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Wojciech Czechowski, Alexander Radchenko,  
Wiesława Czechowska, Kari Vepsäläinen

# The ants of Poland

with reference to the myrmecofauna of Europe



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*Dedicated to  
past generations of Polish myrmecologists  
– on the twentieth anniversary of the death of  
Professor Bohdan Pisarski (1928–1992)*

### **Homage to Bohdan Pisarski**

On August 18<sup>th</sup> 1992, I got an email to Canada — my friend and colleague Professor Bohdan Pisarski had died while carrying out his fieldwork in Finland. The following short, personal recollections aim at illustrating the remarkable bond between Bohdan and Finland. [For a eulogy, see *Memorabilia Zoologica* 48: 3–7 (1994).]

My first meeting with Bohdan was on July 29<sup>th</sup> 1975, when I walked in to his office at Wilcza 64 (Warsaw). First surprise: two polyglots, no common language. The second one: when I switched to my nascent Polish, introduced myself (Bohdan never having heard of me), and invited him to cooperate on the evolutionary ecology of ants, he looked at me with his warm smiling eyes and nodded: *tak*.

Within the next years—when Europe was still long politically divided—I had the opportunity to join the many “western” myrmecologists, who took advantage of the meetings organised by Bohdan in Poland, to get scientists from the east and the west together. Thanks to the Polish and Finnish academies of sciences, our cooperation in the field could start in 1978 and continue during a series of years by community sampling from the Arctic Ocean coast down to the southern tip of Finland. Exotic experiences kept Bohdan alert, e.g. when driving a Russian-made car with Swedish licence plates (borrowed from a Finnish citizen) over to the NATO country Norway and back—without a visa.

Most of Bohdan’s work in Finland took place at Tvärminne Zoological Station and its archipelago off Hanko Peninsula, which he visited yearly. This was the place where he recovered from heavy bureaucratic duties at his home institute. The recovery took place with inexhaustible energy, through “Stakhanovite” work both in the field and in the lab. Related experiences: while Bohdan was looking for nests under a pine trunk, a big viper spurted out. Bohdan only commented that there are seldom two of them, continued searching and took a *Myrmica* nest sample. And being constantly alert? Earlier the same day I had shown Bohdan a newly arrived reprint with the description of a new species, the socially parasitic *Myrmica hirsuta*. In the same evening, Bohdan asked me to look under the microscope—yes, the first find of the new species outside Britain, a female in the sample from the very viper site!

Bohdan's "headquarter of relaxation" was the small cottage on the island Halsholmen, where I and family were living through many Tvärminne summers. Many long evenings and nights rolled by during conversations with Bohdan seated in his favourite rocking chair. These occasions rarely touched myrmecology, rather everything else. In the turbulent 1980s, the discussions swayed back and forth between optimistic futuristic visions, thanks to the birth (and rebirth) of *Solidarność*, and the depressing period of the martial law in between. As an ecologist I could feel the deepest connotations of the immortal aphorism by Stanisław Jerzy Lec: *I lilie na bagnie drżą przed melioracją*. In translation: "And lilies on the mire tremble on the eve of amelioration." Luckily not all mires are drained, and even ditched ones may recover—as may societies. (N.B. – ameliorate, to improve; here a technocratic euphemism for draining, i.e. to severely destroy by ditching.)

Bohdan's summer weeks and months (and short periods wintertime) through 15 years in Finland were at times accompanied by several Polish myrmecologist colleagues. The work and spirit of Bohdan and the impact of Polish myrmecology has been extended and continued in Tvärminne to the next millennium, and in spite of discontinued funding, the present monograph is in part a fruit of the long Polish–Finnish cooperation.

KARI VEPSÄLÄINEN



Professor Bohdan Pisarski and Wojciech Czechowski  
(the Gorce Mts, 1989; photo K. Yamauchi).

# The ants of Poland with reference to the myrmecofauna of Europe

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## ABSTRACT

This book on ants (Hymenoptera: Formicidae) is an updated, corrected and expanded version of the previous monograph of the Polish myrmecofauna (Czechowski et al. 2002). It contains 103 ant species of 25 genera reported in Poland until 2010, the occurrence of which in the country are unquestionable or at least considered by the authors probable. The book consists of four main chapters: (1) a systematic checklist of the ant taxa (subfamilies, genera, species) of Europe, (2) a faunistic catalogue of the ants of Poland, (3) characteristics of the myrmecofauna of Poland, and (4) keys for identification. The checklist is the newest updated list of the European ants, and it displays recent alterations in the ant taxonomy. It contains nine subfamilies, 57 genera and 613 valid species; the list is complemented by 10 recognised but not yet formally described species. The faunistic catalogue provides a taxonomic survey of the Polish ant species together with information about their general distribution in the Palaearctic and the distribution in Poland, with notes on the biology of each species. For some taxa (species, genera), notes on their taxonomic history are provided. The chapter compiles all faunistic data published until the end of the year 2010; published reports are supplemented by confirmed unpublished data available to the authors. For every species maps of their ranges in the Palaearctic and distributions in the geographical regions in Poland are enclosed. The catalogue is closed by a list of the species ever reported in Poland and later owing to a specified reason excluded from the Polish fauna. The next chapter includes zoogeographical and ecological characteristics of the Polish myrmecofauna, with reference to the European myrmecofauna as a whole. The last chapter includes keys for identification of the ant taxa (subfamilies, genera and species), individually for workers, queens and males (when distinguishable). The keys for subfamilies and genera involve all European

taxa of these ranks. The keys for species include all ant species known in Poland, and those not reported from Poland but present in adjacent regions of Central Europe, and recognised as possible to be found in the country. The keys are illustrated with SEM photographs. The main chapters are preceded by the foreword presenting general trends in myrmecological research in the world throughout history, and the introduction, in which the past and the present of Polish myrmecology is outlined.

## KEY WORDS

Ants, biology, checklist, ecology, Europe, faunistics, key, morphology, Poland, systematics, taxonomy, zoogeography.

## CONTENTS

ABSTRACT .....	5
KEY WORDS .....	6
FOREWORD – TRENDS IN MYRMECOLOGY .....	13
INTRODUCTION .....	29
CHAPTER 1. CHECKLIST OF THE ANT TAXA OF EUROPE .....	35
CHAPTER 2. FAUNISTIC CATALOGUE OF THE ANTS OF POLAND .....	53
Subfamily Ponerinae Lepeletier, 1835 .....	54
Tribe Ponerini Lepeletier, 1835 .....	54
Genus <i>Ponera</i> Latreille, 1804 .....	54
Genus <i>Hypoponera</i> Santschi, 1938 .....	59
Subfamily Dolichoderinae Forel, 1878 .....	62
Tribe Dolichoderini Forel, 1878 .....	62
Genus <i>Dolichoderus</i> Lund, 1831 .....	62
Tribe Tapinomini Emery, 1912 .....	65
Genus <i>Tapinoma</i> Förster, 1850 .....	65
Genus <i>Linepithema</i> Mayr, 1866 .....	69
Subfamily Myrmicinae Lepeletier, 1835 .....	71
Tribe Myrmicini Lepeletier, 1835 .....	71
Genus <i>Myrmica</i> Latreille, 1804 .....	71
Genus <i>Manica</i> Jurine, 1807 .....	113
Tribe Pheidolini Emery, 1877 .....	116
Genus <i>Aphaenogaster</i> Mayr, 1853 .....	116
Genus <i>Messor</i> Forel, 1890 .....	118
Tribe Stenammini Ashmead, 1905 .....	121
Genus <i>Stenamma</i> Westwood, 1839 .....	121
Tribe Formicoxenini Forel, 1893 .....	124
Genus <i>Formicoxenus</i> Mayr, 1855 .....	124

Genus <i>Leptothorax</i> Mayr, 1855	127
Genus <i>Temnothorax</i> Mayr, 1861	138
Genus <i>Harpagoxenus</i> Forel, 1893	160
Genus <i>Myrmoxenus</i> Ruzsky, 1902	163
Tribe Solenopsidini Forel, 1893	166
Genus <i>Solenopsis</i> Westwood, 1840	166
Genus <i>Monomorium</i> Mayr, 1855	168
Tribe Myrmeciniini Ashmead, 1905	171
Genus <i>Myrmecina</i> Curtis, 1829	171
Tribe Tetramoriini Emery, 1895	174
Genus <i>Tetramorium</i> Mayr, 1855	174
Genus <i>Anergates</i> Forel, 1874	184
Genus <i>Strongylognathus</i> Mayr, 1853	186
Subfamily Formicinae Latreille, 1809	188
Tribe Formicini Latreille, 1809	188
Genus <i>Formica</i> Linnaeus, 1758	188
Genus <i>Polyergus</i> Latreille, 1804	236
Tribe Camponotini Forel, 1878	239
Genus <i>Camponotus</i> Mayr, 1861	239
Tribe Lasiini Ashmead, 1905	252
Genus <i>Lasius</i> Fabricius, 1804	252
Species excluded from the Polish myrmecofauna	291
CHAPTER 3. CHARACTERISTICS OF THE POLISH MYRMECOFAUNA	293
Species richness and composition	293
Zoogeographical composition	306
Ecological composition	310
The myrmecofauna of Poland relative to those of Europe and selected	
European countries	313
CHAPTER 4. KEYS FOR IDENTIFICATION	333
Key to the European subfamilies	337
Key to the European genera	340
Subfamily Ponerinae	340
Subfamily Dolichoderinae	342
Subfamily Myrmicinae	344
Subfamily Formicinae	351
Key to the Polish species	356
Subfamily Ponerinae	356
Subfamily Dolichoderinae	357
Subfamily Myrmicinae	357
Subfamily Formicinae	371
Plates	387
ACKNOWLEDGEMENTS	443
REFERENCES	444
INDEX OF THE SCIENTIFIC NAMES	485
Names of the ant taxa	485
Names of other animals, fungi, plants and plant associations	496





# Mrówki Polski na tle myrmekofauny Europy

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## STRESZCZENIE

Książka jest nową – zaktualizowaną, poprawioną i rozszerzoną – wersją monografii „The ants (Hymenoptera, Formicidae) of Poland” (Czechowski i in. 2002), przedstawiającą myrmekofaunę krajową w nawiązaniu do myrmekofauny europejskiej. Opracowanie składa się z czterech głównych części. Część pierwszą tworzy pełna lista taksonów mrówek (podrodzin, rodzajów, gatunków) znanych z Europy, podana zgodnie ze stanem układu taksonomicznego z dn. 31 grudnia 2010 r. Wykaz obejmuje 613 opisanych gatunków z 57 rodzajów i dziewięciu podrodzin, a dopełnia go 10 „kryptogatunków” – już zidentyfikowanych, ale jeszcze formalnie nie opisanych. Część drugą stanowi katalog mrówek Polski – taksonomiczny przegląd 103 gatunków z 25 rodzajów i czterech podrodzin, jakie zostały wiarygodnie wykazane z obszaru Polski, poczynając od zarania krajowej myrmekofaunistyki (tj. drugiej połowy XVIII w.) do końca 2010 r. Dla każdego gatunku podana jest synonimika nazw używanych w krajowym piśmiennictwie, informacja o występowaniu w świecie (ilustrowana mapą zasięgu w Palearktyce), informacja o występowaniu w poszczególnych regionach geograficznych Polski (ilustrowana mapą rozmieszczenia w kraju) wraz z wykazem źródeł literaturowych oraz podstawowe dane o biologii. Część trzecia zawiera charakterystykę polskiej myrmekofauny pod względem składu i bogactwa gatunkowego oraz jej profilu zoogeograficznego i ekologicznego. Część czwarta to oryginalne klucze do oznaczania, ilustrowane zdjęciami skaningowymi, opracowane (tam, gdzie to możliwe) osobno dla robotnic, królowych i samców. Klucze do podrodzin i rodzajów obejmują wszystkie europejskie taksony tych szczebli, a klucze do gatunków – wszystkie znane gatunki krajowe oraz dodatkowo te gatunki, których znalezienie (pojawienie się) w Polsce uznano za możliwe. Części merytoryczne poprzedzają rozdziały wstępne, przedstawiające główne kierunki badań nad mrówkami na przestrzeni dziejów oraz nakreślające historię i teraźniejszość myrmekologii w Polsce.

## SŁOWA KLUCZOWE

Biologia, ekologia, Europa, faunistyka, klucz, morfologia, mrówki, Polska, systematyka, taksonomia, wykaz gatunków, zoogeografia.

## SPIS TREŚCI

STRESZCZENIE .....	9
SŁOWA KLUCZOWE .....	10
WPROWADZENIE – GŁÓWNE KIERUNKI MYRMEKOLOGII .....	13
WSTĘP .....	29
ROZDZIAŁ 1. WYKAZ TAKSONÓW MRÓWEK EUROPY .....	35
ROZDZIAŁ 2. KATALOG FAUNISTYCZNY MRÓWEK POLSKI .....	53
Podrodzina Ponerinae Lepeletier, 1835 .....	54
Plemię Ponerini Lepeletier, 1835 .....	54
Rodzaj <i>Ponera</i> Latreille, 1804 .....	54
Rodzaj <i>Hypoponera</i> Santschi, 1938 .....	59
Podrodzina Dolichoderinae Forel, 1878 .....	62
Plemię Dolichoderini Forel, 1878 .....	62
Rodzaj <i>Dolichoderus</i> Lund, 1831 .....	62
Plemię Tapinomini Emery, 1912 .....	65
Rodzaj <i>Tapinoma</i> Förster, 1850 .....	65
Rodzaj <i>Linepithema</i> Mayr, 1866 .....	69
Podrodzina Myrmicinae Lepeletier, 1835 .....	71
Plemię Myrmicini Lepeletier, 1835 .....	71
Rodzaj <i>Myrmica</i> Latreille, 1804 .....	71
Rodzaj <i>Manica</i> Jurine, 1807 .....	113
Plemię Pheidolini Emery, 1877 .....	116
Rodzaj <i>Aphaenogaster</i> Mayr, 1853 .....	116
Rodzaj <i>Messor</i> Forel, 1890 .....	118
Plemię Stenammini Ashmead, 1905 .....	121
Rodzaj <i>Stenamma</i> Westwood, 1839 .....	121
Plemię Formicoxenini Forel, 1893 .....	124
Rodzaj <i>Formicoxenus</i> Mayr, 1855 .....	124
Rodzaj <i>Leptothorax</i> Mayr, 1855 .....	127
Rodzaj <i>Temnothorax</i> Mayr, 1861 .....	138
Rodzaj <i>Harpagoxenus</i> Forel, 1893 .....	160
Rodzaj <i>Myrmoxenus</i> Ruzsky, 1902 .....	163
Plemię Solenopsidini Forel, 1893 .....	166
Rodzaj <i>Solenopsis</i> Westwood, 1840 .....	166
Rodzaj <i>Monomorium</i> Mayr, 1855 .....	168

Plemię Myrmeciniini Ashmead, 1905 .....	171
Rodzaj <i>Myrmecina</i> Curtis, 1829 .....	171
Plemię Tetramoriini Emery, 1895 .....	174
Rodzaj <i>Tetramorium</i> Mayr, 1855 .....	174
Rodzaj <i>Anergates</i> Forel, 1874 .....	184
Rodzaj <i>Strongylognathus</i> Mayr, 1853 .....	186
Podrodzina Formicinae Latreille, 1809 .....	188
Plemię Formicini Latreille, 1809 .....	188
Rodzaj <i>Formica</i> Linnaeus, 1758 .....	188
Rodzaj <i>Polyergus</i> Latreille, 1804 .....	236
Plemię Camponotini Forel, 1878 .....	239
Rodzaj <i>Camponotus</i> Mayr, 1861 .....	239
Plemię Lasiini Ashmead, 1905 .....	252
Rodzaj <i>Lasius</i> Fabricius, 1804 .....	252
Gatunki wykreślone z polskiej myrmekofauny .....	291
CHAPTER 3. CHARAKTERYSTYKA POLSKIEJ MYRMEKOFAUNY .....	293
Bogactwo i skład gatunkowy .....	293
Skład zoogeograficzny .....	306
Skład ekologiczny .....	310
Myrmekofauna Polski na tle myrmekofauny Europy i wybranych krajów europejskich .....	313
CHAPTER 4. KLUCZE DO OZNACZANIA .....	333
Klucz do podrodzin europejskich .....	337
Klucz do rodzajów europejskich .....	340
Podrodzina Ponerinae .....	340
Podrodzina Dolichoderinae .....	342
Podrodzina Myrmicinae .....	344
Podrodzina Formicinae .....	351
Klucz do gatunków krajowych .....	356
Podrodzina Ponerinae .....	356
Podrodzina Dolichoderinae .....	357
Podrodzina Myrmicinae .....	357
Podrodzina Formicinae .....	371
Tablice .....	387
PODZIĘKOWANIA .....	443
PIŚMIENNICTWO .....	444
WYKAZ NAZW NAUKOWYCH .....	485
Nazwy taxonów mrówek .....	485
Nazwy innych zwierząt, grzybów, roślin i zbiorowisk roślinnych .....	496



## FOREWORD – TRENDS IN MYRMECOLOGY

*“To study ants one must love them for themselves  
as well as representatives of organisms”*  
Levins, Pressick and Heatwole (1973)

Together with naturalism, which provides keen observations on nature to answer the question “what?”, ecology is mandatory for comprehending biology. Paraphrasing MacArthur (1972), ecology, as all science, is repeated search for patterns and processes—and their explanation. Accordingly, ecology expands the question to “how?": what mechanisms through which processes cause the patterns we see and describe in nature? The ultimate question “why?” takes the researcher to the realm of evolutionary biology, which endeavours to find the connection between the specifics of the ecological environment and the adaptive features of organisms living there. As Theodosius Dobzhansky (1973) taught us, “Nothing in biology makes sense except in the light of evolution.” He formulated this view already a decade earlier (Dobzhansky 1964) when discussing the relations between molecular and organismic biology—a highly relevant topic still in our times.

Evidently, to understand adaptive patterns and processes in an ecological context, one cannot work without knowing the study organisms, being able to tell them to species—an impossible task without dedicated work of taxonomists through the history of zoology, including myrmecology. Simply, the evolutionary play is acted in the ecological theatre, organisms as actors (Hutchinson 1965). In the following, I try to describe the development of selected fields of myrmecology that all in their own way have contributed to answer the questions “what, how and why”—and thus have expanded our understanding of the life of ants. Hopefully a general trend will become visible; through time many of the earlier isolated fields of myrmecology have increasingly effectively found each other, often joined by ecological and evolutionary-biological research. As a whole, the modern myrmecologist is more than ever a part of a universal scientific community.

### **From proverbs to the superorganism**

The roots of written notes on ants go back in history to Aristotle (*The history of animals*, written 350 B.C.E., translated by D’Arcy Wentworth Thompson), who compared ant and bee societies with those of human societies. More well known to the layperson are the teachings of the Bible (Proverbs), guiding people to follow the behaviour of ants and work industriously. Later observations by committed naturalists, however, have shown that on the contrary worker ants are idle about half of the time, if not most of the time (Wilson 1971). Whereas western human societies work through disciplined hierarchical levels, ant societies are organised in dense heterarchies, where each individual is likely to communicate with any other (Wilson and Hölldobler 1988). Feed-back communication loops work from

down up; much of the decentralised regulation is based on mass communication, information being transmitted from group to group or group to individual. Such an ant society works much by the rule of thumb. The social homeostasis and flexibility such reached includes a large amount of redundancy, which secures the life of societies equally reliably as parallel-series or series parallel operations do in systems engineering (Oster and Wilson 1978).

Evidently, observations on the efficiency of social insects led relatively early to the concept of ant societies as superorganism (Wheeler 1911a), a concept that thrived well until the mid 1900s, after which it was rapidly forgotten. Curiously, no other conception has supplanted the superorganism concept, which has maintained its metaphorical power. For example, competition theory of social insects has included intracolony competition among individuals for energy, when such “competition” could rather be seen as a trade-off of energy inside a superorganism (Vepsäläinen 1980). The superorganism conception was revived and established in a firm theoretical context by Hölldobler and Wilson (1990, 2009), who use it as an all-embracing conceptual framework in explaining “the beauty, elegance, and strangeness of insect societies”.

Let the above catchy attributes describe the fascination of ants experienced already by the early myrmecologists. In the following, after a peek on selective milestones of myrmecology, I try to outline the development of myrmecology through the last half a century.

### **The power of natural history: from observations to encyclopaedic summaries**

The scientific study of ants, based on observation of a naturalist, may be dated to the notes made by René Antoine Ferchault de Réaumur before mid 1700s; his manuscript *Histoire des fourmis* was published as English translation with annotations by Wheeler in 1926, *The natural history of ants*. His observations are still worth of referring to, e.g. in a study where the huge quantities of conifer resin in wood-ant mounds are shown to be prophylactic, and the resin-collecting behaviour of ants seems to have evolved to fight pathogens (Castella et al. 2008).

Pierre-André Latreille made a common mistake of his time by admiring the spectacular industriousness of ants, and merited thus one citation by Wilson (1971) in *The insect societies*. In the cited work, *Histoire naturelle des fourmis et recueil de mémoires et d'observations sur les abeilles, les araignées, faucheurs et autres insectes* (1802) Latreille, however, demonstrates clearly his capacities as a naturalist and taxonomist. In the present times, it is a pity that too few taxonomists have read the above-mentioned work. If they had, they perhaps would not stick to the misnomer *Camponotus ligniperdus* of the carpenter ant *C. ligniperda*. Such degradation most probably is due to the present overemphasis of a single publication language in science, and the negligence of basic taxonomic and linguistic schooling. Clearly, when Latreille (1802) described the species *Formica ligniperda*, he made no mention of *ligniperda* being an adjective. Quite the

contrary, he used the French vernacular “la fourmi ronge-bois”, which is typical of a compound noun in apposition. Thus, under the International Code of Zoological Nomenclature, Article 31.2.2, *ligniperda* must be treated as a noun, and under 31.2.1 and 34.2.1 it must not be changed to agree in gender when combined with *Camponotus*. No matter how frequent is the use of *ligniperdus*, it is mandatory to use the correct original spelling of the noun in apposition.

Pierre Huber was a keen naturalist and skilled observer of the behaviour of ants. His main contribution (1810) was the *Recherches sur les moeurs des fourmis indigènes*. There he was the first to describe, e.g. tending of aphids by ants. His discovery of and narrations on the slave-making *Polyergus rufescens* and *Formica sanguinea* had a strong impact on Charles Darwin, who was stimulated to make his own observations on slave-making. In *On the origin of species* (1859) he formulated a still plausible explanation of the evolution of dulosis (slavery) in ants. Likewise, the strong reproductive inequality between the worker and queen castes was noted by Huber, and the “sterile” worker caste was one of the major critical issues Darwin raised to test his whole theory of natural selection. Darwin’s solution anteceded the theory of kin selection; in his words, “selection may be applied to the family, as well as to the individual, and may thus gain the desired end.”

August Forel published the first edition of *Les fourmis de la Suisse* in 1874, in all a spectacular weighty monograph covering practically all contemporary aspects of European ants (the 2<sup>nd</sup>, revised and corrected edition was published in 1920). Over a human generation later, in 1910, William Morton Wheeler’s *Ants: their structure, development and behavior* laid a solid foundation to future studies in North America. Still two generations later (1971) Edward O. Wilson finished his *The Insect Societies*, which paved the ground to a myrmecology that integrated population genetics and population ecology to account for various aspects of sociality. The subsequent encyclopaedic *The ants* by Bert Hölldobler and Wilson (1990) was published at the dawn of a major breakthrough affecting all biological sciences, when the advanced bioassay techniques, statistically sophisticated algorithms running in powerful computers, and extensive electronic libraries enabling fast and extensive literature searches could transfer myrmecology closer to other fields of biology than ever before. *The ants* was dedicated “for the next generation of myrmecologists”, who were served the end-of-the-second-millennium synthesis of myrmecology, based on the work of many generations of ardent ant students.

### **A simple classification of selected myrmecological topics – the data basis**

As basic data source I have used the Web of Science (WoS, extended, starting with the year 1945). For many reasons, searches in WoS will severely bias the data to favour articles written in English. Also, any combination of search terms will find an embarrassing amount of newer articles, whereas older ones are often missed owing to their lack or scarcity of specific key words. For evident reasons,

my “quick-and-dirty” outline, in its shortness, is deemed to be subjective in its emphasises and omissions. Thus, to put flesh on the review, I have expanded my treatment by using quite a few articles and books (books were lacking from the WoS search) that I know in some detail. Consequently, this review will be fairly much a song of praise to those fields of myrmecology that lie close to my own heart.

The search in WoS extended, starting from 1945 and ending in mid December 2009, returned close to 12900 articles. This basic search used only title words referring to ants, separated by the Boolean search operator “or” and when suitable, the wild card “\*”: ant, ants, Attini, Formicidae, Formicinae, Formica, Camponotus, Lasius, Myrmicinae, Myrmica, Poner\*, Dolichoder\*—evidently, articles with title referring to other subfamilies or genera but not including any of the above search words, were lost from my data base. At this stage, I made no effort to deselect inescapable non-myrmecological articles thus obtained.

Next, a simple try to find relevant articles by topic categories, using specific search words in the topic field (in addition to the general search words given above), resulted in a voluminous and chaotic selection of articles, owing to, e.g. occurrence of the search word in the abstract, but not referring to the main topic of the article. Consequently, I decided to search for topic categories by only using topic words in the title of the article; I made an exception with “kin selection”, which is only occasionally included in the title, but in the topic field of the article usually reveals the theoretical context. Of a substantially extensive topic list, by attempting to minimise article overlaps among the search words, I selected a concise list of 16 topics that included ca. 1480 articles, i.e. 11.5% of all the articles found in the basic search. The percentages of articles found by both the basic and the restricted WoS searches through the chosen six time periods, show a steeply accelerating publishing pace, culminating in about half of the found articles being published in the last decade (Table 1; N% versus n%). For the restricted data, the evenness and diversity measures (based on the amounts and proportions of topics per time period) show with time an increasing diversity and (since 1970 with representative data sizes) evenness of topics covered in myrmecological literature. All this written with the caveat of inherent biases in WoS searches addressing the early decennia.

In the list of 16 main topic categories of ant articles, the highest number of articles is on aphids or coccids (164, 11.1% of all topics), and the lowest on biogeography (31, 2.1%) (Table 2). Invasive species, the fourth topic category ranked by number of articles, is by far most concentrated to the last decennium (96% of all articles; both low diversity and low evenness over the periods). Not surprisingly, the traditional myrmecological topics, taxonomy and systematics, communication, and recruitment, show both high diversity and evenness in their distribution over the time periods. Articles on cuticular hydrocarbons and kin selection have low diversity but high evenness; they are found only in the latest periods, where they are well represented. Articles on competition and social



Table 1. Basic statistics of the WoS search: N – basic search, N% – percentages of articles within time periods of the basic search; n – selected WoS data (see text; used in this review), n% – respective percentages of articles within time periods. The following indices were calculated from the smaller data set: Topics – number of topics with at least one article (max. 16 per time period), EVEN – Smith and Wilson’s evenness index, H’ – Shannon-Wiener diversity index ( $\log 2$ ), NECT – H’ given as the number of equally common topics.

Period	N	N%	n	n%	Topics	EVEN	H’	NECT
All periods	12838	100.0	1474	100.0	16	0.84	3.85	14.41
2000–2009	5903	46.0	838	56.9	16	0.80	3.77	13.63
1990–1999	2970	23.1	337	22.9	16	0.79	3.82	14.13
1980–1989	2192	17.1	188	12.8	14	0.50	3.32	10.01
1970–1979	1191	9.3	82	5.6	10	0.42	2.83	7.10
1960–1969	421	3.3	23	1.6	5	0.89	2.24	4.71
1945–1959	161	1.3	6	0.4	3	0.87	1.46	2.75

parasitism show high diversity but low evenness; they are represented over many periods, but the publications are strongly biased toward later periods. In the following, I try to summarise some main trends of these broad and often heterogeneous main topics through the post-war decades. Only a cursory reading of *The ants* by Hölldobler and Wilson (1990), which outline, among others, the development of main fields of myrmecology through time until the late 1980s, shows that a short review like this one must necessarily remain a superficial one—the less superficial, the more subjective. Constraints set by conciseness also keep the references of the review to a minimum.

### Communication – chemical ecology

In social insects, studies on communication have naturally been well represented through the time periods. Specific topics embrace communication among individuals during trophallaxis (the exchange of alimentary liquid among colony members or guest organisms, either mutually or unilaterally), and in recruitment to food and to defence of nest, food resources or territory, including ritualised combats among individuals of neighbouring societies. Means of communication comprise tactile and acoustic (stridulation) signals, but the primary mode of communication in ants is chemical—in the about a dozen functional categories of communication, most are primarily or entirely based on chemicals (Hölldobler and Wilson 2009). Because chemical communication is included in almost all activities of and among individuals, it has an over a century long research history, but breakthroughs in the field started with development of analytical means, first in the 1950s by the progress of gas chromatography, and more recently by GC-mass spectrometry. This contrasts starkly with “chemical” articles published in the

post-war decennium, when testing of DDT and other insecticides was common on pest ants. Among the diverse subfields of chemical ecology and behaviour in ants and their social symbionts, the role of cuticular hydrocarbons (CHC) has since the 1980s been intensively studied in a variety of contexts.

The integrity of a society necessitates recognition of nest mates (kin) from alien individuals. Here, CHCs function as main semiochemicals. Analyses on levels of colony, species and genera predominate during the present millennium, usually in the context of kin recognition. During the last decades, however, an increasing proportion of CHC research has centred on how alien individuals, social parasitic ants and other organisms, are able to invade an ant nest and live there. Although propaganda, appeasement and repellent substances secreted by pygidial, Poisson or Dufour's glands, are here—depending on the context—important, much of the recent studies have been on CHCs. The review by Lenoir et al. (2001) summarises how much (and still little) was known in the beginning of this millennium about chemical strategies by which parasites break the chemical defence of highly integrated superorganisms. Still at present, much need to be learned about the ontogenesis of CHCs in ants and their parasites and other guest species, e.g. how the chemical cues and signals are coded, and what are the relative (certainly case-specific) roles of the environment, passive or active acquisition of host-specific odour profile, and its synthesis by the parasite itself. Lately, promising breakthroughs have been made, e.g. on integration of the dulotic *Polyergus rufescens* to the host colony by using a flexible chemical signature (D'Ettorre et al. 2002).

Whereas oldest of the few comparative studies on the CHC profiles of slave-making ants and their host ants date back to the early 1990s, chemico-ecological studies on inquiline ants (functionally workerless, obligate parasites) and their host species number not more than a few, and have been published in the last few years. Almost equally rare are studies, all published in the 2000s, on the CHC profiles of lycaenid butterfly caterpillars of the genus *Maculinea*, obligate parasites of their *Myrmica* host species. For a general review on *Maculinea*–*Myrmica* relationships, see Thomas et al. (2005). In all, this expansion of CHC analyses, from kinship studies to intimate relationships between social parasites and their hosts, opens a promising but challenging approach hopefully to better understand how chemical strongholds of superorganisms can be invaded and exploited. A crucial, case-specific, question here is: what are the respective roles of chemical insignificance and chemical mimicry in breaking the chemical defence of ant societies? A concise, up-to-date review of “chemical strategies to deal with ants” is given by Akino (2008); Martin et al. (2009) manage to outline the bewildering diversity of CHCs in ants, and state that “understanding how the cues and signals in chemical communication are encoded is one of the major challenges facing chemical ecologists of the 21<sup>st</sup> century”.

Recent studies have also shown that social parasites of ants may use supplementary means of communication on top of chemical signalling, when integrating to the host society. Thus *Maculinea* caterpillars emit by stridulating acoustic

signals that imitate those produced by *Myrmica* queens (Barbero et al. 2009a,b). Because the queen signalling of the three studied ant species do not differ from each other, caterpillars of different parasitic species may increase their status within the host society by emitting such non-specific, general “myrmicaness” acoustic cues.

## **Kin selection**

Cuticular HC analyses in kin recognition studies started in the mid 1980s, and have, during the last ten years, shown the potential power of combining nest-mate recognition cue studies with traditional genetic studies of relatedness among nest mates. Questions to be solved include, e.g. how strong is actually the bond between genetic relatedness and recognition cues? What is the difference of being genetically kin, genetically similar (without necessarily being kin), and being chemically identical (or similar) for vital cues, being or not being genetically related? Such questions still lay at the outskirts of kin selection studies.

Kin selection theory has its theoretical roots in the 1960s (Hamilton 1964). It saw a burst of development through the 1970s, and was considered a powerful theory to understand evolution of eusociality, queen dominance, and various other aspects of social life of social insects. Proceeding through some up and downs, and many simplistic explanatory hypotheses about sociality and its evolution, kin selection research has incorporated increasingly more realistic scenarios. Kin selection as a topic word (in key words, article title or abstract) returned 110 hits in the WoS search (Table 2), but of these the first article was published as late as in 1991, most (72%) of the articles being published in the last ten years.

The diversification of research in the framework of kin selection is clear, when originally complicating factors to the theory have been included. Thus the common occurrence of polygyny (multiple-queen nests) in ants, and its role in social organisation, necessitated analyses of genetic relatedness; also efforts to explain altruism had to take the number of queens into consideration. Next, cooperation and conflict among nest mates, including worker policing (where eggs laid by workers are eaten by other workers) needed to be understood—when and why cooperation, when and why conflict. Although all these topics are found in some articles published in the mid 1980s, they were included under the umbrella of kin selection theory mainly in the 1990s. The ongoing active research on the social organisation of ants is dominated by the kin selection paradigm, and alternative explanatory frameworks—parental manipulation being the most powerful alternative, see Alexander (1974)—are still waiting for a revival. Interestingly, voices have been raised against the all-explaining role of kin selection in social organisation, foremost by its former main spokesman. Edward O. Wilson named one of his review articles *Kin selection as the key to altruism: its rise and fall* (2005)—a view not received with pleasure by most of the researchers in the field. Anyhow, a research shift from kin to group selection (or rather, not neglecting *a priori* any level of selection) in explaining the evolution of eusociality (Wilson and Hölldobler

Table 2. Statistics of main topics in the myrmecological literature within the space of the last decades: N – number of articles per topic (in descending order), T-% – respective proportion (in %); % 00–09 to % 45–59 – distribution of articles (in %) within each topic over the time periods 2000–2009 to 1945–1959. Periods – for each topic, time periods with at least one publication (max. 6); EVEN – Smith and Wilson’s evenness index, H’ – Shannon-Wiener diversity index (log 2), NECP – H’ given as the number of time periods with equal number of articles [\* – search word in the “topic” field (instead of “title” field)].

Topic	N	T-%	%						Periods	EVEN	H’	NECP
			00–09	90–99	80–89	70–79	60–69	45–59				
Aphids/coccids	164	11.1	55	21	13	5	4	2	6	0.41	1.83	3.56
Social parasitism	147	10.0	41	22	17	14	4	1	6	0.32	2.08	4.24
Community structure	145	9.8	72	16	11	1	0	0	4	0.22	1.16	2.23
Invasive species	126	8.5	96	4	0	0	0	0	2	0.24	0.24	1.18
Competition	125	8.5	39	29	25	6	2	0	5	0.38	1.87	3.67
Recruitment	117	7.9	28	30	27	15	0	0	4	0.95	1.95	3.87
Kin selection*	110	7.5	72	28	0	0	0	0	2	0.86	0.86	1.81
Phylogenetics	86	5.8	66	23	6	5	0	0	4	0.45	1.33	2.51
Speciation	81	5.5	69	28	2	0	0	0	3	0.30	1.02	2.02
Communication	78	5.2	28	23	29	14	5	0	5	0.74	2.14	4.41
Taxonomy/systematics	71	4.8	37	25	15	15	7	0	5	0.81	2.14	4.39
Cuticular hydrocarbons	70	4.7	60	27	13	0	0	0	3	0.76	1.33	2.52
Genetic structure	46	3.1	61	28	9	2	0	0	4	0.36	1.38	2.60
Population structure	39	2.6	67	21	8	0	0	5	4	0.51	1.36	2.57
Maculinea	38	2.6	61	34	5	0	0	0	3	0.47	1.19	2.28
Biogeography	31	2.1	65	23	10	3	0	0	4	0.44	1.38	2.60

2005, Wilson 2008) is welcome, and hopefully will diversify approaches taken in studies of sociality.

### **Taxonomy, systematics and phylogenetics**

Taxonomy and systematics belong to the oldest fields of myrmecology, with a representative cover of time periods (for the post-war time, see Table 2). Whereas basic, alpha-taxonomic activity has, during the last half a century, been low in the New World, the ant taxonomy in the Palaearctic region has developed steadily through the decennia. The pace of group revisions at different taxonomic levels, and description of new species has steeply increased since the early 1980s, thanks to a number of dedicated taxonomists. Two of the most productive ant taxonomists have had an especially strong impetus on the field already through 30 years: Alexander Radchenko and Bernhard Seifert. Many of their and other myrmecologists' taxonomic articles are found in the database of <http://antbase.org/>. The newest large revision concerns the *Myrmica* species of the Old World (Radchenko and Elmes 2010).

Outside the domain of taxonomy, reliable taxonomy and good identification keys to the species level are mandatory in ecological work. At best, the information is published as high-quality regional books and monographs. In this respect, in Central and Northern Europe, Kutter's (1977) and Collingwood's (1979) treatments, respectively, were milestones in their time. The fast progress in ant taxonomy soon called for updated work, the first one of which was *Ameisen: beobachten, bestimmen* (Seifert 1996), followed by *The ants (Hymenoptera, Formicidae) of Poland* (Czechowski et al. 2002)—guides written for neighbouring Central-European countries, but serving well also more northern areas. The former book had soon its successor in *Die Ameisen Mittel- und Nordeuropas* (Seifert 2007) and, now, the latter is seeing its own successor. Even a comparison of the two newest books testifies to an ongoing development in ant taxonomy: even in the taxonomically best known geographical region, in only a few years, the statuses of many species have been re-evaluated, and still new species will most probably be described in the near future.

Clearly, traditional alpha-taxonomy has benefited from supplementing morphological taxonomy with results obtained by newer techniques. Here, species-specific cuticular hydrocarbon profiles (see above) are likely to be increasingly useful. The main complementing data, however, consist of DNA sequences and other molecular-level data, which may reveal sister or "cryptic" species expected on their notable habitat differences in spite of their high morphological similarity. As so often happens, however, new technology in the hands of "myrmecologists" that lack basic taxonomic, faunistic and ecological knowledge, may overemphasise the potential of the new method. In spite of early warnings, the new-millennium barcoding approach in delimiting species has not been rejected by laboratory-oriented people. As comes to ants, Jansen et al. (2009) showed that barcoding may be unable to differentiate morphologically and ecologically well-supported species.

On the other hand, barcoding may help in pinpointing groups that need closer taxonomic study, when the fauna is taxonomically poorly known, as the *Myrmica* of North America (Jansen et al. 2009).

Phylogenetics, the study of evolutionary relationships among organisms, usually among species and higher taxa (though in the field of phylogeography, often among populations within species), historically has its foundation firmly on morphology. The development of molecular methods, first enzyme electrophoresis and other electrophoresis techniques in the 1970s, later molecular phylogenetics—based, e.g. on DNA data from the mid 1990s onward—rendered possible analyses of large data sets, partially thanks to the rapid development of DNA sequencing, fast computers and powerful analytical algorithms.

In phylogenetics, the cladistic method to reconstruct phylogenetic trees has its roots in the early post-war years, and is also with DNA data still used as a “quick-and-dirty” or supplementary method. Cladistics has, however, gradually been superseded by explicit evolutionary models using optimality criteria that are especially suitable with DNA data—hence, the rapid development of molecular phylogenetics. First, maximum likelihood estimates were introduced to biology in the early 1970s and to ant phylogenetics in the mid 1990s. Bayesian inference, which uses very effectively available data to test the conformity of the phylogenetic hypotheses (alternative trees) with the data by starting with a prior probability over hypotheses to reach the posterior probability of a particular hypothesis, has been applied in ant phylogenetics since the early 2000s. Bayesian inference has, together with advanced computational machinery (especially Markov Monte Carlo algorithms) many applications in evolutionary biology; to ant phylogenetics, divergence-time estimates of evolutionary lineages were introduced in the few last years.

The new phylogenetic methods have, in the most recent years, revealed big evolutionary patterns. Almost simultaneously, Moreau et al. (2006) and Brady et al. (2006) published their large phylogenies to illuminate the (early) evolution and divergence of ants. In spite of many similarities, main differences (e.g. for divergence-time estimates, which use fossil data to calibrate the molecular clock) testify to practical difficulties, when morphological, fossil and molecular data render partially conflicting information. This is not always the case, and in many basic phylogenetic reconstructions qualitatively different data end to similar results.

Morphological and molecular data were used in two subsequent studies on the origin of army ants, and both produced the same, main result. Although the traditional view maintains that the army ants of each continent have originated on separate occasions, the new analyses show that army ants have a common origin (Brady 2003, Brady and Ward 2005). The evolution of one of the most fascinating achievements of social insects, the sophisticated agricultural systems in the fungus-growing ants *Attini*, a symbiotic interdependence that has been studied since the late 1800s (Belt 1874, Müller 1874) and later by N. A. Weber (starting in 1954), has likewise been revealed using the above multifaceted and powerful phylogenetic approaches (Schultz and Brady 2008).

## **Evolution of workerless social parasites and speciation**

Social parasitism is one of the first and most fascinating topics in myrmecology, and in the selected list of topics (Table 2) it is surpassed in numbers of articles only by studies on aphids and allied honeydew-producing homopterans. A fundamental issue about social parasites, how they are able to break the defence of the host colony and not be eliminated, is—in its details—still poorly known (see above). Another basic question is the origin of different kinds of social parasites. It has long been known that social-parasitic ants tend to be close relatives to their host species (Emery 1909), and this so-called Emery's rule has (though not without exception) survived even repeated tests by modern phylogenetic methods. Because parasitism in ants is widely spread over ant taxa, it follows that social parasitism has independently evolved many times in ants—this is true for both dulosis (slave-making) and inquilinism, obligate parasitism by (practically) workerless ants.

The evolution of social parasitism in ants is an old question, and for dulotic species alternative explanations were provided by Darwin (1859), Wasmann (1905), Buschinger (1970) and Wilson (1975). Suggested preadaptive characters for dulosis include predation, territorial competition and a polygynous-polydomous life style, including carrying of brood among nests. Which model explains the evolution of dulosis is still a bone of contention, and it is likely that its evolutionary pathway depends on the taxon studied, and that at least in some taxa more than one of the above-mentioned preadaptive behaviours may have worked in concert (for a recent review on slave-making, see D'Ettoire and Heinze 2001).

Likewise, alternative routes have been proposed for the evolution of inquilinism (Wilson 1971). One route would start with territorial aggression, and evolve through enslavement of workers of conspecifics and later of heterospecifics to inquilinism. Alternatively, colony multiplication by adoption of queens, polygyny and budding could have favoured “cheating” queens that produce mainly sexual offspring in a multi-queen nest (see below). A third potential route would proceed from plesiobiosis (close proximity of two or more nests) through xenobiosis (one species living in the nest of another species, keeping its brood separate from the host's brood) to inquilinism. Again, depending on the taxon, one or another route may have been used, though in most cases more studies are needed to solve which one (for a recent review of social parasitism in ants, see Buschinger 2009).

Studies on the evolutionary pathways of social parasitism are, in the near future, likely to obtain more insight through phylogenetic analyses. In this context, an intricate question that has been studied increasingly during the last 15 years is, whether the social parasite and its host are the closest (not only close) relatives to each other. For some of the few parasite-host pairs studied the answer has been negative, for others positive (see Vepsäläinen et al. 2009). The interest in testing the closeness of parasites to their host springs from the evident evolutionary connotation of such a relation. An increasing number of documented sister-species pairs of parasite and host would support hypotheses of speciation of the social parasite from its host in sympatry.

Sympatric speciation through intraspecific parasitism has repeatedly been suggested for inquiline ant species, starting with Wasmann (1909), Buschinger (1970) and Elmes (1978). The prevailing view maintains that polygyny, a derived feature known in about half of all ant species, predisposes ant societies to the evolution of inquilinism. Basically, polygyny may be understood as an ecological adaptation that in specific, often common situations gives a competitive edge by allowing rapid filling of originally competition-free sites by multiplication of nests (budding or fission). Because polygyny involves tolerance of more than one queen in a society, and often acceptance of new queens, some of the queens may, however, abstain from producing workers and instead produce sexual offspring. To succeed in such “cheating”, the sexual offspring must be exceptionally small, comparable to developing workers, not to be selected off by workers that eliminate large larvae determined to develop into gynes (for such “queen control” in *Myrmica*, see Elmes 1991). Thus, miniaturisation of the female would be one step in the evolution of inquilinism. Because in a polygynic population spreading locally by budding, dispersal and independent colony foundation is not needed, and small females can survive—the road to inquilinism is open. For a discussion on ecological and life-history features that may predispose species in the genus *Myrmica* to the evolution of inquilinism in sympatry, and on assigning species rank to an intraspecific inquiline that may be speciating from its host, see Vepsäläinen et al. (2009).

Hypotheses like the one above on the possible sympatric speciation of inquiline *Myrmica* species through intraspecific parasitism are not possible without extensive, detailed knowledge of the ants studied. Present students of various aspects of *Myrmica* species (and many other organisms dependent on these ants) are fortunate to draw from the long and precious series of studies initiated by M. V. Brian in the early 1950s through the 1980s, and continued by Graham Elmes and colleagues. The articles range from all conceivable aspects of ecology and physiology to various details of the social biology of *Myrmica*, including caste determination (larval ontogeny and queen control), production of sexuals, queen size dimorphism and colony structure (polygyny and polycaly). Instead of trying to produce a comprehensive list of the themes approached in the field and by laboratory experiments, I refer to a concise review by Elmes (1991); it should be read by anybody planning studies on *Myrmica*, as a starter to the rich literature on the genus.

A fascinating route to speciation in sympatry is through hybridisation. Although hybrid speciation is common in the plant kingdom, documented cases in animals are few. True, hybridisation in ants has been implied on morphological grounds in about 10% of the Central-European species (Seifert 1999), though fertility of the hybrid offspring may be poor or lost. Recently, morphological interpretation of hybridisation among wood ants (Czechowski and Radchenko 2006a) has been supported by molecular studies that also indicate fertility of the hybrid offspring (Korczyńska et al. 2010). Parallel morphological and molecular studies led Seifert



(2010) to formulate a plausible hypothesis of wood ant speciation through hybridisation. Here, crucial predisposing features include supercoloniality with numerous highly polygynous nests covering tens of hectares, and genotype selection in the hybrid population in local isolation. Consequently, Seifert (2010) suggested that the supercolonial *Formica paralugubris*, which shows morphological traits and nuclear marker patterns intermediate between *F. lugubris* and *F. aquilonia*, but carry an mtDNA close to the latter species, may have speciated within a huge supercolony during Pleistocene isolation via hybridisation and subsequent selection. Perhaps the taxonomic chaos will at last yield to order within the *Formica rufa* group, which was characterised by Vepsäläinen and Pisarski (1981) the *enfants terribles* among the wood ants—or at least become comprehensible.

## Ecology

Ecology is an old field of biological sciences, and very diverse in its topics. Thus in this short survey, I will unabashedly select only a few topics for closer scrutiny. Surprisingly, in myrmecology studies on community structure are relatively new—or rather, this field of myrmecology seems to have expanded at a fast rate. Although in the selected list of topics found in the title of the article (Table 2) it ranks as third counted in the number of articles, 72% of them have been published during the last decennium. For the topic competition (fifth in the number of total articles), the corresponding proportion is only 39%.

The overlap of search words in the title relating to community structure and competition is only ca. 1%, and still only 10%, when the search covers the article topic (i.e. words in the title and the abstract, and key words). Combining these two search terms pairwise with other search words, e.g. such referring to territoriality, neither renders any large overlap between search words. The result may be interpreted such that only relatively lately have community-level ecological studies combined aspects of patterns and processes—of course remembering the caveats due to the heterogeneous search efficiency through the decades. Indeed, even a short peek to the available literature will show that competition studies on ants have long served general competition theory with well-documented case studies.

In the early 1950s, M. V. Brian (1952) had already published a study on the competition among four typical species of the uplands of Britain. The study addressed many factors affecting the structure of ant assemblages (communities): competition for nest sites, distribution of nest sites in relation to microclimate, habitat selection by queens, and causes of replacement of species by another. Elaborating on his own later studies and those of other myrmecologists, Brian (1983) could conclude that “This cursory review of the ant communities in the temperate areas of the world shows that a general design exists based on an interspecies dominance hierarchy.”

The crucial role of interspecific dominance hierarchies in organising ant assemblages has been perceived by many myrmecologists from the 1950s onward. Among

pioneering works one may find, e.g. those of Kaczmarek (1953), Dlussky<sup>1</sup> (1965a), Zakharov (1972), Pisarski (1973) and Reznikova (1983). The comprehensive collection of papers in Pisarski (1982) covers all the main aspects of structure and organisation of ant societies of the mound-building species *Formica exsecta*. Local ant species assemblages moulded by competitive, mutualistic and other relations among species were called coadapted complexes by Dlussky (1981a), who studied ants in different types of deserts in Central Asia and Kazakhstan, and compared assemblages of these areas with those in deserts on the other continents. The monograph is an in-depth treatment of how coadapted complexes of desert ants are formed, but it also helps to understand structuring of other ant communities.

The results and ideas of the many pioneers on structuring of ant communities were formalised by Vepsäläinen and Pisarski (1982), who suggested that a simple three-tiered competitive hierarchy among ant species could serve as a theoretical framework, when studying processes that explain the observed assembly patterns. The concept should not be used without good knowledge of natural history and ecology of ants, because ant assemblages (coadapted complexes) are moulded by many additional factors to competition. Such factors include, e.g. dependence of a substantial proportion of local species on other ant species, either during colony founding or through all life, specifics of the local habitat (e.g. stress and disturbance, and availability of nest sites), and differing dispersal and colonisation potentials of the species. During the latest decades, the competition hierarchy concept has helped to understand, e.g. community assemblages of boreal ants and their structuring (Savolainen and Vepsäläinen 1988 and later, Punntila et al. 1991 and later).

Organisation of ant communities has been studied by Andersen (1995) on a geographical scale by applying the concept of functional groups, originally developed within plant ecology. Such grouping classifies ant species in relation to competition, environmental stress and disturbance. The approach, originally applied in Australia, seems to suit well large-scale comparison of ant communities, and was used later to compare patterns of organisation in North American and Australian ant communities (Andersen 1997).

Traditionally, urbanised areas have been left outside biological studies as "unnatural". Still in the 1970s to 1990s urban myrmecology mainly considered urban pest species. The largest urban ecological study so far was, however, conducted in Warsaw and surrounding rural areas already in the years 1974–1978. Diverse sampling methods covered a large proportion of the invertebrate taxa foraging or living in the soil, on the ground, and above ground in the bush and tree layers. The results on ants were published by Pisarski (1982), who showed that a combination of species classifications—zoogeographical, ecological and

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<sup>1</sup> In this book, we follow ISO 9:1995/GOST 2002 system in the transliteration of names originally in Cyrillic alphabets with one exception. That is, when an author (as e.g. G. M. Dlusskij) has established the romanised spelling of his name in the literature, we use that commonly known spelling (see also the footnote to References).

trophic—describes satisfyingly the attributes of urban ant species—a result reached for most of the other taxa studied within the same big project. Thus, in the studied urban areas, successful ants tended to have a wide food spectrum, and to have large geographic ranges and broad habitat amplitudes. Vepsäläinen et al. (2008) used the same approach in an urban area in Finland, and reached similar general results as Pisarski in Poland. To successfully predict the species composition and community structure of urban ants, one has to know many critical, species-specific attributes of all the regional, rural species. One needs to know to which faunal (zoogeographical) element each species belongs, what its ecological limiting conditions are in relation to the habitats available in the study area, its food spectrum, dispersal and colonisation capacities, competitive relations to other species (position in the competition hierarchy), and possible dependence on other ant species. Naturally, this is basically the same set of information one has to know to predict and comprehend, e.g. the composition of island ant faunas in the archipelago of the Baltic Sea (Vepsäläinen and Pisarski 1982).

Even a short and strongly subjective review of some major trends in myrmecology during the last half a decade can be summarised, again, in a most subjective way. It is a delight to note how naturalists, taxonomists, population geneticists, phylogeneticists, molecular biologists, behavioural biologists, chemical ecologists and community ecologists—especially during the present millennium—have been and are cooperating and contributing with an increasing pace and success to integrate myrmecology to the general field of evolutionary biology.

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