

The Phylogeny and Classification of the Pseudoscorpionida (Chelicerata : Arachnida)

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Abstract

A new pseudoscorpion classification is proposed with two new suborders, Epiocheirata and Iocheirata, based upon a cladistic analysis of relationships within the order. The Epiocheirata contains two superfamilies: Chthonioidea for Chthoniidae, Tridenchthoniidae and Lechtyiidae, stat. nov. (for *Lechytia*), and Feaelloidea for Feaelloidea and Pseudogarypidae. The Iocheirata is divided into two infraorders: Hemictenata Balzan and Panctenata Balzan. The Hemictenata contains a single superfamily, Neobisioidea for Bochicidae, Gymnobisidae, Hyidae, Ideoroncidae, Neobisidae, Parahyidae, fam. nov. (for *Parahya*) and Syarinidae. The Panctenata contains two microorders: Mestommatina, nov. with Garypoidea for Cheiridiidae, Garypidae, Geogarypidae, Larcidae, fam. nov. (for *Archeolarca* and *Larca*) and Pseudochiridiidae, and Olpioidea for Menthidae and Olpiidae; and Ellassommatina, nov. with Sternophoroidea, stat. nov. for Sternophoridae, and Cheliferoidea for Atemnidae, Cheliferidae, Chernetidae and Withiidae. The Vachoniidae is synonymised with the Bochicidae, and the Cheiridioidea is treated as a synonym of Garypoidea. *Philomaoria* Chamberlin and *Philomaoriini* are transferred from the Withiidae to the Cheliferidae. The chthoniid tribe Pseudotyranochthoniini is elevated to subfamily rank, and the systematic position of the Devonian family Dracochelidae is discussed.

Introduction

Few hypotheses concerning pseudoscorpion inter-relationships have been presented in the literature. Simon (1879) placed all known pseudoscorpions into a single family, Cheliferidae, which he divided into three subfamilies, Garypinae, Obisiinae and Cheliferinae. Thorell (1883) divided the order into two suborders, Haplochelonethi for 'Gibbocelloidae' and Diplochelonethi for 'Cheliferoidae'. Hansen and Sørensen (1904) showed that *Gibocellum* Stecker was a fanciful animal, which has since been ignored in the scientific literature. Balzan (1892) proposed two suborders, Panctenodactyli and Hemictenodactyli (as 'Emictenodactyli'), based primarily upon the morphology of the chelicerae, which were accepted and clarified by Hansen (1893) and With (1906).

However, the most lasting classification has been that of Chamberlin (1929, 1930, 1931*a*), in which this distinctive arachnid order was divided into two 'groups' and three suborders: group and suborder Heterosphyronida; and group Homosphyronida, which was subdivided into the suborders Diplosphyronida and Monosphyronida. Chamberlin's subdivisions were primarily based upon the fusion, or lack of fusion, of the pedal tarsi and metatarsi, which resulted in some taxa without apomorphies (Harvey 1988*a*). Beier (1932*a*, 1932*b*) adopted the main components of Chamberlin's classification, but did not recognise the groups Heterosphyronida and Homosphyronida. He proposed three suborders, which he named Chthoninea, Neobisiinea and Cheliferinea. Muchmore (1982*a*) abandoned Chamberlin's subordinal classification, preferring to recognise six superfamilies.

This paper is an attempt to bring together our knowledge of pseudoscorpion relationships above the family level, and to present an hypothesis concerning relationships based upon derived character states. This hypothesis is reflected in a classification which is somewhat different to all previously proposed classifications, in which 24 families are recognised.

Materials and Methods

Many different pseudoscorpion species have been examined as part of this study; many of these are lodged in the Western Australian Museum collections. Some figures have been taken from other sources. Illustrations of right chelae were reversed so that all such figures are from a standard left view.

Specimens were examined using the following techniques: by partial clearing in 50–75% lactic acid or 10% potassium hydroxide and temporarily mounting them on slides in glycerol; by fully dissecting, clearing and mounting them on microscope slides in Euparal; or by cleaning them by sonication and dehydrating them in successive changes of alcohol before air-drying, gold-coating and scanning in a JEOL JSM-35C Scanning Microscope.

Partial synonymies are presented for each superfamily and family; full synonymies are provided by Harvey (1991*a*).

Order PSEUDOSCORPIONIDA de Geer

Diagnosis

Endocephalic spinning apparatus present which discharges through movable cheliceral finger (A*). Pedipalpal tibia and tarsus modified into chela (A). Movable cheliceral finger with 1 submedial or subdistal seta (rarely increased to 3 or 4) (A). Medial eyes absent (A). Cheliceral flagellum present (shared with Solifugida), and composed of several blades (A). Eggs laid into brood sac attached to female genital operculum (A).

Remarks

The classification of this arachnid order, promoted by Chamberlin (1931*a*), was principally based upon the presence or absence of fusion of the pedal tarsi and metatarsi, which has led to considerable difficulties (Muchmore 1982*a*; Harvey 1988*a*). Outgroup comparison with other chelicerates (Shultz 1989, 1990) reveals that the presence of a metatarsus and tarsus is plesiomorphic for the group. As defined by Chamberlin (1931*a*), the Diplosphyronida

*Each component of the diagnoses is labelled (P) denoting a plesiomorphy or (A) denoting an apomorphy.

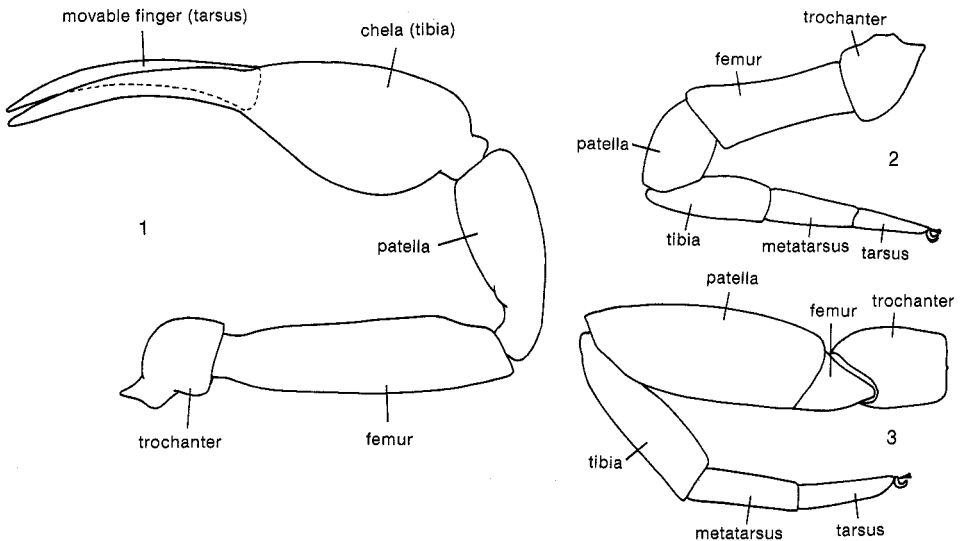
is not based upon an apomorphic character state and is not a monophyletic taxon. Subsequent tarsal and metatarsal fusions have occurred in many groups, principally in Chamberlin's Monosphyronida. Similarly, the Homosphyronida is simply based upon the lack of modification in the metatarsi and tarsi evident in his Heterosphyronida.

The chequered history of the Feaelloidea highlights the dangers of solely relying upon leg structure in reconstructing pseudoscorpion phylogenies. It was placed in the Monosphyronida by Chamberlin (1931*a*) on the basis of the fused metatarsi and tarsi, and in the Diplosphyronida by Beier (1932*a*) on the basis of the presence of four eyes (and a superficial resemblance to a garypid genus). Harvey (1986, 1988*a*) outlined several synapomorphies that united the Feaelloidea as the sister-group of the Chthonioidea; the latter possesses fused metatarsi and tarsi of the anterior legs only, which Chamberlin (1931*a*) had placed in its own taxon, Heterosphyronida.

In the following treatment, Chamberlin's higher taxa (Heterosphyronida, Homosphyronida, Diplosphyronida and Monosphyronida) are replaced with new subordinal names to fully reflect the change from Chamberlin's emphasis on leg character states. One of these suborders is further divided into the infraorders Hemictenata and Panctenata, which are based upon Balzan's (1892) 'tribes', Emictenodactyli [*sic*] and Panctenodactyli. Balzan's names are here abbreviated to make them more euphonious. Table 1 summarises the taxonomic position of each family since 1931.

Terminology of Pedipalpal and Leg Segments

In contrast to all previous nomenclatural systems devised to identify leg segments of pseudoscorpion [most notably, Chamberlin (1930)], Shultz (1989, 1990) has shown that the telofemur is actually a patella. Thus, the legs of a diplosphyronid pseudoscorpion (Figs 2, 3) consist of: coxa, trochanter, femur, patella, tibia, metatarsus (or basitarsus) and tarsus (or telotarsus). Similarly, as shown by Snodgrass (1948), a pseudoscorpion pedipalp consists of: coxa, trochanter, femur, patella, chela (modified tibia) and movable finger (modified tarsus) (Fig. 1). Despite the inconvenience of adopting new names for some segments, all pseudoscorpion workers are urged to follow these systems to allow for more direct comparisons with other Chelicerata.



Figs 1-3. Terminology of pedipalpal and leg segments: 1, pedipalp; 2, leg I; 3, leg IV.

Table 1. Summary of subordinal and infraordinal positions of pseudoscorpion families

	Names in italics not recognised in present study		
	Chamberlin 1931 <i>a</i>	Beier 1932 <i>a,b</i>	This study
Chthoniidae	Heterosphyronida	Chthoniinea	Epiocheirata
Tridenchthoniidae ^A	Heterosphyronida	Chthoniinea	Epiocheirata
Lechytiidae ^B	—	—	Epiocheirata
Feaellidae	Monosphyronida	Neobisiinea	Epiocheirata
Pseudogarypidae	Monosphyronida	Neobisiinea	Epiocheirata
Ideoroncidae	Diplosphyronida	Neobisiinea	Iocheirata: Hemictenata
Bochicidae ^C	—	—	Iocheirata: Hemictenata
<i>Vachoniidae</i> ^D	—	—	—
Hyidae ^E	Diplosphyronida	—	Iocheirata: Hemictenata
Gymnobisiidae ^F	—	—	Iocheirata: Hemictenata
Neobisiidae	Diplosphyronida	Neobisiinea	Iocheirata: Hemictenata
Syarinidae	Diplosphyronida	Neobisiinea	Iocheirata: Hemictenata
Parahyidae ^G	—	—	Iocheirata: Hemictenata
Garypidae	Diplosphyronida	Neobisiinea	Iocheirata: Panctenata: Mestommatina
<i>Synsphyronidae</i> ^H	—	Neobisiinea	—
Larcidae ^I	—	—	Iocheirata: Panctenata: Mestommatina
Cheiridiidae	Monosphyronida	Cheliferinea	Iocheirata: Panctenata: Mestommatina
Pseudochiridiidae ^J	Monosphyronida	—	Iocheirata: Panctenata: Mestommatina
Geogarypidae ^K	—	—	Iocheirata: Panctenata: Mestommatina
Olpiidae	Diplosphyronida	Neobisiinea	Iocheirata: Panctenata: Mestommatina
Menthidae	Diplosphyronida	Neobisiinea	Iocheirata: Panctenata: Mestommatina
Sternophoridae	Monosphyronida	Cheliferinea	Iocheirata: Panctenata: Ellassommatina
Withiidae ^L	—	—	Iocheirata: Panctenata: Ellassommatina
Cheliferidae	Monosphyronida	Cheliferinea	Iocheirata: Panctenata: Ellassommatina
Atemnidae	Monosphyronida	Cheliferinea	Iocheirata: Panctenata: Ellassommatina
<i>Miratemnidae</i> ^M	—	—	—
Chernetidae	Monosphyronida	Cheliferinea	Iocheirata: Panctenata: Ellassommatina
<i>Myrmochernetidae</i> ^N	Monosphyronida	Cheliferinea	—

^A Named Dithidae by Chamberlin (1931*a*); regarded as subfamily of Chthoniidae by Beier (1932*a*).

^B Previously regarded as tribe of Chthoniidae.

^C Regarded as subfamily of Ideoroncidae by Chamberlin (1931*a*) and Beier (1932*a*); elevated to family status by Muchmore (1982*a*).

^D Described as new by Chamberlin (1947); synonymised with Bochicidae (this study).

^E Regarded as subfamily of Ideoroncidae by Beier (1932*a*).

^F Described as new by Beier (1947).

^G Described as new in this paper.

^H Described by Beier (1932*a*) in Fealloidea; synonymised with Garypidae by Chamberlin (1943).

^I Described as new in this paper.

^J Regarded as subfamily of Cheiridiidae by Beier (1932*b*).

^K Regarded as subfamily of Garypidae by Chamberlin (1931*a*) and Beier (1932*a*); elevated to family level by Harvey (1986).

^L Regarded as subfamily of Cheliferidae by Chamberlin (1931*a*) and Beier (1932*a*); elevated to family status by Weygoldt (1970).

^M Elevated to family status by Dumitresco and Orghidan (1970); synonymised with Atemnidae by Harvey (1991*a*).

^N Regarded as junior synonym of Chernetidae by Judson (1985).

What is a Family?

Some authors may object to the number of new families that I have recognised in this revision, particularly as they consist of one or two genera, and one even consists of only a single species. The main criterion I have adopted for the recognition of families (and all other categories) is monophyly. If a taxon cannot be defined by at least one apomorphic character state, then I have attempted to determine an alternative classification which more fully reflects our current knowledge of its affinities. Some of my decisions pose particular

problems. As the Larcidae and Garypidae represent sister-taxa, a feasible solution would be the recognition of a single family, Garypidae, with two subfamilies. My decision was based upon an *a posteriori* judgement that the Larcidae are 'sufficiently different' from the Garypidae to warrant familial status.

The level at which we assign categories to particular points of the cladogram is, in many respects, meaningless, especially when we consider different groups of organisms. How can we reconcile the 200-million-year geological history of the Mammalia, which are conferred the status of Class and divided into 20 or more orders (Honacki *et al.* 1982), with the 400-million-year-old Pseudoscorpionida, which are placed within a single Order? Hennig (1966) argued that once a more complete fossil history is obtained we can arbitrarily assign uniform taxonomic categories to those groups that diverged at a particular time (e.g. Miocene = genus). This information will never become available for most animal groups, including pseudoscorpions, and has doubtful validity given the differing rates of change in different lineages. Hennig further suggested vicariant and parasitological procedures in elucidating absolute age of lineages, but insufficient knowledge of pseudoscorpion vicariance patterns will probably negate this technique. Molecular methods (e.g. biological clocks) may be of some value in this debate, yet the problem seems to be one without an answer.

The Principle of Priority

The strict application of Article 23(d) of the International Code of Zoological Nomenclature (International Commission on Zoological Nomenclature 1985) would require the alteration of three familial and two superfamilial names:

- Microcreagrinae Balzan, 1892 for Neobisiidae Chamberlin, 1930;
- Ideobisiini Banks, 1895 for Syarinidae Chamberlin 1930;
- Garypininae Daday, 1888 for Olpiidae Chamberlin, 1930;
- Microcreagroidea Balzan, 1892 for Neobisioidea Chamberlin, 1930; and
- Garypinoidea Daday, 1888 for Olpioidea Chamberlin, 1930.

I have refrained from adopting these changes as they serve no useful purpose, especially in groups that are very well established and that contain large numbers of species: Neobisiidae and Olpiidae (Harvey 1991a). The maintenance of stability is an explicitly stated function of the Principle of Priority [International Code of Zoological Nomenclature, Article 23(b)], and the Commission has indicated that a register of family-group names may be developed which would preserve long-standing names over little-used senior synonyms (International Commission on Zoological Nomenclature 1990).

Post-embryonic Development

Our knowledge of the nature of post-embryonic trichobothrial development in pseudoscorpions has increased greatly over recent years, and was reviewed by Helversen (1966) and Mahnert (1981). Most authors have determined trichobothrial homologies between taxa on the basis of the relative positions of the trichobothria in adults, which has led to incorrect identifications in some taxa. Harvey (1990) showed that *ist* and *isb* had reversed their positions in several taxa (e.g. *Larca*, *Syarinus*), and provided a sequence of trichobothrial movements to interpret the change. That sequence (Harvey 1990, fig. 6) needs modification as the basal migration of *ist* in Garypidae shown by Harvey (1990, fig. 6d) is in fact plesiomorphic (see below). Geogarypids differ from most other pseudoscorpions in the distal migration of *ist*, which still explains the altered positions of *ist* and *isb*.

The detection of trichobothrial migration poses considerable problems in the nomenclature of individual trichobothria. Should we continue with Chamberlin's (1924a) system, which simply labels trichobothria on the basis of relative positions in the adults? Or should we label homologous trichobothria on the basis of detailed knowledge of post-embryonic development? I advocate the latter, as it has greater predictive and analytical powers in discussing phylogenetic pathways.

Rather than identify trichobothria on the basis of the adult configuration, and then apply them to the nymphal stages, I have summarised our knowledge of post-embryonic development in Table 2 which provides details of the first emergence of individual trichobothria on each series (fixed finger, external; fixed finger, internal; movable finger). This shows that some trichobothria emerge in a constant position in virtually all pseudoscorpions.

Table 2. Summary of known post-embryonic development indicating first appearance of trichobothria

1, protonymph; 2, deutonymph; 3, tritonymph; A, adult

	Fixed, external distal—basal	Fixed, internal distal—basal	Movable distal—basal
Chthoniidae	1 2 3 1	2 1 A 2	1 2 A 3
Tridenchthoniidae	1 2 3 1	2 1 A 2	1 2 A 3
Lechytidae	1 2 3 1	2 1 A 2	1 2 A 3
Feallidae	1 2 3	2 1 1 A 2	2 1 A 3
Pseudogarypidae	1 2 3 1	2 1 A 2	1 3 A 2
Ideoroncidae	1 2 A 3 1	2 1 2	1 3 A 2
Bochicidae	1 2 A 3 1	2 1 2	1 3 A 2
Hyidae	1 2 A 3 1	2 1 2	1 3 A 2
Gymnobisiidae	1 2 A 3 1	2 1 2	1 3 A 2
Neobisiidae	1 2 A 3 1	2 1 2	1 3 A 2
Syarinidae	1 2 A 3 1	2 1 2	1 3 A 2
Parahyidae	1 2 A 3 1	2 1 2	1 3 A 2
Garypidae	1 2 A 3 1	2 1 2	1 3 A 2
Larcidae	1 2 3 1	2 A 1 2	1 3 A 2
Cheiridiidae	1 2 3 1	2 A 1 2	1 3 A 2
Pseudochiridiidae	1 2 3 1	2 A 1 2	1 3 A 2
Geogarypidae	1 2 3 1	2 1 A 2	1 3 A 2
Olpiidae	1 2 A 3 1	2 1 2	1 3 A 2
Menthidae	1 2 A 3 1	2 1 2	1 3 A 2
Sternophoridae	1 2 3 1	2 1 2	1 A 2
Withiidae	1 2 3 1	2 A 1 2	1 3 A 2
Cheliferidae	1 2 3 1	2 A 1 2	1 3 A 2
Atemnidae	1 2 3 1	2 A 1 2	1 3 A 2
Chernetidae	1 2 3 1	2 A 1 2	1 3 A 2

Table 3. Trichobothrial nomenclature and post-embryonic development

	Fixed finger		Movable finger
	External	Internal	
Protonymph	<i>eb et</i>	<i>ist</i>	<i>t</i>
Deutonymph	<i>est</i>	<i>ib it</i>	<i>b</i>
Tritonymph	<i>esb</i>		<i>st</i>
Adult		<i>isb</i>	<i>sb</i>

The trichobothrial nomenclatural system adopted here (Table 3) is modified from Chamberlin (1924a) and takes into account our knowledge of post-embryonic development. That of the fixed finger is fairly straight-forward. The movable finger sequence is here based upon the plesiomorphic condition found in Pseudogarypidae and Icochirata (Character 28).

The hypothesis adopted in this paper assumes that trichobothria have actively shifted their positions on the chelal fingers and hand. The labile nature of trichobothrial location is best exemplified in Chthonioidea, where *ib* and *isb* have moved to the sub-basal region of the hand (Fig. 4). The only other hypothesis that can explain the relative positions in adults assumes that trichobothria emerge at different times during development. Although it is more parsimonious to assume that the trichobothria shift their positions, the alternative hypothesis does not radically alter the arguments presented. As mentioned by Harvey (1990), detailed studies on bothrial or nerve sheath structure may provide valuable information on trichobothrial homologies.

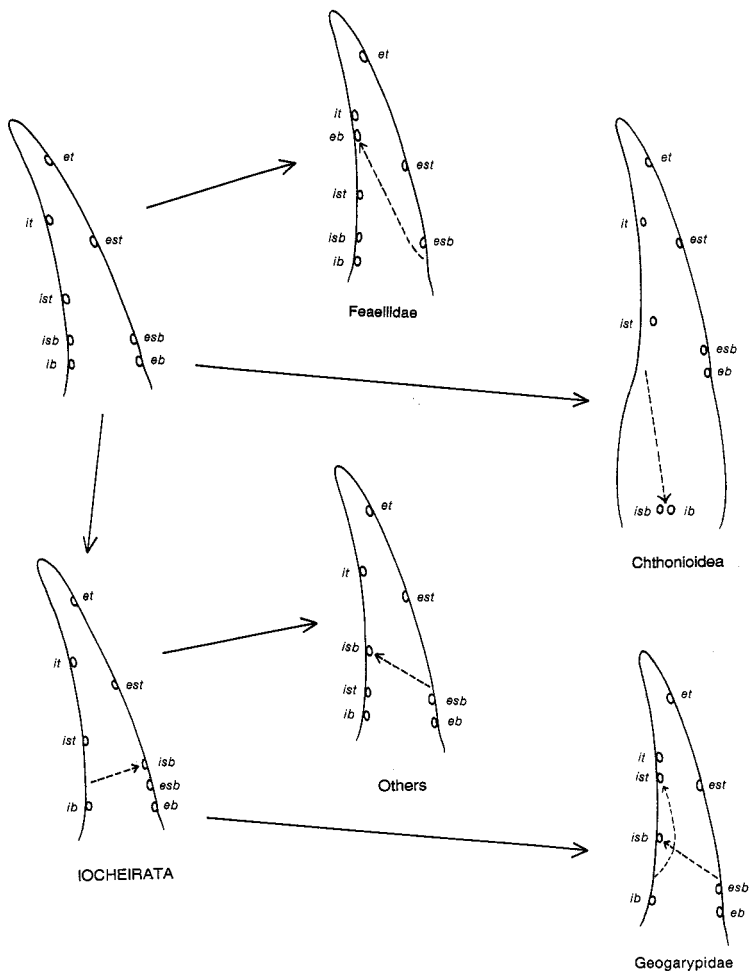


Fig. 4. Fixed chelal finger showing hypothesised movements of trichobothria. See text for explanation.

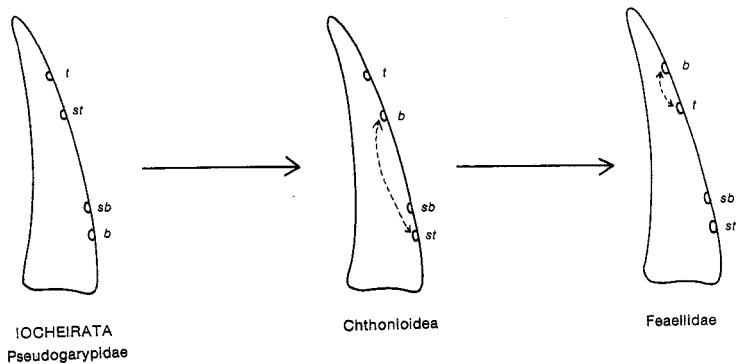


Fig. 5. Movable chelal finger showing hypothesised movements of trichobothria. See text for explanation.

Cladistic Analysis

The phylogenetic analysis presented here was based upon 126 characters and 24 familial taxa, and was conducted with the aid of HENNIG86 (Farris 1988) using the implicit enumeration command (ie). Of the 126 characters, 54 were autapomorphic for individual families and were excluded from the computational analysis; these are represented by 'A' in Table 4. Missing entries ('?' in Table 4) or inapplicable data ('-' in Table 4) were treated as '?' for the analysis, despite the shortcomings of such an approach (Platnick *et al.* 1991).

The main outgroup for the order was the Solifugida, which has been suggested by several workers as the sister-group of the Pseudoscorpionida (e.g. Hammen 1977; Weygoldt and Paulus 1979; Shultz 1989, 1990). Shultz (1990) presented six unique and three convergent synapomorphies that unite these two orders, including:

- chelicerae scissor-like,
- cheliceró-carapacial articulation present,
- rostrum present,
- arolium (empodium) present,
- lateral eyes aggregate, with four facets,
- stigmata present on sternites III and IV,
- coxal endites absent (also in several other orders),
- post genital appendages absent (also in several other orders), and
- tracheal system present (also in several other orders).

As would be expected from a group that is at least 400 million years old (Schawaller *et al.* 1991), there is a large amount of homoplasy in the Pseudoscorpionida data set which has resulted in HENNIG86 producing several trees of similar length. The initial unweighted computation produced four trees of 123 steps (with a consistency index of 0.60 and a retention index of 0.82), which placed the Fealloidea within the Garypoidea as the sister-group to Cheiridiidae + Pseudochiridiidae. These cladograms were rejected because I perceive the apparent similarity between Fealloidea and Garypoidea to be the result of homoplasy.

The second computation included a weighting of 2 for Character 21 (the presence of *xs* in Epiocheirata), which retained the original four cladograms in addition to a further four cladograms which placed the Fealloidea as the sister-group to the Chthonioidea. These trees were of 125 steps, with a consistency index of 0.60 and a retention index of 0.82.

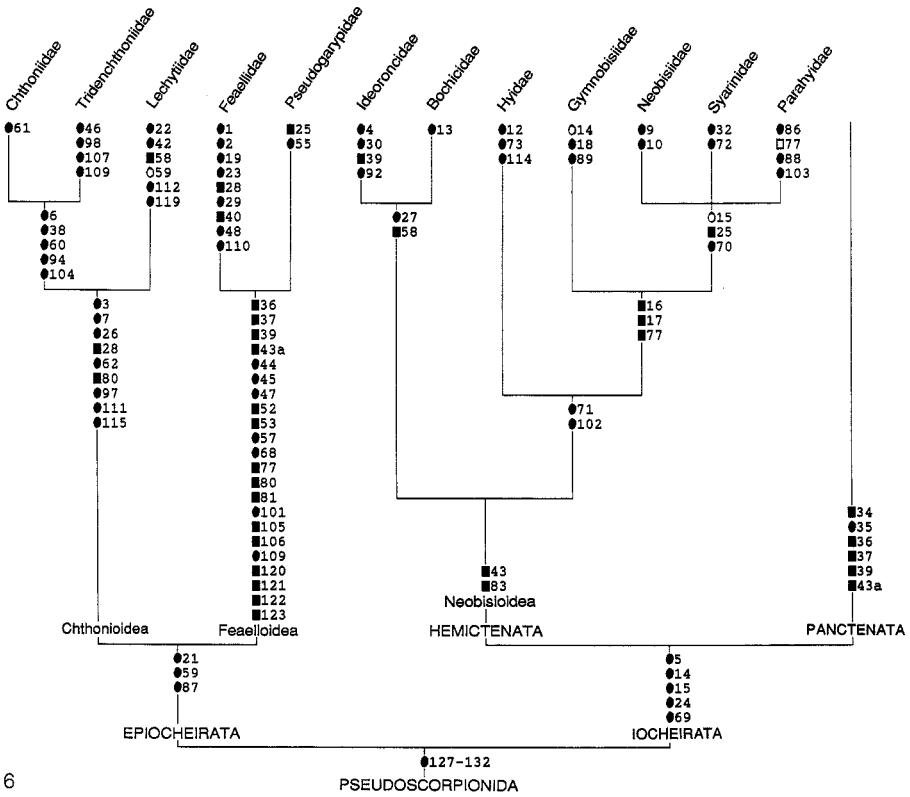
The third computation assigned a weighting of 3 to Character 21 and resulted in four trees with a length of 126 steps, a consistency index of 0.60 and a retention index of 0.82. The preferred cladogram (Figs 6, 7) was selected to best represent the data; all other cladograms differed only by the resolution of two clades, Neobisiidae + Syarinidae + Parahyidae, and Cheliferidae + Chernetidae + Atemnidae, in which the families were variously combined. I prefer to recognise bushes for these two groups, as I could detect no unequivocal apomorphies that unite more than one family with another.

The four trees derived from this computation were further analysed using the 'Nelson' command of HENNIG86 (Farris 1988). The resulting Nelson consensus tree was identical to that selected from the third computation (Figs 6, 7), with identical length, consistency index and retention index.

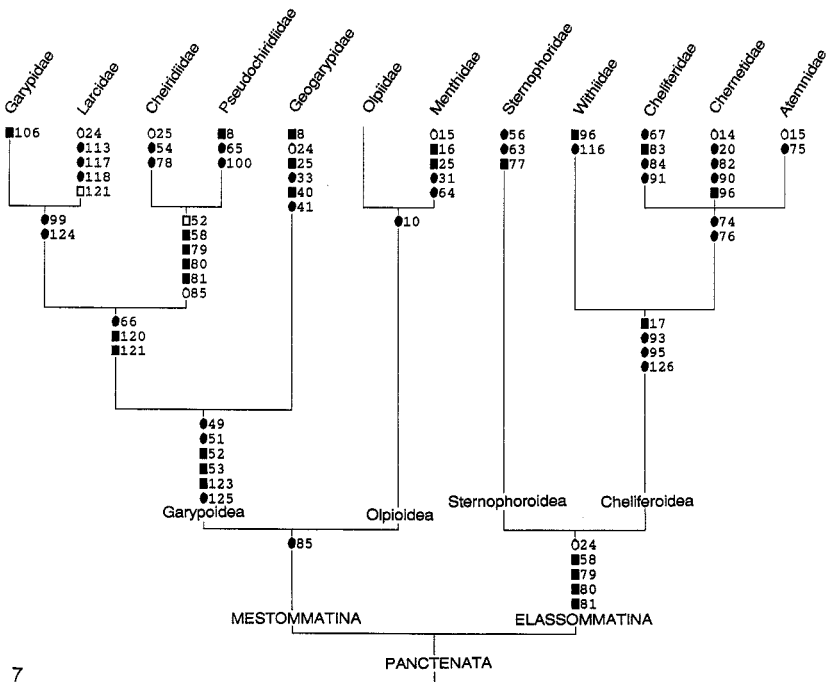
The consistency indices computed for the final computation by HENNIG86 for each character are presented in Table 4. The column labelled 'Condition' indicates whether the character states are autapomorphic for an individual family (A), synapomorphic for one or more families and not found in any family outside of its clade (S), homoplastic (H), or have undergone a reversal (R).

Pedipalps

1. The raptorial pedipalps of Feallidae (Fig. 41) are unique within the order and clearly apomorphic.
2. The median maxillary lyrifissure is only absent in Feallidae. Although this structure is absent in solifugids (Hansen 1893), it seems reasonable to assume that the loss in feallids is apomorphic.



6



Figs 6, 7. Cladograms depicting suggested relationships between families of Pseudoscorpionida. See Table 4 and text for discussion. Autapomorphy (●); reversal (○); homoplasy (■); reversal (□).

Table 4. Character matrix

0, plesiomorphy; 1, 2, apomorphy; ?, not known; -, not relevant; A, autapomorphic for single family; S, synapomorphic; H, homoplasy; R, reversal

	Chthoniidae	Tridenchthoniidae	Lechytiidae	Faeellidae	Pseudogarypidae	Ideonocidae	Bochicidae	Hyidae	Gymnobisiidae	Ncobisiidae	Syariniidae	Parahyidae	Garypidae	Larcidae	Cheiridiidae	Pseudochiridiidae	Geogarypidae	Olniidae	Mentidae	Sternophoridae	Withidae	Cheliferidae	Chernetidae	Atemnidae	Condition	Consistency Index	
PEDIPALPS																											
1. Pedipalps:																											
normal; raptorial	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	A	1.00
2. Median maxillary																											
lyrifissure:																											
present; absent	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	A	1.00
3. Median maxillary																											
lyrifissure: circular/ U-shaped; straight	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	S	1.00	
4. Median maxillary																											
lyrifissure: submedial or subdistal; subbasal	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	A	1.00	
5. Posterior maxillary																											
lyrifissure:																											
absent; present	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	S	1.00	
6. Intermaxillary jugum:																											
short, thick; long, slender	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	S	1.00	
7. Pharyngeal pump,																											
dorsal keel:																											
normal; enlarged	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	S	1.00	
8. Coxal shoulder:																											
absent; present	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	H	0.50	
9. Coxal apex, setae:																											
2; 3+	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	A	1.00	
10. Coxal apex:																											
triangular; rounded	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	A	1.00	
11. Femur, trichobothria:																											
absent; present	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	S	1.00	
12. Femur, 3 (or 2) stout																											
setae: absent; present	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	A	1.00	
13. Femur, sub-basal																											
tubercle:																											
absent; present	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	A	1.00	
14. Venom apparatus, fixed																											
finger: absent; present	0	0	0	0	0	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	SR	0.33	
15. Venom apparatus,																											
movable finger:																											
absent; present	0	0	0	0	0	1	1	1	1	0	0	0	1	1	1	1	1	1	0	1	1	1	1	0	SR	0.25	
16. Venom duct(s):																											
medium length; short	-	-	-	-	-	0	0	0	1	1	1	1	0	0	0	0	0	1	0	0	0	0	0	0	H	0.50	
17. Nodus ramosus:																											
normal; inflated	-	-	-	-	-	0	0	0	1	1	1	1	0	0	0	0	0	0	0	1	1	1	1	1	H	0.50	
18. Movable chelal finger:																											
seta absent; seta present	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	A	1.00	
19. Inwardly directed teeth:																											
absent; present	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	A	1.00	
20. Accessory chelal teeth:																											
absent; present	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	A	1.00	

Table 4 (continued)

	Chthomidae	Tridichthomiidae	Lechytidae	Faeclidae	Pseudogarypidae	Ideoroncidae	Bochidae	Hyidae	Gymnobisidae	Neobisidae	Syarimidae	Parahyidae	Garypidae	Larcidae	Cheiridiidae	Pseudochiridiidae	Geogarypidae	Olipidae	Mentidae	Sternophoridae	Withidae	Cheliferidae	Chernetidae	Atennidae	Condition	Consistency Index
CHELICERAE (continued)																										
43. Serrula exterior: free; partially fused; fused	0	0	0	2	2	1	1	1	1	1	1	1	2	2	2	2	2	2	2	2	2	2	2	2	S	0.50
44. Cheliceral hand: smooth; sculptured	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	S	1.00
45. Fixed finger teeth: several; none	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	S	1.00
46. Galea: 0-1; several	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	A	1.00
CARAPACE																										
47. Anterior lobes: absent; present	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	S	1.00
48. Median anterior lobes: 1; 2-4	-	-	-	1	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	A	1.00
49. Anterior margin: straight or convex; sinuate	0	0	0	-	-	0	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	S	1.00
50. Anterior margin: straight; serrate	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	S	1.00
51. Carapace shape: rectangular; triangular	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	S	1.00
52. Ocular tubercle: absent; present	0	0	0	1	1	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	H	0.33
53. Eye position: nr anterior margin; removed	0	0	0	1	1	0	0	0	0	0	0	1	1	1	1	1	0	0	-	0	0	0	0	0	H	0.50
54. Metazone: not depressed; depressed	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	A	1.00
55. Carapacial alae: absent; present	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	A	1.00
56. Carapacial posterior margin: straight; V-shaped	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	A	1.00
57. Carapace/abdomen articulation: absent; present	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	A	1.00
58. Eyes, maximum number: 4; 2; 0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	1	1	0	0	0	2	1	1	1	H	0.40
LEGS																										
59. Coxal spines: absent; present	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	SR	0.50
60. Intercoxal tubercle: absent; present	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	S	1.00
61. Intercoxal tubercle: monosetose; bisetose	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	A	1.00
62. Coxa I protuberance: absent; present	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	S	1.00
63. Pseudosternum: absent; present	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	A	1.00

Table 4 (continued)

	Chthoniidae	Tridenchthoniidae	Lechytidae	Feallidae	Pseudogarypidae	Idcoronciidae	Bochicidae	Hyidae	Gymnobisiidae	Neobisiidae	Syarinidae	Parahyidae	Garypidae	Larcidae	Cherididae	Pseudochirrididae	Geogarypidae	Olpidae	Menthidae	Sternophoridae	Withidae	Cheliferidae	Chernetidae	Atemnidae	Condition	Consistency Index	
LEGS (continued)																											
64. Coxal articulation: absent; present	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	A	1.00	
65. Coxa IV posteriorly expanded: absent; present	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	A	1.00		
66. Coxal width: I=IV; I<IV	0	0	0	1	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	H	0.50			
67. Coxal sac, ♂: absent; present	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	A	1.00			
68. Femur I and II, slit sensillum: present; absent	0	0	0	1	1	0	?	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	S	1.00			
69. Femur I and II, slit sensillum: sub-basal; subdistal	0	0	0	-	-	1	?	1	?	1	1	1	1	1	1	1	1	1	1	1	1	1	S	1.00			
70. Femur I and II, slit sensillum: perpen- dicular; longitudinal	0	0	0	-	-	0	?	0	?	1	1	1	0	0	0	0	0	0	0	0	0	0	S	1.00			
71. Femur I and II, slit sensilla, group of 3: absent; present	0	0	0	-	-	0	?	1	?	0	1	1	0	0	0	0	0	0	0	0	0	0	S	0.50			
72. Femur I and II, slit sensilla, group of 3: sub-basal; subdistal	0	0	0	-	-	0	?	0	?	0	1	0	0	0	0	0	0	0	0	0	0	0	A	1.00			
73. Femur I and II, slit sensilla mound: absent; present	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	A	1.00			
74. Femur I and II, slit sensilla: straight; semi-circular	0	0	0	-	-	0	?	0	?	0	0	0	0	0	0	0	0	0	0	0	1	1	S	1.00			
75. Femur I and II, slit sensilla: otherwise; circular	0	0	0	-	-	0	?	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	A	1.00			
76. Femur/patella I and II: perpendicular; oblique	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	S	1.00			
77. Femur/patella IV: oblique; perpendicular	0	0	0	1	1	0	0	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	HR	0.25			
78. Femora/patellae: separate; fused	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	A	1.00			
79. Femora/patellae I and II: femur long; patella long	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	1	1	1	1	S	0.50			
80. Metatarsi/tarsi I and II: separate; fused	1	1	1	1	1	0	0	0	0	0	0	0	1	1	0	0	0	1	1	1	1	1	H	0.33			
81. Metatarsi/tarsi III and IV: separate; fused	0	0	0	1	1	0	0	0	0	0	0	0	1	1	0	0	0	1	1	1	1	1	H	0.33			
82. Tarsi, raised slit sensillum: not raised; raised	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	A	1.00			
83. Subterminal tarsal seta: acuminate; dentate	0	0	0	0	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	1	0	0	H	0.50			

Table 4 (continued)

	Chthonidae	Tridionthoniidae	Lechytidae	Feaeidae	Pseudogarypidae	Ideoronctidae	Bochidae	Hyidae	Gymnobisidae	Neobisidae	Syarinidae	Parahyidae	Garypidae	Laridae	Cheiridae	Pseudochirididae	Geogarypidae	Olpidae	Menthidae	Sternophoridae	Withidae	Cheliferidae	Chernetidae	Atennidae	Condition	Consistency Index	
LEGS (continued)																											
84. Claws on tarsus I, ♂:																											
normal; modified	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	A	1.00
85. Arolium and claws:																											
shorter; longer	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	1	1	0	0	0	0	0	0	SR	0.50
86. Arolium, extensions:																											
absent; present	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	A	1.00
MALE GENITALIA																											
87. Longitudinal setal row																											
in atrium:																											
absent; present	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	S	1.00
88. Setal row in atrium:																											
few; many	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	A	1.00
89. Male genitalia:																											
normal; enlarged	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	A	1.00
90. Male genitalia:																											
otherwise; 'chernetid'	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	A	1.00
91. Ram's horn organs:																											
absent; present	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	A	1.00
92. Median genital sac:																											
1; 2	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	A	1.00
93. Sperm mass of																											
spermatophore:																											
simple; complex	0	0	?	?	0	?	?	?	?	?	0	?	?	0	0	?	?	0	?	?	?	1	1	1	1	S	1.00
94. Stalk of spermatophore:																											
simple; complex	1	1	?	?	0	?	?	?	?	0	?	?	0	0	?	?	0	?	?	?	0	0	0	0	0	S	1.00
FEMALE GENITALIA																											
95. Spermathecae:																											
absent; present	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	S	1.00
96. Lateral apodeme:																											
absent; present	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	H	0.50
97. Lateral apodeme frame:																											
absent; present	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	S	1.00
98. Lateral apodeme frame																											
sclerotisation:																											
weak; strong	0	1	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	A	1.00
99. Median cribriform																											
plates: 1; 2 or more	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	S	1.00
ABDOMEN																											
100. Tergites: straight;																											
chevron-shaped	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	A	1.00
101. Tergite XI and sternite																											
XI: separate; fused	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	S	1.00
102. Pleural membrane:																											
striate; granulate	0	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	SR	0.50
103. Pleural membrane:																											
otherwise; pointed	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	A	1.00
104. Pleural membrane:																											
otherwise; papillate	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	S	1.00
105. Pleural sclerites:																											
absent; present	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	S	1.00

3. Most pseudoscorpions, including Fealloidea, possess a circular or U-shaped median maxillary lyrifissure; that of Chthonioidea is straight, which is considered apomorphic.

4. The median maxillary lyrifissure of most pseudoscorpions is submedial or subdistal; the sub-basal position of Ideoroncidae (Chamberlin 1931a, fig. 19g) is considered apomorphic.

5. A posterior maxillary lyrifissure is absent in solifugids, chthonioids and fealloids, but present in all other pseudoscorpions. The possession of a posterior maxillary lyrifissure is here considered apomorphic for Iocheirata.

6. The intermaxillary jugum of most pseudoscorpions is short and stout, never extending past the posterior margin of the pedipalpal coxa (Chamberlin 1931a, figs 25, 26). That of Chthoniidae and Tridenchthoniidae is long and slender (Chamberlin 1931a, figs 22a, 22g, 25a, 25c), which is apomorphic.

7. The dorsal keel of the pharyngeal pump is enlarged in Chthonioidea (Chamberlin 1931a, fig. 22f), which is apomorphic.

8. The pedipalpal coxae of Geogarypidae and Pseudochiridiidae are indented such that a distinct 'shoulder' is present. It appears to have been derived independently in each family.

9. The pedipalpal coxa of virtually all pseudoscorpions bears 2 setae at the apex. Species of Neobisiidae possess 3 or more setae.

10. The apex of the pedipalpal coxa of most pseudoscorpions is triangular. Neobisiids possess a rounded apex, which is apomorphic. *Syarinus* (Syarinidae) also possesses a rounded apex (Muchmore 1982b) which has been independently acquired; as other Syarinidae possess a triangular apex, Syarinidae have been scored with the plesiomorphic condition.

11. 1-2 trichobothria are present on the pedipalpal femur of olpiids and menthids, which are lacking from most other pseudoscorpions.

12. Species of Hyidae possess 3 (occasionally 2) stout sub-basal setae on the posterior margin of the pedipalpal femur (Fig. 81), which are absent from all other families.

13. Some species of Bochicidae possess a sub-basal tubercle on the posterior margin of the pedipalpal femur (Fig. 73). It is present in *Vachonium* spp., *Antillobisium vachoni* Dumitresco and Orghidan and *Troglobochica pecki* Muchmore, and absent in *Paravachonium* spp., *Antillobisium mitchelli* Dumitresco and Orghidan, *Apohya* spp., *Leucohya* spp., *Mexobisium* spp., *Troglobochica jamaicensis* Muchmore and *Troglohya* spp. Without a more detailed study of the species currently placed in the family and their relationships, I prefer to retain the presence of a tubercle as a defining character of the Bochicidae, with subsequent losses in independent taxa.

14 and 15. The presence of a venom apparatus in all pseudoscorpions except Chthonioidea and Fealloidea is considered apomorphic. They are the only known chelicerates with such an apparatus. Chamberlin (1924a, 1924b, 1938) claimed that a venom apparatus was lacking in at least some Cheiridioidea. However, it appears that all cheiridioids possess a venom apparatus (possibly in both chelal fingers) (Mahnert 1982a). All cheiridiids and pseudochiridiids examined by me (*Apocheiridium* spp., *Cheiridium* spp., *Cryptocheiridium* spp., *Pseudochiridium* spp., *Paracheiridium* spp.) clearly possess a venom apparatus. Subsequent losses of the venom apparatus have occurred in several different taxa. It is lost from the fixed finger in Gymnobisiidae, some Bochicidae (*Vachonium*, *Paravachonium*), some Hyidae (*Indohya*) and Chernetidae. It is lost from the movable finger in Neobisiidae, Syarinidae, Parahyidae, Menthidae and Atemnidae.

15. See character 14.

16. The venom ducts of most Iocheirata are quite long, extending much more basally than the level of *et* or *t*. Four families of Neobisioidea (Neobisiidae, Syarinidae, Parahyidae and Gymnobisiidae) differ in possessing very short venom ducts (Figs 93, 103, 113, 123), albeit in different fingers. Menthids and some olpiids also possess short ducts, but these represent separate acquisitions (Olpiidae have been scored as '0').

17. The inflated nodus ramosus of neobisiids, syarinids, parahyids and gymnobisiids (Figs 93, 103, 113, 123) is unique to the Neobisioidea and considered apomorphic. Similarly, the nodus ramosus of cheliferoids is somewhat expanded, this is also deemed apomorphic.

18. Gymnobisiids possess a thickened spine-like seta on the distal end of the movable chelal finger (Fig. 93), which is considered apomorphic.

19. The internal margins of the chelal fingers of Feaellidae bear a number of inwardly directed teeth (Fig. 41), which are considered apomorphic.

20. Both chelal fingers of most Chernetidae possess at least one accessory tooth. The only exception appears to be *Myrmochernes africanus* Tullgren (Judson 1985). Some Geogarypidae (*Geogarypus* and *Indogarypus*, but not *Afrogarypus*) also possess accessory teeth, which represents an independent acquisition.

21. Only chthonioids and fealloids possess the small diploid trichobothrium *xs* on the distal margin of the fixed chelal finger (Figs 11, 21, 31, 41, 51).

22. Trichobothria *eb* and *esb* of most pseudoscorpions are situated on the externo-basal margin of the fixed chelal finger. In Lechytiidae, they have migrated proximally and are situated longitudinally on the chelal hand distally to *ib* and *isb* (Fig. 31).

23. In virtually all pseudoscorpions, trichobothrium *eb* appears in the protonymph at the base of the external margin of the fixed chelal finger. In feallids, trichobothrium *eb* appears on the subdistal region of the internal margin (Figs 4, 47), which is autapomorphic.

24. The plesiomorphic position of trichobothrium *isb* appears to be on the internal face of the fixed chelal finger, as in Fealloidea. It is here hypothesised that the migration of *isb* to the external face of the finger is synapomorphic for Iocheirata (Fig. 4), extending the views of Harvey (1990). Subsequently, *isb* has reverted to the internal face on at least six occasions: *Syarinus* (Syarinidae), Geogarypidae, Cheiridiidae plus Pseudochiridiidae, Larcidae, Garypininae (Olpiidae), and Sternophoroidea plus Cheliferoidea (labelled 'Others' in Fig. 4). The migration in *Syarinus* and Garypininae (Harvey 1990) is not shown on the cladogram, as it is not diagnostic at the family level. The lack of *isb* in all sternophoroids precludes definitive analysis.

25. Trichobothrium *ist* is situated on the sub-basal portion of the fixed chelal finger in Chthonioidea, Feaellidae, some Neobisioidea (Gymnobisiidae, Hyidae, Ideoroncidae, some Neobisiidae, some Syarinidae), Garypoidea (except Geogarypidae), some Olpiidae, Sternophoroidea and most Cheliferoidea. It is situated subdistally or medially in Pseudogarypidae, some Neobisioidea (Bochicidae, some Neobisiidae, some Syarinidae, Parahyidae), Geogarypidae, Menthiidae and some Cheliferoidea. The sub-basal position is here considered plesiomorphic and the submedial or subdistal positions apomorphic. This conformation is apomorphic for Neobisiidae + Syarinidae + Parahyidae, with subsequent reversals to a sub-basal position in most Microcreagrinae (Neobisiidae) and *Syarinus* (Syarinidae); all three families have been coded '1' in the character matrix. The remaining families with both plesiomorphic and apomorphic species have been scored as plesiomorphic in the character matrix.

26. Trichobothria *ib* and *isb* of most pseudoscorpions are situated on the lateral margin of the chelal finger or hand. In chthonioids, they are situated transversely on the dorsal surface of the chelal hand (Figs 4, 11, 21, 31), either basally or sub-basally (most taxa) or distally (Pseudotyranochthoniinae). In *Mexichthonius* spp., they are situated in tandem, with one far in advance of the other (Muchmore 1975a).

27. Trichobothrium *ib* is situated on the dorsum of the chelal hand in several neobisioids: Bochicidae and Ideoroncidae (Figs 61, 73). The independent acquisition of a dorsal *ib* occurs in some Syarinidae (*Nannobisium*, *Alocobisium* and Chitrellinae) (Fig. 110).

28. The post-embryonic development of the trichobothrial pattern of the movable chelal finger differs throughout the order (Fig. 5). In chthonioids, the sequence is *t*, *st*, *b*, then *sb* (protonymph through to adult). In feallids, it is *st*, *t*, *b*, then *sb*; this is clearly a modification of the chthonioid arrangement which differs in the reversal of *st* and *t* (see Character 29). In pseudogarypids and Iocheirata, the sequence is *t*, *b*, *st*, then *sb*. Three equally parsimonious trees are possible: the first treats the Iocheirata and Pseudogarypidae sequence as plesiomorphic, with *b* and *st* reversing their positions independently in Chthonioidea and Feaellidae; the second also treats the Iocheirata sequence as plesiomorphic, with *b* and *st* reversing their positions at the Chthonioidea plus Fealloidea clade, with a subsequent reversal for the Pseudogarypidae; the third treats the Chthonioidea sequence as plesiomorphic, with *st* and *b* independently reversing their positions in Iocheirata and Pseudogarypidae. Which of these three trees represents the most accurate assessment of the situation? The sequence found in Iocheirata and Pseudogarypidae is here interpreted as the plesiomorphic condition, which thus excludes the third tree. Given that the trichobothrial

positions in Feaellidae are fairly labile, it is not out of the question that the movable finger sequence in Feaellidae and Chthonioidea has been derived independently. Therefore, I select the first tree (Fig. 5).

29. The developmental sequence for Feaellidae mentioned above (*st*, *t*, *b*, then *sb*) is clearly autapomorphic.

30. The standard number of chelal trichobothria in adult pseudoscorpions is 12: 8 on the fixed finger (or hand) and 4 on the movable finger. This number is substantially increased in ideoroncids (Fig. 64), which possess 20–31 trichobothria on the fixed finger and hand, and 10–14 trichobothria on the movable finger (Mahnert 1984).

31. Menthids differ from all other pseudoscorpions in possessing three additional trichobothria on the fixed chelal finger (Fig. 192). The only pseudoscorpions (other than ideoroncids and menthids) with a reported trichobothrial number greater than 12 were two *Maorigarypus* spp. (Garypidae, now placed in *Synsphyronus*), which Chamberlin (1930) and Tubb (1937) claimed possessed an additional trichobothrium on the fixed finger. This was refuted by Harvey (1987*a*), who showed that Chamberlin had erred in his estimation [which appeared to have been tacitly followed by Tubb (1937)], and that only eight trichobothria were present on the fixed finger.

32. Trichobothrium *t* of all syarinids is lanceolate, which is autapomorphic.

33. Geogarypids are unique amongst pseudoscorpions in the possession of pit-like structures on the external margin of the fixed chelal finger (Harvey 1986, figs 9, 30, 50).

Chelicera

34. A cheliceral velum is absent from solifugids, chthonioids, feaelloids and neobisioids, but is present in garypoids, sternophoroids, cheliferoids and most olpioids (e.g. Figs 127, 177, 196, 206). It is apomorphic for the Panctenata and has been subsequently lost in some olpioids (e.g. *Amblyolpium*).

35. Similarly, the lamina exterior is absent from solifugids, chthonioids, feaelloids and virtually all neobisioids, but is present in garypoids, olpioids, sternophoroids, cheliferoids, and some genera of the neobisioid family Ideoroncidae. It appears to be apomorphic for Panctenata, with an independent occurrence in some Ideoroncidae; the latter have been scored '0' in Table 4 due to the lack of a lamina exterior in several genera.

36. The movable cheliceral finger bears a number of teeth on the internal margin in most Chelicerata, including Solifugida. Amongst pseudoscorpions, they are found only in Chthonioidea and Neobisioidea (e.g. Figs 9, 98). The two subsequent reductions to a subapical lobe have occurred in Feaelloidea (Figs 39, 49) and Panctenata (e.g. Figs 127, 216).

37. The movable cheliceral finger of pseudoscorpions bears a single seta (*gs*) (some taxa possess several *gs*, e.g. some Chernetidae and Cheliferidae), which is situated submedially in Chthonioidea and Neobisioidea (e.g. Figs 9, 98). In all other pseudoscorpions it is situated subdistally near the tip of the finger (e.g. Figs 39, 127). Outgroup comparison with solifugids fails to identify the plesiomorphic condition, but I have scored the submedial position as plesiomorphic. As noted by Chamberlin (1931*a*), it seems to be highly correlated with the degree of fusion of the serrula exterior.

38. The flagellar areole of Chthoniidae and Tridenchthoniidae is elliptical, and the blades insert in two indistinct rows (Figs 10, 20). The areole of all other pseudoscorpions (including Lechtyiidae) is narrow, and the blades insert linearly (e.g. Fig. 30). The elliptical configuration is apomorphic.

39. The cheliceral flagellum of Chthonioidea and Neobisioidea usually consists of many blades (often more than 6; e.g. Fig. 10), which is here interpreted as the plesiomorphic state. Several independent reductions have occurred (see also Character 40): feaelloids possess 1 or 2 blades (Figs 40, 50), Ideoroncidae possess 4 blades (Fig. 60), and members of Panctenata possess at most 4 blades (e.g. Fig. 207). These reductions are independent and synapomorphic.

40. The cheliceral flagellum of feaelids and geogarypids is reduced to a single blade (Figs 40, 168), which are independent apomorphies. Some *Mexobisium* spp. (Bochicidae) possess a single blade (Muchmore 1986) which is not shown on the character matrix as all other species of the family possess at least 2 blades.

41. The cheliceral flagellum of geogarypids lacks spinules along the shaft (Fig. 168), a feature found in all other taxa.

42. The penultimate blade of the flagellum of Lechytiidae is curved and recumbent (Fig. 30).

43. The serrula exterior arises from a small areole in Chthonioidea and is free for most of its length (Chamberlin 1931a, fig. 16d). It is fused to the movable finger for half to $\frac{2}{3}$ of its length in Neobisioidea (Chamberlin 1931a, fig. 16e), and is completely fused to the finger in Feaelloidea, Garypoidea, Olpioidea, Sternophoroidea and Cheliferoidea (Chamberlin 1931a, figs 16f-h). This appears to represent a transition series (full fusion is labelled 'a' in Figs 6, 7).

44. The chelicera of Feaelloidea bears distinctive sculpturing (Figs 39, 49) that is absent in other pseudoscorpions.

45. The internal margin of the fixed cheliceral finger is usually furnished with several small teeth (e.g. Fig. 9). The major exception is the Feaelloidea where the subdistal teeth have been reduced and apparently consolidated into a strong terminal tooth (Figs 39, 49).

46. The movable cheliceral finger of nymphal tridenchthoniids bears a number of galeal blades, which is autapomorphic.

Carapace

47. The anterior carapacial margin of most pseudoscorpions is straight, slightly convex, or sinuate. However, that of feaelloids bears 3-6 anterior lobes (Figs 38, 48), which are considered apomorphic.

48. Pseudogarypids bear 3 anterior carapacial lobes, while feaelids bear 2-6 lobes. The lateral lobes common to both groups are reduced in *Feaella krugeri* Beier (Beier 1966). The median lobe typical of pseudogarypids is divided into two in most feaelids, while *Feaella mirabilis* Ellingsen and *F. mombasica* Beier (Ellingsen 1906; Beier 1955b) bear 4 such lobes. The division of the medial lobe in feaelids is apomorphic (Fig. 38).

49. The anterior carapacial margin of garypoids is sinuate such that a prominent medial sulcus is present (Figs 126, 136, 146, 156, 166); it is less apparent in pseudochiridiids. Apart from feaelloids (which are discussed above), all other pseudoscorpions possess a straight or convex anterior margin.

50. The anterior carapacial margin is raised and serrate in virtually all chthonioids (Figs 8, 18, 28), although some chthoniids such as *Lagynochthonius* have a much reduced epistome.

51. The carapace of most pseudoscorpions is subrectangular. That of garypoids is subtriangular (Figs 126, 136, 146, 156, 166), which is clearly apomorphic.

52. The eyes of pseudoscorpions (when present) are placed flat upon the lateral margin of the carapace. However, those of feaelloids and most garypoids are situated on ocular tubercles (e.g. Figs 38, 48, 126, 136, 166). This apomorphic state has appeared twice. Cheiridiids and pseudochiridiids lack the tubercles (Figs 146, 156), but this appears to be associated with the reduction in the number of eyes.

53. The eyes of most pseudoscorpions (when present) are situated near the anterior margin of the carapace. The eyes of feaelloids and garypoids are independently removed from the anterior margin by about $\frac{1}{3}$ the length of the carapace (Figs 38, 48, 126, 136, 146, 156, 166), which is here considered apomorphic.

54. The carapacial metazone of cheiridiids bears a distinct circular depression that appears to be unique amongst pseudoscorpions (Fig. 146). I have not been able to confirm this character state in *Pycnocheiridium mirum* Beier (the sole representative of the Pycnocheiridiinae).

55. The carapacial alae of pseudogarypids are clearly unique amongst pseudoscorpions (Fig. 48).

56. The posterior carapacial margin of sternophoroids is V-shaped (Fig. 195), which fits into tergite I. A similar structure in Goniochernetinae (Chernetidae) is clearly a parallelism (Heurtault 1983; Harvey 1985).

57. The carapace/abdominal junction of feaelids (Chamberlin 1931a, figs 7c-f) is unique to that group.

58. Many pseudoscorpions possess two pairs of corneate eyes situated on the lateral margin of the carapace, which is clearly plesiomorphic. This condition is found in at least some species of the following families: Chthoniidae, Tridenchthoniidae, Fealloidae, Pseudogarypidae, Neobisiidae, Gymnobiidae, Syarinidae, Parahyidae, Hyidae, Garypidae, Larcidae, Geogarypidae, Olpiidae and Menthidae. Separate reductions to one pair of corneate eyes, to one pair of eyespots, or to total blindness, have occurred in a variety of taxa (e.g. some Chthoniidae, some Tridenchthoniidae, Lechtyiidae, some Neobisiidae, some Syarinidae, Ideoroncidae, some Hyidae, Bochicidae, Cheiridiidae, Pseudochiridiidae, some Olpiidae, some Menthidae, Sternophoridae, and all Cheliferoidea). Amongst the Epiocheirata, Neobisioida, Garypoida and Olpioidea, eye reduction is most apparent in cavernicolous and soil-dwelling forms. Most of these families retain species with four eyes, which have been scored as '0' in Table 4. However, Lechtyiidae, Pseudochiridiidae, Cheiridiidae, Bochicidae, Ideoroncidae, Sternophoroidea and Cheliferoidea either lack eyes or possess only two eyes or eye-spots.

Legs

59. Coxal spines are found on the pedipalpal coxae and pedal coxae I-III in chthonioids and fealloids, but are completely absent from the other groups. This constitutes a synapomorphy for the Epiocheirata. Some chthonioids lack coxal spines (e.g. Lechtyiidae, *Sathrochthonius* spp.), but traces of their original presence may remain in the form of granulations (Chamberlin 1962).

60. Chamberlin (1931a) considered the intercoxal tubercle to be a 'primordial sternum', but the lack of a true sternum or any sclerotised region between the coxae in most other arachnid orders (including Solifugida) and all other pseudoscorpions suggests that the tubercle is autapomorphic for Chthoniidae plus Tridenchthoniidae. Although the tubercle has been independently lost in many taxa, it is still present in several genera (Chthoniidae: *Allochthonius*, *Aphrastochthonius*, *Chthoniella*, *Chthonius*, *Mundochthonius*, *Pseudotyrannochthonius*, *Sathrochthonius* and *Selachochthonius*; Tridenchthoniidae: *Compsaditha*, *Ditha*, *Dithella*, *Neoditha*, *Paraditha* and *Tridenchthonius*).

61. The intercoxal tubercle of Tridenchthoniidae, when present, is invariably monosetose, whereas that of Chthoniidae is bisetose. The latter is considered apomorphic. Individual specimens of Chthoniidae may possess a monosetose tubercle, such as the male holotype of *Aphrastochthonius tenax* Chamberlin (Chamberlin 1962; but not the female allotype), and the holotype of *Mundochthonius holsingeri* Benedict & Malcolm (1974).

62. Chthonioids possess an anterior protuberance on coxa I, which is considered apomorphic.

63. Sternophorids possess a pseudosternum (Harvey 1985, fig. 10) which is a unique coxal structure apparently formed by desclerotisation of the medial portion of the coxae, rather than a separate entity between the coxae.

64. The unusual condylar articulation between coxae II and III is unique to the Menthidae (Chamberlin 1931a, figs 7b, 7h).

65. The coxae of pseudochiridiids are expanded posteriorly, often to an enormous degree, which is clearly apomorphic. Slight protuberances occur in some cheliferoids (e.g. *Megachernes* spp. and *Protochelifer* spp.), but these are little more than a swelling of the coxal margin.

66. The coxae of all pseudogarypids and garypoids except geogarypids diverge posteriorly such that coxa IV is much wider than coxa I. A similar condition is found in some cheliferids [e.g. *Chelifer cancroides* (Linnaeus)]. The coxae of all other pseudoscorpions do not diverge posteriorly, and coxa IV is approximately the same width as coxa I. The former condition is considered apomorphic.

67. Most cheliferid males possess a sac in each coxa IV that opens via a pore situated on the mesal surface of the coxa. This apomorphic structure is not present in some cheliferids (e.g. *Philomaoria* spp., *Ellingsenius indicus* Chamberlin), and presumably has been secondarily lost.

68. All pseudoscorpions, except Fealloidea, possess one or more slit sensilla on femur I and II. The loss in fealloids is apomorphic.

69. This femoral slit sensillum is sub-basal in Chthonioidea, and is subdistal in Iocheirata. The lack of such a slit sensillum in Solifugida (Hansen 1893) makes the determination of polarity difficult, but I here consider the subdistal position to be apomorphic.

70. The primary femoral slit sensillum of legs I and II is perpendicular to the long axis in Chthonioidea, Garypoidea, Olpioidea, Sternophoroidea, Cheliferoidea and all Neobisioidea except Neobisiidae, Syarinidae and Parahyidae. In these three families it lies longitudinally or at most diagonally along the dorsal surface of the segment.

71. In addition to the primary femoral slit sensillum, most species of Neobisiidae, Syarinidae, Parahyidae and Hyidae possess a group of three small slit sensilla, which is unique amongst the Neobisioidea. This group is absent in some syarinids (e.g. *Ideoblothrus*, *Chitrella*), which appears to be a secondary loss. I have not had the opportunity to examine any gymnobisiids or bochicids.

72. The group of three small slit sensilla is sub-basal in Neobisiidae, Parahyidae and Hyidae, and subdistal in Syarinidae; the latter is apomorphic.

73. The group of three slit sensilla of Hyidae is situated on a distinct sub-basal mound on the anterior margin of femur I and II (Fig. 82). This is absent from all other pseudoscorpions and is apomorphic.

74. The primary slit sensillum of femora I and II is straight in most pseudoscorpions, and strongly curved in Cheliferidae, Chernetidae and Atemnidae, which is apomorphic.

75. The primary slit sensillum is semi-circular in Cheliferidae and Chernetidae, and virtually circular in Atemnidae. The latter is apomorphic.

76. The junction between the femur and patella of legs I and II of most pseudoscorpions is perpendicular. It is oblique in Cheliferidae, Atemnidae and Chernetidae (Figs 219, 229, 239).

77. The junction between femur and patella IV is oblique in most families. In several independent taxa (Fealloidea, Gymnobisiidae, Neobisiidae, some Syarinidae, and Sternophoridae), this junction is perpendicular (Figs 43, 53, 92, 102, 101, 200), which is here considered apomorphic. Amongst the neobisioids, the perpendicular suture appears to have been acquired prior to the Gymnobisiidae, Neobisiidae, Syarinidae plus Parahyidae clade, and subsequently reverted to an oblique suture in Parahyidae and some Syarinidae (e.g. *Syarinus*). The latter family have been scored as '1' due to the presence of at least some species with a perpendicular suture (e.g. *Nannobisium*, some *Ideobisium*, some *Ideoblothrus*).

78. The pedal femora and patellae of legs I and II of cheiridiids are fused into a single podomere (Figs 150, 151); a remnant suture line can sometimes be observed (Mahnert 1982a).

79. The femora of the anterior legs are longer than the patellae in most families. In Cheiridiidae, Pseudochiridiidae, Sternophoroidea, Cheliferoidea, most Garypidae (all except *Garypus*) and some Olpiidae (e.g. *Xenolpium*), the patella is longer than, or equal in length to, the femur, and the two segments are 'submobile'. The latter condition appears to have independently arisen several times. Garypidae and Olpiidae have been scored as '0', as at least some representatives possess the plesiomorphic condition.

80 and 81. Most chelicerates possess a distinct metatarsus and tarsus (Shultz 1989, 1990), as do many pseudoscorpions. However, in several groups these segments have become fused into a single structure. This has occurred independently in fealloids, some garypoids (e.g. some *Synsphyronus* spp., *Geogarypus connatus* Harvey, cheiridiids and pseudochiridiids), sternophoroids and cheliferoids (e.g. Figs 42, 43, 150, 151, 199, 200, 219, 220), and in the anterior legs of chthonioids (e.g. Fig. 12). The inclusion of all monotarsate taxa into a single taxon (i.e. Chamberlin's Monosphyronida) is clearly untenable, as more-convincing synapomorphies clearly unite taxa with varying degrees of tarsal fusion (e.g. Chthonioidea and Fealloidea; Cheiridiidae and Pseudochiridiidae with other Garypoidea). Garypidae and Geogarypidae are scored as '0' in Table 4, due to the retention of separate segments in most taxa. Characters 80 (legs I and II) and 81 (legs III and IV) have been treated separately to assist in tracing the differential fusion of metatarsi and tarsi, especially in Chthonioidea.

81. See Character 80.

82. The tarsi of Chernetidae bear a raised proximal slit sensillum, which is not raised in all other taxa.

83. The subterminal tarsal seta of most pseudoscorpions is simple and acuminate, whereas it is dentate in neobisioidea and most cheliferids. The latter condition is considered apomorphic.

84. The claws of leg I are asymmetrical in most male cheliferids, and are used during mating. Although some male cheliferids lack the modified claws (e.g. *Aperittochelifer*, *Australochelifer*, *Nannochelifer*, *Philomaoria*, *Protochelifer*), these are considered to represent secondary reductions.

85. The pedal arolium is generally shorter than, or equal to, the length of the claws. In some taxa, the arolium is lengthened and extends beyond the claws: Garypidae (except *Garypus*), Larcidae, Geogarypidae, Olpidae, Menthidae (except *Paramenthus*), and most Ideoroncidae (e.g. Figs 141, 171, 181). The long arolium appears to be synapomorphic for the Mestommatina, and has been secondarily shortened in *Garypus*, *Paramenthus* and Cheiridiidae plus Pseudochiridiidae. The lengthened arolium of some Ideoroncidae (*Ideoroncus*, *Shravana*, *Nhatrangia*, *Typhloroncus*, *Afroroncus*, *Nannoroncus*, *Negroroncus* and some *Albiorix*) is considered an independent acquisition, which has not been included in the data matrix, because of the retention of a short arolium in other genera (*Dhanus* and some *Albiorix*). However, it may be more plausible to suggest that a lengthened arolium is synapomorphic for Ideoroncidae which has been subsequently reduced in *Dhanus* and some species of *Albiorix*. Until suitable hypotheses are available concerning the relationships of ideoroncid genera, I prefer to code them as '0'.

86. The pedal arolium of Parahyidae bears two long distal extensions (Figs 121, 122), which are not found in any other family.

Male Genitalia

87. Chthonioids and fealloids possess a longitudinal row of setae on each side within the male genital atrium that appear to be synapomorphic for that group. Similar setae are found in hyids (Chamberlin 1946), but they are not homologous.

88. Unlike all other pseudoscorpions, the setae within the male genital atrium of *Parahya submersa* (Bristowe) are numerous and placed on elliptical platelets (Harvey 1991b, fig. 12).

89. Male gymnobisiids possess greatly enlarged male genitalia (W. Muchmore, personal communication; author's observation) that are unique to that group.

90. The male genitalia of chernetids are of a type that is unique within the order.

91. Male cheliferids possess lateral evaginations of the posterior ventral diverticulum termed ram's horn organs which are everted during mating. Chamberlin (1931a) and other authors incorrectly suggested that they were formed from the lateral genital sacs (Legg 1975). The lack of these structures in some cheliferids (e.g. *Australochelifer*, some *Ellingsenius* spp., *Philomaoria*, *Protochelifer*) appears to represent secondary reductions.

92. The median genital sac of Ideoroncidae consists of two sacs (Mahnert 1984), which is virtually unique within the order. Some Chitrellinae (Syarinidae) possess two sacs (Vachon 1938, 1954, 1969; Chamberlin 1952; Mahnert 1980), but the family has been scored as '0' because of the presence of a single sac in many genera.

93. The spermatophore produced by males varies in morphology (Weygoldt 1969, 1970). In Chthonioidea, Fealloidea, Neobisioidea and Garypoidea it consists of a slender stalk surmounted by the spherical sperm mass. In Cheliferoidea, the sperm mass possesses a complex structure. The latter is considered apomorphic. The morphology of the spermatophore is not known for the Sternophoroidea.

94. The spermatophore stalk is normally simple, and lacks any adornments. In Chthoniidae and Tridenchthoniidae, the top of the stalk is embellished with a collar or sharp protuberances (Weygoldt 1969, fig. 52), which is apomorphic. Although the structure of the spermatophore is unknown in Lechytiidae, they too may be found to possess a complex stalk.

Female Genitalia

95. Spermathecae are absent from most female pseudoscorpions, but are found in most cheliferoids (exceptions include some cheliferid genera where the spermathecae are much reduced or lost). The presence of spermathecae is considered apomorphic.

96. Female withiids and chernetids possess lateral apodemes (Judson 1985) that are lacking in all other pseudoscorpions. This may suggest a sister-group relationship between the two families, which would require that Withiidae have lost the oblique femur/patella junction characteristic of Cheliferidae, Atemnidae and Chernetidae.

97. Female chthonioids possess a characteristic lateral apodeme frame that is unique to that group.

98. The lateral apodeme frame of tridenchthoniids is much thickened, and clearly apomorphic.

99. Harvey (1985) suggested that a single median cribriform plate was plesiomorphic for pseudoscorpions, and that a division into two (or more) separate plates was apomorphic. This has occurred on several separate occasions (Garypidae and Larcidae, and some Sternophoridae, Withiidae, Chernetidae, Cheliferidae, Atemnidae, Cheiridiidae and Neobisiidae). Only the division into two plates for the Garypidae plus Larcidae is shown on the cladogram, as all other families possess at least some species with an undivided plate.

Abdomen

100. The tergites of most pseudoscorpions are relatively straight; those of pseudo-chiridiids are somewhat chevron-shaped, especially the anterior tergites.

101. Tergites XI and sternite XI are fused in fealloids, with no trace of any division visible. Although a similar, independent state is found in other families, these have been excluded from Table 4.

102. The pleural membrane of most pseudoscorpions is longitudinally striate, which Chamberlin (1931a) considered to be the plesiomorphic condition. It is found in Ideoroncidae, Bochicidae, Olpiidae, Menthiidae and some Syarinidae (e.g. *Syarinus*, *Ideoblothrus*). It is granulate in Gymnobisiidae, Hyidae, Neobisiidae, some Syarinidae (e.g. *Ideobisium*) and Parahyidae. The latter condition is apomorphic for all Neobisioidea except Bochicidae and Ideoroncidae, and has been subsequently lost in some Syarinidae.

103. The pleural membrane of Parahyidae possesses pointed papillations (Harvey 1991b, fig. 5), which is apomorphic.

104. Unlike Lechytiidae and all other pseudoscorpions, the pleural membrane of Chthoniidae and Tridenchthoniidae is minutely papillate.

105. Fealloids possess distinct sclerites in the pleural membrane that are lacking in most other pseudoscorpions. Some pseudogarypids have reduced sclerites (Benedict and Malcolm 1978). The only other taxa that possess similar structures are some garypoids, such as *Anagarypus* spp. (Muchmore 1982c) and Geogarypidae. The structures found in the garypoids are little more than sclerotised bases where the pleural setae insert, and accordingly have been scored as '0'.

106. The presence of a stigmatic spiracular helix is widespread amongst most pseudoscorpion groups, and has been independently lost in Fealloidea and Garypidae.

107. A spiracular guard sclerite is found in Tridenchthoniidae, but not in other Chthonioidea or other pseudoscorpions.

108. The spiracles of tridenchthoniids are oblique, while those of all other Epiocheirata are transverse. The former condition is considered apomorphic. The situation is more complicated within the Iocheirata where obliquely situated spiracles occur across many different groups. This complicated situation is further confused by the occurrence of transverse anterior spiracles and oblique posterior spiracles in some taxa (e.g. Harvey 1985, fig. 10). Although this character has been scored for most families (Table 4), it has only been included on the cladogram for Tridenchthoniidae.

109. The spiracles of fealloids have been 'disassociated' from sternites III and IV, and have moved backwards towards sternites IV and V (see also Character 110).

110. The spiracles of fealloids are fused to sternites IV and V, which, along with Character 109, represents a transformation series.

111. Pseudoscorpions are equipped with two pairs of tracheae which open via spiracles situated on the third and fourth sternites. Each trachea is separate and terminates in smaller tracheoles. Solifugids possess a networked tracheal system (Bernard 1896; Millot and Vachon 1949) that opens via paired spiracles situated on sternites III and IV, in addition to those

located between coxa II and III, and a single spiracle on sternite V. The coxal spiracles of Solifugida are unique to that group. The respiratory system of most pseudoscorpions (including the Fealloidea) consists of thickened anterior tracheae that ramify into tracheoles near the posterior coxae (in fealloids they are quite short and ramify before the coxae). The posterior tracheae ramify into tracheoles almost immediately. The tracheae of Chthonioidea are narrow, and do not terminate in numerous tracheoles. The anterior tracheae extend well into the coxal region, with individual tracheoles emerging along its length; this is considered apomorphic.

112. The setae that border the posterior genital operculum of male Lechyiidae are bifurcate, in contrast to those of all other pseudoscorpions.

113. Larcids possess a row of setae along the posterior margin of sternites III and IV, which is apomorphic for the group.

114. The setae on the genital operculae of female hyids are extremely small (less than 0.003 mm) and very difficult to observe, whereas the setae of other pseudoscorpions are of normal proportions.

115. The posterior genital operculum of male chthonioids is deeply cleft, which is apomorphic.

116. Male, female and tritonymphal withiids possess discrete patches of sensory setae on the sternites that are lacking from other groups (usually very reduced in females and tritonymphs). The lack of such patches from male *Protowithius* and *Termitowithius* (Beier 1955a; Muchmore 1990a) may represent a secondary loss, but may also represent an out-group relationship with the remainder of the family.

117. All larcids possess a desclerotised region surrounding the anal plate (Gardini 1983) that is unique to the group.

118. Sternite XI in larcids lacks elongate lyrifissures, even though small lyrifissures are present (Gardini 1983). This is considered apomorphic.

119. Sternite XI is virtually absent in Lechyiidae, which is autapomorphic for the family.

120. The anus of most pseudoscorpions is situated between tergite XI and sternite XI at the distal end of the abdomen. The anus of four garypoid families (Garypidae, Larcidae, Cheiridiidae and Pseudochiridiidae) is enclosed by sternite XI and is subventral. This condition is also found in Fealloidea where tergite XI and sternite XI are fused (Character 101).

121. The anal rim of garypids, cheiridiids and pseudochiridiids is raised, which is considered apomorphic. Similarly, it is raised in Fealloidea, which is an independent acquisition. The Larcidae are here included in a clade with Garypidae, Cheiridiidae and Pseudochiridiidae, and the loss of a raised anal rim is here considered a reduction, probably associated with the desclerotisation of sternite XI (see Character 117).

122. The anal plates (tergite XII and sternite XII) of fealloids are unique amongst pseudoscorpions in being heavily sclerotised.

123. The abdomen of most pseudoscorpions is subrectangular, such that the abdomen is not much wider than the carapace. However, the abdomen of fealloids and garypoids is ovoid, which is considered apomorphic. It appears to have been acquired independently.

General

124. Pseudoderm (or exocuticle) is present in Garypidae and Larcidae.

125. The dorsal vestitural setae of most pseudoscorpions are straight. In virtually all Garypoidae they are curved, which is considered apomorphic. Several genera of Garypidae (e.g. *Synsphyronus*, *Paragarypus*) possess straight setae, which indicates a secondary reversal. Some cheliferoids possess slightly curved setae, but the curvature never approaches that of the Garypoidae.

Behaviour

126. The mating dance of cheliferoids is unique to the group. The male produces a spermatophore only in the presence of a receptive female, and usually grasps the pedipalps of the female during the dance. Sperm transfer data are not known for Lechyiidae,

Feallidae, Pseudochiridiidae, Menthidae, Sternophoridae, and all Neobisioidea except Neobisiidae. Despite this sizeable gap in our knowledge, it seems reasonable to postulate that only cheliferoidea perform a mating dance.

Ordinal Synapomorphies

127. The endocephalic spinning apparatus is unique to the Pseudoscorpionida.

128. The pedipalpal tibia and tarsus of pseudoscorpions are modified to form a grasping appendage, the chela, analogous to that of scorpions.

129. The movable cheliceral finger of solifugids (and many other chelicerates) bears a number of setae. Pseudoscorpions possess a single seta (*gs*), situated submedially or subdistally. In a few isolated taxa, *gs* is increased to 3 or 4.

130. Medial eyes absent. Apart from blind forms, few chelicerates lack medial eyes (e.g. Palpigradida, Schizomida, Acarina, Ricinuleida).

131. Flagellum with several blades. Solifugids and pseudoscorpions bear a cheliceral flagellum which in the latter group is composed of several blades. These have been reduced in some taxa (Feallidae, Geogarypidae) to a single blade. Some solifugids, such as some Rhagodidae, Melanoblossidae and Eremobatidae, possess multiple blades (Muma 1976), which is undoubtedly convergent.

132. Female pseudoscorpions lay their eggs into a brood sac attached to the genital operculum. Although some other arachnids construct a brood sac (e.g. Amblypygida), this is considered convergent.

Key to Recent Families of Pseudoscorpionida

1. Chelal fingers without venom apparatus (e.g. Fig. 14); trichobothrium *xs* present (e.g. Fig. 14) Suborder Epiocheirata 2
- One or both chelal fingers with venom apparatus (e.g. Fig. 64); trichobothrium *xs* absent (e.g. Fig. 64) Suborder Iocheirata 6
- 2(1). Carapace with anterior lobes (Figs 38, 48); tergite XI and sternite XI fused and surrounding anus; all legs with metatarsi and tarsi fused (e.g. Figs 42, 43) Fealloidea 3
- Carapace without anterior lobes (Figs 8, 18, 28); tergite XI and sternite XI not fused and neither surrounding anus; only legs I and II with metatarsi and tarsi fused (e.g. Figs 12, 13) Chthonioidea 4
- 3(2). Carapacial alae absent (Fig. 38); carapace and abdomen with unusual articulation Feallidae
- Carapacial alae present (Fig. 48); carapace and abdomen with normal articulation Pseudogarypidae
- 4(2). Trichobothria *eb* and *esb* on dorsum of hand (Fig. 31); flagellum arising in straight line, with penultimate blade curved and recumbent (Fig. 30) Lechytiidae
- Trichobothria *eb* and *esb* at base of fingers (Figs 11, 21); flagellum arising from elliptical areole, with penultimate blade not noticeably curved or recumbent (Figs 10, 20) 5
- 5(4). Spiracles transverse; carapace with few setae (Fig. 8); female lateral apodeme frame not sclerotised Chthoniidae
- Spiracles oblique; carapace with numerous setae (Fig. 18); female lateral apodeme frame sclerotised Tridenchthoniidae
- 6(1). Movable cheliceral finger with several teeth (e.g. Fig. 59); *gs* submedial (e.g. Fig. 59); serrula exterior attached for $\frac{1}{2}$ to $\frac{2}{3}$ of its length; chelicera without velum or lamina exterior (e.g. (Fig. 98) (present in some Ideoroncidae) Infraorder Hemictenata Neobisioidea 7
- Movable cheliceral finger with 1–2 subapical teeth (e.g. Fig. 127); *gs* subdistal (e.g. Fig. 127); serrula exterior attached entire length; chelicera with velum and lamina exterior (lost in some Olpiidae) Infraorder Panctenata 13
- 7(6). Venom ducts very short, not extending past *et* (e.g. Figs 93, 103); nodus ramosus expanded (e.g. Figs 93, 103) 8
- Venom ducts long, extending well past *et* (e.g. Fig. 64); nodus ramosus not expanded (e.g. Fig. 64) 11
- 8(7). Venom apparatus only present in fixed chelal finger (e.g. Fig. 103) 9
- Venom apparatus only present in movable chelal finger (Fig. 93) Gymnobisiidae
- 9(8). Apex of pedipalpal coxa with 2 setae 10
- Apex of pedipalpal coxa with 3 or more setae Neobisiidae

- 10(9). Arolium without distal extensions (Figs 111, 112); trichobothrium *t* lanceolate ... Syarinidae
 Arolium with distal extensions (Figs 121, 122); trichobothrium *t* acuminate ... Parahyidae
- 11(7). Chelae with 30–45 trichobothria (Fig. 64) Ideoroncidae
 Chelae with 12 trichobothria (Figs 74, 84) 12
- 12(11). Femur I and II with small sub-basal mound (Fig. 82); female anterior genital operculum with
 minute setae Hyidae
 Femur I and II without small sub-basal mound (Fig. 68); female genital opercula with
 normal setae Bochicidae
- 13(6). Carapace subtriangular (e.g. Fig. 126); abdomen subovate; eyes situated away from anterior
 margin of carapace (e.g. Fig. 126) Garypoidea 14
 Carapace subrectangular (e.g. Fig. 176); abdomen subrectangular; eyes situated near anterior
 margin of carapace (e.g. Fig. 176) 18
- 14(13). Anal plate surrounded by sternite XI; coxa IV much wider than coxa I 15
 Anal plate situated between tergite XI and sternite XI; coxa IV approximately same width
 as coxa I Geogarypidae
- 15(14). Two eyes (Figs 146, 156) 16
 Four eyes (Figs 126, 136) 17
- 16(15). Tergites chevron-shaped; coxa IV much enlarged posteriorly Pseudochiridiidae
 Tergites not chevron-shaped; coxa IV not enlarged posteriorly Cheiridiidae
- 17(15). Sternite XI with desclerotised region surrounding anus Larcidae
 Sternite XI without desclerotised region surrounding anus Garypidae
- 18(13). Pseudosternum present Sternophoroidea Sternophoridae
 Pseudosternum absent 19
- 19(18). Spermathecae absent; pedipalpal femur with 1–2 trichobothria, usually, in basal half
 Olpioidea 20
 Spermathecae present; pedipalpal femur without trichobothria in basal half
 Cheliferoidea 21
- 20(19). Venom apparatus present in both chelal fingers (Fig. 182); fixed chelal finger with at most
 8 trichobothria (Fig. 182); specialised articulation joint absent between coxae II and III
 Olpiidae
 Venom apparatus only present in fixed chelal finger (Fig. 192); fixed chelal finger with
 11 trichobothria (Fig. 192); specialised articulation joint present between coxae II and III
 Menthidae
- 21(19). Femur/patella I and II junction perpendicular (Fig. 209); male sternites generally with discrete
 patches of sensory setae Withiidae
 Femur/patella I and II junction oblique (Figs 209, 229, 239); male sternites without discrete
 patches of sensory setae 22
- 22(21). Venom apparatus present in both chelal fingers (Fig. 221); males generally with coxal sacs
 and ram's horn organs Cheliferidae
 Venom apparatus generally absent from at least one chelal finger (Figs 231, 250); males
 without coxal sacs or ram's horn organs 23
- 23(22). Venom apparatus generally present in movable chelal finger only (Fig. 231); tarsi with
 proximal raised slit sensillum; chelal fingers normally with at least one accessory tooth
 Chernetidae
 Venom apparatus present in fixed chelal finger only (Fig. 241); tarsi without proximal raised
 slit sensillum; chelal fingers without accessory teeth Atemnidae

Suborder **EPIOCHEIRATA**, nov.

Diagnosis

Venom apparatus absent (P). Trichobothrium *xs* present (A). Coxal spines usually present (A). Male genital atrium with a longitudinal row of setae on each side (A).

Remarks

This suborder corresponds to Chamberlin's Heterosphyronida (= Chthonioidea) plus part of his Monosphyronida (= Fealloidea). The monophyly of the two superfamilies was first suggested by Harvey (1986), but Weygoldt (1969) proposed that the fealloids were a problematic group that 'originated either close to the Heterosphyronida or somewhere between Heterosphyronida and Diplosphyronida'. The recognition of a united suborder that is cladistically distinct from the other suborder, Iocheirata, is pivotal to our understanding

of pseudoscorpion phylogeny, and hence classification. Epiocheirata is well supported by a number of synapomorphies, and includes the earliest known pseudoscorpion, *Dracocheila deprehendor* Schawaller, Shear & Bonamo.

Etymology

The name refers to the lack of a venom apparatus in the chelal fingers (*epios* Greek, gentle, kind; *cheirus* Greek, hand).

Superfamily **CHTHONIOIDEA** Daday

Chthonioidea Daday. — Chamberlin, 1931a: 209.

Diagnosis

Trichobothrium *ib* and *isb* on dorsum of chelal hand (A). Median maxillary lyrifissure straight (A). Female lateral apodeme frame present (A). Coxa I with anterior protuberance (A).

Remarks

The three Recent families included in this superfamily are easily distinguished by the presence of *ib* and *isb* on the dorsal surface of the chelal hand (Figs 11, 21, 31). These trichobothria are placed medially or sub-basally in most chthonioids, but are situated sub-distally in Pseudotyranochthoniinae (Chthoniidae). The Lechytiidae represent the sister-group to the remaining two families because of the presence of two apomorphies in Chthoniidae and Tridenchthoniidae that are lacking in Lechytiidae: flagellar blades arising from an elliptical areole (Schawaller *et al.* 1991, fig. 22), and the elongate intermaxillary jugum (Chamberlin 1931a, figs 22a, 25a, 25c).

Schawaller (1980) presented a phylogenetic analysis of the Chthonioidea that differs from the one presented here, mainly due to the small number of characters utilised in his analysis. His suggestion that the Pseudotyranochthoniini were not part of a clade that contained the Chthoniini and Lechytiini was based upon the belief that the distal position of *ib* and *isb* in the pseudotyranochthoniines was plesiomorphic. Outgroup comparison with the Tridenchthoniidae and Lechytiidae indicates that this position is apomorphic.

The recently described Dracocheilidae (Schawaller *et al.* 1991) appear to belong to this superfamily and are discussed below.

Family **CHTHONIIDAE** Daday

Chthoniinae Daday, 1888: 133.

Chthoniidae Daday. — Hansen, 1893: 232.

Diagnosis

Intercoxal tubercle (when present) bisetose (A). Transverse spiracles (P). Female lateral apodeme frame not strongly sclerotised (P).

Remarks

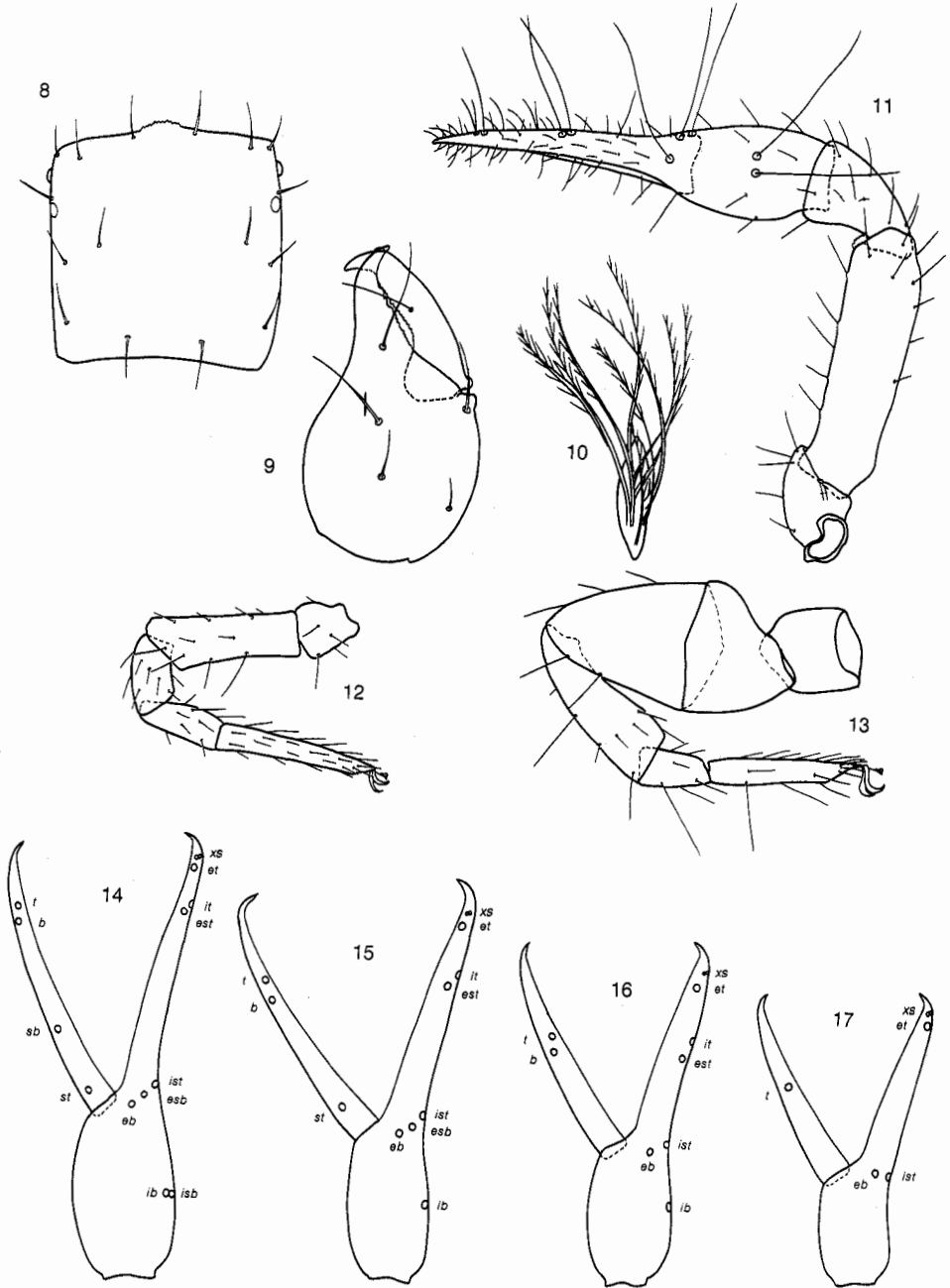
The Chthoniidae are a large, diverse group currently represented by 31 genera, which appear to be united by the possession of a bisetose intercoxal tubercle, which has subsequently been lost in numerous genera. The Pseudotyranochthoniini is here elevated to subfamilial level, Pseudotyranochthoniinae, stat. nov., on the basis of the subdistal position of trichobothria *ib* and *isb* on the chelal hand. This group may deserve familial status once its relationship with other chthoniids is fully resolved.

Family **TRIDENCHTHONIIDAE** Balzan

Tridenchthoniidae Balzan, 1892: 505.

Diagnosis

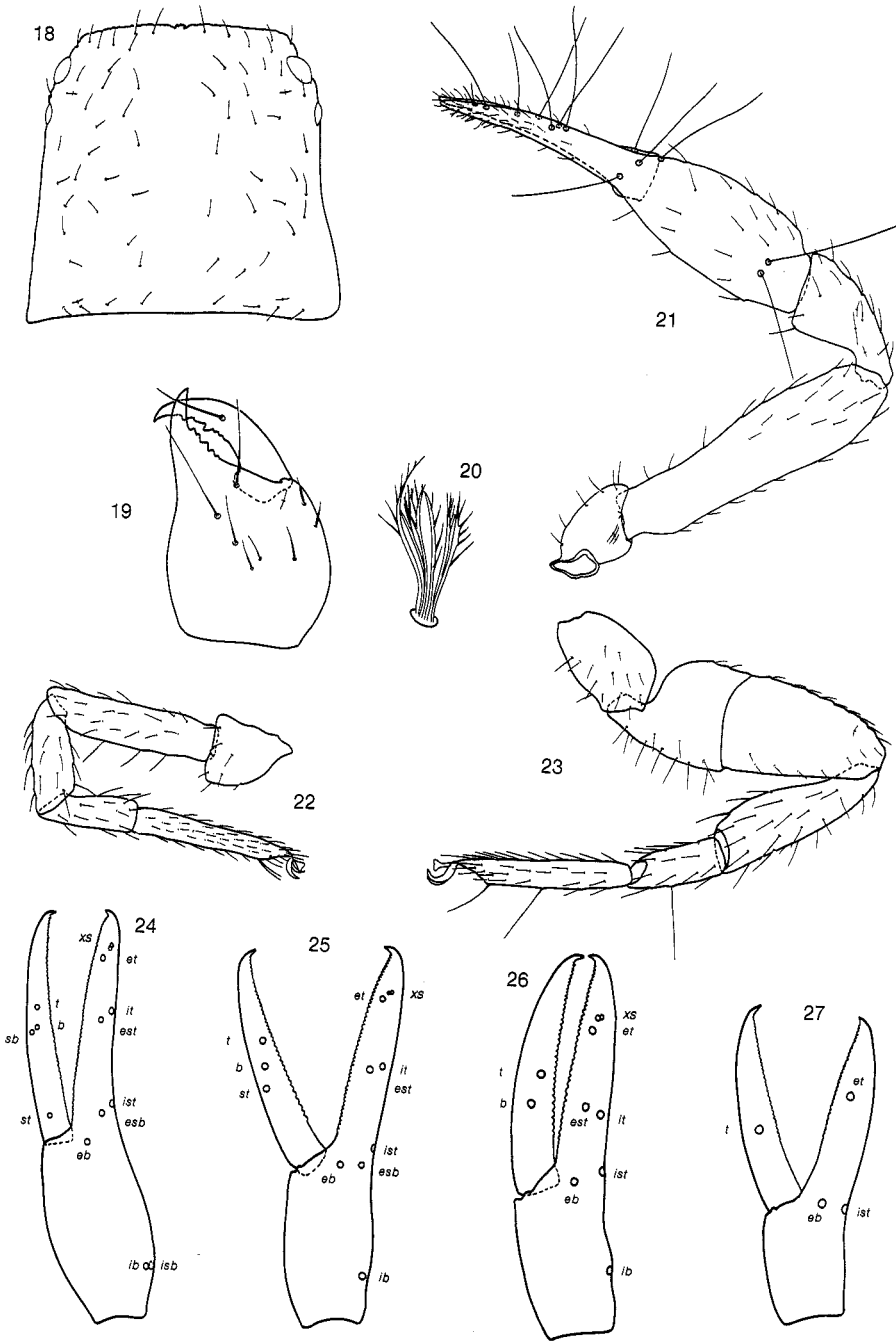
Intercoxal tubercle (when present) monosetose (P). Numerous carapacial setae (A). Oblique spiracles (A). Female lateral apodeme frame strongly sclerotised (A). Movable cheliceral finger of nymphs usually with at least 2 galeae (A).



Figs 8-17. Chthoniidae. 8-13, *Austrochthonius australis* Hoff: 8, carapace; 9, chelicera; 10, flagellum; 11, right pedipalp; 12, leg I; 13, leg IV; 14-17, *Chthonius ischnocheles* (Hermann), left chela, after Gabbutt and Vachon (1963): 14, adult; 15, tritonymph; 16, deutonymph; 17, protonymph.

Remarks

This family of 17 genera is largely tropical in distribution, and is distinguished from the Chthoniidae and Lechyiidae by the strongly sclerotised female lateral apodeme frame. Chamberlin and Chamberlin (1945) divided the family into two subfamilies, Cecodithinae



Figs 18–27. Tridenchthoniidae. 18–23, *Pycnodithella harveyi* Kennedy: 18, carapace; 19, chelicera; 20, flagellum; 21, right pedipalp; 22, leg I; 23, leg IV; 24–27, *Compsaditha aburi* Chamberlin and Chamberlin, left chela, after Vachon (1952) and Mahner (1978): 24, adult; 25, tritonymph; 26, deutonymph; 27, protonymph.

and Tridenchthoniinae, and further divided the latter into two tribes, Tridenchthoniini and Verrucadithini, based upon the nature of the chelal teeth. The number of galeae on the movable cheliceral finger of the nymphs was used by Mahnert (1983) to further separate these tribes.

Family **LECHYTIIDAE** Chamberlin, stat. nov.

Lechyitini [*sic*] Chamberlin, 1929: 76.

Diagnosis

Trichobothria *eb* and *esb* on dorsum of hand (A). Flagellar blades in straight row (P). Penultimate flagellar blade curved and recumbent (A). Anterior apical seta of pedipalpal coxa bifid (A). Setae bordering genital operculum of male bifid (A). Sternite XI much reduced (A).

Remarks

The Lechytiini (sole genus *Lechytia*) are here removed from the Chthoniidae and elevated to family status to fully reflect their relationships with the remaining Chthonioidea. Muchmore (1975*b*) first suggested that *Lechytia* may deserve familial status. They are excluded from the Chthoniidae and Tridenchthoniidae because of the lack of an elliptical flagellar areole, and the short inter-maxillary jugum (Chamberlin 1931*a*, fig. 25*d*). Over 20 species of *Lechytia* are known, and a fossil Oligocene species from the Dominican Republic was described by Schawaller (1980).

Family **DRACOCHELIDAE** Schawaller, Shear & Bonamo

Dracochelidae Schawaller, Shear & Bonamo, 1991: 3.

Diagnosis

Serrula interior blades of chelicera smooth. Flagellar blades in straight row (P).

Remarks

This family is known from only a single species of *Dracochela* from the Middle Devonian of Gilboa, New York, U.S.A. (Schawaller *et al.* 1991). Due to our lack of knowledge of many character states for the family, it has not been included in the phylogenetic analysis or cladogram. As discussed by Schawaller *et al.* (1991), *Dracochela* can be excluded from the Feaelloidea because it lacks the synapomorphies of that group. At present, it seems best to place it within the Chthonioidea. The linear flagellar blades (Schawaller *et al.* 1991, fig. 3) exclude *Dracochela* from the Chthoniidae and Tridenchthoniidae, and the positions of the trichobothria exclude it from the Lechytiidae. It may represent a basal clade within the Chthonioidea.

Schawaller *et al.* (1991) suggest that the anterior legs of *D. deprehendor* Schawaller, Shear & Bonamo possess a separate metatarsus and tarsus. However, the illustrations provided by Schawaller *et al.* (1991, figs 6, 18) indicate that the anterior metatarsi and tarsi are fused, which would clearly place the Dracochelidae within the Chthonioidea.

Superfamily **FEAELLOIDEA** Ellingsen

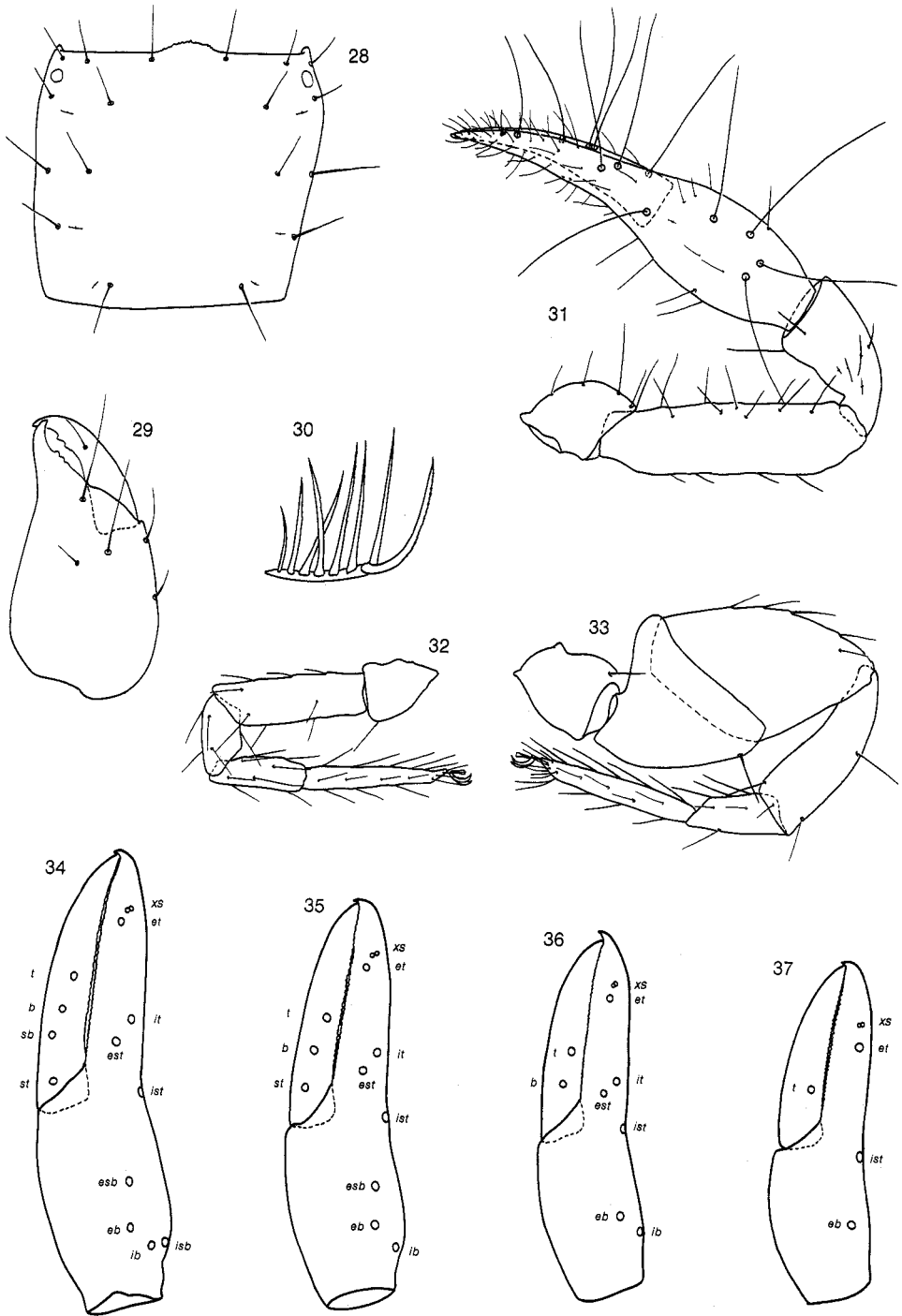
Feaelloidea Ellingsen. — Chamberlin, 1931*a*: 230.

Diagnosis

Carapace with 3–6 anterior lobes (A). Spiracles separate from sternites III and IV, and near sternites IV and V (A). Anal plate surrounded by fused tergite XI and sternite XI (A). Anal plates (tergite XII and sternite XII) heavily sclerotised (A). Pleural membrane usually with platelets (A).

Remarks

This easily recognised superfamily is defined by a suite of synapomorphies. The pleural membrane platelets are reduced in females of some *Pseudogarypus* spp. (Benedict and Malcolm 1978).



Figs 28–37. Lechytidae. 28–33, *Lechytia* sp.: 28, carapace; 29, chelicera; 30, flagellum, after Muchmore (1975b); 31, right pedipalp; 32, leg I; 33, leg IV; 34–37, *Lechytia maxima* Beier, left chela, after Mahnert (1986): 34, adult; 35, tritonymph; 36, deutonymph; 37, protonymph.

Family **FEALLIDAE** Ellingsen

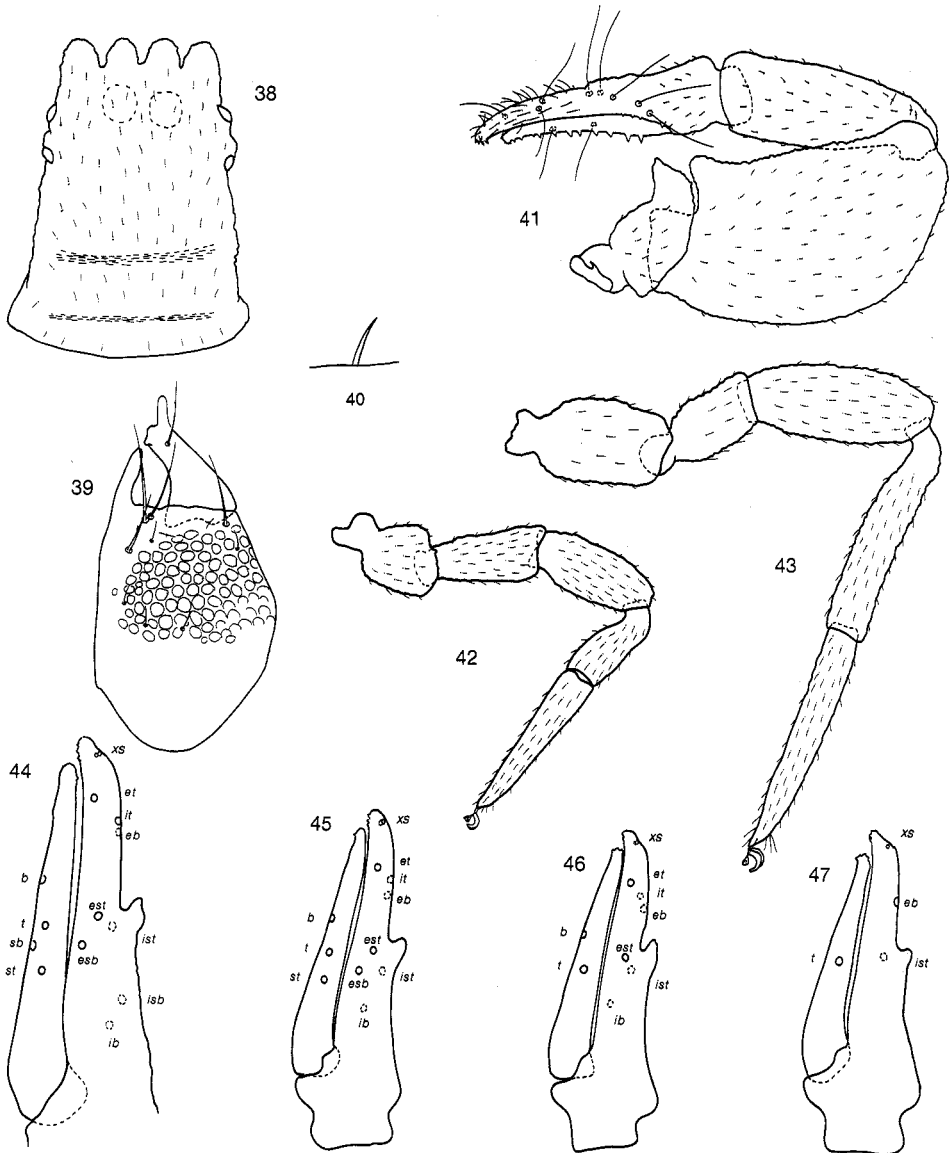
Faellidae Ellingsen, 1906: 259-60.

Diagnosis

Pedipalps raptorial (A). Median maxillary lyrifissure absent (A). Cheliceral flagellum consists of a single blade (A). Anterior margin of carapace with 2 or more medial lobes (A). Carapace and tergite I with unusual articulation joint (A). Spiracles fused to sternites IV and V (A).

Remarks

The Feallidae currently contain a single genus, *Fealla* Ellingsen.

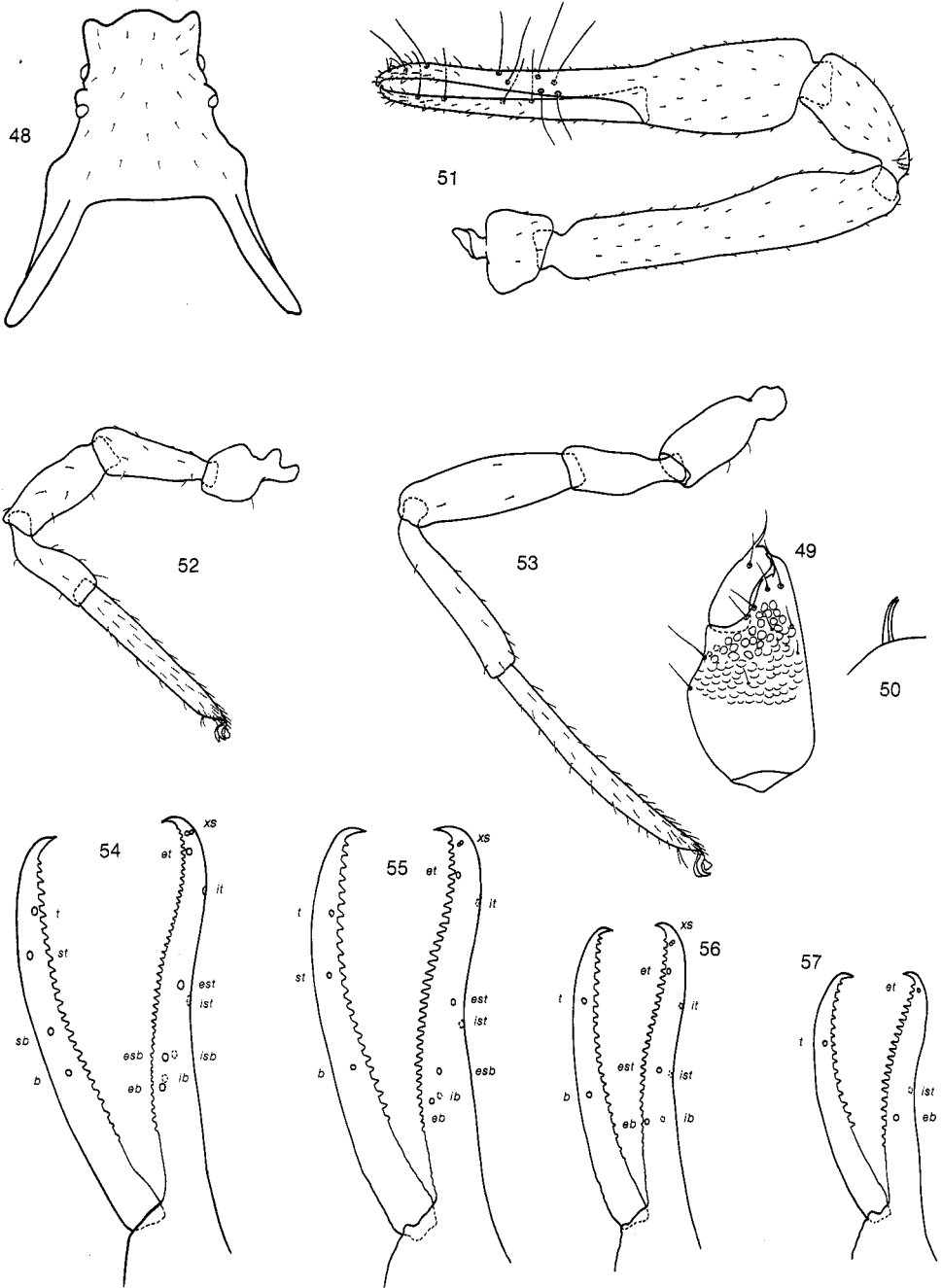


Figs 38-47. Feallidae. 38-43, *Fealla anderseni* Harvey: 38, carapace; 39, chelicera; 40, flagellum; 41, right pedipalp; 42, leg I; 43, leg IV; 44-47, *Fealla perreti* Mahnert, left chela, after Mahnert (1982b): 44, adult; 45, tritonymph; 46, deutonymph; 47, protonymph.

Family **PSEUDOGARYPIDAE** Chamberlin

Pseudogarypinae Chamberlin, 1923a: 161.

Pseudogarypidae Chamberlin. — Chamberlin, 1931a: 230.



Figs 48–57. Pseudogarypidae. *Neopseudogarypus scutellatus* Morris: 48, carapace; 49, chelicera; 50, flagellum; 51, right pedipalp; 52, leg I; 53, leg IV; 54–57, left chela: 54, adult; 55, tritonymph; 56, deutonymph; 57, protonymph.

Diagnosis

Carapacal alae present (A).

Remarks

The Pseudogarypidae currently contain two genera, *Pseudogarypus* Banks and *Neopseudogarypus* Morris, found in North America and Tasmania respectively. Several species have been recorded from Oligocene Baltic Amber.

Suborder **IOCHEIRATA**, nov.*Diagnosis*

Venom apparatus present in one or both chelal fingers (A). Posterior maxillary lyrifissure present (A).

Remarks

This large assemblage of pseudoscorpions is characterised by the presence of a chelal venom apparatus, which is unique within the Chelicerata. The venom apparatus has been subsequently lost in one finger of several groups of Iocheirata, but the only iocheirid that totally lacks a venom apparatus is *Myrmochernes africanus* Tullgren (Chernetidae). Its clear relationship with other chernetids (Judson 1985) indicates that the loss is secondary.

Etymology

The name refers to the presence of a chelal venom apparatus (*ios* Greek, poison; *cheirus* Greek, hand).

Infraorder **HEMICTENATA** Balzan

Emictenodactyli [*sic*] Balzan, 1892: 539.

Diagnosis

Subterminal tarsal seta dentate (A).

Remarks

This suborder is revalidated for the Neobisioidea, which is the sister-group to the remaining Iocheirata. The only known synapomorphy for the group is the dentate subterminal tarsal seta.

Balzan (1892) consistently used 'Emictenodactyli', which was altered to 'Hemictenodactyli' by With (1906). The name is here modified to render it more euphonious.

Superfamily **NEOBISIOIDEA** Chamberlin

Neobisioidea Chamberlin, 1930: 9.

Diagnosis

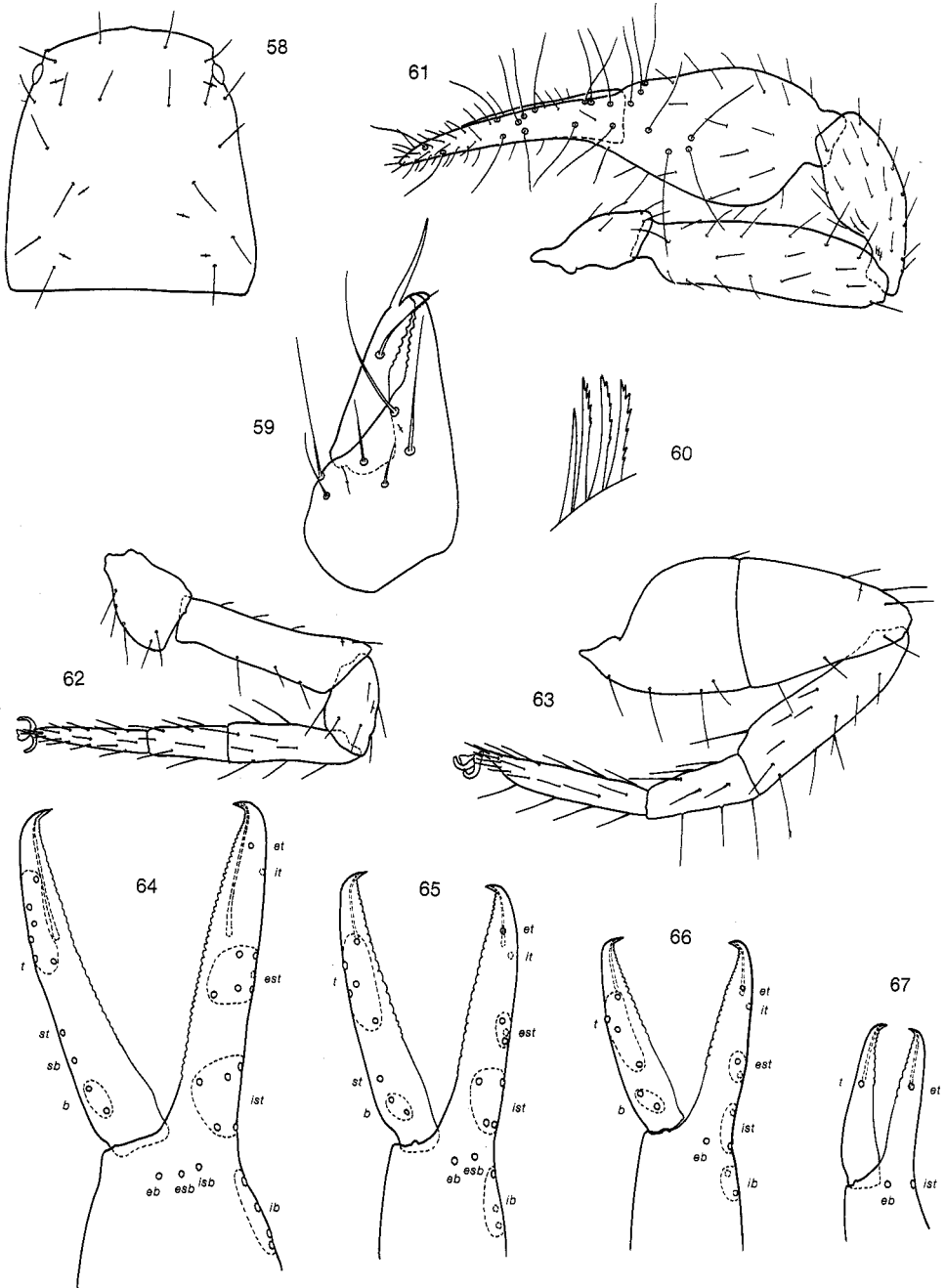
As for infraorder.

Remarks

This superfamily consists of seven families, four of which (Gymnobisiidae, Neobisiidae, Syarinidae and Parahyidae) are united by the short venom ducts and an inflated nodus ramosus (Muchmore 1972). The latter three families are further united by the lack of a venom apparatus in the movable chelal finger. Amongst this clade, it is impossible at present to fully resolve the trichotomy. The Neobisiidae is distinct on the basis of the larger number of setae on the rounded apex of the pedipalpal coxa; many Syarinidae possess a lanceolate *t*; and Parahyidae possess a small suite of apomorphies, including distal extensions on the arolia, and papillate pleural membrane.

These four families and the Hyidae are united by the presence of a group of three slit

sensillae on femora I and II. The Bochicidae and Ideoroncidae are tenuously united by the position of *ib* on the dorsum of the chelal hand, a character state that is also found in some Syarinidae.



Figs 58–67. Ideoroncidae. *Dhanus siamensis* (With): 58, carapace; 59, chelicera; 60, flagellum; 61, right pedipalp; 62, leg I; 63, leg IV, without trochanter; 64–67, left chela: 64, adult; 65, tritonymph; 66, deutonymph; 67, protonymph.

Family **IDEORONCIDAE** Chamberlin

Ideoroncidae Chamberlin, 1930: 42.

Diagnosis

Chelal fingers with numerous trichobothria: 20–31 on fixed finger and hand, and 10–14 on movable finger (A).

Remarks

This is an extremely well-defined family that currently contains nine genera (Mahnert 1984): *Afroroncus* Mahnert, *Albiorix* Chamberlin, *Dhanus* Chamberlin, *Ideoroncus* Balzan, *Nannoroncus* Beier, *Negroroncus* Beier, *Nhatrangia* Redikorzev, *Shravana* Chamberlin and *Typhloroncus* Muchmore.

Family **BOCHICIDAE** Chamberlin

Bochicinae Chamberlin, 1930: 43.

Vachoniidae Chamberlin, 1947: 3–4. Syn. nov.

Bochicidae Chamberlin.—Muchmore, 1982a: 98.

Diagnosis

Pedipalpal femur often with sub-basal tubercle on the posterior margin (A).

Remarks

The sole criterion for distinguishing the Bochicidae from the Vachoniidae is the lack of a functional venom apparatus in the fixed chelal finger of the latter, even though a trace of the venom duct remains (Chamberlin 1947, fig. 8). Muchmore (1982a) first suggested that the two families were closely related and intimated that they may be synonymous. As discussed above, the sole apomorphy for the family has subsequently been lost in several groups.

The Bochicidae are found in central America as far north as Texas, mostly occurring in caves. Nine genera have been described: *Antillobisium* Dumitresco & Orghidan, *Aphoya* Muchmore, *Bochica* Chamberlin, *Leucohya* Chamberlin, *Mexobisium* Muchmore, *Paravachonium* Beier, *Troglobochica* Muchmore, *Troglohya* Beier and *Vachonium* Chamberlin.

Family **HYIDAE** Chamberlin

Hyidae Chamberlin, 1930: 41.

Diagnosis

Femur I and II with sub-basal mound (A). Female anterior genital opercula with minute setae (A). Pedipalpal femur with 3 (occasionally 2) stout setae on posterior-basal margin (A).

Remarks

This family was recently restricted to two named genera, *Hya* Chamberlin and *Indohya* Beier (Harvey 1991b), and an undescribed cavernicolous genus is known from Australia. *Indohya* and the new genus lack a venom apparatus in the fixed chelal finger.

Family **GYMNOBISIIDAE** Beier

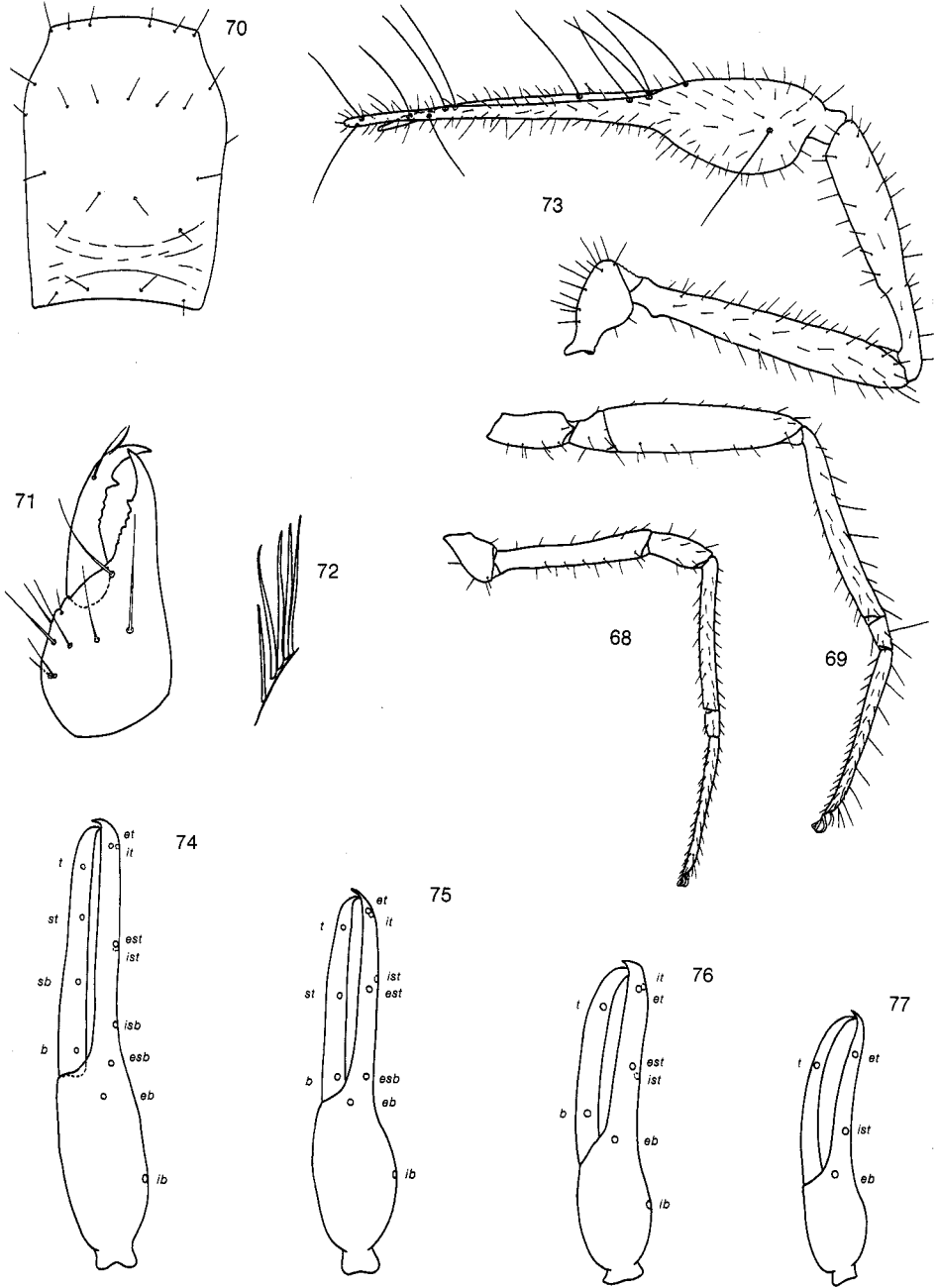
Gymnobisiidae Beier, 1947: 287–8.

Diagnosis

Movable chelal finger with distal, thickened spine-like seta (A). Male genitalia greatly enlarged (A). Venom apparatus lacking from fixed chelal finger (A).

Remarks

The Gymnobiidae are found only in southern South America and South Africa. Four genera are currently recognised: *Beierobisium* Vitali-di Castri, *Gymnobisium* Beier, *Mirobisium* Beier and *Vachonobisium* Vitali-di Castri. Males of some genera possess modified chelae (e.g. Fig. 90), which may represent a synapomorphy for a subfamilial grouping.



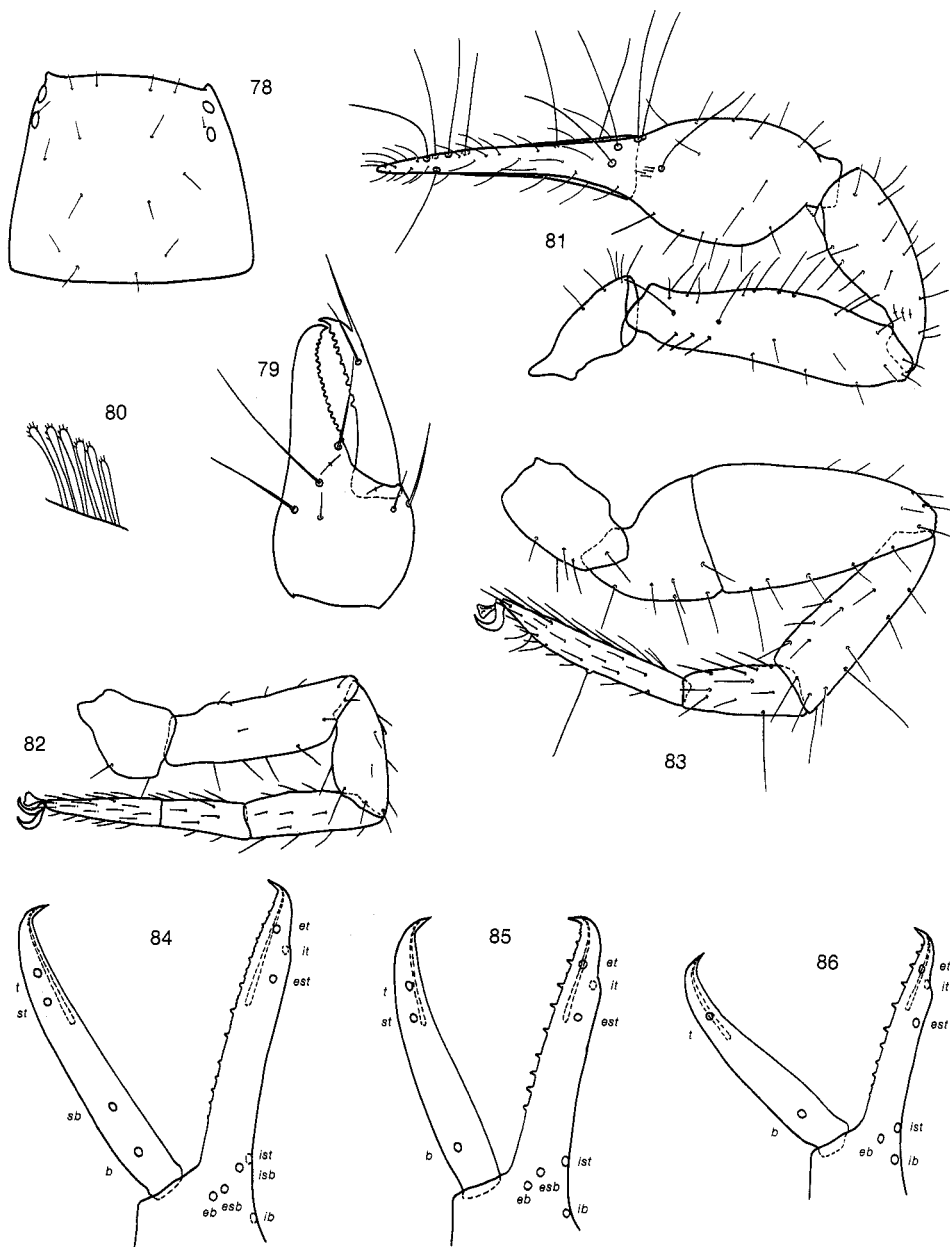
Figs 68-77. Bochicidae. 68-69, *Vachonium boneti* Chamberlin, after Chamberlin (1947): 68, leg I; 69, leg IV; 70-77, *Antillobisium vachoni* Dumitresco and Orghidan, after Dumitresco and Orghidan (1977): 70, carapace; 71, chelicera; 72, flagellum; 73, right pedipalp; 74-77, left chela: 74, adult; 75, tritonymph; 76, deutonymph; 77, protonymph.

Family **NEOBISIIDAE** Chamberlin

Neobisiidae Chamberlin, 1930: 9.

Diagnosis

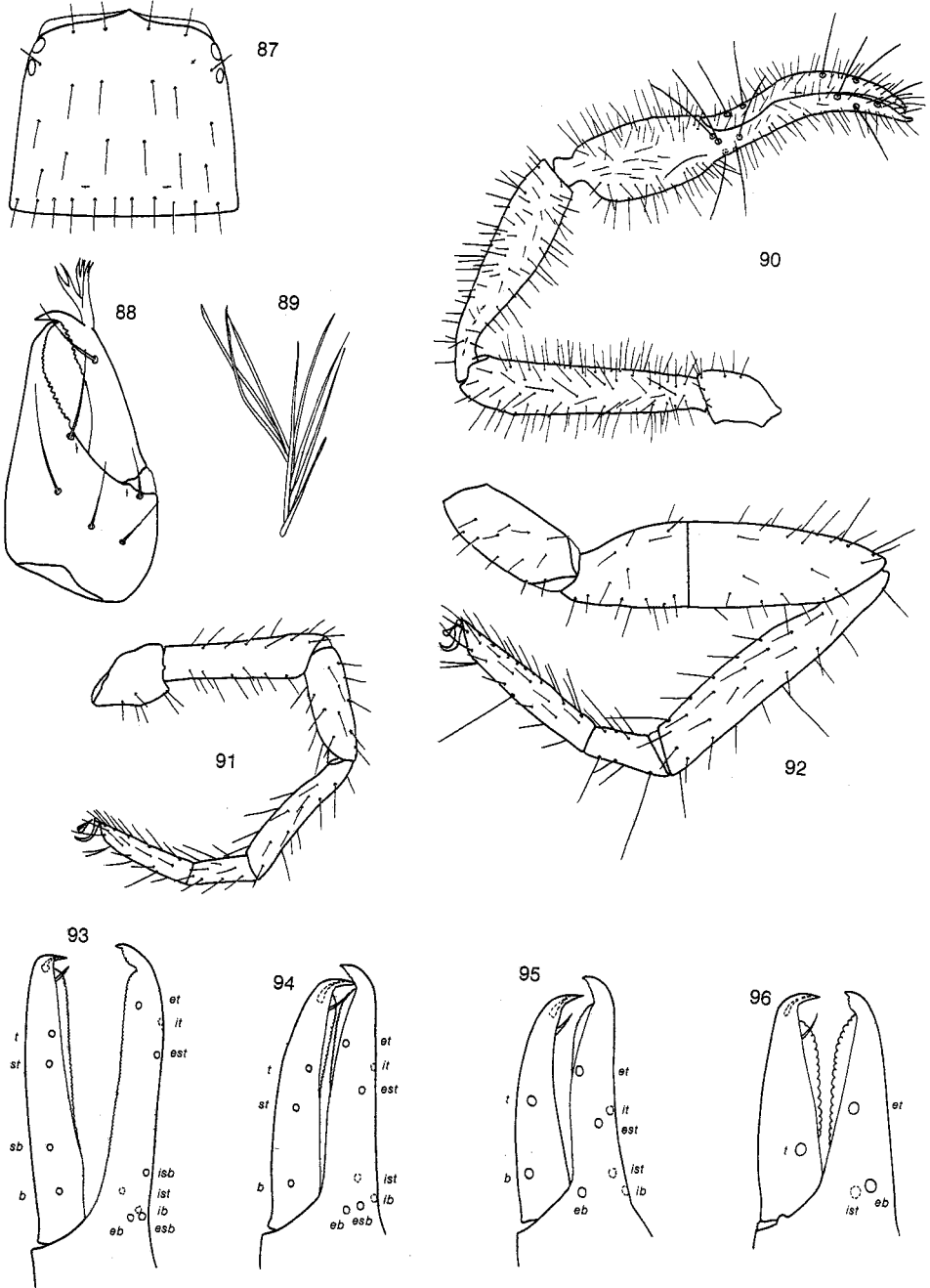
Apex of pedipalpal coxa with 3 or more setae (A). Apex of pedipalpal coxa rounded. Venom apparatus absent from movable chelal finger (A).



Figs 78–86. Hyidae. *Hya minuta* (Tullgren): 78, carapace; 79, chelicera; 80, flagellum; 81, right pedipalp; 82, leg I; 83, leg IV; 84–87, left chela: 84, adult; 85, tritonymph; 86, deutonymph.

Remarks

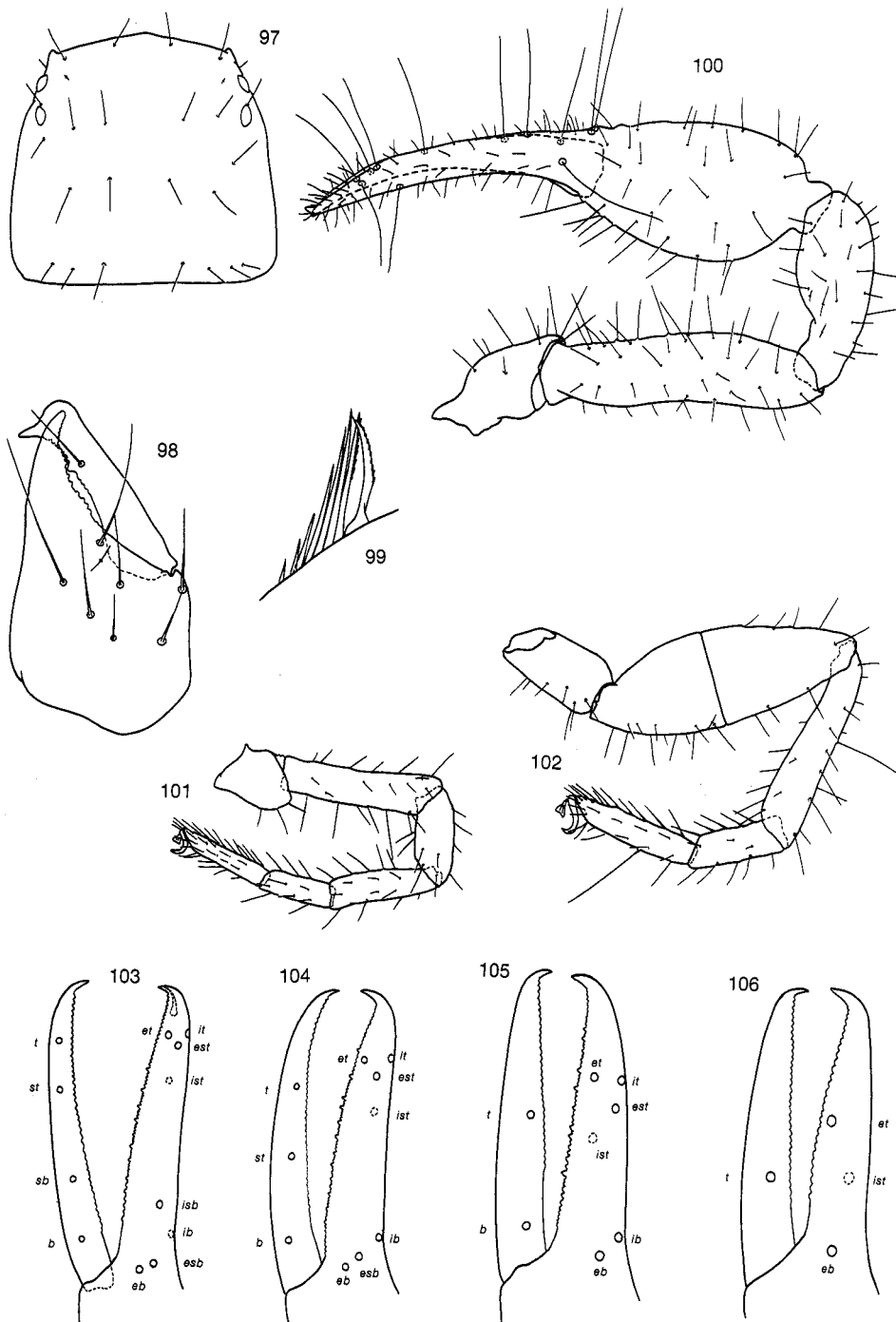
This large family is diagnosed satisfactorily, and can be divided into two major groups, Neobisiinae (galea reduced to sclerotic knob) and Microcreagrinae (trichobothrium *ist* usually sub-basal). The maintenance of Neobisiidae Chamberlin, 1930 over Microcreagrinae Balzan, 1892 is discussed above.



Figs 87-96. Gymnobsiidae. *Vachonobisium troglophilum* Vitali-di Castri, after Vitali-di Castri (1963): 87, carapace; 88, chelicera; 89, flagellum; 90, left pedipalp; 91, leg I; 92, leg IV; 93-96, left chela: 93, adult; 94, tritonymph; 95, deutonymph; 96, protonymph.

Family SYARINIDAE Chamberlin

Syarinidae Chamberlin, 1930: 38.



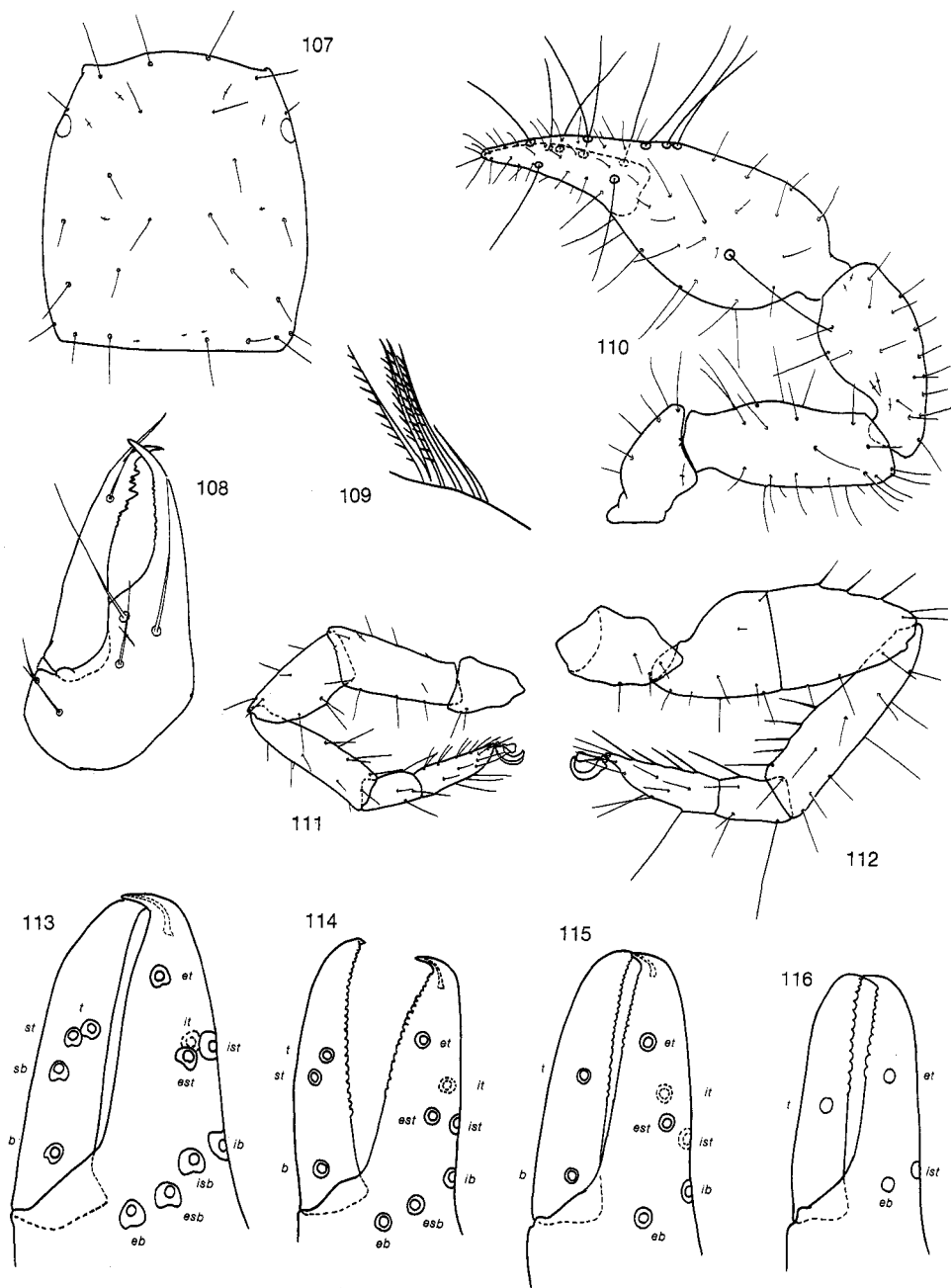
Figs 97–106. Neobisiidae. *Neobisium carcinoides* (Hermann) (Neobisiidae): 97, carapace; 98, chelicera; 99, flagellum; 100, right pedipalp; 101, leg I; 102, leg IV; 103–106, left chela, after Gabbutt and Vachon (1965): 103, adult; 104, tritonymph; 105, deutonymph; 106, protonymph.

Diagnosis

Venom apparatus absent from movable chelal finger (A). Trichobothrium *t* lanceolate (A).

Remarks

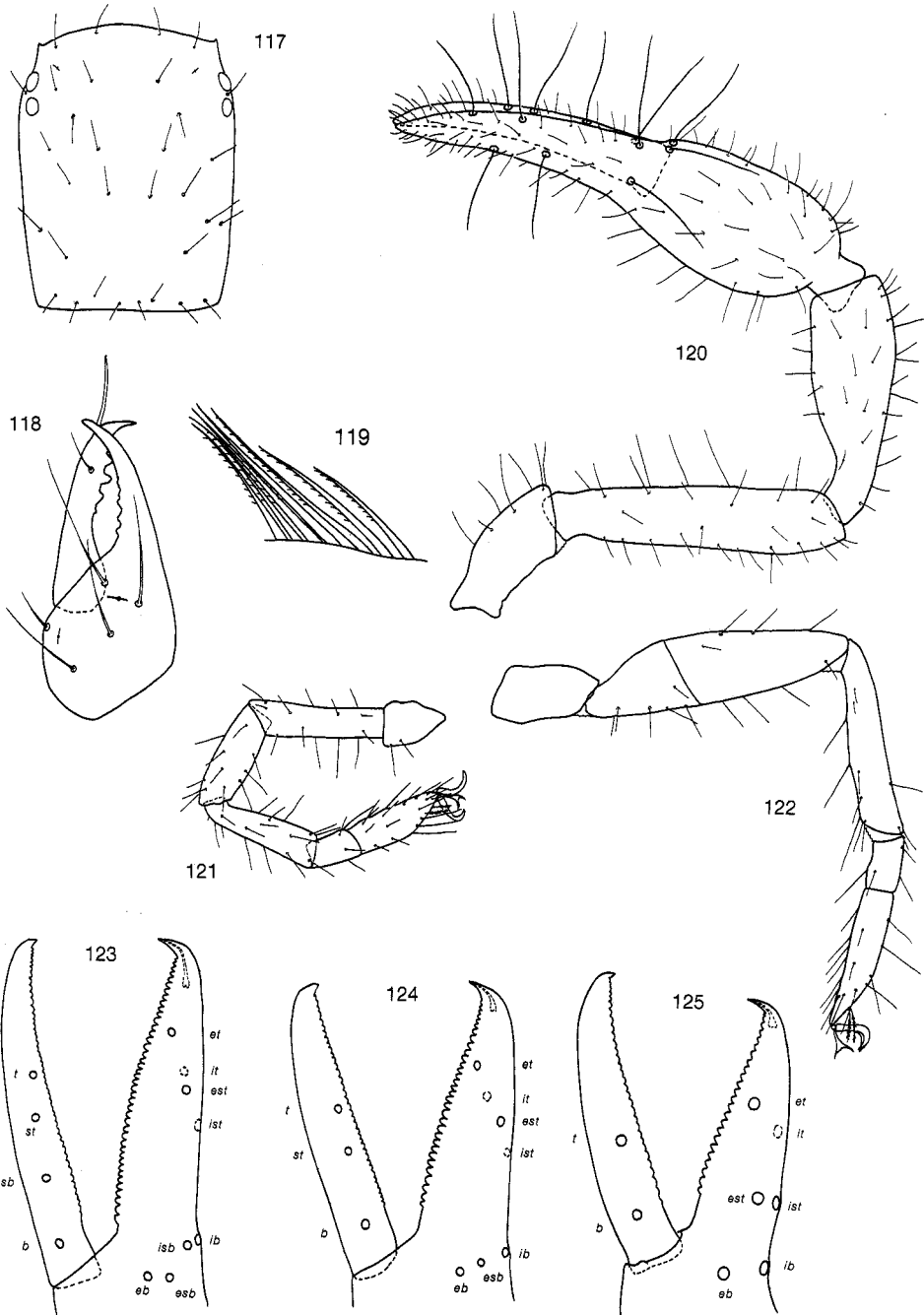
Muchmore (1982*b*) attempted to provide a comprehensive diagnosis that fully distinguished the Syarinidae from the Neobisiidae. The main synapomorphy used in this analysis is the lanceolate *t*. This, however, has been lost on a number of occasions, particularly amongst



Figs 107–116. Syarinidae. *Nannobisium* sp.: 107, carapace; 108, chelicera; 109, flagellum; 110, right pedipalp; 111, leg I; 112, leg IV; 113–116, *Ideoblothrus amazonicus* (Mahnert) and *I. caecus* (Mahnert), left chela, after Mahnert (1979): 113, adult; 114, tritonymph; 115, deutonymph; 116, protonymph.

the cavernicolous forms. Further work is necessary to unravel the complex relationships of the syarinid genera.

The maintenance of Syarinidae Chamberlin, 1930 over Ideobisiinae Banks, 1895 is discussed above. The enigmatic genus *Hyarinus* Chamberlin cannot be placed in an existing family until material becomes available for study (Muchmore 1982b).



Figs 117–125. Parahyidae. *Parahya submersa* (Bristowe), mostly after Harvey (1991b): 117, carapace; 118, chelicera; 119, flagellum; 120, right pedipalp; 121, leg I; 122, leg IV; 123–125, left chela: 123, adult; 124, tritonymph; 125, deutonymph.

Family **PARAHYIDAE**, nov.

Type genus: *Parahya* Beier, 1957.

Diagnosis

Arolium with distal extensions (A). Suture between femur and patella IV oblique (A). Venom apparatus absent from movable chelal finger (A).

Remarks

Parahya Beier was placed in the Hyidae by Beier (1957) and in Neobisiidae by Harvey (1991b). However, the only known species, *P. submersa* (Bristowe), lacks the synapomorphies of both families; in particular, the three or more manducatory setae characteristic of the Neobisiidae, and the minute setae on the female anterior genital operculum found in Hyidae. *Parahya* can be excluded from the Syarinidae because of the lack of a lanceolate trichobothrium *t*. Therefore, I prefer to recognise a separate family, Parahyidae, rather than force the genus into a pre-existing family.

The oblique suture between femur and patella IV is virtually unique within the Neobisiidae, Parahyidae plus Syarinidae clade, although some syarinids (e.g. *Syarinus* and some *Ideoblothrus* and *Ideobisium*) possess an oblique line.

Infraorder **PANCTENATA** Balzan

Panctenodactyli Balzan, 1892: 509.

Diagnosis

Velum present (A). Lamina exterior present (A). Movable cheliceral finger with 1–2 distal teeth or lobes (A). Seta *gs* of movable cheliceral finger subdistal (A). Serrula exterior completely fused to movable cheliceral finger (A).

Remarks

This taxon includes four superfamilies and 12 families, and is easily separated by the cheliceral characters listed above, although the last three character states are also found in the Fealloidea. It is virtually equivalent in scope to Panctenodactyli (Balzan 1892), which has been contracted to render it more euphonious.

Two microorders are recognised, Mestommatina and Ellassommatina.

Microorder **MESTOMMATINA**, nov.*Diagnosis*

Generally with 4 eyes (P). Arolium generally longer than claws (A).

Remarks

This micro-order corresponds to Chamberlin's (1931a) Garypoidea plus Cheiridiidae and Pseudochiridiidae, and is best diagnosed by the long arolia [subsequently reduced in *Garypus* (Garypidae), *Paramenthus* (Menthidae), Cheiridiidae and Pseudochiridiidae]. It may also be distinguished from the Ellassommatina by the plesiomorphic retention of four eyes (reduced to two in Cheiridiidae, Pseudochiridiidae and some Olpioidea).

Etymology

This group takes its name from the plesiomorphic retention of four eyes in most of its included taxa (*mestos* Greek, full, abundance; *omma* Greek, eye).

Superfamily **GARYPOIDEA** Simon

Garypoidea Simon.—Chamberlin, 1930: 585.

Cheiridioidea Hansen.—Chamberlin, 1931a: 234–5. Syn. nov.

Diagnosis

Carapace subtriangular (A). Eyes set on ocular tubercles (reduced in Cheiridiidae and Pseudochiridiidae) (A). Eyes situated away from anterior margin of carapace (A). Abdomen subovate (A). Vestitural setae curved (subsequently lost in some Garypidae) (A). Anterior margin of carapace sinuate (A).

Remarks

Chamberlin (1931*a*) included three families within the Garypoidea: Garypidae, Olpiidae and Menthiidae. The latter two families are here transferred to a separate superfamily (see below). The Garypidae were divided into two families, Garypidae and Geogarypidae, by Harvey (1986). Two further families (Cheiridiidae and Pseudochiridiidae) are added here, and *Larca* and *Archeolarca* are transferred to the Larcidae.

The Geogarypidae appear to represent the sister-group of the remaining garypoids, and are defined by the presence of numerous synapomorphies. The remaining four families are united by the anus being surrounded by sternite XI. The Larcidae apparently represent the sister-group to the remaining three families, which are united by the raised rim surrounding the anus. Cheiridiidae and Pseudochiridiidae share several apomorphies, including two eyes, metatarsi and tarsi fused and arolium shorter than claws.

Family **GARYPIDAE** Simon

Garypinae Simon, 1879: 42.

Garypidae Simon.—Hansen, 1893: 231–2.

Synsphyronidae Beier, 1932*a*: 238.

Diagnosis

Stigmatic helix absent (A).

Remarks

This family is here restricted to a group of genera defined by the lack of a stigmatic helix. Ten genera are currently recognised (*Ammogarypus* Beier, *Anagarypus* Chamberlin, *Elattogarypus* Beier, *Eremogarypus* Beier, *Garypus* L. Koch, *Meiogarypus* Beier, *Neogarypus* Vachon, *Paragarypus* Vachon, *Synsphyronus* Chamberlin and *Thaumastogarypus* Beier), but some of these will be reduced in synonymy in a forthcoming review of the family (Harvey, unpublished data).

Family **LARCIDAE**, fam. nov.

Type genus: *Larca* Chamberlin, 1930.

Diagnosis

Anal plate surrounded by desclerotised region (A). Sternites III and IV with a row of setae along posterior margin (A). Lyrifissures of sternite XI small (A).

Remarks

Two genera are currently included in the family: *Larca* Chamberlin and *Archeolarca* Hoff & Clawson.

Family **CHEIRIDIIDAE** Hansen

Chiridiinae [*sic*] Hansen, 1893: 232.

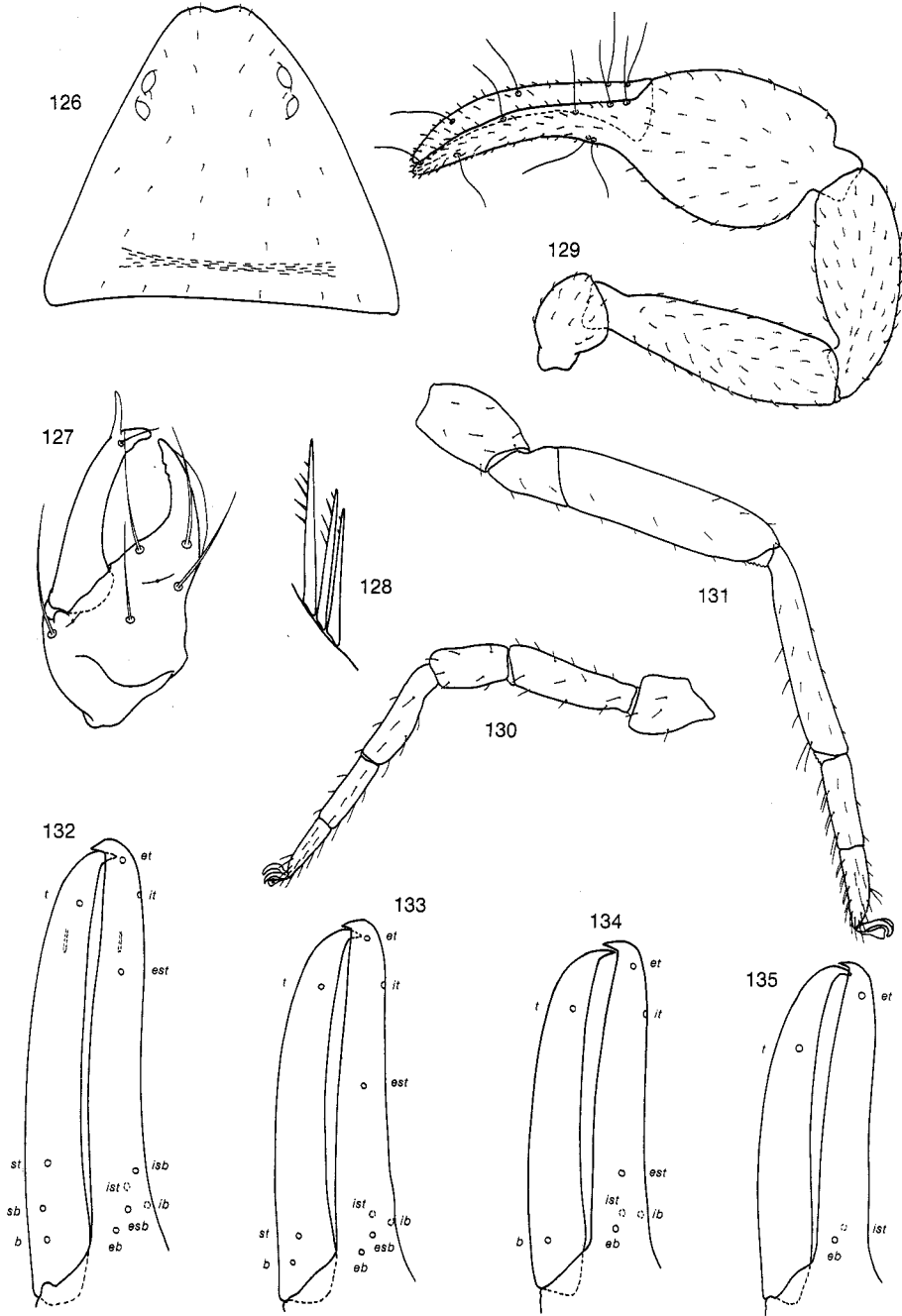
Cheiridiidae Hansen.—Chamberlin, 1931*a*: 236.

Diagnosis

Carapacal metazone present (A). Pedal femora and patellae I–IV fused (A).

Remarks

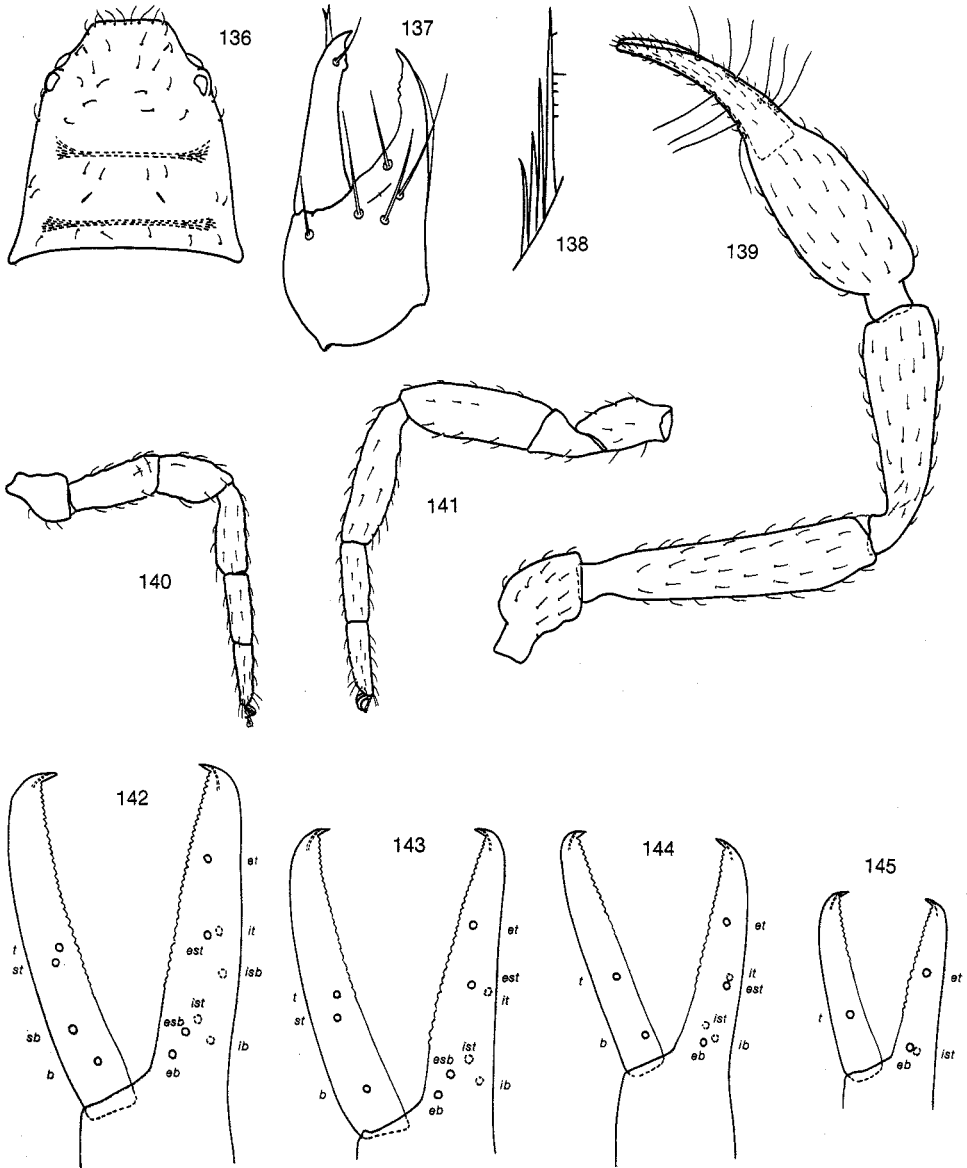
Chamberlin (1931a) suggested that the venom apparatus is lacking in the movable chelal finger in cheiridiids; this has subsequently been shown to be incorrect (e.g. Chamberlin 1938; Mahnert 1982a).



Figs 126–135. Garypidae. 126–131, *Garypus sini* Chamberlin: 126, carapace; 127, chelicera; 128, flagellum; 129, right pedipalp; 130, leg I; 131, leg IV; 132–135, *Garypus ocellatus* Mahnert, left chela, after Mahnert (1984): 132, adult; 133, tritonymph; 134, deutonymph; 135, protonymph.

Family **PSEUDOCHIRIDIIDAE** ChamberlinPseudocheiridiinae [*sic*] Chamberlin, 1923*b*: 370.Pseudocheiridiidae [*sic*].—Chamberlin, 1931*a*: 235–6.**Diagnosis**

Coxae expanded posteriorly (A). Tergites chevron-shaped (A).

RemarksTwo genera are currently recognised, *Pseudochiridium* With and *Paracheiridium* Vachon.

Figs 136–145. Larcidae. 136–141, *Larca granulata* (Banks): 136, carapace; 137, chelicera; 138, flagellum; 139, right pedipalp; 140, leg I; 141, leg IV; 142–145, *Archeolarca aalbui* Muchmore, left chela: 142, adult; 143, tritonymph; 144, deutonymph; 145, protonymph.

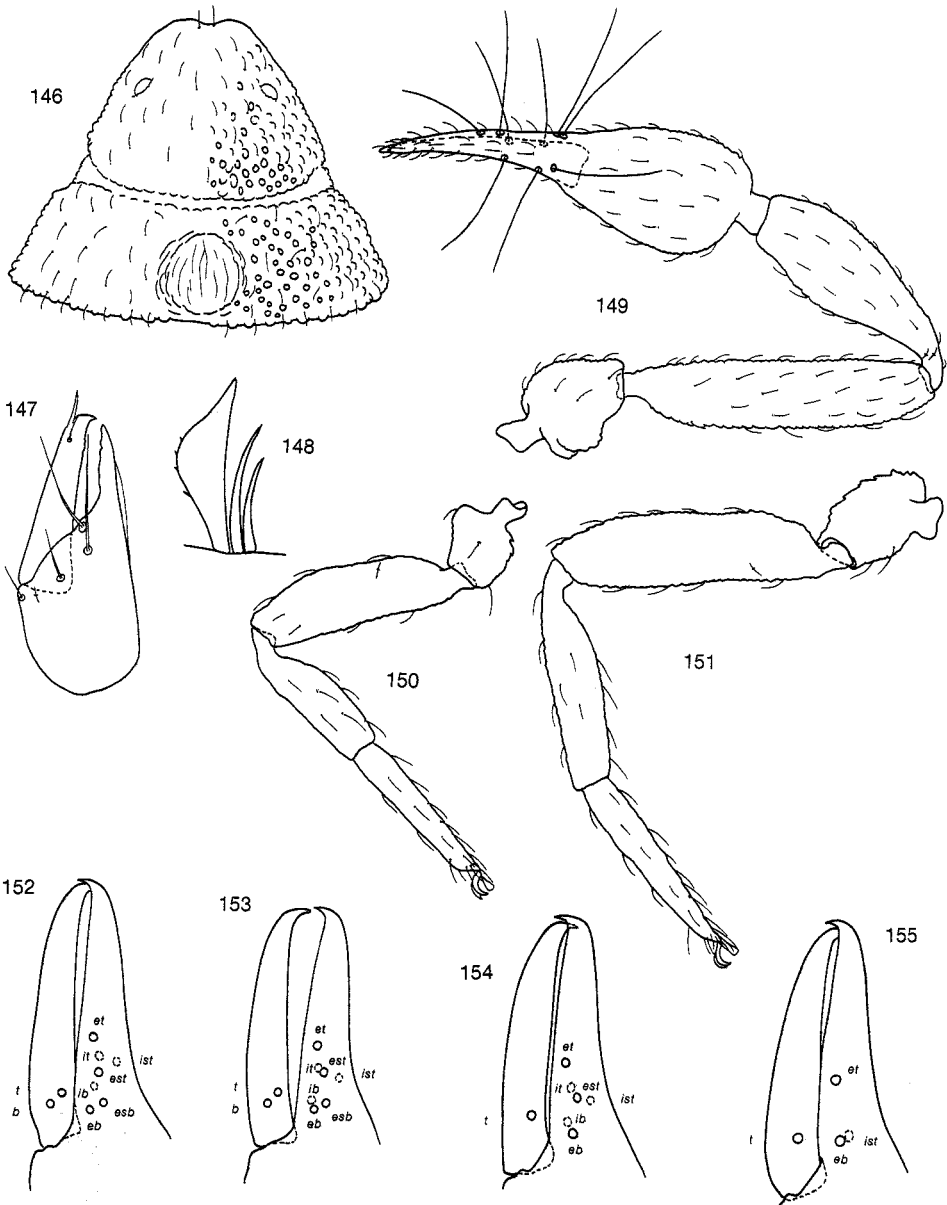
Family **GEOGARYPIDAE** Chamberlin

Geogarypinae Chamberlin, 1930: 609.

Geogarypidae Chamberlin. – Harvey, 1986: 754.

Diagnosis

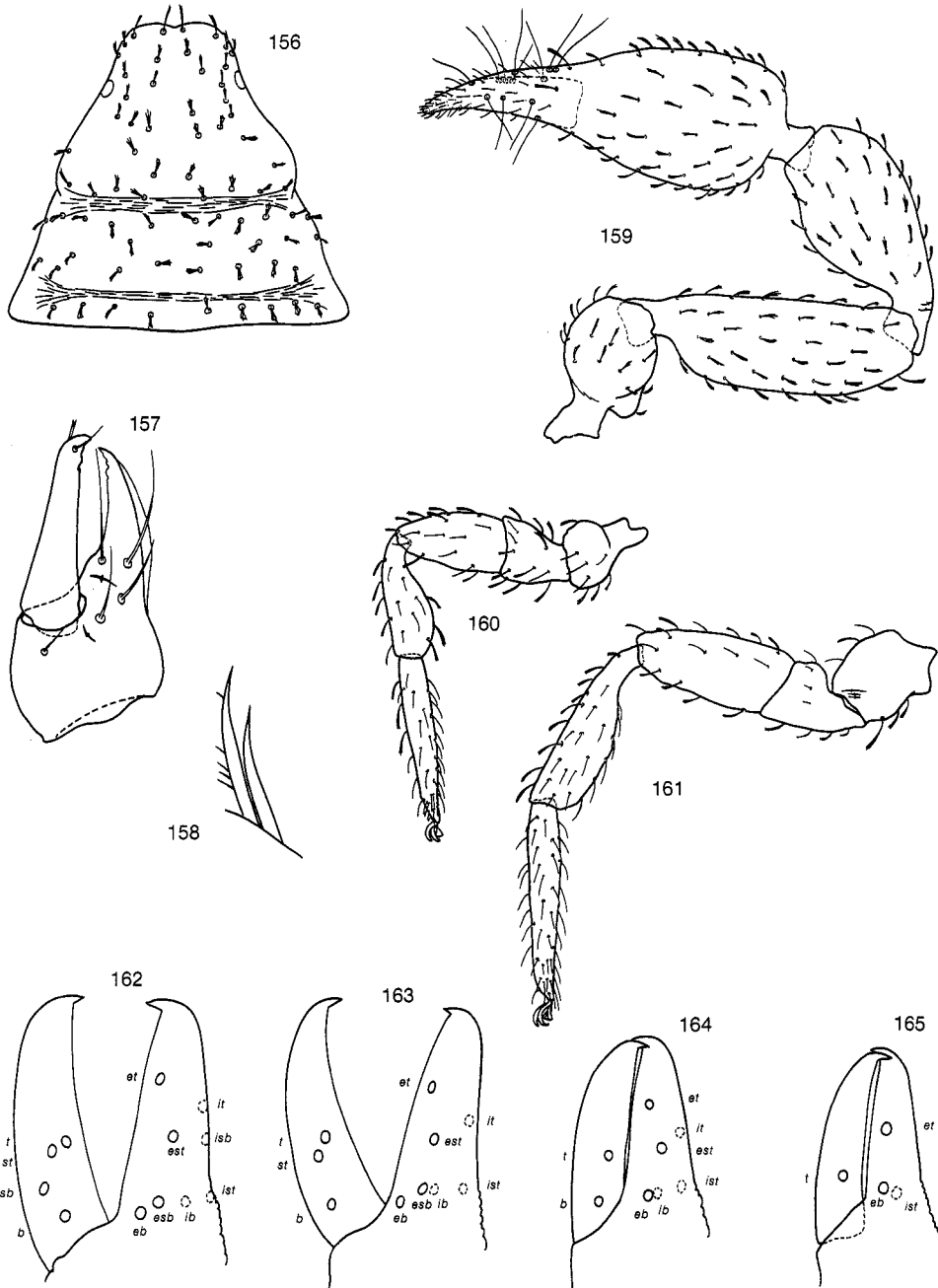
Fixed chelal finger with pit-like structures on external margin (A). Cheliceral flagellum of single blade (A), without spinules (A).



Figs 146–155. Cheiridiidae. 146–151, *Cheiridium museorum* (Leach): 146, carapace; 147, chelicera; 148, flagellum; 149, right pedipalp; 150, leg I; 151, leg IV; 152–155, *Cryptocheiridium elgonense* Beier, left chela, after Mahnert (1982a): 152, adult; 153, tritonymph; 154, deutonymph; 155, protonymph.

Remarks

Geogarypids are generally litter-dwelling pseudoscorpions. Three genera were recognised by Harvey (1986): *Geogarypus* Chamberlin, *Afrogarypus* Beier and *Indogarypus* Beier.

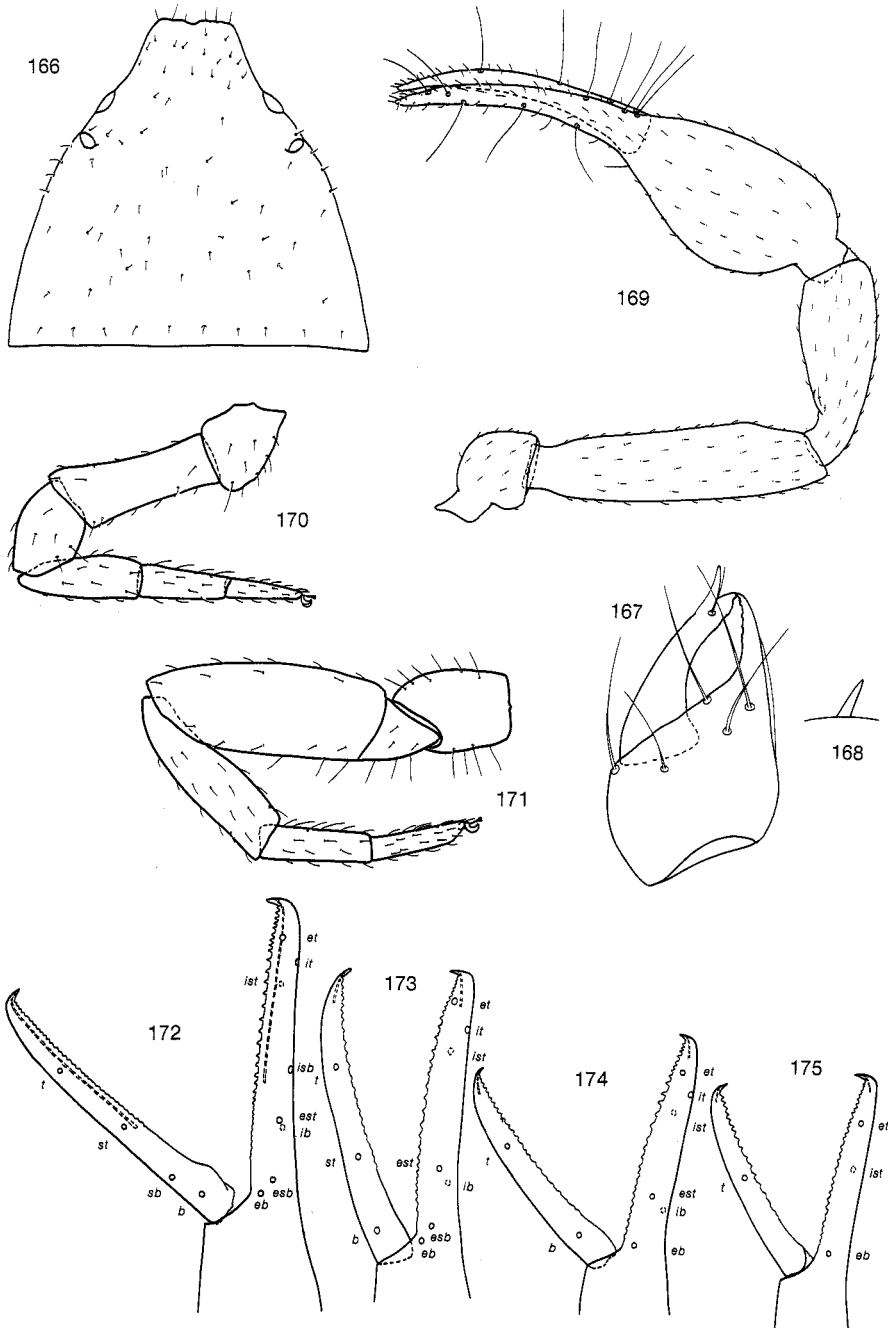


Figs 156–165. Pseudochiridiidae. 156–161, *Pseudochiridium clavigerum* (Thorell): 156, carapace; 157, chelicera; 158, flagellum; 159, right pedipalp; 160, leg I; 161, leg IV; 162–165, *Pseudochiridium heurtaultae* Vitali-di Castri, left chela, after Vitali-di Castri (1970): 162, adult; 163, tritonymph; 164, deutonymph; 165, protonymph.

Superfamily **OLPIOIDEA** Banks, stat. nov.

Diagnosis

1-2 trichobothria present on basal half of pedipalpal femur (A). Carapace subrectangular (P). Eyes not set on ocular tubercles (P). Eyes situated near anterior margin of carapace (P). Abdomen subrectangular (P). Anterior margin of carapace straight (P).



Figs 166-175. Geogarypidae. *Geogarypus taylori* Harvey, mostly after Harvey (1986): 166, carapace; 167, chelicera; 168, flagellum; 169, right pedipalp; 170, leg I; 171, leg IV; 172-175, left chela: 172, adult; 173, tritonymph; 174, deutonymph; 175, protonymph.

Remarks

The sole apomorphy identified for this taxon is the femoral trichobothria. Chamberlin (1930, 1931a) included the Olpiidae and Menthidae in the Garypoidea, but all characters listed by him to define the superfamily were simply symplesiomorphies.

Family **OLPIIDAE** Banks

Olpiinae Banks, 1895: 2.

Olpiidae Banks.—Chamberlin, 1930: 588.

Diagnosis

Specialised condylar articulation joint absent between coxae II and III (P). Venom apparatus present in both chelal fingers (P). Adults without three accessory trichobothria on fixed chelal finger and hand (P).

Remarks

At present, this large family lacks any synapomorphies. The maintenance of Olpiinae Banks, 1895 over Garypininae Daday, 1888 is discussed above.

Family **MENTHIDAE** Chamberlin

Menthidae Chamberlin, 1930: 585.

Diagnosis

Specialised condylar articulation joint between coxae II and III (A). Venom apparatus absent from movable chelal finger (A). Adults with three accessory trichobothria on fixed chelal finger and hand (A).

Remarks

A recent review of the Menthidae (Harvey and Muchmore 1990) recognised four genera: *Menthus* Chamberlin, *Oligomenthus* Beier, *Paramenthus* Beier and *Thenmus* Harvey.

Microorder **ELASSOMMATINA**, nov.*Diagnosis*

Two or no eyes (A). Arolium shorter than claws (P).

Remarks

This group of two superfamilies is united by a number of apomorphies, none of which is unique to the group.

Etymology

The name refers to the presence of only two or no eyes in all of its members (*elasso* Greek, lessen, diminish; *omma* Greek, eye).

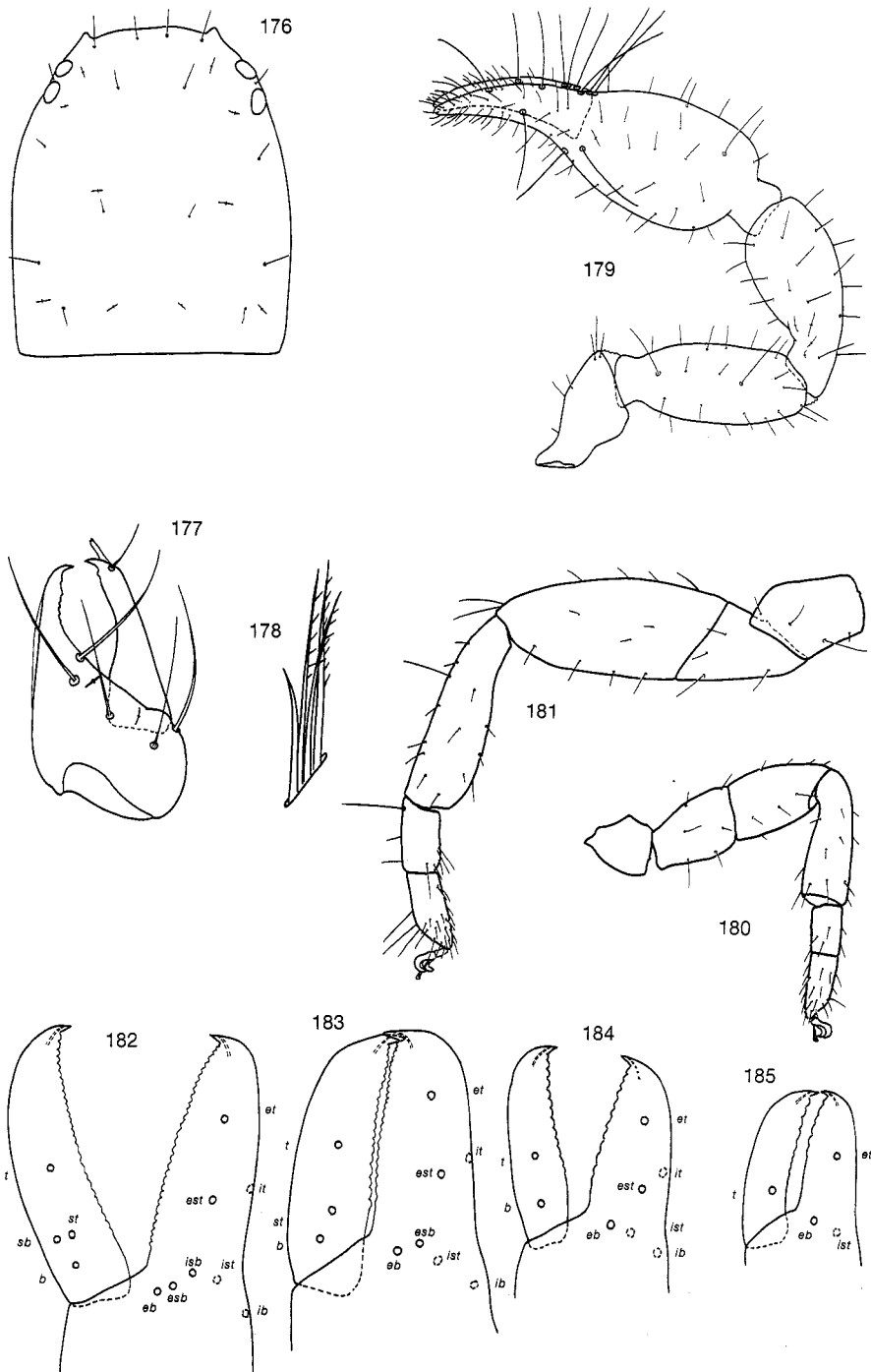
Superfamily **STERNOPHOROIDEA** Chamberlin, stat. nov.*Diagnosis*

Pseudosternum present (A). Posterior margin of carapace V-shaped (A).

Remarks

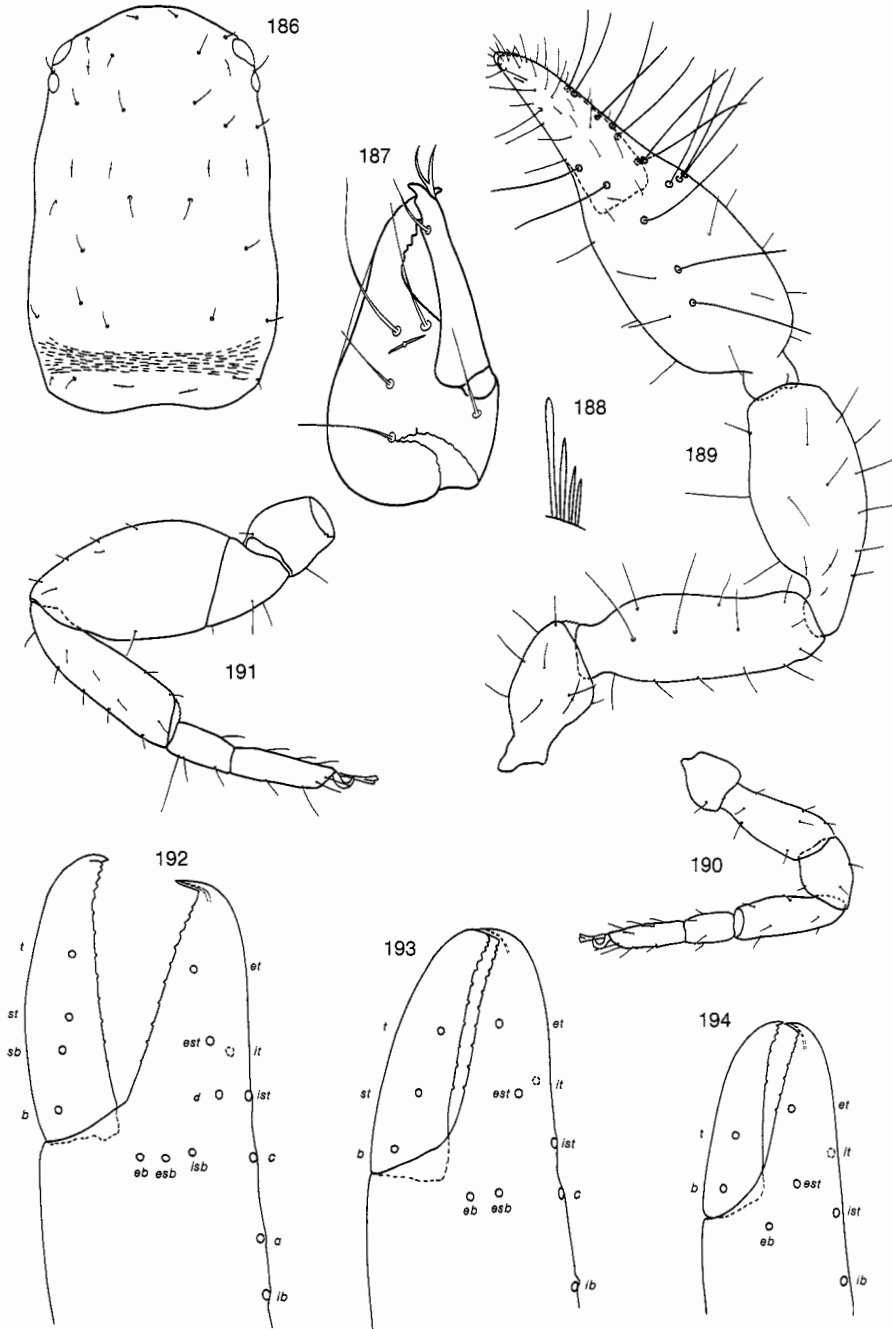
Chamberlin (1931a) placed the Sternophoridae within the Cheiridioidea on the slender grounds that all three families were 'homofemorate', i.e. the femora (now femur/patella) of legs I and II were morphologically similar to those of III and IV. In most other respects, the Sternophoridae are dissimilar to cheiridiids and pseudocheiridiids, which are here transferred to the Garypoidea (see above). They are here united with the Cheliferoidea in the

Elassommatina, which is distinguished by the presence of two or no eyes, the femur of the anterior legs being shorter than the patella, and the fusion of the metatarsi and tarsi. While none of these characters is completely limited to these two superfamilies, the paedomorphic



Figs 176–185. Olpiidae. 176, 179, 182–185, *Beierolpium oceanicum* (With), after Harvey (1988b); 177, 178, 180, 181, *Protogarypinus* sp.: 176, carapace; 177, chelicera; 178, flagellum; 179, right pedipalp; 180, leg I; 181, leg IV; 182–185, left chela: 182, adult; 183, tritonymph; 184, deutonymph; 185, protonymph.

tendencies of the Sternophoridae (such as lack of trichobothria *isb* and *sb*) ensure that their relationships to other superfamilies remain obscure. Although they lack spermathecae (which excludes them from the Cheliferoidea as currently recognised), details of their mating habits and spermatophore morphology are unknown. Beier (1954) suggested that they may be related to the Chernetidae, but this was dismissed by Heurtault (1983) and Harvey (1985).



Figs 186–194. Menthidae. *Thenmus aigialites* Harvey, after Harvey and Muchmore (1990): 186, carapace; 187, chelicera; 188, flagellum; 189, right pedipalp; 190, leg I; 191, leg IV; 192–194, left chela: 192, adult; 193, tritonymph; 194, deutonymph.

Family **STERNOPHORIDAE** Chamberlin

Sternophorinae Chamberlin, 1923*b*: 370–1.

Sternophoridae Chamberlin.—Chamberlin, 1931*a*: 238.

Diagnosis

As for superfamily.

Remarks

Sternophorids are small, pale, and extremely flattened. They are found under bark of trees or logs, and the family currently contains three genera (Harvey 1985): *Garyops* Banks, *Idiogaryops* Hoff and *Afrosteronphorus* Beier.

Superfamily **CHELIFEROIDEA** Risso

Cheliferoidea Risso.—Chamberlin, 1931*a*: 239–40.

Diagnosis

Spermathecae present (A). Spermatophore complex (A). Mating dance performed (A).

Remarks

Female withiids and chernetids possess a pair of lateral apodemes on the lateral margins of the genital region that are lacking in all other pseudoscorpions (including other Cheliferoidea). This may constitute a synapomorphy for these two families, which would contradict the hypothesis that the Chernetidae belong in a clade with the Cheliferidae and the Atemnidae, based upon the oblique junction between the femur and patella of the anterior legs.

Family **WITHIIDAE** Chamberlin

Withiinae Chamberlin, 1931*b*: 290.

Withiidae Chamberlin.—Weygoldt, 1970: 253.

Diagnosis

Males (and occasionally females) with sensory setae on posterior sternites (A).

Remarks

Males of three genera, *Protowithius* Beier, *Juxtachelifer* Hoff and *Termitowithius* Muchmore, lack the abdominal sensory setae characteristic of the family. However, they appear to be true members of the Withiidae.

Family **CHELIFERIDAE** Risso

Cheliferidae Risso, 1826: 157.

Diagnosis

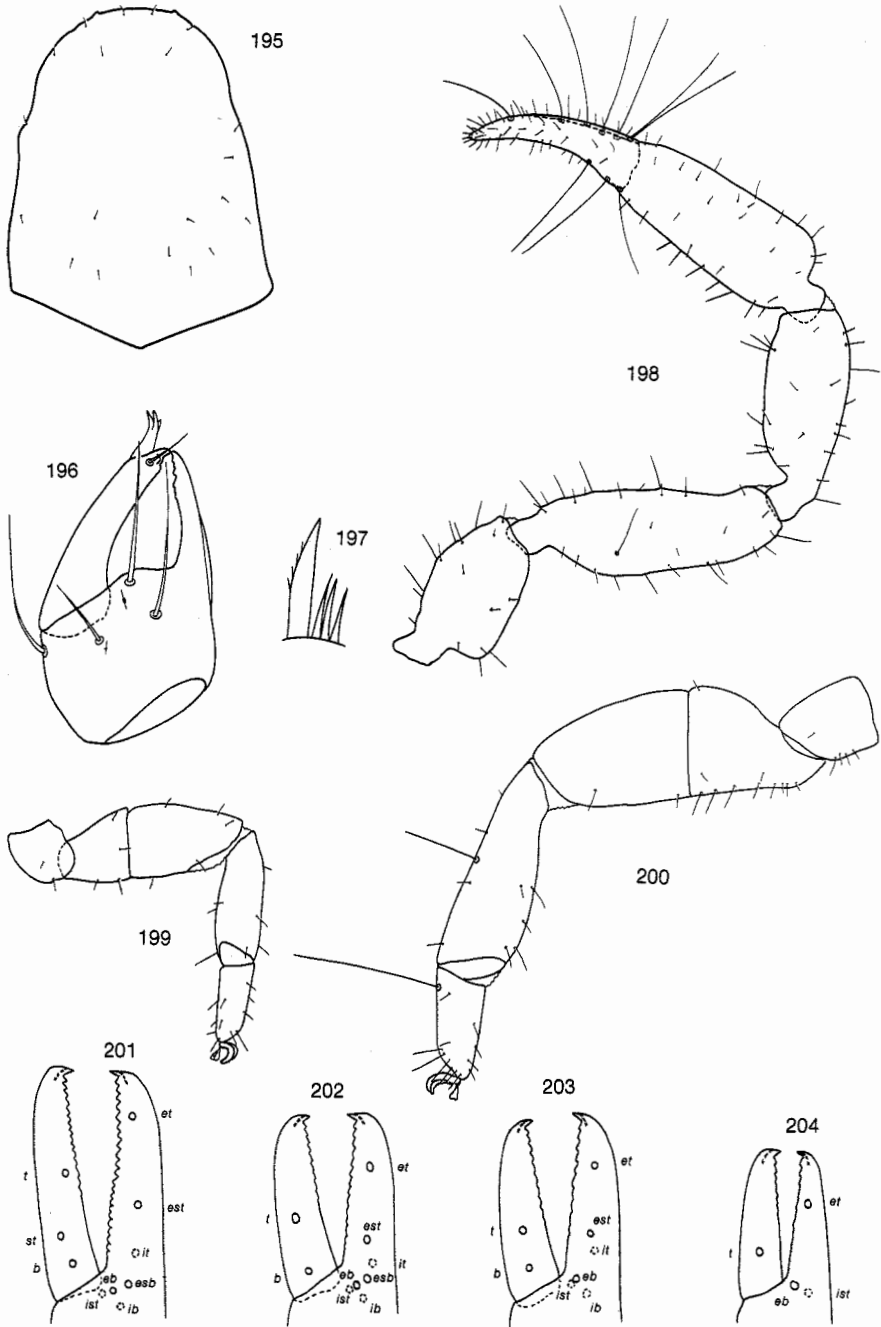
Male genitalia with ram's horn organs (A). Coxa IV of males with coxal sac (A). Claws of leg I assymetrical in males (A).

Remarks

Some taxa included in this family lack one or more of the three synapomorphies cited above.

Philomaoria Chamberlin (along with the *Philomaoriini* Chamberlin) was originally placed in the Withiinae (Chamberlin 1931*b*). Examination of the type material of *Philomaoria pallipes* (White) and *P. novazealandica* Chamberlin reveals the possession of an oblique

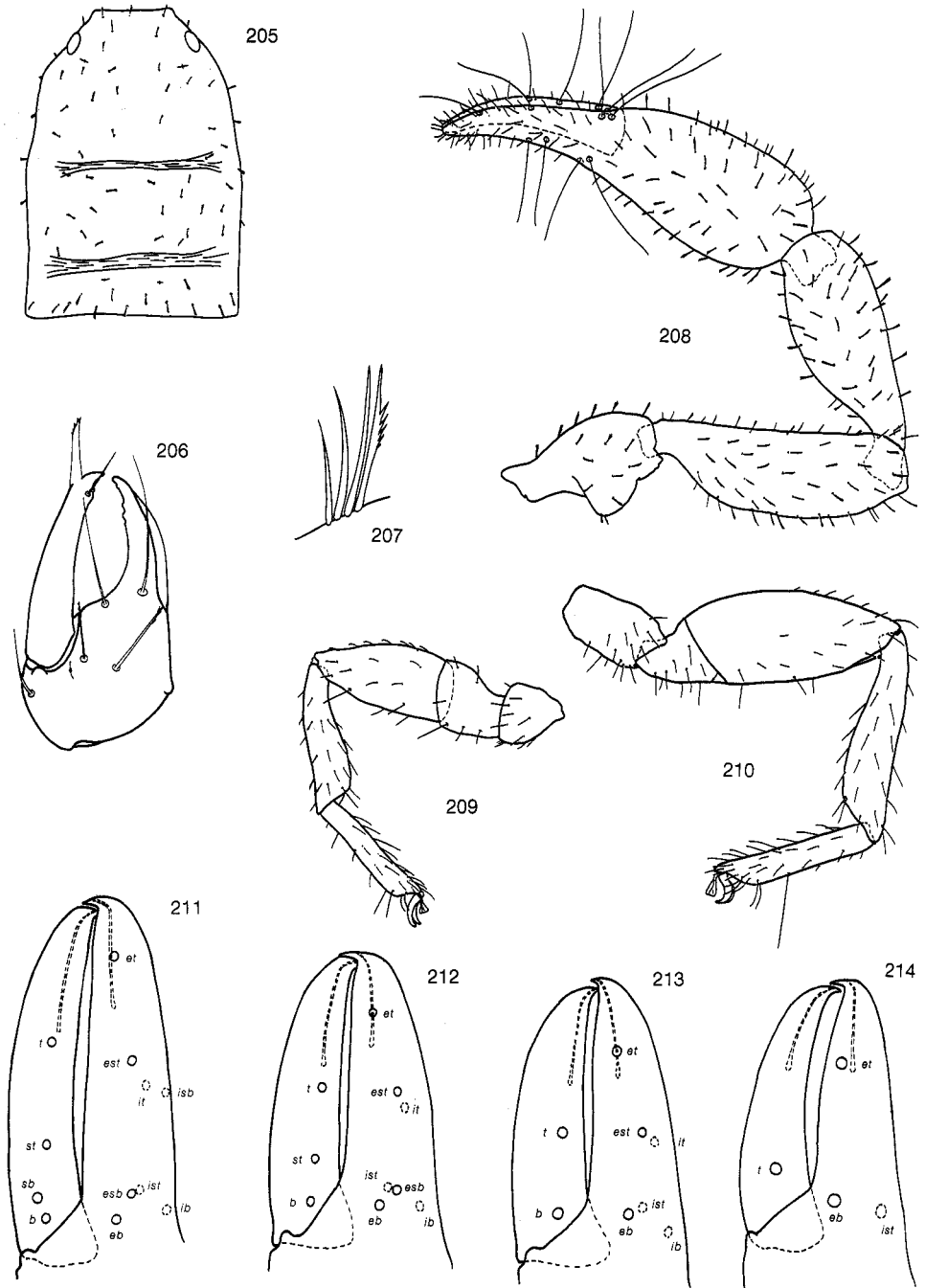
suture line between the anterior femora and patellae and a lack of abdominal sensory setae. Although *Philomaoria* lacks all three synapomorphies cited above, it is here transferred to the Cheliferidae. The form of the male genitalia supports this opinion.



Figs 195–204. Sternophoridae. 195–198, *Garyops depressus* Banks: 195, carapace; 196, chelicera; 197, flagellum; 198, right pedipalp; 199–200, *Garyops sini* (Chamberlin): 199, leg I; 200, leg IV; 201–204, *Afrosternophorus hirsti* (Chamberlin), left chela: 201, adult; 202, tritonymph; 203, deutonymph; 204, protonymph.

Family **CHERNETIDAE** Menge

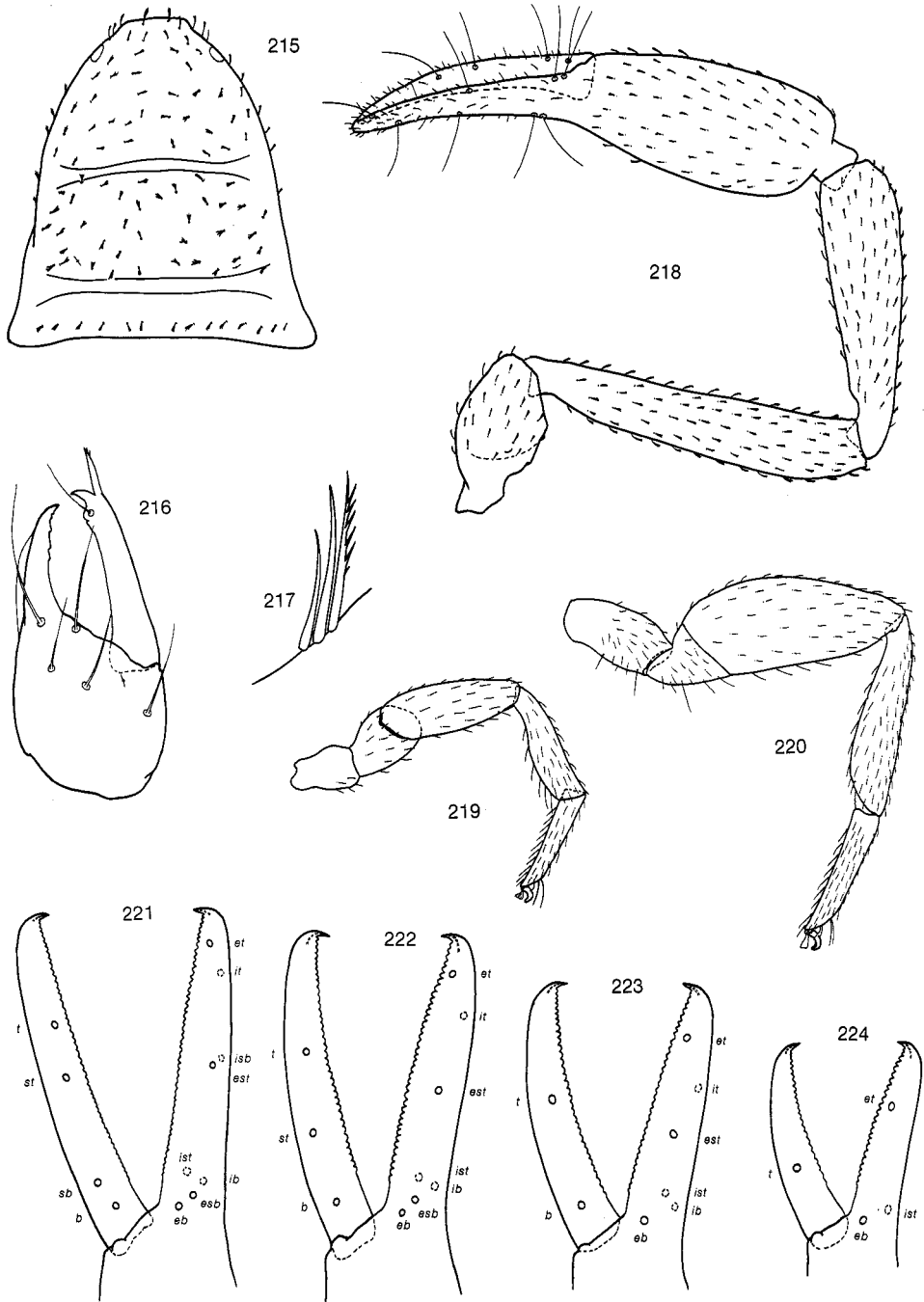
Chernetidae Menge, 1855: 22.



Figs 205–214. Withiidae. 205–210, *Withius piger* (Simon): 205, carapace; 206, chelicera; 207, flagellum; 208, right pedipalp; 209, leg I; 210, leg IV; 211–214, *Dolichowithius mediofasciatus* Mahnert, left chela, after Mahnert (1979): 211, adult; 212, tritonymph; 213, deutonymph; 214, protonymph.

Diagnosis

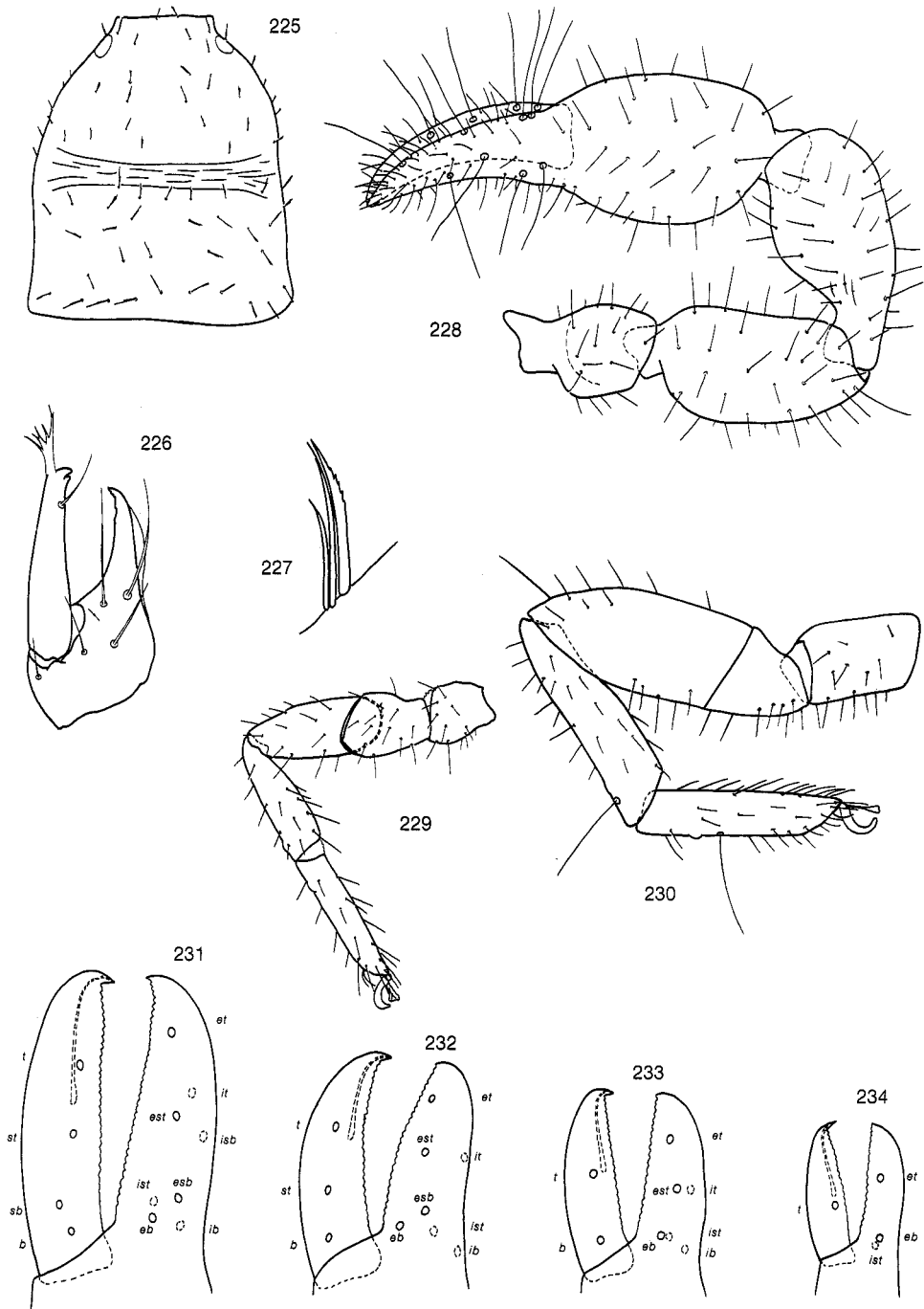
Tarsi with proximal raised slit sensillum (A). Venom apparatus absent from or substantially reduced in fixed chelal finger (A). Chelal fingers usually with at least one accessory tooth (A). Male genitalia of 'chernetid' type (A).



Figs 215–224. Cheliferidae. *Protochelifer victorianus* Beier: 215, carapace; 216, chelicera; 217, flagellum; 218, right pedipalp; 219, leg I; 220, leg IV; 221–224, left chela: 221, adult; 222, tritonymph; 223, deutonymph; 224, protonymph.

Remarks

The presence of accessory teeth appears to be an excellent synapomorphy for the family, although they appear to be absent in some taxa, such as *Myrmochernes africanus* Tullgren



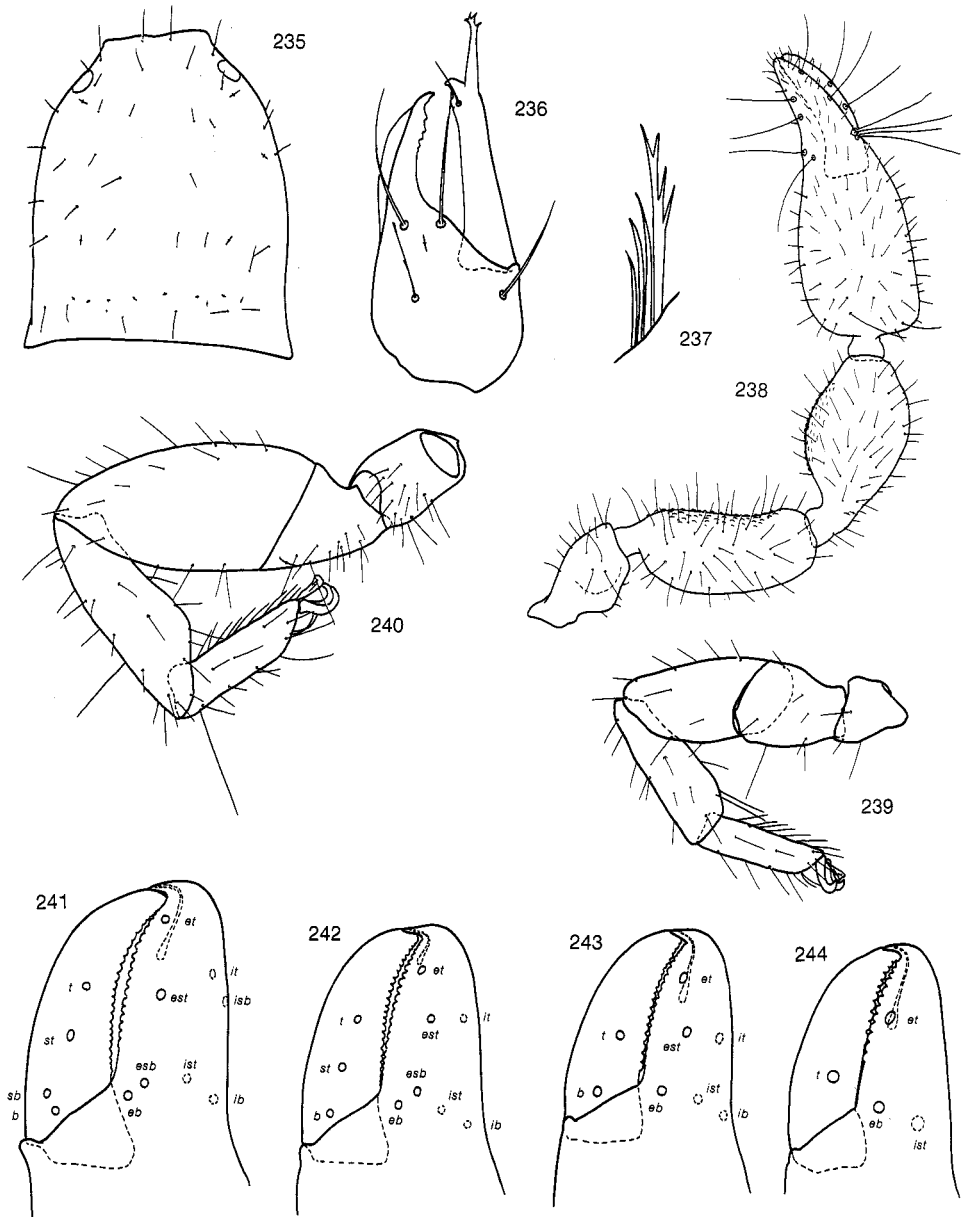
Figs 225–234. Chernetidae. *Lamprochernes savignyi* (Simon), mostly after Harvey (1987b): 225, carapace; 226, chelicera; 227, flagellum; 228, right pedipalp; 229, leg I; 230, leg IV; 231–234, left chela: 231, adult; 232, tritynymph; 233, deutonymph; 234, protonymph.

(Judson 1985), *Reischekia* spp. (Beier 1965) and *Cacoxylus echinatus* (Beier) (Beier 1965). Hoff's (1949) claim that *Wyochernes hutsoni* lacks accessory teeth was refuted by Muchmore (1990b). Another synapomorphy is the lack of a venom apparatus from the fixed chelal finger. However, Judson (1985) has shown that *Myrmochernes africanus* Tullgren lacks a venom apparatus from both chelal fingers.

Family ATEMNIDAE Chamberlin

Atemnidae Chamberlin, 1931a: 243-4.

Miratemnidae Beier. — Dumitresco and Orghidan, 1970: 134.



Figs 235-244. Atemnidae. *Oratemnus curtus* (Beier): 235, carapace; 236, chelicera; 237, flagellum; 238, right pedipalp; 239, leg I; 240, leg IV; 241-244, left chela: 241, adult; 242, tritonymph; 243, deutonymph; 244, protonymph.

Diagnosis

Venom apparatus absent from movable chelal finger (A).

Remarks

The Atemnidae were divided into two families (Atemnidae and Miratemnidae) by Dumitresco and Orghidan (1970). The Miratemnidae was defined by the presence of a peculiar Barrois' organ, 'baguettes latérales' (lateral rod) of the male genitalia extending forward and not united anteriorly, and two carapacial furrows (Dumitresco and Orghidan 1970). As briefly mentioned by Harvey (1991a), I prefer to reduce the Miratemnidae to subfamily status within the Atemnidae, as I believe that the diagnostic characters are not particularly useful at the family level. Only one miratemnine species has been examined to determine the nature of Barrois' organ, and further data on a variety of different atemnid genera are necessary before we can fully assess the utility of this character. The anteriorly directed lateral rod found in miratemnines (Chamberlin 1933; Vachon 1938; Dumitresco and Orghidan 1969) is apparently not unique to the Miratemninae, as the atemnid *Paratemnoides assimilis* (Beier) also has anteriorly directed lateral rods (Harvey 1988b).

Chamberlin (1933) listed two additional characters to distinguish the Miratemninae from the Atemninae: cheliceral hand with five setae (four in Atemninae), and tactile seta of leg IV submedial (sub-basal in Atemninae). Neither of these characters warrant the separation of the two subfamilies to familial level. Therefore, I regard Miratemnidae as a synonym of Atemnidae.

Acknowledgments

This review would not have been possible without the examination of numerous specimens borrowed from or donated by colleagues. In particular, Dr Jacqueline Heurtault (Paris), Mr Paul Hillyard (London), Mr Mark Judson (Leeds), Dr Volker Mahnert (Geneva), Dr W. Muchmore (Rochester) and Dr Norman Platnick (New York) provided much material. Dr Heather Proctor assisted with sperm transfer data, and Dr William B. Muchmore, Dr V. Mahnert and Dr Robert Raven kindly reviewed a draft of the manuscript.

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