künstlichen Belichtungsbedingungen. – Zool. Anz. 177: 367-379. **[5,6]**

Weber, F. 1966b Die tageszeitliche Aktivitätsverteilung des dunkelaktiven *Carabus problematicus* (Coleoptera, Ins.) nach Phasenumkehr des Zeitgebers. – Zool. Beitr. 12: 161-179. **[5,6]**

Weber, F. 1966c Zur Verbreitung von *Carabus irregularis* Fabr. im Teutoburger Wald und Eggegebirge (Westfalen). – Entomol. Bl. 62 (1): 1-5. **[6]**

Weber, F. 1966d Beitrag zur Karyotypanalyse der Laufkäfergattung *Carabus* L. (Coleoptera). – Chromosoma 18: 467-476. **[6]**

Weber, F. 1967 Zur Polymorphie eines Chromosoms innerhalb von Populationen des Laufkäfers *Carabus auronitens* Fabr. – Experientia 23: 1-4. **[6]**

Weber, F. 1968a Circadian-Regel und Laufaktivität der Caraben (Ins. Coleoptera). – Oecologia (Berl.) 1: 155-170. **[6]**

Weber, F. 1968b Die intraspezifische Variabilität des heterochromatischen Armes eines Chromosoms bei der Gattung *Carabus* L. (Coleoptera). – Chromosoma 23: 288-308. **[6]**

Weber, F. 1970 Die circadiane Laufperiodik der *Carabus*-Arten bei konstanten Umweltbedingungen. – Faun. Oekol. Mitt. 3: 337-347. **[5]**

Weber, F. 1973 Beitrag zur Karyotypanalyse der Laufkäfergattung *Carabus* L. (Coleoptera). – Chromosoma 18: 466-476. **[5]**

Weber, F. 1983 Die tageszeitliche Aktivitätsverteilung von *Carabus problematicus* im Laborexperimet und im natürlichen Habitat. – In: Brandmayr, P., P.J. den Boer & F. Weber (eds.): Report 4th Symp. Carab. '81: 59-74. **[6]**

Weber, F. & U. Heimbach 2001 Behavioural, reproductive and developmental seasonality in *Carabus auronitens* and *Carabus nemoralis* (Col., Carabidae). A demographic comparison between two co-existing spring breeding populations and tests for intra- and interspecific competition and for synchronizing weather events. – Mitteilungen aus der Biologischen Bundesanstalt für Land- und Forstwirtschaft Berlin Dahlem, 382. **[5,A]**

Weber, F. & I. Weber 1966 Wiederentdeckung des Laufkäfers *Carabus variolosus* F. im Arnsberger Wald. – Natur und Heimat 26: 69-70. **[9]**

Weidemann, G. 1965 Ökologische und biometrische Untersuchungen an Proctotrupiden (Hymenoptera, Proctotrupidae s. str.) der Nordseeküste und des Binnenlandes. – Z. Morphol. Ökol. Tiere 55: 425-514. **[6]**

Westheide, W. & R. Rieger (eds.) 1996 Spezielle Zoologie, Teil 1: Einzeller und Wirbellose Tiere. – Stuttgart: Fischer Verlag: 1-909. **[6]**

Weygolt, P. 1996 Chelicerata, Spinnentiere. – In: Westheide, W. & R. Rieger (eds.): Spezielle Zoologie, Teil 1: Einzeller und Wirbellose Tiere. – Stuttgart: Fischer Verlag: 449-497. **[6]**

Wiley, E.O. 1981 Phylogenetics, the theory and practice of phylogenetic systematics. – New York: John Wiley & Sons: XV + 439 pp. **[8]**

Wilson, E.O. 1988 Biodiversity. – Washington D.C.: Nat. Academy Press. **[1]**

Wright, S. 1931 Evolution in Mendelian populations. – Genetics 16: 97-159. **[9]**

Yamashita, T. & K. Kanehisa 1979 Studies in the daily rhythmic activity and food habitat of *Carabus yaconicus* Bates (Coleoptera, Carabidae). – Ber. Ohara Inst. Landwirtsch. Biol. Okayama Univ. 17: 195-200. **[6]**

Yatsentkovsky, E. 1906 Predvaritel'moe soobschenie o zhukakh Khersonskoi gubernii (A preliminary report on the beetles of Herson province) – Sb. Stud. Biol. Kruz. 1: 142-179. [In Russian]. **[5]**

Yuferev, G.I. 1980 Fauna zhuzhelits (Coleoptera, Carabidae) Kirovskoi oblasti. (The ground-beetle fauna (Coleoptera, Carabidae) of the Kirov Province) – In: Issledovaniya entomofauny Srednego Povolzh'ya. Kazan': 38-44. [In Russian]. **[5]**

Yurtsev, B.A. 1975 Nekotorye tendentsii razvitiya metoda "konkretnoi flory" (Some trends in the development of the concrete flora method) – Bot. Zhurn. 60: 69-83. [In Russian]. **[8]**

Zaballos, J. P. & C. Jeanne 1994 Nuevo catalogo de los carabidos (Coleoptera) de la Peninsula Iberica. – Monografias S. E. A.-1: 1-159. **[3,5,6,9]**

Zagaikevich, I.K. V.B. Rizun & V.I. Yavornitsky 1989 K izucheniyu zhuzhelits (Carabidae, Coleoptera) nekotorykh lesnykh ekosistem zapada USSR. (To a study on ground-beetles in some forest ecosystems of the western part of the Ukrainian SSR) – In: Ekologiya i taksonomiya nasekomykh Ukrainy. Sborn. nauchn. trud. 3: 84-86. [In Russian]. **[5]**

Zarapkin, S.R. 1934 Zur Phänoanalyse von geographischen Rassen und Arten. – Arch. Naturgesch. (N.F.) 3: 161-186. **[6]**

Zherebtsov, A.K. 1979 Fauna i ekologiya zhuzhelits estestvennykh biogeotsenozov Raifskogo uchastka Volzhsko-Kamskogo zapovednika. (Fauna and ecology of ground-beetles in natural biogeocenoses of the Raifa part of the Volga-Kama Reserve) – Avtoref. kand. diss. Moscow: 1-25. [In Russian]. **[5]**

Zhuravlev, S. 1914 Materialy po faune zhukov Ural'skoi oblasti. (Contributions à la faune des Coléoptères de la Province d'Uralsk) – Tr. Russk. entomol. obshch. 41 (3). [In Russian]. **[5]**

Zinovjev, E.V. 1991 Ground beetles of the midflow of the Ai-river. – In: Olshvang, V.N. (ed.). Ekologhicheskie gruppirovki v estestvennykh i antropoghennykh landshaftakh Urala: Sbornik nauchn. trudov. Sverdlovsk: Uralsk otd. Akad. nauk. SSSR: 23-29. [In Russian]. **[5]**

Zinovjev, E.V. 1997 Novyi vid zhuzhelits roda *Carabus* (Coleoptera, Carabidae) s Yuzhnogo Urala. – Uspehi entomologii na Urale. Ekaterinburg: 35-38. **[5,t]**

Author's index

Alphabetical list of authors, cited in the text. The numbers **[2,3,4...,10]** between square brackets refer to the chapter(s) where the respective author has been cited. No difference has been made with respect to first and following authorships. The indication **[maps]** means that one or more papers of this author was used to construct the European and/or Russian maps in Chapter 5, and thus not necessarily have been mentioned in the text. The indication **[t]** means that one or more papers of this author has been used to construct the ecological transects of Chapter 8. **[A]** means mentioned in the Addendum.

Taxonomic index

INDEX OF SUBGENERAAND OTHER SUPRASPECIFIC GROUPS

Only valid subgenera and most important synonyms (in italic) are listed. Supraspecific groups are given in bold. Page numbers in bold refer to those pages, where the most important information about a taxon is listed, i.e. in Chapter 2. *Checklist*, Chapter 3. *Key to the adults*, Chapter 4.' *Key to the larvae* and Chapter 5. *Species accounts*, respectively.

INDEX OF SPECIES AND SUBSPECIES

Valid species present in Europe are given in bold. Major subspecies are marked with 'ssp.'. Questionable subspecies are given in italic and matched with '(ssp.)'. The valid species not present in Europe are in normal font. Page numbers in bold refer to those pages, where the most important information about a taxon is listed, i.e. in Chapter 2. *Checklist*, Chapter 3. *Key to the adults*, Chapter 4. *Key to the larvae* and Chapter 5. *Species accounts*, respectively.