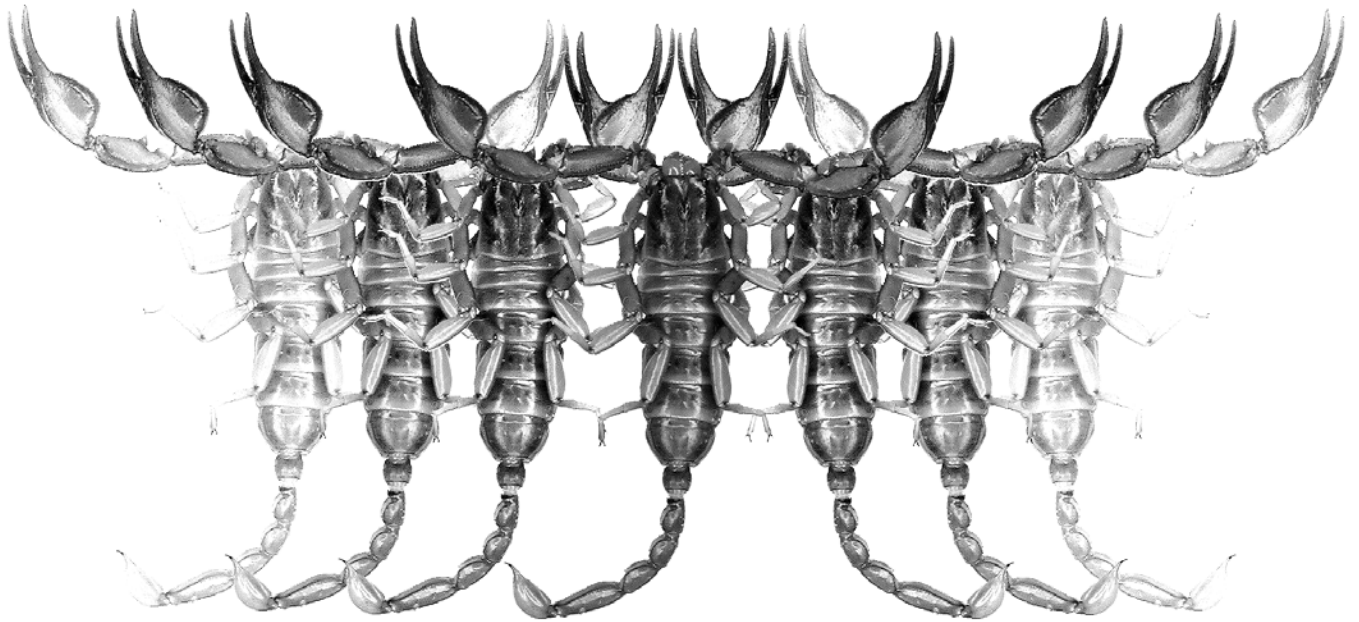


Euscorpius

Occasional Publications in Scorpiology



**High-Level Systematics and Phylogeny of the
Extant Scorpions (Scorpiones: Orthosterni)**

Michael E. Soleglad and Victor Fet

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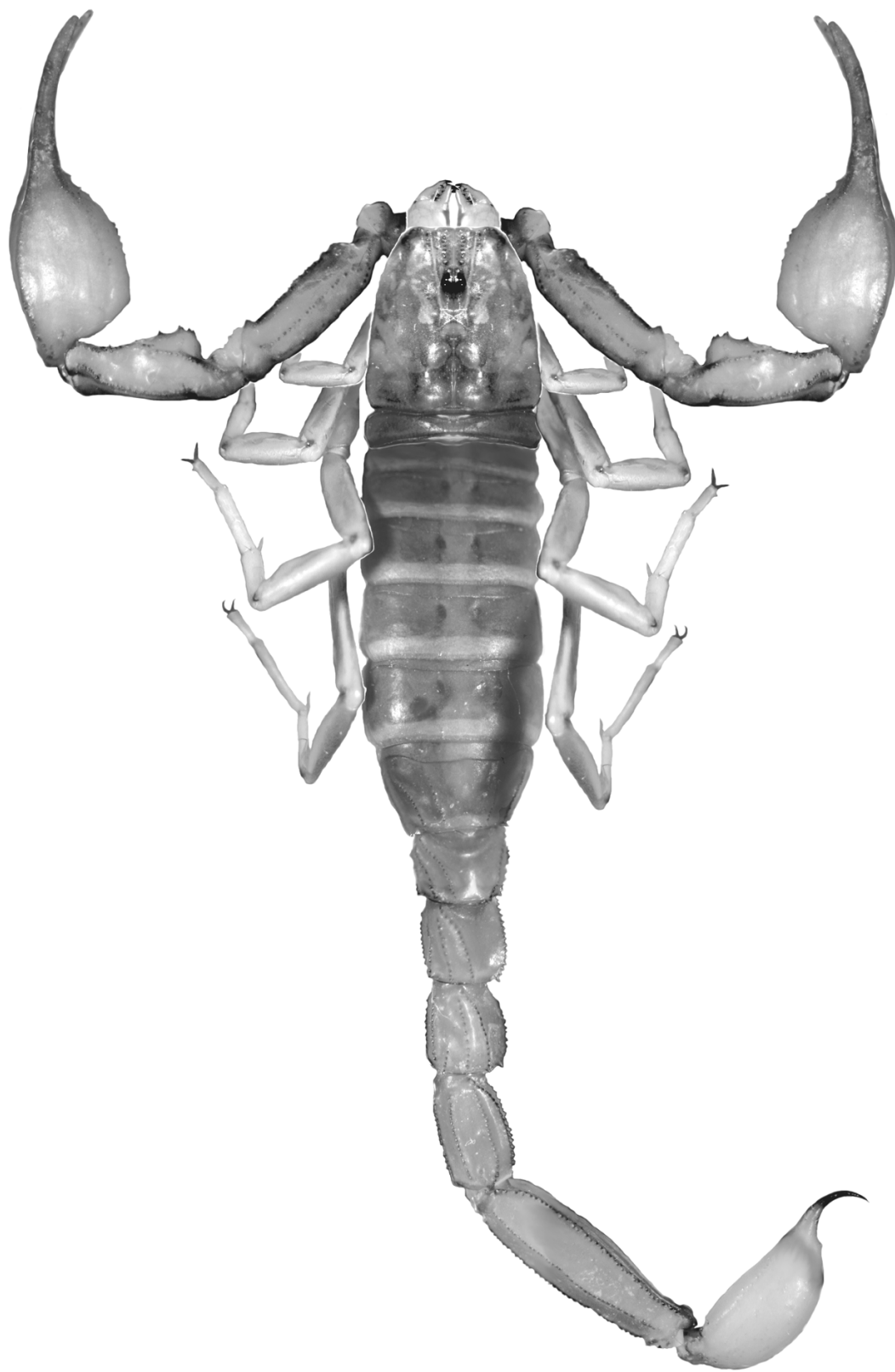
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- **ZISP**, Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia
- **WAM**, Western Australian Museum, Perth, Australia
- **NTNU**, Norwegian University of Science and Technology, Trondheim, Norway



Pseudochactas ovchinnikovi Gromov ♀



To the memory of

ALEXEI ANDREEVICH BYALYNITSKII-BIRULYA

(A. BIRULA)

(2 November 1864, Babkovo, Mogilev Region – 18 June 1937, Leningrad),

a great Russian zoologist

High-level systematics and phylogeny of the extant scorpions (Scorpiones: Orthosterni)

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“...there is the naturalist’s interest in disentangling the life histories of little-known insects, in learning about their habits and structure, and in determining their position in the scheme of classification—a scheme which can be sometimes pleasurably exploded in a dazzling display of polemical fireworks when a new discovery upsets the old scheme and confounds its obtuse champions. ...”

(Vladimir Nabokov, interview with Alvin Toffler, *Playboy*, January 1964).

Summary

A number of authors (e. g. Birula, 1917a, 1917b; Mello-Leitão, 1945; Stockwell, 1989) addressed above-level systematics of extant scorpions, and accepted the grouping of scorpion families in several superfamilies. At the same time, Kjellesvig-Waering (1986) classified all extant scorpions under the same superfamily, Scorpionoidea. Sissom (1990) and Fet et al. (2000) did not list any superfamilies, considering the systematic situation above family (and often at the family level as well) unresolved. Most recently, Lourenço (2000a) listed six superfamilies, largely following the unpublished but important study of Stockwell (1989). The goal of this paper is to address scorpion systematics and phylogeny above genus level. We conducted a comprehensive, cladistic morphological analysis of 90 extant genera (over 150 species) of scorpions belonging to all recognized families. We especially concentrated on relationships among so-called “chactoid” scorpions, where subfamilies, tribes, and subtribes were revised and/or established. The family Chactidae was given a special attention due to the number of phylogenetic and taxonomic issues that were revised. In addition, we addressed the status of a recently discovered, unique relict family Pseudochactidae, and the systematic relationships within Iuridae. As a result of intensive study, we propose a number of sweeping changes in current scorpion taxonomy; the results of analyses leading to these changes are discussed in detail. The category of **parvorder**, subordinate to infraorder, is introduced for the first time in arachnid systematics. Four extant parvorders are recognized within the scorpion infraorder Orthosterni: Buthida, Chaerilida, Pseudochactida, and Iurida. Six extant **superfamilies** are recognized: Buthoidea, Chactoidea (=Vaejovoidea, **syn. n.**), Chaeriloidea, Iuroidea (**new**), Pseudochactoidea (**new**), and Scorpionoidea (=Bothriuroidea, **syn. n.**). Parvorders Buthida, Chaerilida and Pseudochactida are monotypic, each including a single superfamily; parvorder Iurida includes three superfamilies (Chactoidea, Iuroidea, and Scorpionoidea). We recognize 14 extant scorpion **families**: Bothriuridae, Buthidae, Caraboctonidae, Chactidae, Chaerilidae, Euscorpiidae, Iuridae, Liochelidae, Microcharmidae, Pseudochactidae, Scorpionidae, Superstitioniidae, Urodacidae, and Vaejovidae. Superfamilies Chaeriloidea and Pseudochactoidea are monotypic; superfamily Buthoidea includes two families (Buthidae and Microcharmidae). Superfamily Iuroidea includes two families (Caraboctonidae and Iuridae); subfamily Caraboctoninae (formerly in Iuridae) is elevated to the family rank. Superfamily Chactoidea includes four families: Chactidae, Euscorpiidae, Superstitioniidae (=Troglotayosicidae, **syn. n.**), and Vaejovidae. Within Chactidae, three subfamilies are established: Chactinae, Brotheinae, and Uroctoninae. Within Chactinae, two tribes are established: Chactini and Nullibrotheini, **new tribe** (monotypic). Within new subfamily Brotheinae, two tribes are established: Brotheini and Belisariini (monotypic). Within Brotheini, two subtribes are established: Brotheina and Neochactina, **new subtribe**; the latter is based on a new genus, *Neochactas*, **gen. n.** Within Brotheina, genera *Cayooca*, *Guyanochactas*, and *Taurepania* are synonymized with *Broteochactas*. Subfamily Uroctoninae is restored from synonymy under Vaejovidae and transferred to Chactidae; it includes genera *Uroctonus* and *Anuroctonus* (the latter transferred from the erstwhile Iuridae). Family Troglotayosicidae is abolished, and its two genera are transferred to other families: *Troglotayosicus*, to Superstitioniidae; and *Belisarius*, to Chactidae. Subfamily Belisariinae is downgraded to the tribe rank and transferred to Chactidae (subfamily Brotheinae). Superfamily Scorpionoidea includes four families: Bothriuridae, Liochelidae (=Hemiscorpiidae, **syn. n.**), Scorpionidae (=Diplocentridae, **syn. n.**), and Urodacidae (=Heteroscorpionidae, **syn. n.**). Family Diplocentridae is downgraded to the subfamily rank in Scorpionidae. Subfamily Nebinae is downgraded to the tribe rank in Diplocentrinae. Family Hemiscorpiidae is downgraded to the subfamily rank in Liochelidae. Family

Heteroscorpionidae is downgraded to the subfamily rank in Urodacidae. We provide detailed classification, taxonomic history, and diagnoses of all recognized scorpion taxa above genus level. The phylogeny and biogeographic implications are discussed. As an addition, we present, among other materials, results of the first pilot high-level scorpion DNA phylogeny, including representatives of seven families spanning all four parvorders. Both morphological analysis and DNA sequence analysis support the primitive nature of parvorders Pseudochactida, Buthida, and Chaerilida, as opposed to the derived position of parvorder Iurida. Especially remarkable is the parvorder Pseudochactida, which exhibits many primitive features. Within Iurida, the superfamily Iuroidea is firmly established as a basal group, and Scorpionoidea, as the most derived group. Phylogeny within Chactoidea shows ancient nature of many clades, as our analysis reveals hitherto unexpected relationships between a number of genera and tribes.

Introduction

Current literature on scorpion taxonomy recognizes 16 formally valid extant scorpion families (some including extinct genera or species): Bothriuridae, Buthidae, Chactidae, Chaerilidae, Diplocentridae, Euscorpidae, Hemiscorpiidae, Heteroscorpionidae, Iuridae, Liichelidae, Microcharmidae, Pseudochactidae, Scorpionidae, Superstitioniidae, Troglotayosicidae, and Urodacidae (Fet et al., 2000; Lourenço, 1998a, 1998b, 2000a; Prendini, 2000, 2001, 2003; Soleglad & Sissom, 2001; ICZN, 2003). This increase from nine families recognized only a decade ago (Sissom, 1990) indicates a considerable activity in high-level scorpion taxonomy. This activity was marked by a discovery of entirely new families such as Pseudochactidae (Gromov, 1998); elevating in rank existing subfamilies such as Euscorpinae and Superstitioniinae (Stockwell, 1992), Heteroscorpioninae (Lourenço, 1996a), Hemiscorpiinae and Urodacinae (Prendini, 2000; Lourenço, 2000a); and creating new taxa of family rank for genera formerly placed in other families, such as Microcharmidae and Troglotayosicidae (Lourenço, 1996a, 1998a, 1998b). Monophyly and rank of some newly created families are disputable—see e.g. Prendini (2000, 2001, 2003a, 2003b) and Lourenço (2000a) on family status of Hadogenidae and Lisposomidae.

Relevant to the systematics of extant scorpion families is the recent progress in reassessment of existing fossil scorpion taxa, and description of new ones. Kjellesvig-Waering (1986) revised all fossil scorpions, majority of which belong to now extinct lineages at the level of suborders and infraorders. The subsequent work of Stockwell (1989) and Jeram (1994a, 1994b, 1998) confirmed that only a small portion of fossil scorpion taxa, belonging to the infraorder Orthosterni (also spelled as Orthosternina) can be placed among ancestors of extant families. However, the dearth of orthostern fossils presented the dramatic gap for any such analysis—none were listed by Kjellesvig-Waering (1986) between the Carboniferous and the Tertiary. This is why especially important are the recent discoveries of Cretaceous orthostern scorpions from Brazil (Campos, 1986; Carvalho & Lourenço, 2001), Lebanon (Lourenço, 2001c), Burma (Lourenço, 2002a; Santiago-Blay et al.,

in press), and France (Lourenço, 2003). Other, more recent fossils belong to extant families, among which Buthidae predominate in Tertiary amber inclusions (Lourenço & Weitschat, 1996, 2000, 2001).

In addressing the high-level scorpion phylogeny and systematics, the unpublished work of Stockwell (1989) stands alone as the most important treatment, and the first which employed the Hennigian cladistic methods. Stockwell's approach and interpretations clearly set a new standard for scorpion phylogenetic work. Equally important was Stockwell's inclusion of fossil taxa in his analysis, which has not been attempted before by any modern scorpion systematist. Availability by the time of Stockwell's work of the monumental volume of Kjellesvig-Waering (1986) allowed Stockwell (1989) to include informed statements on fossil scorpions, especially on infraorder Orthosterni. Importance of the evaluation of the orthostern fossils as relevant to extant scorpions became even clearer with the emergence of brilliant works by Jeram (1994a, 1994b, 1998) who described in a great detail a number of Carboniferous taxa.

In the last decade, a dramatic activity has been seen in re-evaluating generic composition of traditional families such as the most recent cladistic revisions of superfamily Scorpionoidea by Prendini (2000), and of family Euscorpidae by Soleglad & Sissom (2001). Many other families, including the most diverse scorpion family, Buthidae, are still awaiting vigorous reassessment of intrafamilial relationships. At the same time, phylogeny at the higher level, i.e. among the families of the extant scorpions, is not well resolved (Fet et al., 2000). Recently, we (Soleglad & Fet, 2001) published a cladistic analysis of scorpion phylogeny based on trichobothrial characters—one of the most comprehensive character sets in scorpions. Our later work (Soleglad & Fet, 2003) addressed another important character, scorpion sternum, and its phylogenetic importance. The goal of the present paper is to clarify the high-level phylogeny and systematics of all extant scorpions. We seek to expand the morphological analysis to an exhaustive list of morphological character sets. We also provide and discuss a preliminary molecular (DNA) data analysis. Further detailed information on scorpion taxonomy at genus level and below can be found in the "Catalog of Scorpions of the World" (Fet et al., 2000).

Historical interpretations of high-level phylogeny of extant scorpions

Already some early (“pre-cladistic”) phylogenetic schemes for the scorpion order allowed to see the recurrent pattern of several emerging branches, especially emphasizing Buthidae as a very separate branch of scorpions—superfamily Buthoidea, or “buthoids” (Birula, 1917a, 1917b; Vachon, 1952). The separate status of Buthidae as opposed to other scorpion families has been since confirmed by broad biological evidence from many different areas, including morphology, reproductive anatomy, gametogenesis, and toxins (Farley, 2001).

Thorell (1876a: 5) stated “Scorpions form so compact and uniform group that it is extremely difficult, perhaps impossible to say with certainty which of them are the highest and which the lowest”. However, at the same time, Thorell (1876b: 86) was the first to introduce a Darwinian “tree-thinking” style in the issue of scorpion evolution. He presented a simple phylogenetic tree (“arbre généalogique”) of arachnids, where monophyletic (as we would say now) scorpions formed the branching order (Telegonoidae, (Androctonoidae, (Vejovoidae, Pandinoidea))). This scheme in later terminology corresponds exactly to the superfamilies of Mello-Leitão (1945) if presented as (Bothriuroidea, (Buthoidea, (Chactoidea, Scorpionoidea))). Of course, we are far from assigning cladistic values to this “phylogenies”, as they are clearly phenetic: the very fact that Thorell (1876b) and Mello-Leitão (1945) considered Bothriuroidea a separate lineage is based undoubtedly on the unique sternum shape—a derived feature, as we now realize (Soleglad & Fet, 2003). However, a separate branch for the family Buthidae (=Androctonoidae) on a tree, whether phenetic or cladistic, remains the major feature of any scorpion phylogeny today – the “grade” differences of Buthidae from other extant families proved to be its “clade” differences.

Thorell’s tree was modified and elaborated by Kraepelin (1905) who emphasized separate position of Buthidae by deriving it from a different group of Carboniferous scorpions (Apoxypodes) than all other scorpions (which he derived from Anthracoscorpia). This view at polyphyly of extant scorpions did not survive to our days; all orthostern scorpions are now considered monophyletic (Jeram, 1994a, 1994b). In Kraepelin’s scheme, the family Buthidae was for the first time clearly presented as a separate basal branch of modern scorpions. Birula (1917b: 88) also depicted a phylogeny (“a graphic representation”), based on his superfamilial classification, and confirming Kraepelin’s basal placement of Buthidae. His tree included six families with a topology (Buthidae, (Bothriuridae, (Chactidae, Vaejovidae, (Diplocentridae, Scorpionidae))).

Lamoral (1980) was the first to offer a simplified Hennigian, cladistic interpretation of scorpion order,

with only three branches; two of them (“buthoids” and “chaeriloids”) included only one family each, and the third (“diplocentroids”), included Diplocentridae, Scorpionidae, Chactidae, Bothriuridae, and Vaejovidae. The branching order in the Lamoral’s interpretation was: (Buthidae, (Chaerilidae, (Diplocentridae, Scorpionidae), (Bothriuridae, (Chactidae, Vaejovidae))). One of the major new assumptions in this model was that “chaeriloids” (Chaerilidae) were treated as a sister group to “diplocentroids”. Sissom (1990: 152, Fig. 3.34) reproduced the cladogram of Lamoral (1980) without changing its branching order, but adding families Ischnuridae and Iuridae. Sissom (1990) emphasized that, within the “diplocentroids”, Ischnuridae, Diplocentridae and Scorpionidae formed a monophyletic group, while the relationships of Iuridae, Chactidae and Vaejovidae remained obscure. The phylogeny of Sissom (1990) was also later reproduced by Farley (2001, Fig. 2.6).

Stockwell (1989), in an unpublished Ph.D. dissertation, distinguished four superfamilies: Buthoidea (Buthidae, Chaerilidae), Chactoidea (Chactidae, Euscorpidae, Scorpionsidae), Vaejovoidea (Superstitionidae, Iuridae, Vaejovidae), and Scorpionoidea (Bothriuridae, Ischnuridae, Diplocentridae, Scorpionidae, Urodacidae). Stockwell’s phylogeny (Buthoidea, (Chactoidea, (Vaejovoidea, Scorpionoidea))) emphasized the distinction between “primitive” (Buthoidea) and derived scorpion families.

One of the issues for extant scorpion phylogeny has been its rooting with the fossil taxa. Many earlier authors had no reservation to root it directly with Paleozoic taxa, sometimes even deriving extant scorpions from more than one fossil ancestor (e.g. Kraepelin, 1905). Among fossil scorpions, the Carboniferous Palaeopisthacanthidae Kjellesvig-Waering, 1986 has been identified as a sister group of all extant scorpions, or infraorder Orthosternina (Kjellesvig-Waering, 1986); thus, extant scorpions are considered monophyletic. Jeram (1994a: 513) stated that the careful re-examination of the Carboniferous scorpifera “will facilitate more accurate assessment of the relationships between modern scorpion genera”. In his analysis of fossil scorpions, Jeram (1994a: Text-Fig. 1) followed the phylogeny suggested by Stockwell (1989) with fossil Palaeopisthacanthidae as a sister group to all extant (“crown group”) scorpions. Among the “crown group”, two clades were distinguished (Text-Fig. 1): one included Buthidae and Chaerilidae, i.e. Stockwell’s superfamily Buthoidea; another, three clades with vernacular names, in the topology (chactoids (vaejovoids, diplocentroids)).

Most recently, Prendini (2000, 2003a), in a detailed cladistic analysis of taxa within Scorpionoidea, placed Bothriuridae as a basal group of this superfamily, and gave a family rank to scorpionid subfamilies Hemiscorpiinae and Urodacinae. The resulting scheme of relation-

ships within Scorpionoidea was as follows: (Bothriuridae, ((Heteroscorpionidae, Urodacidae), ((Hemiscorpiidae, Ischnuridae), (Diplocentridae, Scorpionidae))))). This conflicted with the decision of Lourenço (2000a) to establish family ranks for Hadogenidae and Lisposomidae.

Our recent work (Soleglad & Fet, 2001) on the evolution of orthobothriotaxy further elaborated Vachon's (1974) three trichobothrial "types" and identified two more fundamental "types": Type D for the recently described, unique extant family Pseudochactidae Gromov, 1998, and Type P for the fossil Palaeopisthacanthidae. This work also included information on important, recently described Cretaceous fossil taxa: *Protoischnurus* Carvalho & Lourenço, 2001 (family Protoischnuridae Carvalho & Lourenço, 2001) and *Archaeobuthus* Lourenço, 2001 (family Archaeobuthidae Lourenço, 2001).

At the moment of this writing, the high-level scorpion phylogeny and taxonomy was still unresolved, and division of extant scorpions into above-family groups was not finalized. The following issues remain especially important: (a) position of Chaerilidae ("Type B"); (b) position of Pseudochactidae ("Type D"); and (c) relationships among the group including six currently valid families: Iuridae, Chactidae, Vaejovidae, Euscorpionidae, Superstitioniidae, and Troglotayosicidae, i.e. "Type C minus Scorpionoidea".

Scorpion superfamilies: the nomenclatural history

Simon (1879: 92) was the first to use a superfamily category in scorpion systematics as he mentioned the name Buthoidea (based on family Buthides C. L. Koch, 1837, now Buthidae), thus indicating for the first time a separate position of Buthidae as compared to all other scorpions. Birula (1917a: 161-164, 1917b: 54-57) divided all extant scorpions into three superfamilies (Birula, 1917a), or "series" (Birula, 1917b). These were: Buthoidea, Chactoidea (based on subfamily Chactini Pocock, 1893, now family Chactidae), and Scorpionoidea (based on family Scorpionides Latreille, 1802, now Scorpionidae). They were distinguished on the basis of several features, including not only characters of external morphology but also those of reproductive system and venom glands. It is important to note that superfamily Buthoidea was monotypic, i.e. included only family Buthidae. Superfamily Chactoidea included Vaejovidae (now Vaejovidae), Bothriuridae and Chactidae, while superfamily Scorpionoidea included Scorpionidae and Diplocentridae. Mello-Leitão (1945) adopted Birula's system of three superfamilies, and introduced a fourth one, Bothriuroidea (based on family Bothriuridae Simon, 1880), which was monotypic. Mello-Leitão's opinion (1945: 133) that the name Bothriuroidea was

already introduced by Birula is incorrect; thus, Mello-Leitão is the first author who used this name.

Within the next several decades, no change has been seen in formal high-level scorpion taxonomy, and existing names of superfamilies (or their vernacular form) have been used occasionally, e.g. Vachon (1952: 42) divided all scorpions into "buthoids" and "chactoids"; Petrunkevitch (1955: P73) used the name Scorpionoidea. At the same time, the exhaustive analysis of morphology led to further understanding of a special position of Buthidae and Chaerilidae (formerly in Chactidae) as different from all other scorpion families. Vachon (1963) demonstrated the important systematic role of cheliceral dentition; there are four unique patterns characterizing Buthidae, Chaerilidae, and Iuridae, and the remaining families (Sissom, 1990). Further, the establishment of fundamental orthobothriotaxic trichobothrial patterns by Vachon (1974) divided all extant scorpion families into three unequal "types", A, B and C. Type A included only Buthidae, Type B, only Chaerilidae, and Type C, all the remaining families. These "types" have been since often treated by scorpion systematists as important if informal groups close or equal in rank to superfamilies (Lamoral, 1980; Sissom, 1990). The trichobothrial patterns continue to play the most prominent role in scorpion systematics (Soleglad & Fet, 2001; Soleglad & Sissom, 2001).

Lamoral (1980), considering phylogeny of modern scorpions, separated them into three lineages strictly according to Vachon's "types", and addressed these lineages as "buthoids", "chaeriloids" and "diplocentroids". Thus Lamoral (1980) came one step short of introducing a formal superfamily name for Chaerilidae (Type B), since names Buthoidea and Scorpionoidea (the latter Lamoral called "diplocentroids") already existed to accommodate all other families. Stockwell (1989: 75) was incorrect in interpreting Lamoral's English vernaculars as valid Latin superfamily names.

The vernacular names have been occasionally used in scorpion systematics even if a Latin name has never been published (e.g. Jeram (1994a: 519) used words "chactoids", "vaejovoids", and "diplocentroids", although only the Chactoidea existed as an available Latin superfamily name). The term "buthoids" (or Buthoidea) has been used as well, usually as an equivalent of Type A (family Buthidae) (Selden, 1993: 303; Lourenço, 1996a: 45; Lourenço & Weitschat, 2000, 2001). Since Lourenço (1998b) separated family Microcharmidae from Buthidae, "buthoids" (or Buthoidea) technically included two families. Lourenço (2001c) included the Cretaceous Archaeobuthidae under Buthoidea, which in our opinion (Soleglad & Fet, 2001) was not justified; see also Santiago-Blay et al. (in press). Lourenço (2003) also included the Cretaceous Palaeoeuscorpionidae under Chactoidea, which in our opinion was not justified as well.

In a comprehensive analysis of all fossil scorpions, Kjellesvig-Waering (1986: 232) in passing “lumped” all extant scorpions under the same superfamily, Scorpionoidea (where he also included the Carboniferous family Palaeopisthacanthidae Kjellesvig-Waering, 1986). Such a radical move is understandable from a paleontologist’s viewpoint as Kjellesvig-Waering (1986) established not less than 48 families and 21 superfamilies of fossil scorpions, grouped into five infraorders and two suborders. This division of fossil taxa was criticized (Stockwell, 1989; Jeram, 1994b, 1998) and probably is overly detailed. On the other hand, placement of all modern families into one superfamily by Kjellesvig-Waering (1986) was definitely not satisfactory from the perspective of extant scorpion systematics. Kjellesvig-Waering (1986: 15) further suggested that all extant scorpions should be treated as just three families (Buthidae, Scorpionidae, and Bothriuroidea); the latter was singled out based solely on its derived sternum shape; see Soleglad & Fet, (2003).

The need for the superfamily category persisted, as was expressed by Stockwell (1989) who recognized four superfamilies: Buthoidea, Chactoidea, Vaejovoidea, and Scorpionoidea. The only new name introduced by Stockwell (1989) was Vaejovoidea, and he synonymized Bothriuroidea with Scorpionoidea. However, Stockwell’s important work was not published, and therefore taxonomic changes proposed in it were not valid according to the International Code of Zoological Nomenclature (ICZN, 1999). Some, but not all, family-group and genus-group changes proposed by Stockwell (1989) were published by this author later (Stockwell, 1992).

As a result, there is currently no consensus on usage of superfamily category in scorpions. In their major reference works, Sissom (1990) and Fet et al. (2000) did not list any valid superfamilies. Fet et al. (2000) were compelled, for formal taxonomic purposes, to follow the opinion of Kjellesvig-Waering (1986), thus listing three available at this time superfamily names (Buthoidea, Chactoidea, and Bothriuroidea) as synonyms of the single extant superfamily, Scorpionoidea.

Prendini (2000) provided an extensive cladistic analysis of the restricted superfamily Scorpionoidea (*sensu* Stockwell, 1989) but did not discuss other superfamilies, implicitly restricting the scope of overly inflated Scorpionoidea *sensu* Kjellesvig-Waering (1986) in favor of the unpublished cladistic classification of Stockwell.

Most recently, Lourenço (2000a) published a list of six scorpion superfamilies (Buthoidea, Chactoidea, Chaeriloidea, Vaejovoidea, Bothriuroidea, and Scorpionoidea), in part following Stockwell (1989), but without separate justifications or diagnoses. Two new superfamily names formally introduced by Lourenço (2000a) were Vaejovoidea (based on family Vejovidae Thorell, 1876, now Vaejovidae), which included Vaejovidae and

Luridae; and Chaeriloidea (based on subfamily Chaerilini Pocock, 1893, now family Chaerilidae), which included Chaerilidae and Pseudochactidae. Prendini (2003a) doubted the validity of Bothriuroidea.

Scorpion nomenclature above the family-group

Phylogenetic relationships within the ancient and diverse subphylum Chelicerata are currently highly controversial, and scorpions have long been a focus of this controversy (Shultz, 1990; Selden & Dunlop, 1998; Wheeler & Hayashi, 1998; Giribet & Ribera, 2000; Dunlop & Braddy, 2001; Giribet et al., 2001). Scorpions, known from the Silurian, have been traditionally treated as an order of class Arachnida (Kjellesvig-Waering, 1986; Sissom, 1990; Fet et al., 2000). Kjellesvig-Waering (1986) established an elaborate system of suborders, infraorders, and superfamilies among fossil scorpion taxa. Starobogatov (1990) treated scorpions and eurypterids as two superorders, and recognized for scorpions two orders: Palaeophoniformes and Scorpioniformes. Stockwell (1989) proposed a scheme, which raised scorpions to a class Scorpionida (as first proposed by Van der Hammen (1977)), with three orders: Protoscorpiones, Palaeoscorpiones and Scorpiones. Of these, the order Scorpiones was divided in two suborders, Mesoscorpionina (extinct) and Neoscorpionina. The latter included two infraorders, Palaeosterni (extinct) and Orthosterni. This system was adopted by Selden (1993) and Jeram (1994a, 1994b), who also treated scorpions as class Scorpionida. Jeram (1994a) commented that “more space is available in the taxonomic hierarchy for the grouping of fossil forms into monophyletic clades”. Most recently, Jeram (1998) conducted a cladistic analysis of all known genera of the Silurian and Devonian scorpions in which all scorpions again were treated as an order, and the suborder name Mesoscorpionina was used.

We should note here that the category of superfamily is the highest rank category under the formal nomenclatural regulation of the Code (ICZN, 1999). On the other hand, order-group and class-group taxa are not regulated in terms of priority and synonymy. There was a considerable discussion on status of scorpions as either a class (with several orders) or a single order (see Stockwell, 1989; Selden, 1993; Jeram, 1994a, 1994b; Fet et al., 2000). It is not our goal here to discuss the order-group and higher categories, as the extant scorpion systematics is not directly relevant to these categories.

Following the existing consensus, we place all extant superfamilies under the infraorder Orthosterni (known from the Carboniferous to present). This infraorder name, preferred here, was used originally by Pocock (1911), and later by Stockwell (1989), Selden (1993), Jeram (1994a, 1994b) and Soleglad & Fet (2003), while the alternative name Orthosternina was

used by Kjellesvig-Waering (1986), Sissom (1990) and by Fet et al. (2000). One of the reasons we prefer to use the name *Orthosterni* is to avoid confusion as we introduce *subtribe* category here with ending “-ina” as accepted traditionally in many taxonomic groups (Coleoptera, Lepidoptera, Mammalia). (By the same reason we prefer to use the suborder name *Neoscorpiones* rather than *Neoscorpionina*). A number of extinct families also are placed in *Orthosterni* but we do not establish any new above-family taxa for those. Our new nomenclatural scheme is given further in this paper; it is based on our proposed phylogeny (Fig. 114).

The necessity of multiple intermediate categories for taxa of rank higher than the family-group has been long recognized by many cladists (McKenna, 1975). For mammals, McKenna & Bell (1997) use not less than 16 subordinated named categories between class and superfamily, which are as follows: subclass, infrafamily, superlegion, legion, sublegion, infralegion, supercohort, cohort, magnorder, superorder, grandorder, mirorder, order, suborder, infraorder, and parvorder. We feel that at least some of these categories may prove useful in arachnid classification.

Our current attention is focused on the infraorder *Orthosterni*, and the need of an intermediate category between the infraorder and superfamily compels us to introduce a category of **parvorder**, new for the arachnid systematics. Some examples of the recent use of this category come from vertebrate systematics. Sibley & Monroe (1990) in their classification of the world's birds accept a number of parvorders. Parvorders are recognized also in the latest phylogenetic classification of mammals (McKenna & Bell, 1997), e.g. elephants are placed into parvorder Proboscidea, infraorder Behemota, and suborder Tethytheria of the order Uranotheria. Even we, as it happens, belong to the superfamily Hominoidea, parvorder Catarrhini, infraorder Anthropeoidea, and suborder Haplorhines of the order Primates (McKenna & Bell, 1997). Since there is no standard ending for parvorders, we choose the ending “-ida” as it is done for birds by Sibley & Monroe (1990).

Methods & Material

Cladistic analysis software packages

Software package PAUP* Version 4 (Beta) (Swofford, 1998) was used for Maximum Parsimony (MP) analysis of morphology based character codings, tree searches, consensus trees, and bootstrap and jackknife resampling sequences. Winclada Version 0.9.3 (Nixon, 1999) was used to generate the resulting PAUP* MP cladogram showing distribution of all characters and their states. Cladograms for the molecular sequences from

PAUP* were generated by TreeView (Win 32) Version 1.5.2 (Page, 1998).

SEM microscopy

To investigate the leg tarsal armament, legs (usually III or IV) were removed from the animals and fixed for 12 hours in 0.1M sodium cacodylate with 2.5% gluteraldehyde (freshly prepared). After rinse/soak for 12 hours in plain 0.1 M sodium cacodylate, specimens were post-fixed for 2 hours in freshly prepared 1% osmium tetroxide again in sodium cacodylate. Specimens were rinsed three times with distilled water and dehydrated in an ethanol series (50, 75, 95, and two changes of 100%) before being dried and coated with gold/palladium (ca. 10 nm thickness) in a Hummer sputter coater. Digital SEM images were acquired with a JEOL JSM-5310LV at Marshall University, West Virginia. Acceleration voltage (10–20 kV), spot size, and working distance were adjusted as necessary to optimize resolution, adjust depth of field, and to minimize charging.

Material examined

We examined a large set of taxa representing all major groups of Recent scorpions. The following scorpions (well over 150 species spanning 90 genera) were examined in this study for either structure analysis and/or illustration. The family and genus assignments presented below, in alphabetical order, are based on *current classification*, therefore they do not reflect the taxonomic changes established further in this paper. See this section for locality data of species-level illustrations.

Bothriuridae (7 genera, 11 species): *Bothriurus araguayae* Vellard, 1934, Minas Gerais, Brazil, ♀ (VF); *Bothriurus burmeisteri* Kraepelin, 1894, Gobernador Costa, Chubut, Argentina, (VF); *Brachistosternus ehrenberghii* (Gervais, 1841), Tarapaca Province, Valle de Azapa, Chile, ♂ (VF); *Brachistosternus* sp., Antofagasta Province, Rio Loa, Chile, (VF); *Centromachetes pocockii* (Kraepelin, 1894), Lebu, Arauco, Chile, (VF); *Cercophonius squama* (Gervais, 1843), Engadine, Sidney, Australia, ♀ (VF); *Cercophonius* sp., Mt. Field National Park, Tasmania, Australia, (USNM); *Orobothriurus* sp., Ancash Dept., Laguna Llangancco, Peru, (MES); *Phoniocercus pictus* Pocock, Valdivia Nancul, Fundo El Linque, Chile, ♀ (VF); *Phoniocercus sanmartini* Cekalovic, 1973, Concepcion Province, Estero Nonguen, Chile, (VF); *Urophonius granulatus* Pocock, 1898, Ultima Esperanza, Laguna Amarga, Chile, ♂ (VF).

Buthidae (30 genera, 37 species): *Alayotityus nanus* Armas, 1973, Santiago, Cuba, (VF); *Androctonus bicolor* Ehrenberg, 1828, Lhav, Israel, ♂ (MES);

Anomalobuthus rickmersi Kraepelin, 1900, Bukhara, Uzbekistan, (VF); *Apistobuthus pterygocercus* Finnegan, 1932, Oman, (VF); *Babycurus exquisitus* Lowe, 2000, Oman, ♂ (NMB); *Buthacus yotvatensis* Levy, Amitai & Shulov, 1973, Abu Dhabi, United Arab Emirates, ♂ (VF); *Buthus occitanus* (Amoreux, 1789), Casablanca, Morocco, (MES); *Centruroides anchorellus* Armas, 1976, Río la Mula, Guamá, Santiago de Cuba, ♀ (VF); *Centruroides exilicauda* (Wood, 1863), Cabo San Lucas, Baja California Sur, Mexico, ♀ (MES); *Centruroides hentzi* (Banks, 1910), Panama City, Florida, USA, ♂ (MES); *Compsobuthus matthiesseni* (Birula, 1905), Baghdad, Iraq, ♀ (VF); *Grosphus bistratus* Kraepelin, 1900, Ihotry, Madagascar, ♀ (VF); *Grosphus hirtus* Kraepelin, 1901, Tamatave Province, Perinet, Madagascar, ♀ (MES); *Hottentotta minax* (L. Koch, 1875), Eritrea, ♂ (VF); *Isometrus maculatus* (DeGeer, 1778), Diego Garcia, Chagos Arch., ♀, ♂ (USNM), Indonesia, ♀ (VF); *Isometrus* sp., Papua New Guinea, ♀ (MES); *Karasbergia methueni* Hewitt, 1913, Uapur Upington, South Africa, ♂ (LP); *Kraepelinia palpator* (Birula, 1903), Badghyz, Turkmenistan, ♀ (VF); *Leiurus quinquestriatus* (Ehrenberg, 1828), Saudi Arabia, (VF); *Liobuthus kessleri* Birula, 1898, Chardara, Kazakhstan, (VF); *Lychas* sp., Viti Levu, Fiji, ♀ (MES); *Lychas* sp., Indonesia, (VF); *Lychas* sp., Rime Road, Singapore, ♂ (VF); *Mesobuthus caucasicus* (Nordmann, 1840), Chardara, Kazakhstan, ♀ (VF); *Mesobuthus eupeus* (C.L. Koch, 1839), Repetek, Turkmenistan, ♀ (VF); *Microbuthus* sp., Jabal Bani Jabir, Oman, ♀ (GL); *Microtityus jaumei* Armas, 1974, Santiago, Cuba, (VF); *Odontobuthus* sp., Oman, ♀ (GL); *Orthochirus scrobiculosus* (Grube, 1873), Israel, (MES); *Parabuthus* sp., Kenya, (VF); *Paraorthochirus glabrifrons* (Kraepelin, 1903), Oman, ♀ (GL); *Polisius persicus* Fet, Capes & Sissom, 2001, Zahedan, Iran, holotype ♂ (USNM); *Razianus zarudnyi* (Birula, 1903), Gachsaran, Fars, Iran, (VF); *Rhopalurus junceus* (Herbst, 1800), Camaquey, Sibanidi, Cuba, ♀ (VF); *Tityus nematochirus* Mello-Leitão, 1940, Bucaramangó, Colombia, ♂ (MES); *Uroplectes vittatus* (Thorell, 1876), Doddiebum, Zimbabwe, ♂ (VF); *Vachoniolus globimanus* Levy, Amitai & Shulov, 1973, Oman, ♂ (VF).

Chaerilidae (1 genus, 6 species): *Chaerilus celebensis* Pocock, 1894, Luzon, Philippines, ♂ (WDS); *Chaerilus chapmani* Vachon & Lourenço, 1985, Palawan Island, Philippines, ♀ (FK); *Chaerilus petrzelkai* Kovařík, 2000, Saigon Province, Vietnam, holotype ♀ (FK); *Chaerilus tichyi* Kovařík, 2000, Pahang, Malaysia, ♀ paratype (FK); *Chaerilus tryznai* Kovařík, 2000, Bomi env., Tibet, ♀ paratype (FK); *Chaerilus variegatus* Simon, 1877, Indonesia, ♂ (MES), Java (FK).

Chactidae (7 genera, 7 species): *Broteochactas delicatus* (Karsch, 1879), Grande Île, French Guiana, ♂ (MES); *Brotheas granulatus* Simon, 1877, Grande Île,

French Guiana, ♀ (MES); *Chactas* sp., Darien, Panama, ♂ and ♀ (MES); *Hadrurochactas schaumii* (Karsch, 1880), Petite Île, French Guiana, ♂ (MES); *Nullibrotheas allenii* (Wood, 1863), Cabo San Lucas, Baja California Sur, Mexico, ♂ and ♀ (MES), Los Planes, Baja California Sur, Mexico, ♂ (MES); *Teuthraustes oculus* Pocock, 1900, Latacunga, Ecuador, ♀ (WDS); *Vachoniochactas* sp., Alto Río Mavaca, Amazonas, Venezuela (CAS).

Diplocentridae (5 genera, 6 species): *Bioculus comondae* Stahnke, 1968, Loreto, Baja California Sur, Mexico, ♂ (MES); *Cazierius gundlachii* (Karsch, 1880), San Juan, Santiago de Cuba, Cuba, ♂ (VF); *Didymocentrus leseurii* (Gervais, 1844), Martinique, ♀ (VF); *Diplocentrus ochoterenai* Hoffmann, 1931, Oaxaca, Mexico, ♀ (MES); *Diplocentrus whitei* (Gervais, 1844), Cuatro Ciénegas, Coahuila, Mexico, ♂ (MES); *Nebo hierichonticus* (Simon, 1872), Haifa, Israel, ♀ (VF).

Euscorpiidae (9 genera, 14 species): *Alloscorpiops lindstroemii* (Thorell, 1889), Tak Province, Umphang, Thailand, ♀ (CAS); *Chactopsis insignis* Kraepelin, 1912, Loreto, Peru, ♀ (MNHN); *Euscorpiops binghamii* (Pocock, 1893), Misty Hollow, Dawna Hills, Burma, ♀ (WDS); *Euscorpius flavicaudis* (DeGeer, 1778), Banyuls, France, ♂ (MES); *Euscorpius gamma* (Caporiacco, 1950), Slovenia (VF); *Euscorpius italicus* (Herbst, 1800), Agarone, Ticino, Switzerland, ♂ (MES); *Euscorpius naupliensis* (C.L. Koch, 1837), Kalidona, Peloponnese, Greece, ♀ (MES); *Euscorpius tergestinus* (C.L. Koch, 1837), Slovenia (VF); *Megacormus gertschi* Díaz Nájera, 1966, Zacualtipan, Hidalgo, Mexico, ♀ (MES); *Megacormus granosus* (Gervais, 1843), San Andreas, Veracruz, Mexico, ♀ (AMNH); *Neoscorpiops tenuicauda* (Pocock, 1894), Maharashtra, Bhimashankar, India, ♂ (CAS); *Plesiochactas dilutus* (Karsch, 1881), Portillo Nejapa, Oaxaca, Mexico, ♂ (AMNH); *Scorpiops tibetanus* Hirst, 1911, Lhasa, Tibet, ♂ (USNM); *Troglocormus willis* Francke, 1981, Cueva de la Llorona, Yerbabuena, Tamaulipas, Mexico, ♀ (WDS).

Hemiscorpiidae (1 genus, 1 species): *Hemiscorpiops maindroni* (Kraepelin, 1900), Wadi Bani Kharus, Oman, ♀ (GL), Wadi Mistal, Oman, ♂ (GL).

Heteroscorpionidae (1 genus, 1 species): *Heteroscorpion opisthacanthoides* (Kraepelin, 1896), Madagascar, ♀ (MES).

Iuridae (6 genera, 13 species): *Anuroctonus phaiodactylus* (Wood, 1863), Oneida Co., Idaho, USA, ♂ (MES), Beaver Co., Utah, USA, ♂ (MES), Tooele Co., Utah, USA, ♂ and ♀ (CAS); *Anuroctonus* sp., Anza-Borrego Desert State Park (ABDSP), California, USA, ♂ (MES), Ojos Negros, Baja California, Norte, Mexico, ♂ and ♀ (CAS); *Calchas nordmanni* Birula, 1899, Megisti Island, Greece (VF), Anamur, Turkey, ♀ and ♂ (NHMW), Baykau, Turkey, ♀ (NHMW), Antalya, Turkey, ♀ (NHMW); *Caraboctonus keyserlingi*

Pocock, 1893, Chili, ♂ (MES); *Hadruroides charcasus* (Karsch, 1879), Peru, ♀ (MES); *Hadruroides maculatus* (Thorell, 1876), Huancayo, Peru, ♂ and ♀ (MES); *Hadrurus arizonensis* Ewing, 1928, Maricopa Co., Arizona, USA, (MES), ABDSP, California, USA, ♀ (MES); *Hadrurus aztecus* Pocock, 1902, Tehuacan, Puebla, Mexico, ♂ (MES); *Hadrurus concolor* Stahnke, 1969, Santa Rosalia, Baja California Sur, Mexico, ♀ (MES); *Hadrurus hirsutus* (Wood, 1863), Cabo San Lucas, Baja California Sur, Mexico, ♀ (MES); *Hadrurus obscurus* Williams, 1970, ABDSP, California, USA, ♂ and ♀ (MES); *Hadrurus pinteri* Stahnke, 1969, Oakies Landing, Baja California Norte, Mexico, ♀ (MES); *Iurus dufourei* (Brullé, 1832), Turkey, ♂ (MES).

Liochelidae (4 genera, 6 species): *Cheloctonus* sp., St. Lucia, Kwazulu, Natal, ♀ (VF); *Hadogenes troglodytes* (Peters, 1861), Johannesburg, South Africa, ♀ (MES); *Liocheles australasiae* (Fabricius, 1775), Sidemen, Karangasem, Bali, Indonesia, ♀ (VF); *Liocheles* sp., Papua New Guinea, ♀ (MES); *Liocheles* sp., Guadalcanal, Solomon Islands, ♂ (MES); *Opisthacanthus lepturus* (Beauvois, 1805), Canal Zone, Panama, ♀ (MES).

Microcharmidae (1 genus, 1 species): *Microcharmus hauseri* Lourenço, 1996, Lokobe Natural Reserve, Île Nosy Be, Madagascar, holotype ♂ (MHNG).

Pseudochactidae (1 genus, 1 species): *Pseudochactas ovchinnikovi* Gromov, 1998, Babatag, Uzbekistan, ♂ and ♀ (VF).

Scorpionidae (4 genera, 5 species): *Heterometrus longimanus* (Herbst, 1800), Mindanao, Philippines, ♂ (MES); *Heterometrus petersii* (Thorell, 1876), Palawan, Philippines, ♂ (USNM); *Opisthophthalmus* sp., Johannesburg, South Africa, ♀ (MES); *Pandinus imperator* (C. L. Koch, 1841), ♀ (MES); *Scorpio maurus* Linnaeus, 1758, Tel-Yezucham, Israel, ♀ (MES), Galil, Israel, ♀ (VF).

Superstitioniidae (2 genera, 2 species): *Superstitionia donensis* Stahnke, 1940, ABDSP, California, USA, ♀ (MES), Peralta Canyon, Pinal Co., Arizona, USA, ♀ (MES), Arizona, USA, ♂ (VF); *Alacran tartarus* Francke, 1982, Huantla Sistema, Sotano de San Agustín, Oaxaca, Mexico, ♀ (WDS).

Troglotayosicidae (1 genus, 1 species): *Belisarius xambeui* Simon, 1879, Vidra, Gerona, Catalunya, Spain, ♀ (WDS), Fogars de Monclús, Montseny, Barcelona, Spain, ♀ (VF).

Urodacidae (1 genus, 1 species): *Urodacus manicatus* (Thorell, 1876), Australia, (VF).

Vaejovidae (10 genera, 48 species): *Paravaejovis pumilis* (Williams, 1970), Ciudad Constitution, Baja California Sur, Mexico, ♂ (MES); *Paruroctonus arnaudi* Williams, 1972, El Socorro, Baja California Norte, Mexico, ♂ (MES); *Paruroctonus boreus* (Girard, 1854), Mercury, Nevada, USA, ♂ (MES); *Paruroctonus*

gracilior (Hoffmann, 1931), Cochise Co., Arizona, ♂ (MES); *Paruroctonus luteolus* (Gertsch & Soleglad, 1966), ABDSP, California, USA, ♂ (MES); *Paruroctonus silvestrii* (Borelli, 1909), ABDSP, California, USA, (MES); *Paruroctonus stahnkei* (Gertsch & Soleglad, 1966), Maricopa Co., Arizona, USA, (MES); *Pseudouroctonus andreas* (Gertsch & Soleglad, 1972), ABDSP, California, USA, (MES); *Pseudouroctonus angeleus* (Gertsch & Soleglad, 1972), Ventura Co, California, USA, (BH); *Pseudouroctonus apacheanus* (Gertsch & Soleglad, 1972), Cochise Co., Arizona, USA, ♀ (MES); *Pseudouroctonus minimus castaneus* (Gertsch & Soleglad, 1972), San Diego Co., California, USA, ♂ (MES); *Pseudouroctonus reddelli* (Gertsch & Soleglad, 1972), Conal Co., Texas, USA, ♂ and ♀ (MES), Travis Co., Texas, USA, ♂ (MES); *Serradigitus calidus* (Soleglad, 1974), Cuatro Ciénegas, Coahuila, Mexico, ♀ paratype (MES); *Serradigitus gertschi gertschi* (Williams, 1968), ABDSP, Chariot Canyon, California, USA, ♀ (MES); *Serradigitus joshuaensis* (Soleglad, 1972), ABDSP, California, USA (MES); *Serradigitus minutis* (Williams, 1970), Cabo San Lucas, Baja California Sur, Mexico, ♂ and ♀ (MES); *Serradigitus subtilimanus* (Soleglad, 1972), ABDSP, California, USA, (MES); *Serradigitus wupatkiensis* (Stahnke, 1940), Coconino Co., Arizona, USA, ♀ (MES); *Smeringurus aridus* (Soleglad, 1972), ABDSP, California, USA, ♂ (MES); *Smeringurus grandis* (Williams, 1970), Oakies Landing, Baja California Norte, Mexico, ♂ (MES); *Smeringurus mesaensis* (Stahnke, 1957), ABDSP, California, USA, ♀ (MES); *Syntropis macrura* Kraepelin, 1900, Ensenada Marquer, Isla Carmen, Baja California Sur, Mexico, ♀ (WDS); *Uroctonites huachuca* (Gertsch & Soleglad, 1972), Huachuca Mtns., Arizona, USA, ♂ (MES); *Uroctonites monterey* (Gertsch & Soleglad, 1972), Monterey Co., California, USA, ♂ (MES); *Uroctonus mordax mordax* Thorell, 1876, Yosemite National Park, California, USA, ♂ and ♀ (MES), Weott, California, USA, ♂ (MES); *Uroctonus mordax pluridens* Hjelle, 1972, Santa Clara Co., California, USA, ♂ (MES); *Vaejovis bruneus* Williams, 1970, Loreto, Baja California Sur, Mexico, ♀ (MES); *Vaejovis carolinianus* (Beauvois, 1805), Haralson Co., Georgia, USA, ♀ (MES); *Vaejovis eusthenura* (Wood, 1863), Cabo San Lucas, Baja California Sur, Mexico, ♀ (MES); *Vaejovis cazieri* Williams, 1968, Cuatro Ciénegas, Coahuila, Mexico, ♀ (MES); *Vaejovis gravicaudus* Williams, 1970, Santa Rosalia, Baja California Sur, Mexico, ♀ (MES); *Vaejovis hirsuticauda* Banks, 1910, ABDSP, California, USA, ♂ and ♀ (MES); *Vaejovis intrepidus cristimanus* Pocock, 1898, Autlán, Jalisco, Mexico, ♀ (MES); *Vaejovis jonesi* Stahnke, 1940, Coconino Co., Arizona, USA, ♀ (MES); *Vaejovis mexicanus mexicanus* (C.L. Koch, 1836), Aculco, Distrito Federal, Mexico, ♀ (MES); *Vaejovis nigrescens* Pocock, 1898, Rioverde,

San Luis Potosí, Mexico, ♂ (MES); *Vaejovis nitidulus* C. L. Koch, 1843, Cuicuitlan, Oaxaca, Mexico, ♀ (MES); *Vaejovis occidentalis* Hoffmann, 1931, Acapulco, Guerrero, Mexico, ♀ (MES); *Vaejovis paysonensis* Soleglad, 1973, Gila Co., Arizona, ♀ (MES); *Vaejovis punctatus* Karsch, 1879, Acatlan, Puebla, Mexico, ♀ (MES); *Vaejovis punctipalpi* (Wood, 1863), Cabo San Lucas, Baja California Sur, Mexico, ♀ (MES); *Vaejovis puritanus* Gertsch, 1958, ABDSP, California, USA (MES); *Vaejovis spinigerus* (Wood, 1863), Alamos, Sonora, Mexico, ♀ (MES); *Vaejovis solegladi* Sissom, 1991, Teotitlan, Oaxaca, Mexico, ♀ (MES); *Vaejovis viscainensis* Williams, 1970, Los Bombas, Baja California Sur, Mexico, ♂ and ♀ (MES); *Vaejovis vittatus* Williams, 1970, Cabo San Lucas, Baja California Sur, Mexico, ♂ (MES); *Vaejovis vorhiesi* Stahnke, 1940, Cochise Co., Arizona, USA, ♀ (MES); *Vaejovis waeringi* Williams, 1970, ABDSP, California, USA, ♂ (MES); *Vaejovis longiunguis* (Williams, 1969), Los Bombas, Baja California Sur, Mexico, ♂ (MES).

Abbreviations

List of depositories: AMNH, American Museum of Natural History, New York, New York, USA; BH, Personal collection of Blaine Hébert, Los Angeles, California, USA; CAS, California Academy of Science, San Francisco, California, USA; GL, Personal collection of Graeme Lowe, Philadelphia, Pennsylvania, USA; FK, Personal collection of František Kovářik, Prague, Czech Republic; LP, Personal collection of Lorenzo Prendini, New York, New York, USA; MES, Personal collection of Michael E. Soleglad, Borrego Springs, California, USA; MHNG, Museum d'Histoire Naturelle de Geneve, Geneva, Switzerland, NHMW, Naturhistorisches Museum, Vienna, Austria; VF, Personal collection of Victor Fet, Huntington, West Virginia, USA; USNM, United States National Museum (Smithsonian Institution), Washington, DC, USA; WDS, Personal collection of W. David Sissom, Canyon, Texas, USA.

Character Description and Evaluation

This section presents the results of new character analyses conducted during this study. In particular, most of these analyses are germane to fundamental characters that have the most impact on determining the upper-level phylogeny of Recent scorpions such as parvorders and superfamilies. These analyses include, although not limited to, metasomal carination, leg tarsus armament, cheliceral dentition, and trichobothrial patterns. In addition, some of these analyses are also applicable to the lower-level taxonomies involving the superfamily Chactioidea. Other structures and their characterizations

not discussed specifically in this section but used in the cladistic analysis presented herein are discussed briefly in **Appendix A**, where each character and its set of assigned state values are provided.

It is important to note here that for purposes of comparative analyses and the coherent presentation of the material, *the taxonomic name-groups and their relationships as established in this paper are used throughout this discussion*. The section on classification formally establishes our taxonomic emendations. Finally, for the sake of brevity in writing, the superfamily Chactioidea, whose phylogeny is (((Chactidae, Euscorpidae), Superstitioniidae), Vaejovidae), is divided as follows: **Vaejovidae** and **Chactioidea(-V)** (= Chactidae + Euscorpidae + Superstitioniidae). This abbreviation is necessary due to the frequency of structural comparisons between these clades.

Metasoma

The metasoma as seen in the Silurian scorpions has gone through subtle but significant changes to produce the metasoma now present in Recent scorpions. We can categorize these changes (or more appropriately derivations) into three groups: 1) the gradual lengthening of the more terminal metasomal segments, 2) a gradual tapering of the metasomal segments, and 3) the loss of metasomal carinae on the more terminal segments.

Fossil Scorpions: The typical metasoma found in a Silurian scorpion, for example *Proscorpius osborni* (Whitfield) (see Kjellesvig-Waering, 1986, Text-Fig. 8-C), exhibits five segments all roughly the same width and length — providing a somewhat stocky appearance. In addition to the overall segment proportions, Kjellesvig-Waering also described the basic carinal ornamentation found in this scorpion: four pairs of carinae, which we interpret here as the dorsal, dorsal lateral, ventral lateral, and ventral median carinae. These four carinal pairs were found on *all* five metasomal segments of *P. osborni*, again emphasizing little or no difference from one segment to another. Although the exact carination, i.e., which carinae are present on a segment by segment basis, is not clear on most fossils studied by Kjellesvig-Waering, the generally stocky and similarly proportioned segments are quite evident in many fossil scorpion genera spanning the major infraorders he recognized (these are all illustrated in Kjellesvig-Waering, 1986): Holosternina: *Allopalaeophonon* (early Silurian, 443–430 Ma), *Proscorpius*, *Archaeophonon*, *Stoermeroscorpion* (late Silurian, 430–417 Ma), *Garnettius* (late Carboniferous, 323–290 Ma); Lobosternina: *Palaeophonon* (early Silurian), *Eskiscorpio* (early Carboniferous, 354–323 Ma), *Boreoscorpion*, *Eoscorpion*, *Paraisobuthus* (late Carboniferous); Meristosternina: *Palaebobuthus* (late Carboniferous). Jeram (1994b) described the large

Carboniferous scorpion *Pulmonoscorpium kirktonensis* which also exhibits somewhat stocky metasomal segments, all roughly the same length and width. In this species Jeram (1994b: 293) was able to discern the same number of carinal pairs as that reported by Kjellesvig-Waering for the Silurian scorpion *Proscorpium osborni*, except in this case the dorsal carinae were absent on segment V. Jeram (1994b), using Stockwell's (1989) classification, placed this species in infraorder Mesoscorpionina (order Scorpiones).

In the suborder Neoscorpionina (following Stockwell's classification), scorpions have developed an elongated metasomal segment V. This condition, in fact, is stated as a synapomorphy for this suborder (Jeram, 1994b, Fig. 1). It is not clear whether this gradual elongation occurred initially on all segments, or just on segment V. In Kjellesvig-Waering (1986), we see that the Carboniferous genera *Eoctonus* (Text-Fig. 35-A, B) and *Buthiscorpium* (Text-Fig. 40-A) (i.e., Holosternina under Kjellesvig-Waering's classification or Palaeosterni under Stockwell's) segments I–III are approximately the same length, IV is equal or slightly longer, and V is noticeably longer. Jeram (1994a: 532) described the metasoma of Carboniferous scorpion *Compsoscorpium elegans* Petrunkevitch (infraorder Orthosterni) as "... segments are short, but increase slightly in length posteriorly along the tail. The fifth metasomal segment (preanal) is twice as long as the fourth ...".

Jeram (1994a: 532, Text-Fig. 3-B, C) described the metasomal carination for *Compsoscorpium elegans* "Dorsal carinae are very prominent ... pairs of superior-lateral, inferior lateral and inferior median carinae are also present, making a total of ten carinae per segment ...". Although Jeram only lists four pairs of carinae (implying eight carinae, not ten), in Text-Fig. 3-G, he illustrates five pairs, the *median lateral* (ml) not being mentioned specifically in the text. This observation, as well as those for *Pulmonoscorpium kirktonensis* and *Proscorpium osborni*, is important since they show that in general the number of metasomal carinae in fossil scorpions did not vary across the metasomal segments. This observation is somewhat intuitive since we see the conspicuous tapering that is evident in Recent scorpions is essentially absent in fossil scorpions, thus the metasomal segments of fossil scorpions could accommodate the full complement of carinae.

In summary, we see one major derivation in the metasoma of fossil scorpions: the gradual lengthening of the segments in a basal to terminal direction, especially exhibited in segment V. In addition, although the more terminal segments became elongated, tapering is not evident and therefore a full complement of carinae is typically found throughout all five segments, including a paired set of ventral median carinae on segment V. Jeram (1994a, Text-Fig. 3-B) illustrates these paired

carinae on segment V for *Compsoscorpium elegans*. In Fig. 4 we illustrate a *hypothetical* carinal configuration of metasomal segments I, IV and V as reported by Jeram (1994a) for *C. elegans*.

Recent Scorpions – General: In Recent scorpions, we see a significant progressive lengthening of metasomal segments starting with segment I and continuing to segment V, clearly the longest segment in the metasoma. In addition, the segments are in general progressively thinner beginning with segment I. The loss of metasomal carinal pairs is also evident in Recent scorpions, especially on the more terminal segments. We can categorize this loss of metasomal carinae into four groups, ordered by their presumably phylogenetic importance: 1) the loss of the dorsal carinal pair on segment V; 2) the progressive partial loss of the lateral carinae starting from the basal segment and continuing to segment IV; 3) the loss of one of the paired ventral median carinae on segment V (i.e., it is single); and 4) the localized (i.e., occurring in some scorpion groups) loss of one of the paired ventral median carinae on segments I–IV. Following is a general depiction of the metasomal segment carinae configuration found in a large majority of Recent scorpions for segments I through V (see **Appendix C**).

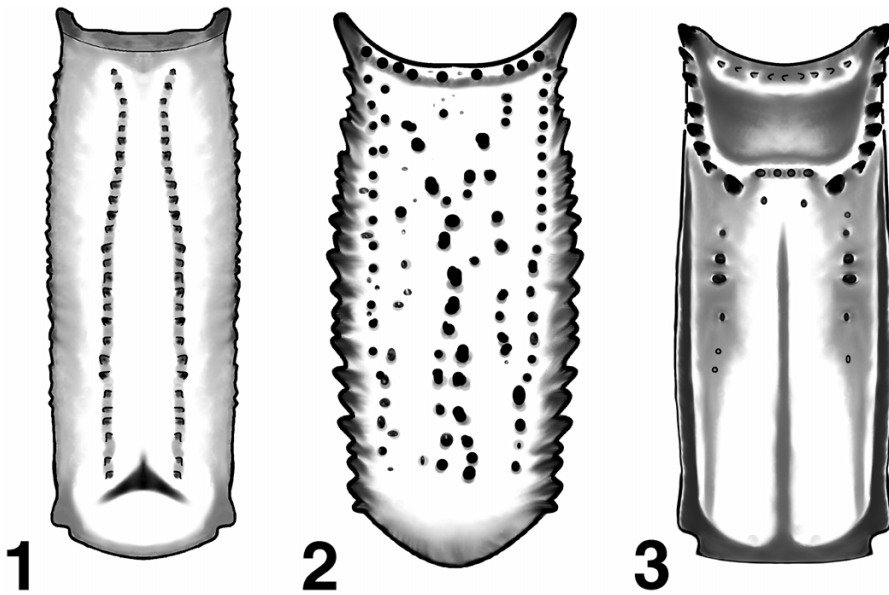
Metasomal segment I: This segment always exhibits the complete complement of metasomal carinae, five pairs (in some cases, the ventral median carina is single). It is usually the shortest and widest segment in the metasoma—we hypothesize that this segment, from a carinal armament perspective, represents a form closest to that exhibited in fossil scorpions across all segments.

Metasomal segment II: This segment is similar to segment I but longer, thinner and, in general, the lateral carinae are reduced or absent altogether. The lateral carinae, if present, exists from a posterior to anterior direction, exhibiting development anywhere from total obsolescence to complete development, but in general occurs for less than 60% of the segment's length.

Metasomal segment III: As with segments I and II, this segment becomes longer, thinner, and the lateral carinal pair is even more reduced, on an average, present for less than 30% of the segment's length.

Metasomal segment IV: This segment is usually noticeably longer and a little thinner than the preceding segment with almost always showing complete obsolescence of the lateral carinae.

Metasomal segment V: Segment V is quite unique in Recent scorpions, considerably longer than the other segments and in many cases exhibiting a slight tapering towards the telson (although a lot of variability is present in the latter). In addition, this segment is void of the dorsal carinal pair, the ventral median carinae is single (with one exception which is discussed below), and the lateral carinae are variable either absent or present in



Figures 1-3: Metasomal segment V, ventral view. **1.** *Pseudochactas ovchinnikovi*, showing paired ventral median carinae. **2.** *Chaerilus petzelskai*, showing Y-shaped terminus of single ventral median carina. **3.** *Biloculus comondae*, showing crescent-shaped ventral transverse carina.

variously degrees in an anterior to posterior direction. Closely inspecting the dorsal aspect of segment V (Figs. 4–5), we see that the most dorsal carinae are quite rounded, suggesting the possible remnants of another more dorsal carinae pair. Therefore, based on this observation as well as comparison with segment I, we hypothesize that the dorsal carinae are absent in segment V (i.e., the most dorsal carinae on segment V are the dorsal lateral carinae).

In Recent scorpions a unique articulation mechanism is found between metasomal segments IV and V. This unique structure, forming a ball (an *articulation condyle* on segment IV) and open socket (an *articulation socket* on segment V) mechanism, provides a special “hinge-like” function between these two segments, forcing a restricted vertical 90+ degree motion. The articulation socket is a conspicuous smooth and shiny ball-like cuticle projection emanating from the dorsal lateral carinae terminus. The articulation socket is a smooth shiny concave structure projecting from the anterior base of the dorsal lateral carinae (concave area faces dorsal aspect). This mechanism is not found on the other three metasomal segments (i.e., I–III) or between segments III and IV which move in a more free form rotating motion. Other similar articulation mechanisms, where presumably precise articulation is required, are also found on Recent scorpions; e.g., the base of the chelal movable finger (two mechanisms, *external* and *internal condyles*), the cheliceral movable finger base, and on the legs connecting various segments. It is not known whether this mechanism of the metasoma is found in fossil scorpions.

We suggest here that the tapering seen in the metasomal segments of Recent scorpions has caused, in part, the loss of carinae, especially in the terminal segments. The most elongated segments, IV and V, are essentially

devoid of the lateral carinal pair, and in segment V, the lateral carinae, if present, begin at the anterior aspect. Segment V, usually the longest and thinnest of all segments, shows the most derivation, losing the dorsal carinal pair and the ventral median carinal pair found in fossil scorpions has been reduced to a single carina.

Also of interest, but occurring in much lower phylogenetic levels than the derivations discussed above, is the reduction in segments I–IV of the ventral median carinal pair to a single carina. This condition is observed across a varied assemblage of Recent scorpion genera, e.g. in scorpionoids: *Heteroscorpion*, *Hemiscorpius*, *Habibiella*, and *Urodacus* (Fig. 5); in euscorpids: *Euscorpis* (Fig. 5), *Megacormus*, and *Plesiochactas*; and in vaejovids: *Syntropis* and *Vejovoidus* (Fig. 5). In general we consider these derivations localized to the groups in which they occur, and in particular, we suspect this condition as seen in the vaejovoid genera *Syntropis* and *Vejovoidus* to be caused, in part, by a radical adaptation to their microhabitat; ultralithophilic for the former and ultrapsammophilic for the latter. This conclusion is based on the presumed close relationship of *Syntropis* to *Vaejovis* and related genera, and *Vejovoidus* to *Paruroctonus* and related genera, i.e., they do not exhibit any other significant differences except in this character.

Recent Scorpions – major groups, the parvorders: Above we outlined the basic structure of the metasoma for Recent scorpions; here we discuss the metasoma on a major scorpion group basis, the parvorder, starting with the presumed primitive Recent scorpions—the pseudochactids, buthoids and chaerilids. See **Appendix C** for a detailed chart of the metasomal carinae configuration for all five metasomal segments representing a large assemblage of Recent scorpion species.

Pseudochactida: The very interesting species *Pseudochactas ovchinnikovi* (Figs. 1 and 4) has a unique

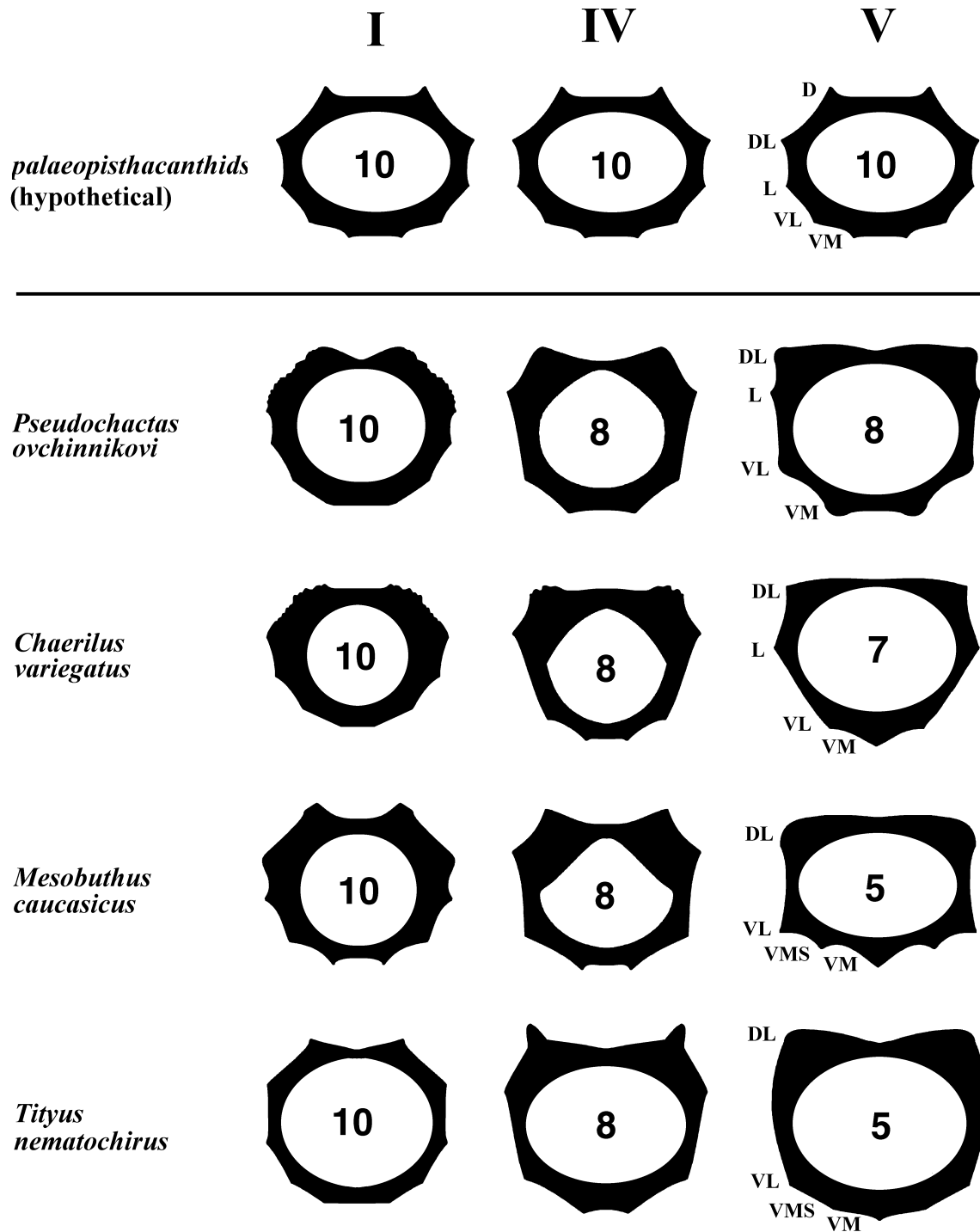


Figure 4: Diagrammatic cross-section of metasomal segments I, IV and V of the palaeopisthacanthids and primitive Recent scorpions. Although the diagrams supplied for the palaeopisthacanthids are hypothetical only, they do depict the five carinal pairs reported by Jeram (1994a) for the complete metasoma. Of particular interest, note paired ventral median carinae (VM) exhibited on segment V for genus *Pseudochactas*, lateral carinae (L) on segment V for genera *Pseudochactas* and *Chaerilus*, which is absent in the two buthoids, and ventral median secondary (VMS) carinae on segment V on buthoid genera *Mesobuthus* and *Tityus*. Note, although individual segment diagrams are to scale, they are not necessarily to scale between or within a species. Numbers inside diagrams refer to number of primary carinae present, and therefore excludes VMS carinae; D = dorsal, DL = dorsal lateral, L = lateral, VL = ventral lateral, VM = ventral median, VMS = ventral median secondary.

condition of a set of paired ventral median carinae on metasomal segment V, unprecedented in Recent scorpions. In Figure 1 we can see that this well-developed carinal pair tapers slightly posteriorly, towards the telson. We believe that this tapering suggests these carinae are in the process of becoming single, which presents an intermediate between the paired condition found in the palaeopisthacanthids and the single condition found on all other Recent scorpions. To support this hypothesis, the tapering occurs in the same direction as the reduction of the lateral carinae on this segment. We consider these paired ventral median carinae to be a plesiomorphic condition, directly inherited from a fossil lineage as that exhibited, for example, in the palaeopisthacanthids. Otherwise, *Pseudochactas* metasomal carinae ornamentation is typical of Recent scorpions, segment V is equipped with lateral carinae for 50% of its length, and, on segments I–IV, the lateral carinae reduce progressively, becoming obsolete on segment IV.

Chaerilida: Segment V (Fig. 4) is equipped with lateral carinae, developed from 70–80% of the segments length (based on the examination of three species). The lateral carina exhibits the typical progressive reduction from segment I to segment IV where it is obsolete. In many species of *Chaerilus* (as reported by Kovařík, 2000), the ventral median carina of metasomal segment V bifurcates posteriorly, forming a wide Y-shaped pattern. This pattern is evident in the three species examined in this study. We do not consider this bifurcation found in some *Chaerilus* species to be evidence of a paired ventral median carinae evolving however, (or, for that matter, in the process of disappearing) since it is not consistent within the genus. Plus, the true paired carinae as found in *Pseudochactas* are more indicative of paired carinae that appear to be in the process of becoming single, as evidenced by their subtle *posterior* tapering. Kovařík also reported paired ventral median carinae for segment V in new species *C. petzelkai*. We examined this species and noted that the carina is doubled in places (Fig. 2) caused by the intense exaggerated granulation found on this little scorpion. However, the spacing is much too close to be considered homologous to paired carinae. This is also indicated when compared to the spacing of the paired carinae found on segment IV, which are more separated, and, when segment V is viewed from the terminal end, it clearly has a single carina.

Buthida: In Fig. 4 we illustrate diagrammatically the key metasomal segment carination for an Old and a New World buthid. In these diagrams we see that the lateral carinae are obsolete in segments IV and V. **Appendix C** presents 24 buthoid genera metasomal carinae configurations, only three, *Hottentotta*, *Alayotityus* and *Microcharmus*, exhibit lateral carinae, in part,

on these segments (segment IV for the former and segment V for the latter two). Although these observations are based on solitary species within the genus, we suspect that in general the complete loss of the lateral carinae on segment V is indicative of the buthoids (note this carinal pair is usually present, in part, on all other Recent scorpion groups). On metasomal segment V of many buthids is found a pair of ventral median secondary (VMS) carinae, flanking the single ventral median carina. These carinae do not completely traverse the entire segment, showing development on the anterior aspect only. For those cases where these carinae extend towards the posterior half, there is sometimes a transverse line of connecting granules forming a crescent-shaped pattern, a *ventral transverse carina* (VTC). In **Appendix C**, ten genera (out of 24) exhibit VMS, and two of these, *Mesobuthus* (weakly) and *Buthacus*, exhibit the ventral transverse carina.

Iurida: In general, this parvorder conforms to the typical carinal pattern as described above, the progressively reduced lateral carinae on segments I–IV and the presence of lateral carinae, in part, on segment V. Of particular interest here is the presence of lateral carinae on metasomal segment IV for two New World iuroid genera, *Hadrurus* (Fig. 5) and *Hadruroides*, which is essentially unprecedented in Recent scorpions. As indicated in **Appendix C**, these carinae are present for 40–60% of the segment's length. For the scorpionoids there is a tendency for complete obsolescence of the lateral carinae on segments I–IV, but they are usually present, in part, on segment V. *Diplocentrus ochoterenai* and *Bioculus comondae* (Fig. 3) exhibit a ventral transverse carina on segment V but it is not accompanied by ventral median secondary carinae. Francke (1978) also reports this condition in several diplocentrids (i.e., *Oiclus*, *Cazierius*, *Tarsoporus*, and *Didymocentrus*). In contrast, the genus *Heteronebo* does not exhibit a ventral transverse carina (Francke, 1978) but instead, the ventral median carina forms an irregular Y-shape bifurcation on the posterior aspect of segment V on some species. In general, the chactids, euscorpids and vaejovids all comply with the standard metasoma carinae configuration—exhibiting the progressively reduced lateral carinae on segments I–IV and usually some trace of the lateral carinae on segment V. The metasomal carina configuration is variable in the superstitioniids: in *Superstitionia* the dorsal and dorsal lateral carinae are present, the lateral and ventral carinae are essentially smooth to obsolete; the typhlochactines only exhibit weakly developed dorsal carinae, the others are obsolete. The metasomal carinae are quite unusual in the troglobitic genus *Alacran*. The five segments are very elongated, “rectangular” when viewed from the end, exhibiting highly crenulated dorsal and ventral lateral carinae as “corners” of the segment. There is no trace of the ventral median carinae

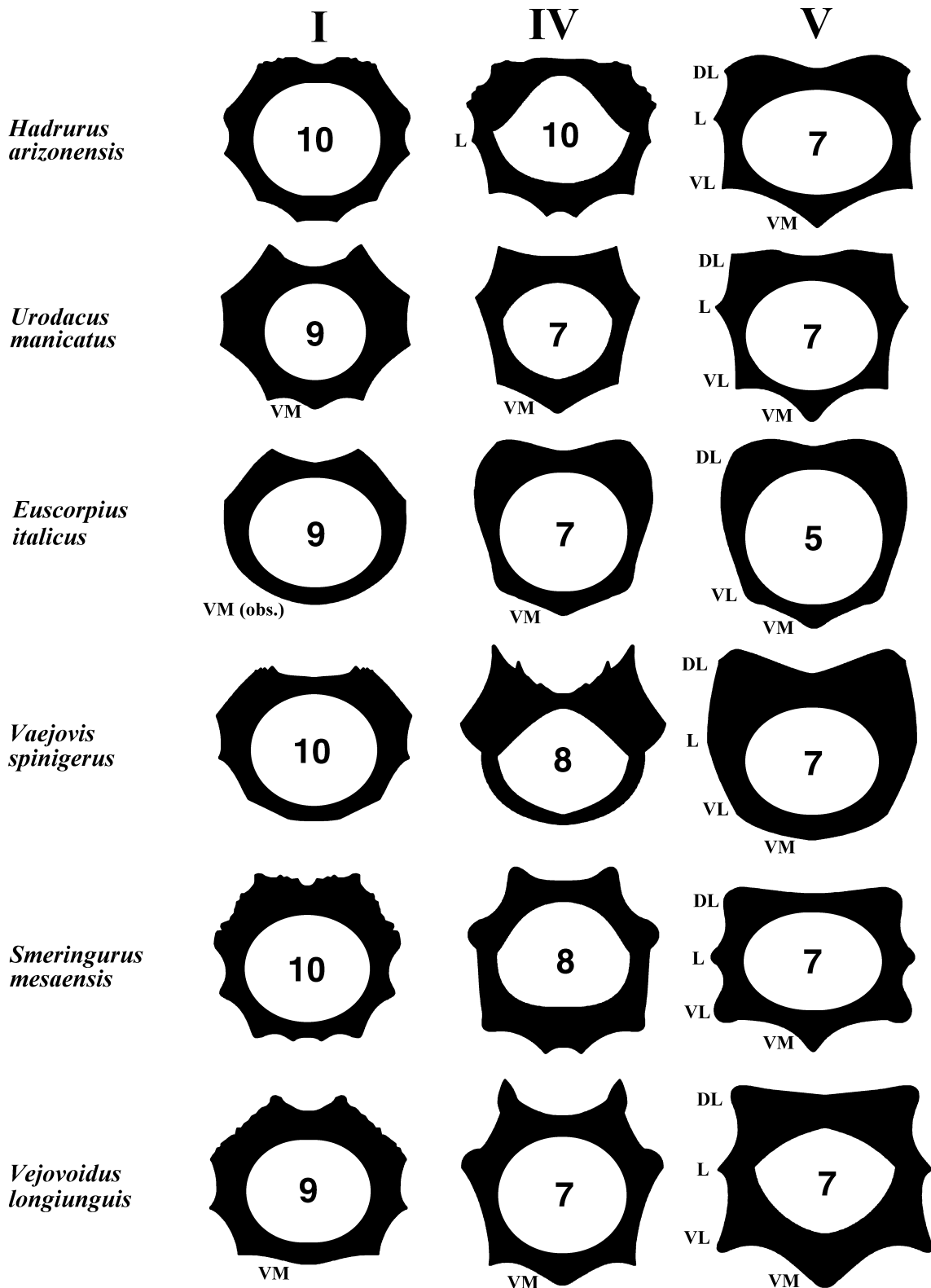


Figure 5: Diagrammatic cross-section of metasomal segments I, IV and V of “non-primitive” Recent scorpions, parvorder Iurida. Of particular interest, note lateral (L) carinae present on segment IV for genus *Hadrurus*; single ventral median (VM) on segments I and IV for genera *Urodacus*, *Euscorpium* and *Vejovoidus*; and the close proximity of ventral median (VM) carinae in genus *Smeringurus*. Note, although individual segment diagrams are to scale, they are not necessarily to scale between or within a species. Numbers inside diagrams refer to number of primary carinae present, and therefore exclude VMS carinae; *obs.* = obsolete, see Fig. 4 for definition of other terms.

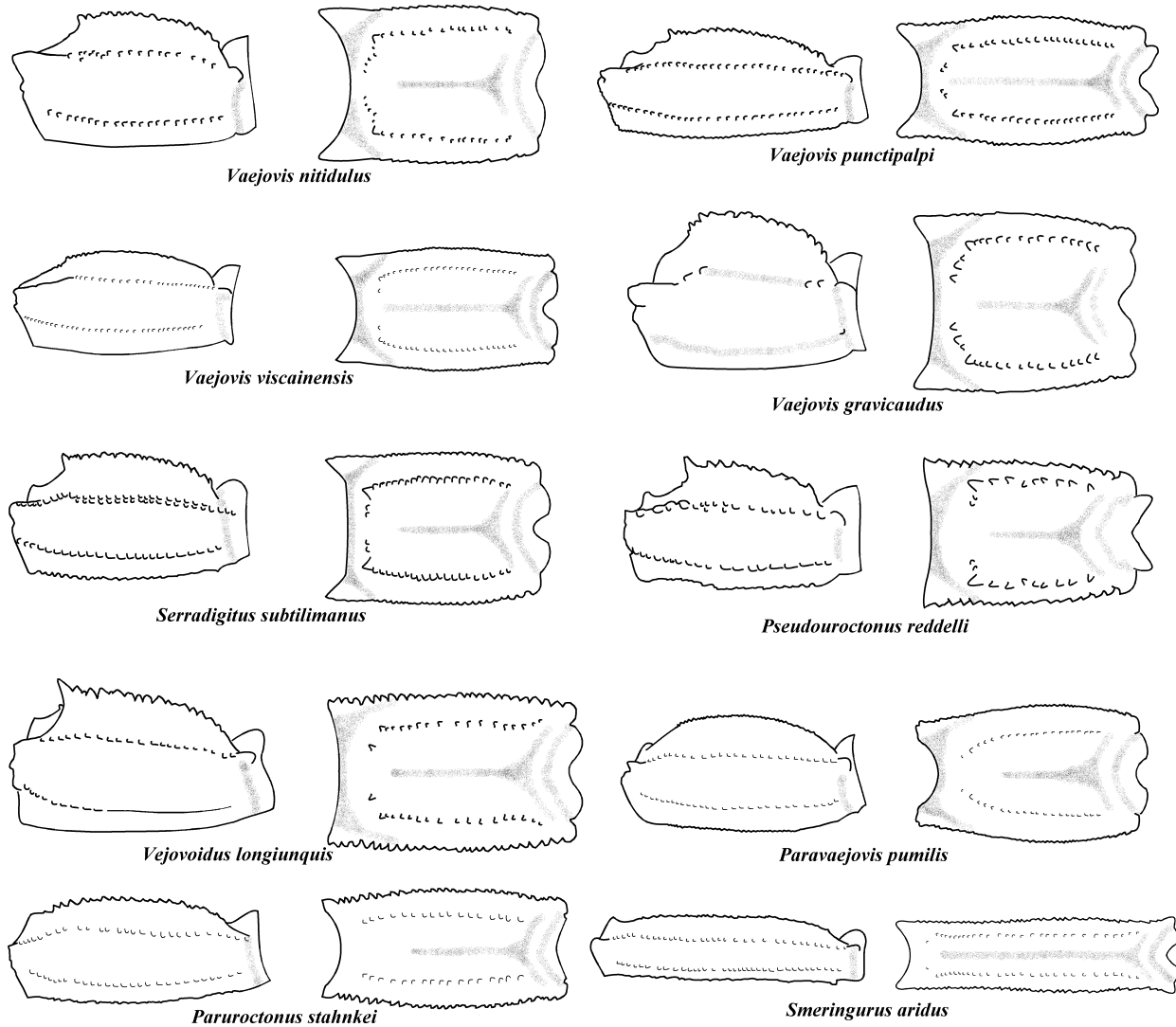


Figure 6: Metasomal segment IV of a representative set of vaejovoid genera. Lateral (left) and dorsal (right) views. Note that the extreme posterior aspect of the dorsal lateral carina is highly developed, exhibiting a “flared terminus” in all major vaejovoid groups, *Serradigitus*, *Pseudouroctonus*, and to a more limited degree, in *Vejovoidus* and *Paravaejovis*. This condition, however, is absent on *Paruroctonus* and *Smeringurus*. Compare these figures with those of the chactids illustrated in Fig. 7.

on any of the five segments, the ventral surface quite smooth and flat. There is a slight trace of the dorsal lateral carinae on segment I which reduces to a slight posterior remnant on segments II–III.

Recent Scorpions – families Vaejovidae and Chactidae: The terminus of the dorsal lateral carinae of metasomal segment IV is quite distinct on a major cross section of vaejovoid scorpions. The extreme posterior edge of this carina (i.e., the “terminus”) is flared extending above the articulation condyle of the segment. Viewing this segment from a dorsal aspect we can see that it also flares outward exhibiting a somewhat flat pointed extremity, or spine. This unique condition of the dorsal lateral carinae terminus is found in all *Vaejovis* groups, *Serradigitus*, *Syntropis*, *Pseudouroctonus*, *Uroctonites*, *Vejovoidus*, and *Paravaejovis* (see Fig. 6). It is

absent, however, in the related genera *Paruroctonus* and *Smeringurus* (Fig. 6). The more exaggerated form of this condition is found in the “nitidulus” group and some members of the “eusthenura” group of *Vaejovis*, *Pseudouroctonus*, and *Serradigitus*, exhibiting lesser development on *Vejovoidus* and *Paravaejovis*. Scorpions of the families Chactidae, Euscorpidae and Superstitioniidae do not exhibit this condition (*Superstitionia* is the only exception to this, showing minor flaring of the dorsal lateral carina terminus). For these families, the dorsal lateral carina terminus meets with the articulation condyle (Fig. 7).

Stahnke (1974) first pointed out the unique terminus of the dorsal lateral carinae of metasomal segment IV for the genus *Vaejovis*, stating (p. 134): “... the distal terminus of superior lateral keels of segment IV flat, subtrian-

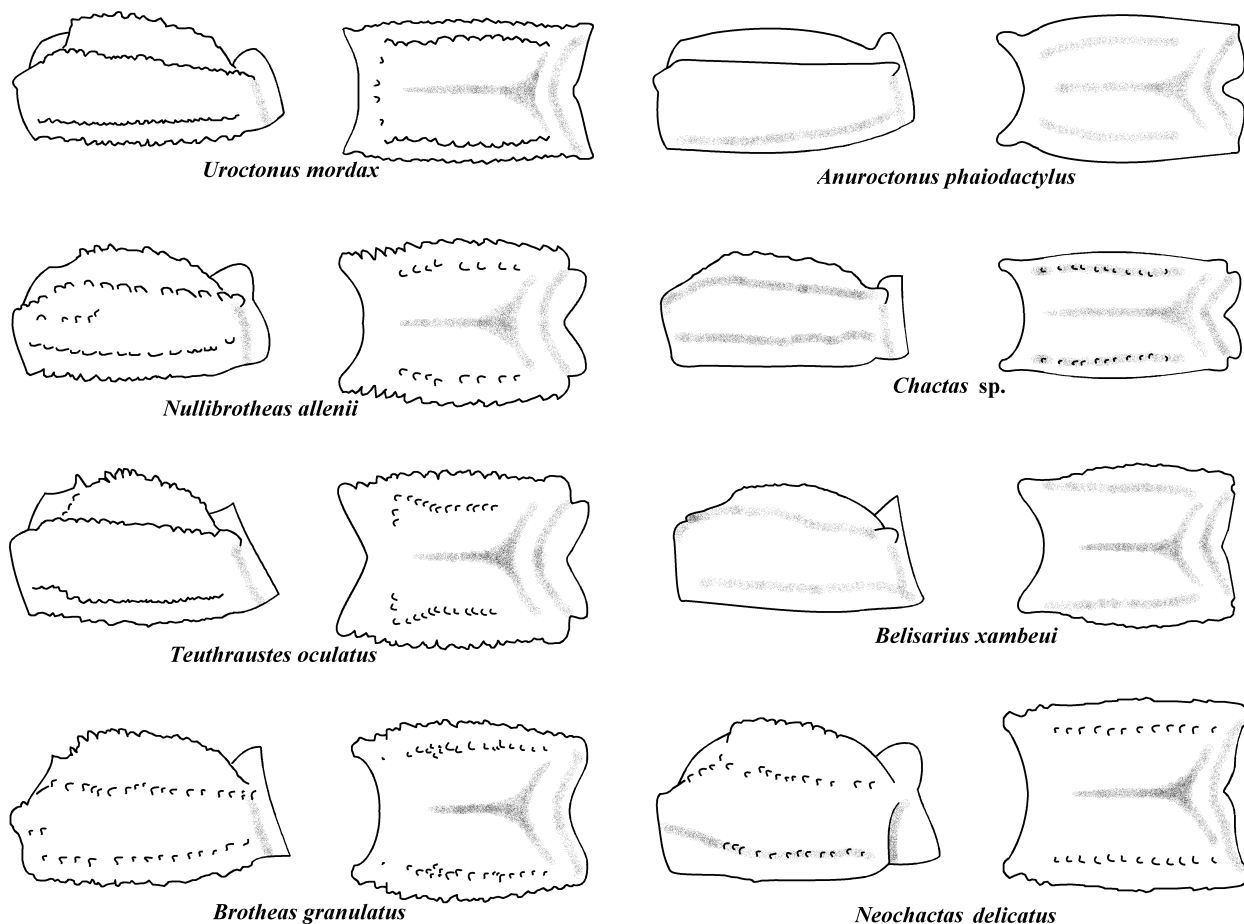


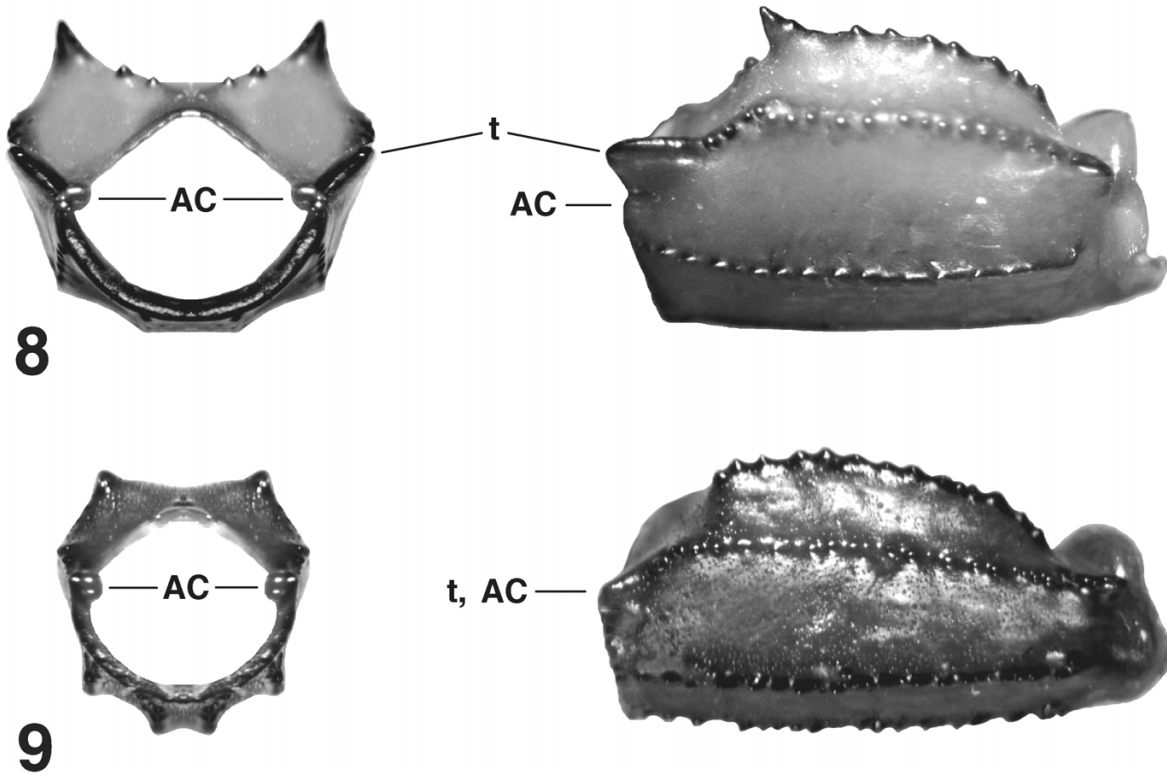
Figure 7: Metasomal segment IV of a representative set of chactid genera. Lateral (left) and dorsal (right) views. Compare the dorsal lateral carina terminus with that illustrated for the vaejovids in Fig. 6.

gular and projecting somewhat laterad ...". Stahnke also established (1974, p. 137) that the genus *Paruroctonus* does not have this unique condition: "... nor is the distal terminus of the dorsal keel on segment V flat and subtriangular ..." (this appears to be a mistake in the text: one should read *segment IV*, not segment V). Stahnke illustrated this character in two species of *Vaejovis* (his Figs. 7-D, F) as well as the lack of same for *Uroctonus* (his Fig. 7-A). Figures 6 and 7 in this paper illustrate this feature for various vaejovoid and chactid species, respectively.

Figures 8–9 illustrate in detail the relationship of the dorsal lateral carina terminus with the posterior articulation condyle. The condyle on segment IV connects with its counterpart located on the anterior end of metasomal segment V. In Figs. 8–9, we illustrate this character in detail for the vaejovoid *Vaejovis intrepidus cristimanus* and the chactid *Uroctonus m. mordax*. In the vaejovoid we see the dorsal lateral carina terminus extends considerably above and posterior of the articulation condyle, whereas in the chactid this carina terminates at the condyle, typical of Chactoidea(-V).

Leg tarsus armature

The setal and spinule armature of scorpion legs has historically been used as an important taxonomic character. In this study we concentrate on the ventral aspect of the tarsus. Very little is known about the tarsus armature in fossil orthostern scorpions; in particular, the tarsus is unknown for the palaeopisthacanthids. However, we do have a detailed description of the leg of *Pulmonoscorpium kirktonensis* Jeram (suborder Mesoscorpionina). Jeram (1994b: 293) reports "... The telotarsus (= tarsus) bears a single inferior row of fixed thorns ..." In addition, Santiago-Blay et al. (in press) reports the following for Cretaceous fossil scorpion *Palaeoburmesebuthus grimaldii* Lourenço: "...tarsus exhibits two delicate rows of ventral spinules (areolae were not visible so we are assuming here that these are spinules, not setae) ..." Based on this limited data from the fossil record, we cannot definitively hypothesize a primitive state for the ventral aspect of the leg tarsus.



Figures 8-9: Metasomal segment IV, posterior end (left) and lateral (right) views. **8.** *Vaejovis intrepidus cristimanus*. **9.** *Uroctonus mordax mordax*. Note the “flared” terminus of the dorsal lateral carinae that extends considerably above the articulation condyle in *V. i. cristimanus*; in *U. m. mordax*, the terminus is not flared coinciding with the articulation condyle. *AC* = articulation condyle; *t* = terminus of dorsal lateral carina.

Definition of Terms. Following are definitions of special terms used in this study to describe the scorpion leg tarsus.

Spinule: A smooth tapering eruption from the cuticle, forming a point at its extremity, exhibiting various thickness and lengths; spinules may have minor longitudinal striations or be smooth. No socket is present. Short, blunt spinules are equivalent to what usually is termed to “denticles” in other scorpion body parts (carapace, pedipalp).

Seta: A tapering bristle that originates from a “socket” in the cuticle, exhibiting various thickness and lengths, from a large thick rigid “spinoid” seta to that of a thin elongated flexible bristle-like seta; seta may have longitudinal striations or be smooth. Unlike spinules, many setae are innervated and carry a mechano- and/or chemoreceptory function (Farley, 1999).

Spinule Cluster: A group of spinules formed in a median row, either situated in irregular groups, or in highly concentrated clusters (i.e., “tufts”). In general these spinules are long, thin either tapering to a point or truncated distally.

Socket: A round mound shaped projection from the cuticle, exhibiting a circular orifice at its distal center from which a seta originates; sockets may be quite large extending considerably from the cuticle base, or may be a small shallow rim-like projection situated at the cuticle

base surrounding the extending seta. Some sockets have small blunt spinules circumscribing their orifice.

Striations: Evenly distributed semi-parallel, dense, shallow longitudinal indentations extending most of a seta or spinule’s shaft length, most prominent basally.

Ridges: Unevenly distributed, medium to deep longitudinal grooves originating proximally and extending to the midpoint of a spinule(s) shaft.

Figure 10 depicts several setal and spinule forms, illustrating many of these special components.

Setal/spinule configurations. In Recent scorpions we recognize five basic fundamental setal/spinule configurations. We consider these basic configurations relevant at the parvorder and superfamily levels. Other hypothesized derivations *within* these configurations are discussed below.

Pseudochactida

1. two median rows of spinules – superfamily **Pseudochactoidea**

Buthida, Chaerilida

2. two or more irregularly positioned rows of setae with medium to large sockets) – superfamilies **Buthoidea, Chaeriloidea**

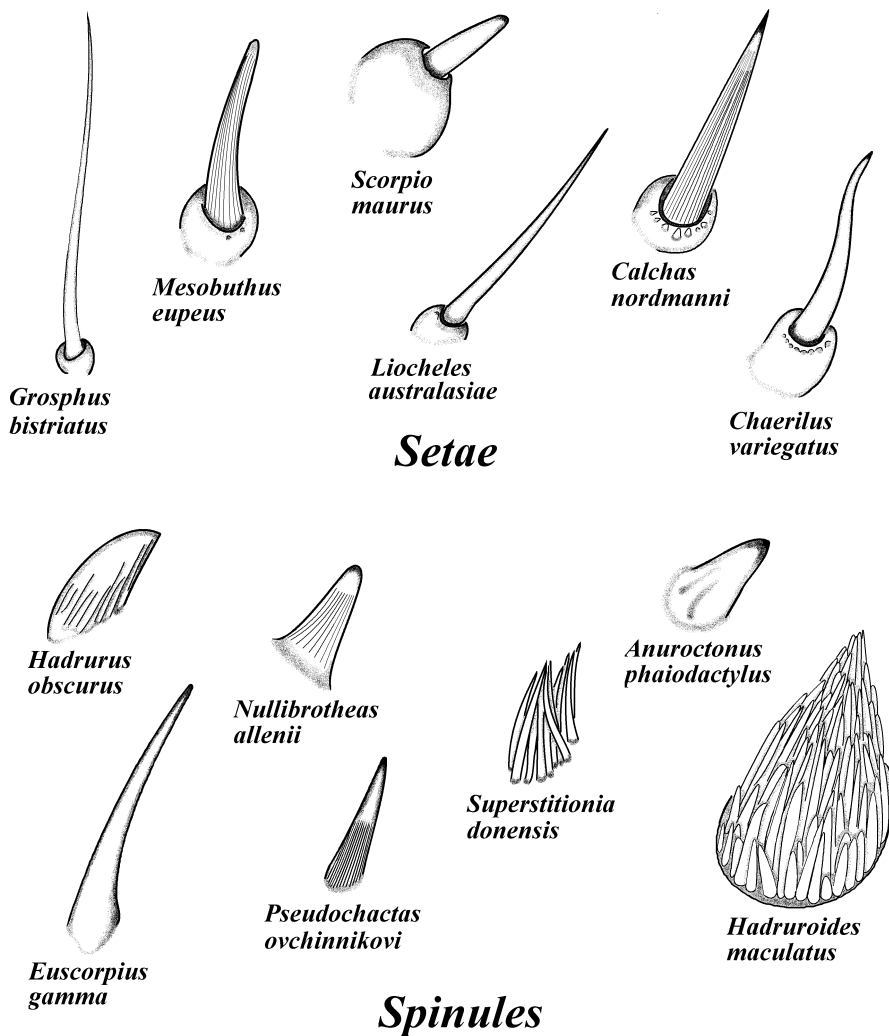


Figure 10: Leg tarsus, ventral view. *Setae* and *spinules* from representative Recent scorpion genera. Of particular interest, note the spinule clusters in genera *Superstitionia* and *Hadruidoidea*; the deep irregular ridges in genus *Hadrurus*; the large limbatic socket surrounding the seta of *Scorpio*; and the fine striations present in both *setae* and *spinules*.

Iurida

3. medially oriented row of spinule clusters (irregular, concentrated clusters, or fused) – superfamily **Iuroidea**
4. paired lateral rows of rigid “spinoid” setae originating from large limbatic sockets, with or without a median row of spinules – superfamily **Scorpionoidea**
5. paired lateral rows of small to medium setae with small sockets accompanied by a median row of spinules – superfamily **Chactoidea**

Pseudochactida: *Pseudochactas*, the sole member of this parvorder, conforms to *configuration 1*: two essentially parallel submedian rows of small spinules extending the entire length of the ventral aspect of the tarsus (Figs. 11–12). Each spinule exhibits subtle

striations basally, extending to the midpoint or further (Figs. 10 and 12). This form is unique in all Recent scorpions. However, its evolutionary polarity is not determinable, and therefore, this character is either autapomorphic to this monotypic genus or is inherited (i.e., plesiomorphic) from an ancestor. Jeram (1994a) illustrates similar dual rows of small spinules on the ventral aspect of the leg tibia and basitarsus (= protarsus) for Carboniferous fossil *Composcorpium elegans* (Text-Fig. 5, E & H); however the tarsus is unknown in this fossil family. In line with this simple configuration, we see that the basitarsus of *Pseudochactas* also has two ventral rows of spinules matching in size and position as those found on the tarsus (Gromov, 1998, Fig. 3.7). If this pattern of “matching spinule rows” across leg segments holds up for the palaeopisthacanthids, then it implies that this spinule configuration is plesiomorphic to the pseudochactids, again exhibiting another primitive

character found on this Recent scorpion “relic”. In addition, the description of the dual spinule rows in fossil scorpion *Palaeoburmesebuthus* by Santiago-Blay et al. (in press) may imply that the dual rows exhibited in *Pseudochactas* are indeed primitive, however, the authors were not completely sure about the true identity of these tiny structures, i.e., spinules versus setae.

Buthida: The scorpions of this parvorder conform to *configuration 2*: two or more irregularly oriented rows of conspicuous socketed setae. In general, these setae are somewhat elongated and striated, originating from well-developed sockets (Figs. 10 and 15–18). For *Mesobuthus* (Fig. 15) we see two irregular rows of fairly stout setae projecting from well-developed sockets. In genera *Grosphus*, *Isometrus* and *Centruroides* (Figs. 16–18), the number of irregular rows increase, the setae are longer, thinner, and the sockets are smaller. There is no evidence of any spinule development on the ventral aspect of the tarsus in buthoids.

Chaerilida: As the buthoids, the chaerilids conform to *configuration 2*: two irregular rows of stout heavy socketed setae (Figs. 10, 13–14). In Figs. 10 and 14 we see the setal sockets are partially rimmed by minute blunt spinules and the setal shaft exhibits subtle striations. On the distal two-thirds of the ventral aspect of the tarsus, we see a median row of small blunt spinules (Fig. 13).

Iurida: The three superfamilies comprising parvorder Iurida present a wide variety of setal/spinule arrangements representing three fundamental configurations.

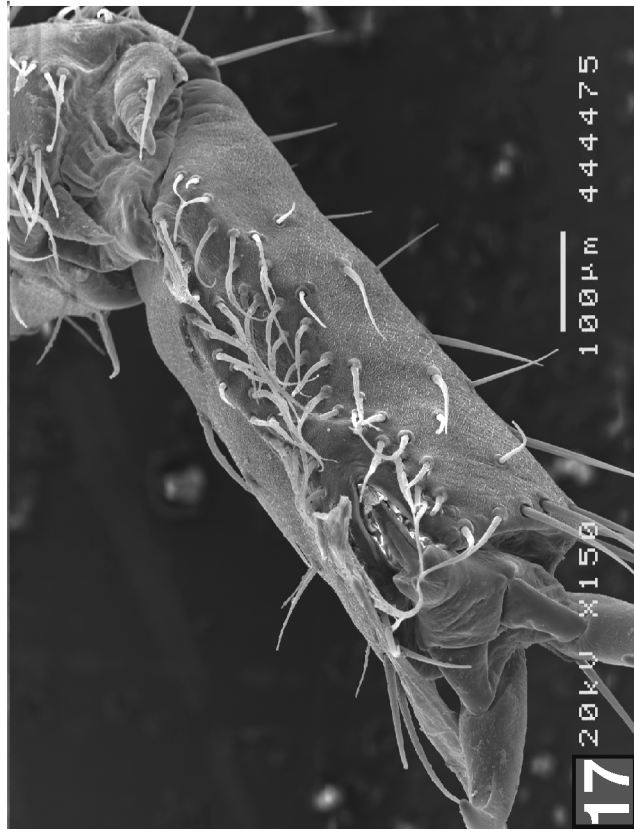
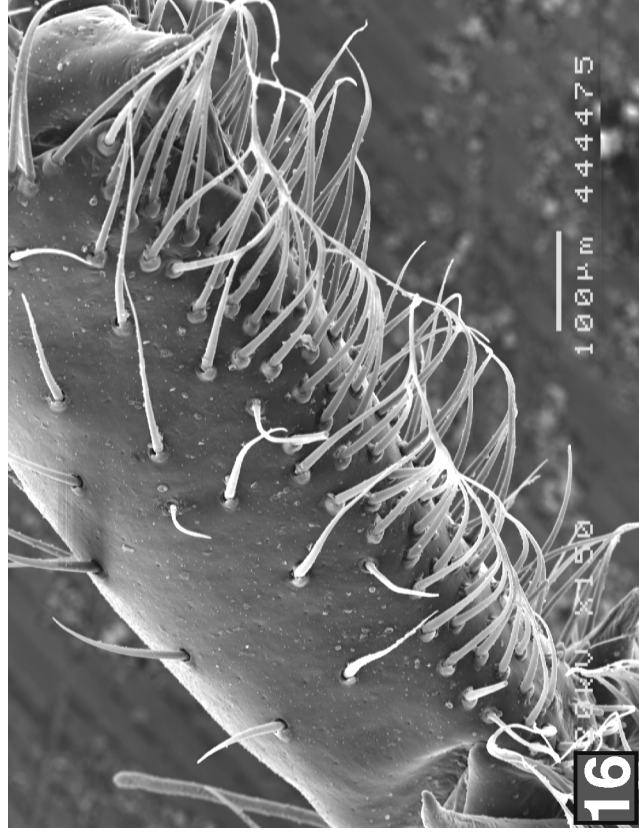
Iuroidea – Scorpions of this superfamily conform to setal/spinule *configuration 3*: median row of spinule clusters. Although the iuroids are a small (albeit, widely dispersed) group of scorpions, the variety of spinule cluster forms exhibited is exceptional. No less than three distinct forms are present, and one of these can be divided further into two subforms: 1) an irregular median row of grouped setal clusters (two to four) found in juvenile to subadult *Calchas*; 2) a median row of highly concentrated setal clusters, forming “setaceous tufts”, found in genera *Iurus*, *Caraboctonus* and *Hadruioides*; and a median row of “fused” setal clusters, forming individual “spinule-looking” protuberances, found in genus *Hadrurus*. The configuration found in *Calchas* is quite interesting (Figs. 19 and 23). This genus exhibits a considerable number of irregularly positioned large socketed setae (Fig. 10). In adults, the median row of clustered spinules is essentially obsolete except for the proximal aspect. In subadults and juveniles, the spinule clusters are quite apparent being surrounded by the larger and heavier setae (Fig. 23). The tarsus of adult *Calchas* specimens is very similar to that found in *Chaerilus*, both with a domination of socketed setae. As pointed out above, *Chaerilus* also exhibits a small partial median row of blunt spinules, but they are neither clustered nor elongated as seen in *Calchas*. In the Old

World iurid genus *Iurus* and the New World caraboctonines, *Caraboctonus* and *Hadruioides*, the spinule clusters are highly concentrated forming distinct “tufts” of elongated spinules (Figs. 10, 20–21). In both of these iuroid groups, the individual clusters are situated on low-profile bases or platforms, which form a subtle ring around the cluster (Figs. 10). In *Iurus*, the spinules are truncated, presenting a squared-off look to the cluster terminus. In *Caraboctonus* and *Hadruioides*, the individual spinules are tapered and of various lengths, forming an overall pointed looking spinule cluster (Fig. 10). For all three genera, the number of spinules per cluster and their lengths are reduced considerably on younger specimens. For very early instar specimens (see Fig. 24 for *Hadruioides charcasus*), the spinules in a cluster are reduced to minimal numbers, approximating those seen in *Calchas*. On mature specimens the individual spinules may number as high as 100+. When viewing the ventral aspect of the tarsus in genus *Hadrurus* under regular magnification (10–30x), one sees a closely grouped median row of spinules, typical of that seen in most vaejovids or chactids (Fig. 22). However, under high magnification, we see a somewhat blunt “spinule” with conspicuous irregularly formed *ridges* originating at its base and continuing most of its length (Figs. 10 and 25). It is clear that these ridges are not the typical symmetric semi-parallel striations found on many setae and some spinules. Under close examination of the base of these ridges, we see that they are three-dimensional, exhibiting a relief almost separate from the other ridges forming the base. We hypothesize here that these ridges are residual spinules fused into a solid structure, presumably originating from the highly concentrated spinule clusters found in *Hadrurus*’s sister group, Caraboctoninae. Note that this very unique set of derivations of the iuroid tarsus briefly described here is being further analyzed in detail in an upcoming paper involving extensive SEM micrography (Fet et al., in progress). In this analysis, multiple species are investigated, each spanning different ontogenetic stages.

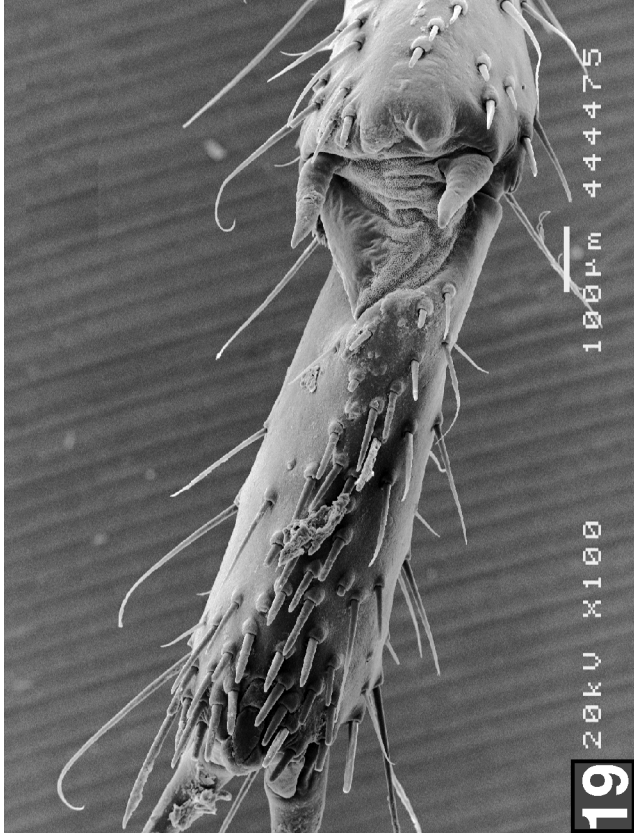
Scorpionoidea – This superfamily conforms to setal/spinule *configuration 4*: two parallel lateral rows of heavy spinoid setae emanating from well-developed limbated sockets (Figs. 10, 27–30). A median spinule row is optional. The number and lengths of these setal pairs are highly variable dependent on the group within this superfamily; they are quite numerous in the scorpionines and diplocentrines, and less numerous in the bothriurids and hemiscorpiines. Of particular interest is the reduction of these spinoid setae to thinner, more bristle-like setae, originating from smaller sockets in certain scorpionoid genera such as *Brachistosternus*, *Iomachus* and *Liocheles* (Fig. 30). Close inspection of these setal bases show that they still exhibit a somewhat substantial socket, but smaller, lower-profile, due to the much thinner seta.



Figures 11-14: Leg tarsus, lateral-ventral view of *Pseudochactas* and *Chaerilus* showing setal/spinule arrangements. **11 & 12.** *Pseudochactas ovchinnikovi*. **13 & 14.** *Chaerilus variegatus*.



Figures 15-18: Leg tarsus, lateral-ventral view of representative buthid genera showing socketed setal arrangements. **15.** *Mesobuthus eupeus*. **16.** *Grosphus bistriatus*. **17.** *Isometrus maculatus*. **18.** *Centruroides anchorellus*.



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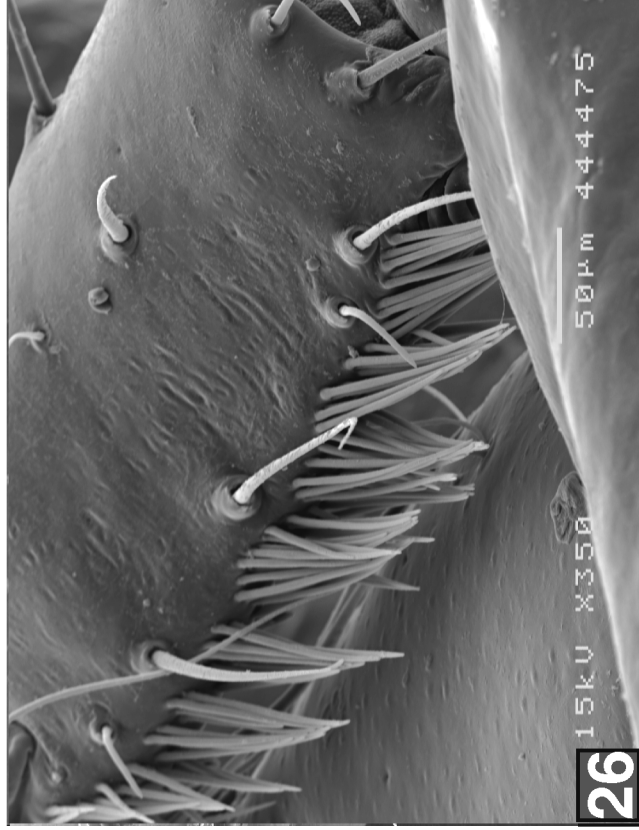
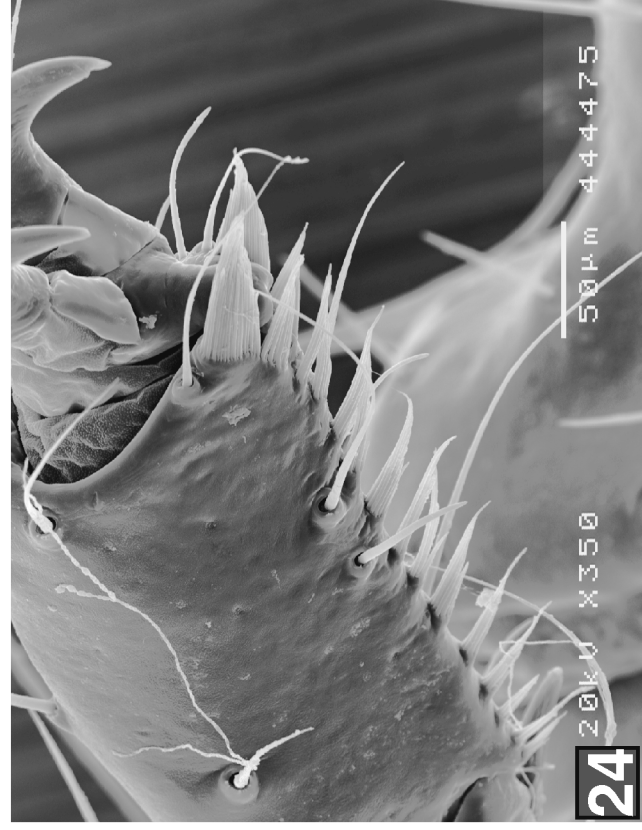
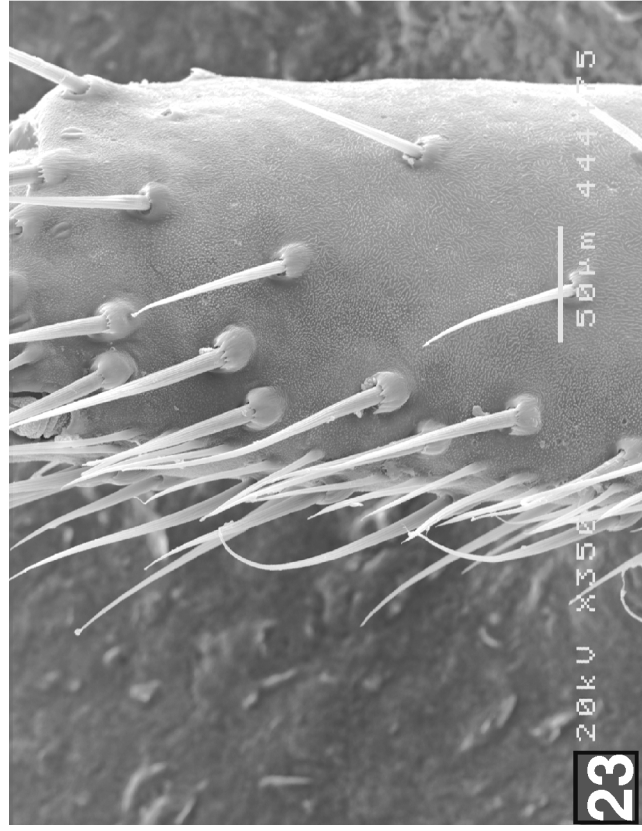


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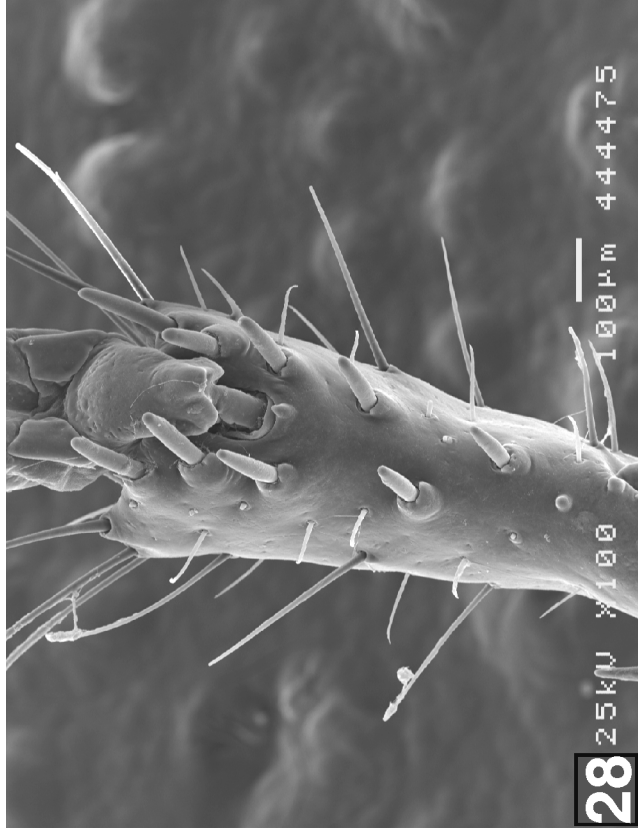


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Figures 19-22: Leg tarsus, lateral-ventral views of iuroid genera showing setal and spinule cluster arrangements. **19.** *Catelchus nordmanni*. **20.** *Iurus difoureus*. **21.** *Caraboctonus keyserlingi*. **22.** *Hadrurus hirsutus*.



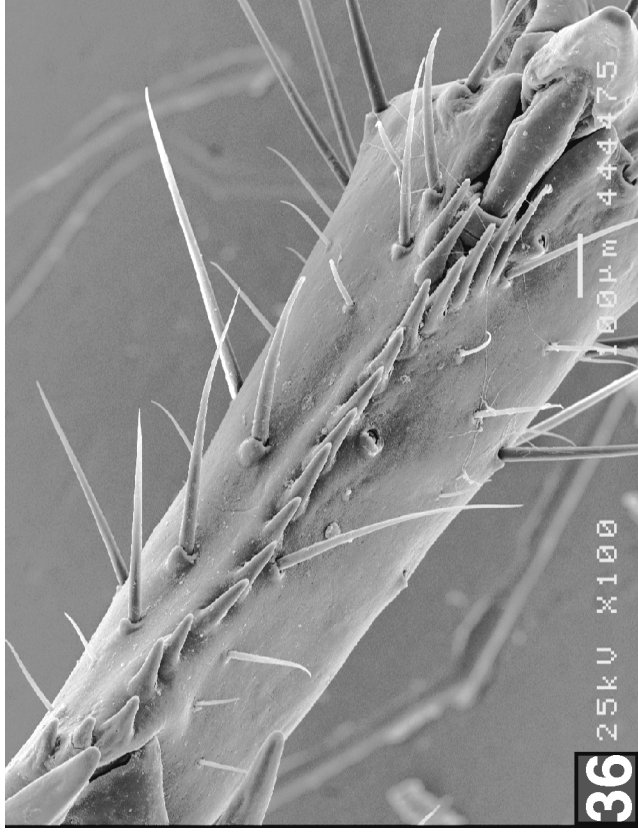
Figures 23-26: Leg tarsus, lateral-ventral view of iuroid and superstitionid genera showing closeup of spinule cluster configurations. **23.** *Calchas nordmanni*, juvenile. **24.** *Hadruroides charcastis*, instar-2. **25.** *Hadrurus obscurus*. **26.** *Superstitionia donensis*.



Figures 27-30: Leg tarsus, lateral-ventral view of representative scorpionoid genera showing socketed setal arrangements. **27.** *Scorpio maurus*. **28.** *Biocutlus comondae*. **29.** *Centromachetes pocockii*. **30.** *Liocheles australasiae*.



Figures 31-34: Leg tarsus, lateral-ventral view of euscorpriid and chactid genera showing setal and spinule configurations. **31.** *Euscorprius tergustinus*. **32.** *Nullibrotheas allenii*. **33.** *Belisarius xambeui*. **34.** *Anuroctonus* sp.



Figures 35-38: Leg tarsus, lateral-ventral view of vaejoivid genera showing setal and spinule configurations. **35.** *Vaejoivis punctatus*. **36.** *Pseudouroctonus reddelli*. **37.** *Smeringurus gertschi*. **38.** *Smeringurus grandis*.

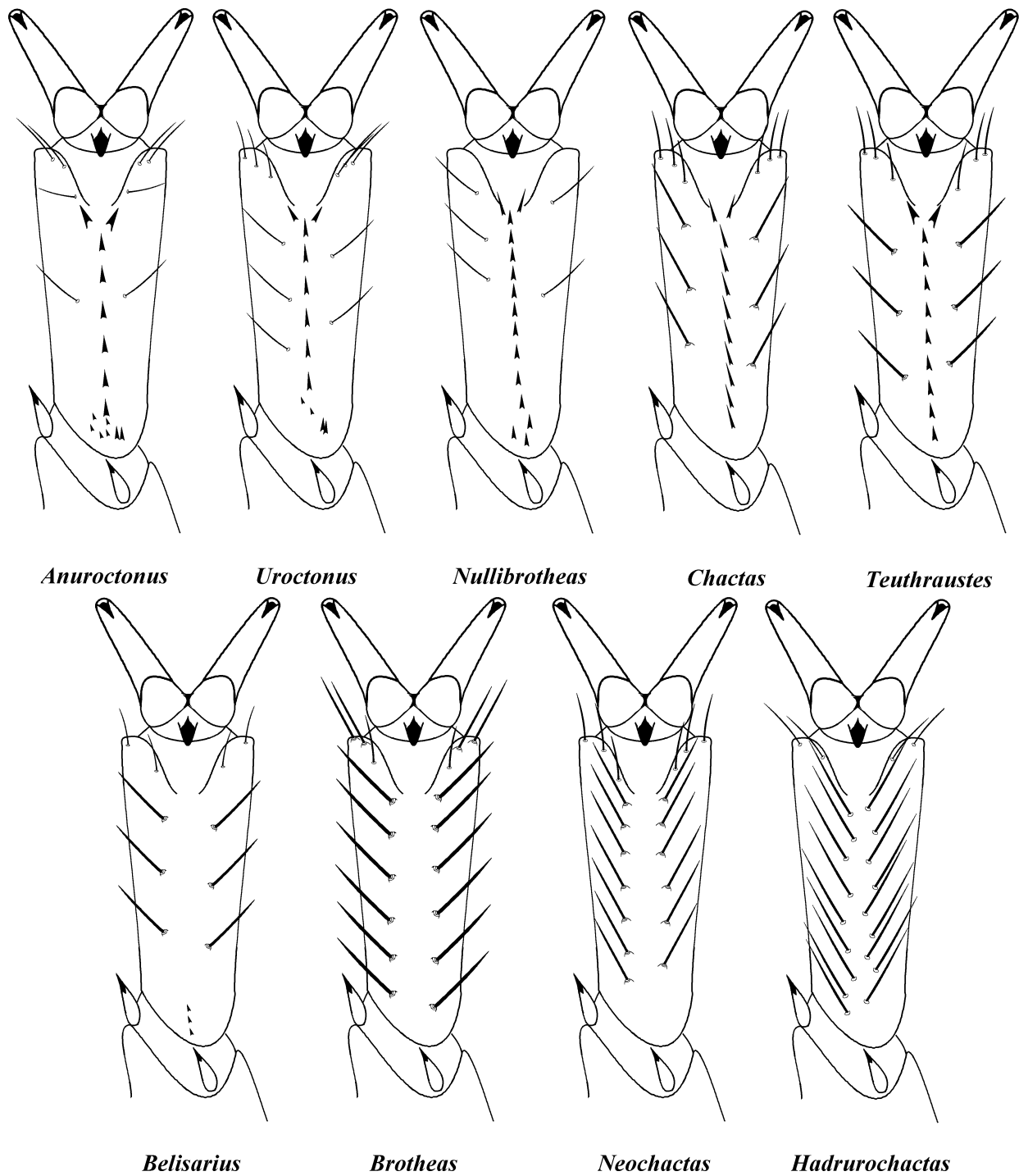


Figure 39: Diagrammatic ventral view of leg tarsus showing the basic arrangement of *setal/spinule* configurations of representative chactid genera.

Chactoidea – This superfamily complies with *setal/spinule configuration 5*: moderate to well-developed lateral pairs of setae and a median row of spinules. The sockets of the setal pairs are of small to moderate development, never as large or significant as those seen in the spinoid setae of the scorpionoids or as

that seen in most buthoids and chaerilids. The ventral median spinule row is present in all vaejooids and in a large majority of the euscorpoids and chactids as well. The dominance of setal pairs versus the median spinule row creates several sub-configurations within these two large assemblages of taxa (Figs. 31–39). The spinule

median row is present in all vaejovids, the lateral setal pairs are of weak to moderate development. Within the vaejovids, the number of *ventral distal spinule pairs* is considered an important taxonomic character, separating some of the vaejovid genera and *Vaejovis* groups. Both one-pair and multiple-pair groups are illustrated in Figs. 35–38: *Vaejovis punctatus* and *Pseudouroctonus reddelli* (Figs. 35–36), and *Serradigitus gertschi* and *Smeringurus grandis* (Figs. 37–38), multiple-pair and one-pair, respectively. This character also proved to be important in the distinction of some euscorpoid genera (Soleglad & Sissom, 2001: 62–64). Williams & Savary (1991) defined the vaejovid genus *Uroctonites* based, in part, on the slightly heavier setal pairs found on the ventral aspect of the tarsus, in contrast to those found in other species of *Pseudouroctonus*. The chactid subfamilies Chactinae and Uroctoninae are similar to the vaejovids, all equipped with a median spinule row terminated by a single pair of distal spinules; the setal pairs are weakly developed in Uroctoninae (represented by *Anuroctonus* in Fig. 34) and well-developed on most Chactinae (represented by *Nullibrotheas* in Fig. 32). Subfamily Brotheinae has essentially lost the median spinule row showing a strong emphasis on the setal pair configuration: *Brotheas* and *Belisarius* (Fig. 33) with strongly developed setal pairs, and the other genera (e.g., *Neochactas*, *Hadrurochactas*) with thinner but more numerous setal pairs (see Fig. 39 for the overall configurations of setal and spinule arrangements for family Chactidae). In the superstitioniids we see three configurations. In subfamily Typhlochactinae (which includes *Alacran*), the median spinule row is essentially absent (minor development is reported in *T. mitchelli* (Sissom, 1988)) and the setal pairs are prevalent, but never as well-developed or numerous as those seen in the brotheines. In subfamily Superstitioniinae, which includes *Superstitionia* and *Troglotayosicus*, we see two patterns. In *Superstitionia*, we see a very unique, dense clustering of elongated spinules, which is similar, under normal magnification, to the spinules clusters seen in young *Calchas* specimens, although more dense and continuous but never forming concentrated clusters of setae as seen in some of the other iuroids (Figs. 10 and 26). The *Troglotayosicus* tarsus has not been examined by us so our observations are based solely on the description and illustration provided by Lourenço (1981: 654, Fig. 43): although the figure shows socketed setae, the text uses the term “spinules (spiniformes)”; whether they are setae, spinules, or a mixture of both, they are in any case quite numerous, elongated, and irregularly positioned. If these “setae” turn out to be spinules, at least for the median area, then we can possibly see a taxonomic connection between this form and that exhibited by *Superstitionia*—both spinule sets would be exceptionally elongated and closely set, which is unprecedented in the chactoids.

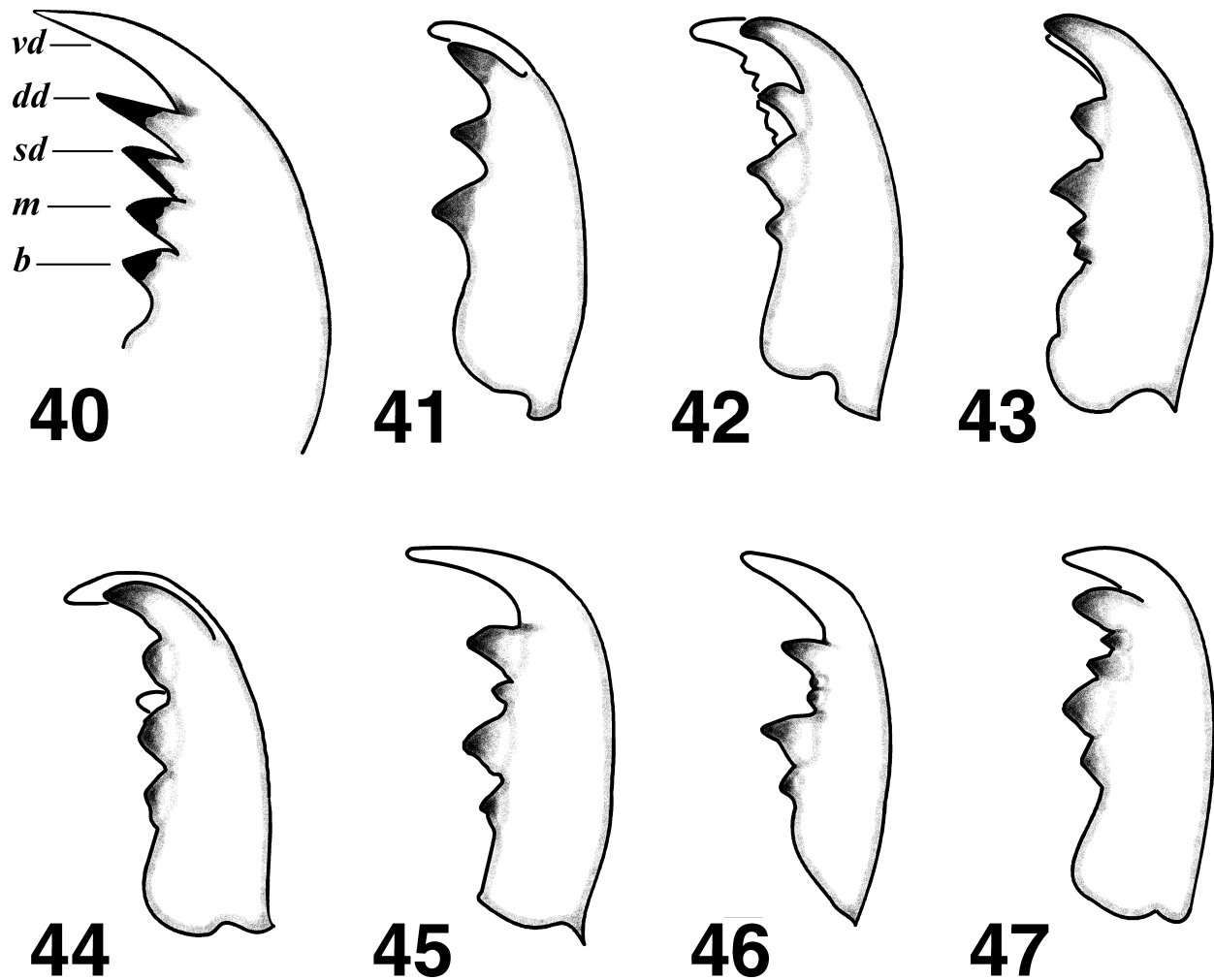
Chelicerae

The chelicerae are an important taxonomic structure in the diagnoses of high-level as well as low-level scorpion taxonomic groups. Vachon (1963) formally defined the basic cheliceral configurations found in Recent scorpions as well as established a nomenclature for identifying various denticles found on this structure. In our analysis, which proposes the palaeopisthacanthids as a primitive form for cladistic purposes, four important aspects of cheliceral dentition are considered: the dorsal and ventral aspects of the movable finger, and the dorsal and ventral aspects of the fixed finger. Of particular importance are: the presence or absence of fundamental denticles on the dorsal edge of the movable finger, the dentition on the ventral edge of the movable finger, the orientation of the denticles of the fixed finger, and the presence or absence of accessory denticles (i.e., “protuberances”) on the ventral surface of the fixed finger. As a character of lesser importance, we also consider the relative alignment of the distal denticles terminating the dorsal and ventral edges of the movable finger.

Kjellesvig-Waering (1986) and Jeram (1994a) described and illustrated the chelicerae of two Carboniferous palaeopisthacanthid scorpions. Kjellesvig-Waering (1986: 233, Text-Fig. 103-E) illustrated the chelicerae for *Palaeopisthacanthus schucherti*, and Jeram (1994a: 534, Text-Fig. 4-E) described and illustrated the chelicerae for *Compsoscorpium elegans*. Of particular importance here is the fact that the chelicerae of these two fossil genera match quite closely in overall structure and dentition. We adopt these descriptions and illustrations as the primitive condition for this important structure, using both genera as a composite when necessary to complete the information.

Movable finger. The cheliceral movable finger has two distinct cutting edges (dorsal and ventral), which enclose the denticulate edge of the fixed finger when a chelicera is closed. These two edges exhibit variability in their overall development as well as in specific dentition configurations.

Dorsal edge. In Fig. 40, we show *Palaeopisthacanthus schucherti* as illustrated by Kjellesvig-Waering (1986). In this diagrammatic drawing we see that the dorsal edge is considerably reduced, the ventral distal denticle extending well beyond the dorsal distal denticle. All four dorsal denticles are well-developed, however, especially a somewhat large subdistal denticle. For fossil scorpion *Compsoscorpium elegans*, Jeram (1994a) writes: “... moveable finger has a superior row of five teeth which increases in size distally ...”. We take exception to Jeram’s count of five denticles for this edge. We suspect that, when viewing the movable finger from the dorsal aspect, that the ventral distal denticle was included in this count. We therefore propose here that *Compsoscorpium* has four denticles on the dorsal edge, as

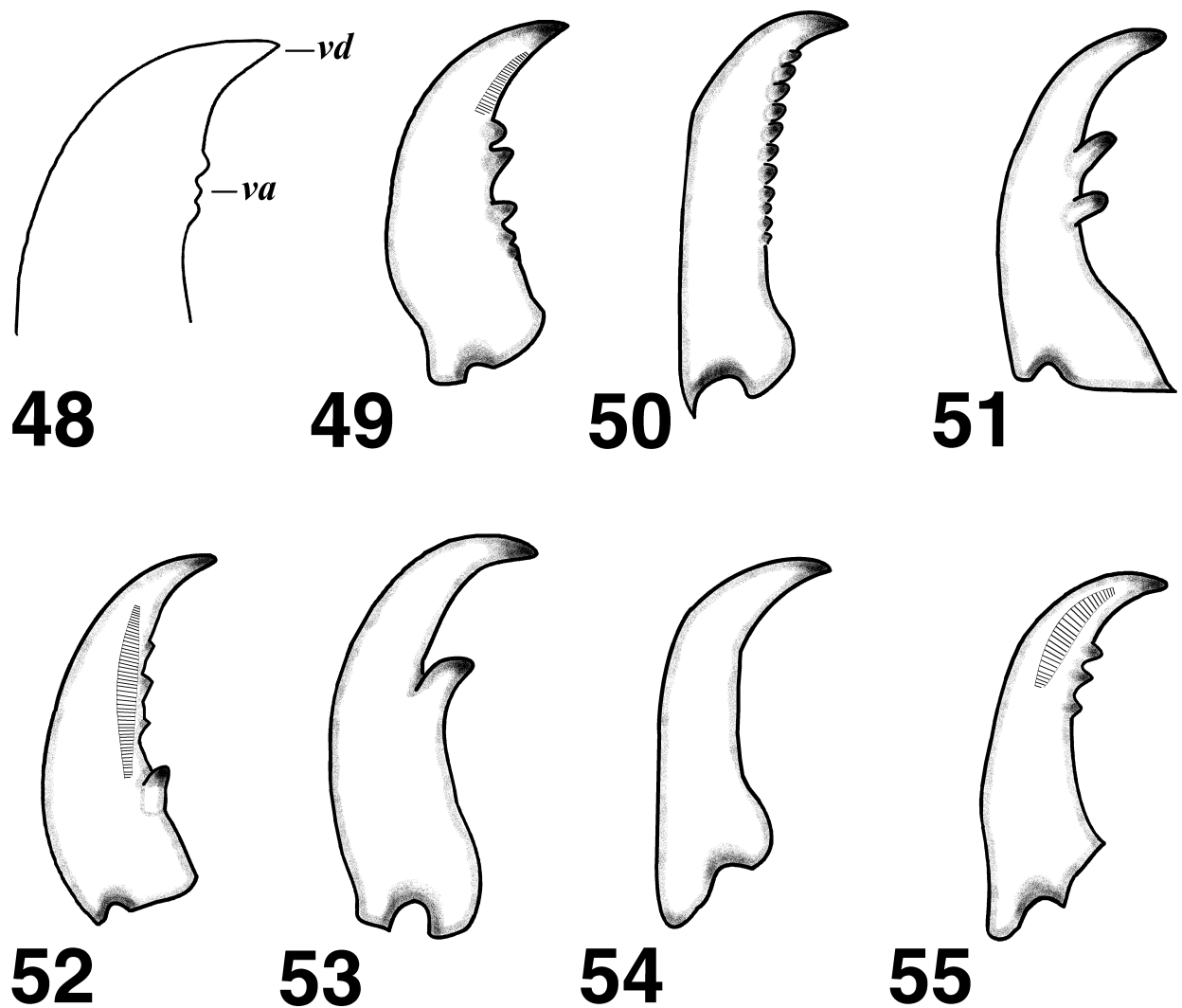


Figures 40–47: Cheliceral movable finger, dorsal aspect. **40.** *Palaeopisthacanthus schucherti* (after Kjellesvig-Waering, 1986: Text-Fig. 103-E, in part). **41.** *Pseudochactas ovchinnikovi*. **42.** *Chaerilus variegatus*. **43.** *Androctonus bicolor*. **44.** *Iurus dufourei*. **45.** *Scorpio maurus*. **46.** *Brachistosternus ehrenbergii*. **47.** *Hadrurus aztecus*. Note that the ventral edge is not shaded in order to contrast it with its dorsal counterpart. *vd* = ventral distal (denticle), *dd* = dorsal distal, *sd* = subdistal, *m* = median, *b* = basal.

that reported and illustrated for *Palaeopisthacanthus*. If one views Kjellesvig-Waering's (1986: Text-Fig. 103-E) original illustration of the chelicerae, which shows all denticles pigmented, the dorsal/ventral edges are not discernable when viewed from the dorsal aspect. Only when viewed internally (a view also shown in this figure) do the two edges become apparent. Jeram's observation that the denticles increase in size distally is consistent with our illustration of *Palaeopisthacanthus* (Fig. 40). Therefore, we see consistency within the two palaeopisthacanthid genera in the dentition of the cheliceral dorsal edge of the movable finger. We consider this configuration of four denticles a primitive condition: dorsal distal (*dd*), a single subdistal (*sd*), median (*m*), and single basal (*b*) denticles.

In Figures 40–47, we illustrate the dorsal edge of the movable finger of several Recent scorpion groups. In Fig. 40 (*Palaeopisthacanthus schucherti*) we illustrate

the hypothesized primitive condition, as discussed above. We see that the primitive condition of four denticles is found in parvorder Chaerilida (Fig. 42), Old World iuroids, and in most scorpionoids. We consider this configuration plesiomorphic for these groups. This primitive condition, which exhibits single subdistal (*sd*) and basal (*b*) denticles, is found in both Old World iuroid genera, *Iurus* (Fig. 44) and *Calchas*, and consistently in scorpionoid families Scorpionidae (represented by *Scorpio* in Fig. 45) and Liochelidae, as well as in some bothriurid genera (i.e., *Bothriurus*, *Timogenes*, and *Vachonia* (Prendini, 2000: 48)). However, Prendini considered the occurrence of a single subdistal denticle in these three bothriurid genera as derived from a two subdistal denticle state (i.e., a reversal, since these genera formed the most internal aspect of his bothriurid clade (see Prendini's Fig. 2)). Two primitive Recent scorpion parvorders, Pseudo-



Figures 48-55: Cheliceral movable finger, ventral aspect. **48.** *Palaeopisthacanthus schucherti* (after Kjellesvig-Waering, 1986: Text-Fig. 103-E, in part). **49.** *Pseudochactas ovchinnikovi*. **50.** *Chaerilus variegatus*. **51.** *Androctonus bicolor*. **52.** *Calchas nordmanni*. **53.** *Iurus dufourei*. **54.** *Liocheles* sp. (Papua New Guinea). **55.** *Nullibrotheas allenii*. The dorsal edge is not shown. *vd* = ventral distal (denticle), *va* = ventral accessory denticle (s).

chactida and Buthida, do not comply entirely with the hypothesized primitive condition. In Pseudochactida (Fig. 41), we see a single subdistal denticle, but the basal denticle is *missing*. We consider the absence of the basal denticle a derivation for this parvorder. In Buthida (represented by *Androctonus* in our Fig. 43), we also see a single subdistal denticle but the basal denticle is *doubled*, clearly a derived condition for this parvorder. For New World iuroids (represented by *Hadrurus* in Fig. x), and most bothriurid genera (represented by *Brachistosternus* in Fig. 46), we have two subdistal denticles. With a few exceptions, all chactoids have two subdistal denticles, which we consider a synapomorphy for this superfamily. For superstitioniid subfamily Typhlochactinae we see several species with a single subdistal denticle (i.e., *Sotanochactas elliotti*, *Typhlochactas cavicola*, *T. sylvestris*, and *T. granulosus*); and one minute species, *T. mitchelli*, has three dorsal

denticles, presumably missing the basal denticle. Interestingly, species *T. rhodesi* and *T. reddelli* are equipped with two subdistal denticles (see Sissom & Cokendolpher (1998: Table 1)). Due to the cave adaptation of these highly specialized scorpions, we do not consider the number of subdistal denticles of a particular taxonomic importance. Clearly, this somewhat arbitrary condition exhibited in this scorpion group is derived from a two subdistal denticle configuration. Gertsch & Soleglad (1972: Fig. 36) illustrated a single subdistal denticle for vaejovid *Uroctonites montereus* and also reported it as single in *U. sequoia*.

Ventral edge. As with the dorsal edge, we have good information on the dentition of the ventral edge of the movable finger for the two fossil Carboniferous genera, *Palaeopisthacanthus* and *Compsoscorpium*. In our Figure 48, showing *Palaeopisthacanthus schucherti* (after Kjellesvig-Waering, 1986), we see an edge with

three small crenulations or denticles. For *Compsoscorpis elegans*, Jeram (1994a) writes: "... inferior dentition consists of the large distal tooth and an inferior row of approximately twelve small accessory teeth ...". Again this is consistent with *Palaeopisthacanthus*, both fossil genera exhibiting a crenulated ventral edge and an enlarged distal denticle. We consider this condition primitive.

Figure 48 illustrates the primitive ventral edge for fossil *Palaeopisthacanthus schucherti*. Figures 49–55 illustrate the ventral edge of the cheliceral movable finger for several Recent scorpion groups. We see the primitive condition of several accessory denticles exhibited in parvorders Pseudochactida (Fig. 49) and Chaerilida (Fig. 50). We considered this crenulation to be plesiomorphic for these two parvorders. In parvorder Buthida (represented by *Androctonus* in our Fig. 51), we see two well-developed denticles, which is clearly a derivation for this parvorder. The presence of these distinct denticles is essentially conserved in Buthida, representing well over 75 genera. In parvorder Iurida, we have two fundamental configurations for the ventral edge of the movable finger: 1) a large single basal denticle, and, 2) a smooth edge. Superfamily Iuroidea is equipped with a large single denticle on the ventral edge (Figs. 52–53). The denticle is the most developed in the genus *Iurus* (Fig. 53) where it is situated midfinger and flares outward almost forming a tripod when the finger edge is viewed internally (i.e., the tripod is formed by the dorsal and ventral distal denticles and this large ventral denticle). In the genus *Calchas* (Fig. 52), the denticle is smaller and more basal. In addition, in some specimens of *Calchas*, we see irregular crenulation similar to that exhibited in the primitive condition (this is illustrated in Fig. 52). One could hypothesize that this relict genus retained the primitive state. In New World iuroids, genera *Hadrurus* and *Hadruidoidea* have a well-developed basal denticle situated on the proximal half of the segment, and in genus *Caraboctonus*, the denticle is smaller and more basally situated. Superfamilies Scorpionoidea (represented by *Liocheles* in Fig. 54) and Chactoidea have a smooth ventral edge of the movable finger. In Chactoidea there are several examples of ventral crenulations in various forms. These are all considered secondary development, having been derived from a smooth edge. This same hypothesis was proposed by Soleglad & Sissom (2001: 73–74). In family Euscorpidae, Soleglad & Sissom (2001: Fig. 207) proposed two separate derivations of a crenulated ventral edge, for subfamilies Megacorminae and Scorpipinae, respectively. In this paper, we also propose two separate crenulated ventral edge derivations for the family Chactidae, subfamily Uroctoninae and tribe Nullibrotheini (subfamily Chactinae) (Fig. 55). In the family Vaejovidae, several genera exhibit ventral crenulations to one degree or another: *Paruroctonus* and related

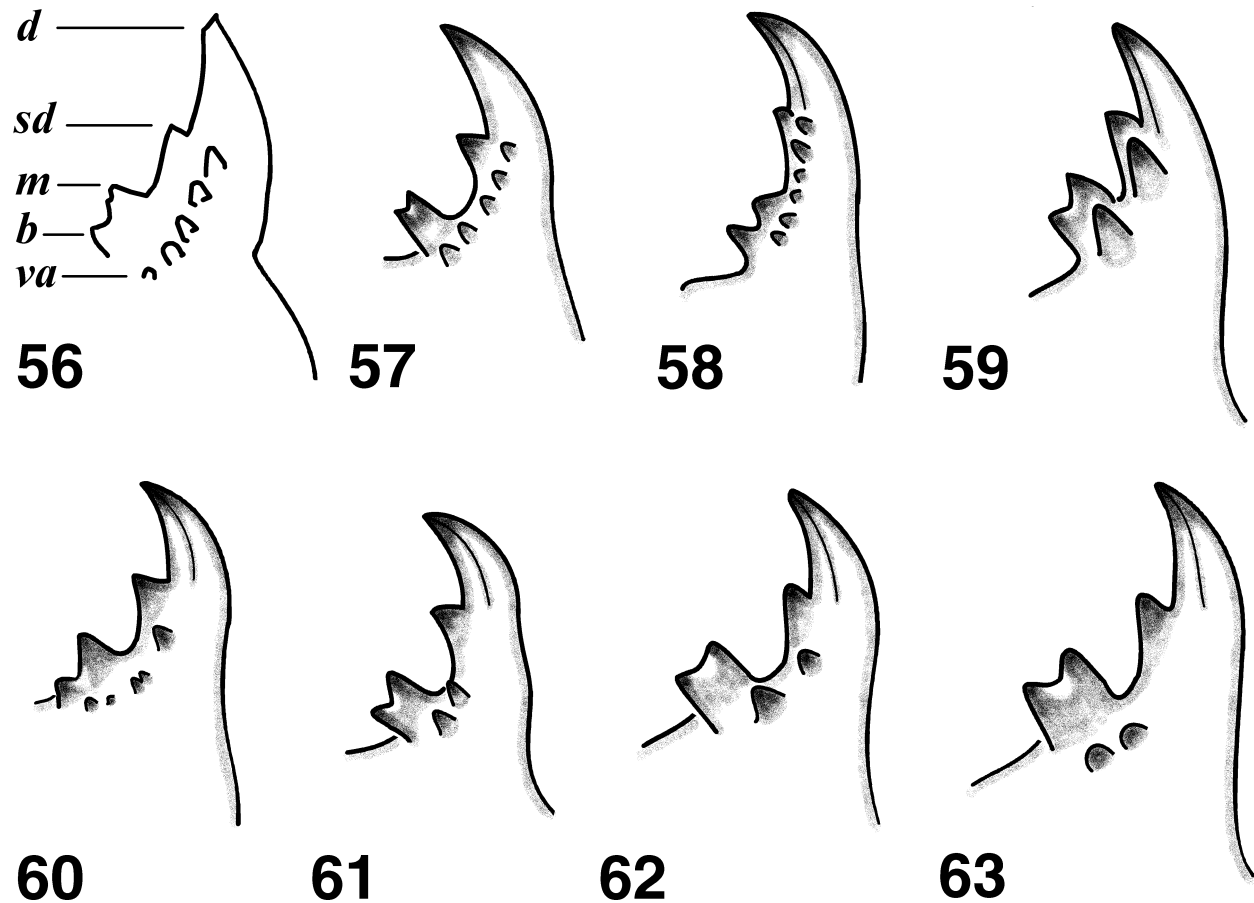
genera (*Smeringurus* and *Vejovoidus*), and *Pseudo-uroctonus* (in part) and *Uroctonites*.

Dorsal/ventral distal denticle alignment. For fossil genera *Palaeopisthacanthus* and *Compsoscorpis*, Kjellesvig-Waering (1986) and Jeram (1994a) reported an enlarged ventral distal denticle, contrasted to a smaller, more offset dorsal distal denticle (Fig. 40). This feature, again, illustrates consistency in the chelicerae of these two palaeopisthacanthid genera.

In Recent scorpions, the relative proportional development of the dorsal and ventral distal denticles has diagnostic value in some scorpion groups. For the three primitive parvorders, Pseudochactida (Fig. 41), Chaerilida (Fig. 42), and Buthida (represented by *Androctonus* in Fig. 43), we see a well-developed dorsal distal denticle, slightly offset from its ventral counterpart. In particular, in Buthida, the dorsal distal denticle often extends beyond the ventral denticle, which is, in general, a characteristic of this large scorpion group. Interestingly, none of these three primitive parvorders exhibit the primitive state as seen in the palaeopisthacanthids, the significantly offset dorsal edge. In superfamily Iuroidea we see a well-developed dorsal distal denticle in genus *Iurus* (Fig. 44), with lesser development in other genera. In the scorpionoids we see that family Liochelidae and subfamily Heteroscorpioninae have a well-developed dorsal distal denticle, approximately the same length as its ventral counterpart. In contrast, other scorpionoids have a very reduced dorsal distal denticle (represented by *Scorpio* and *Brachistosternus* in Figs. 45–46). The relative proportions of these two distal denticles were used as a diagnostic character by Soleglad & Sissom in Euscorpidae (2001: 57–59) for distinguishing the very developed dorsal distal denticle exhibited in the subfamily Scorpipinae. At a more localized scale, several species of the vaejovid genus *Paruroctonus* have a very reduced dorsal edge of the movable finger (e.g., *P. gracilior*, *P. stahnkei*, *P. becki* (see Gertsch & Soleglad, 1966: Figs. 34, 37, 40), *P. williamsi*, and *P. pecos* (see Sissom & Francke, 1981: Figs. 28, 32)). This may possibly provide some diagnostic rationale for grouping two or more of these species.

Fixed finger. The cheliceral fixed finger has only one denticulate cutting edge, which we refer to in this paper as the dorsal edge. The dentition of the fixed finger, in general, is quite static in scorpions, only exhibiting subtle variations in their configuration, thus providing some diagnostic value. The ventral surface of this finger does not form a cutting edge; it may be smooth or be equipped with one or more denticles of variable development (sometimes referred to as "protuberances").

Dorsal edge. The dorsal edge of the fixed finger has been illustrated for both fossil genera discussed above, both exhibiting four fundamental denticles: distal (*d*),



Figures 56-63: Cheliceral fixed finger, ventral aspect. **56.** *Compsoscorpium elegans* (after Jeram, 1994a: Text-Fig. 4-E, in part). **57.** *Pseudochactas ovchinnikovi*. **58.** *Chaerilus variegatus*. **59.** *Androctonus bicolor*. **60.** *Troglocormus willis*. **61.** *Pseudo-uroctonus reddelli*. **62.** *Smeringurus grandis*. **63.** *Vejovoidus longiunguis*. *d* = distal (denticle), *sd* = subdistal, *m* = median, *b* = basal, *va* = ventral accessory.

single subdistal (*sd*), median (*m*), and basal (*b*) denticles. In our Figure 56 of *Compsoscorpium elegans* (after Jeram, 1994a), we see that the median and basal denticles are conjoined on a common trunk, a configuration usually found in Recent scorpions. Kjellesvig-Waering (1986) illustrates the fixed finger for *P. schucherti* with the median and basal denticles somewhat flush with the finger edge. Kjellesvig-Waering (1986: 233) reports: "... the fixed ramus seems to correspond closely to the arrangement in the genus *Chaerilus* ...". He was referring to the flush orientation of the median and basal denticles of the dorsal edge of the fixed finger, a diagnostic character for the genus *Chaerilus* (Fig. 58).

All Recent scorpions exhibit the fundamental four denticles of the dorsal edge of the cheliceral fixed finger (Figs 57-63) (one exception, see below). Parvorder Chaerilida has a separate, non-conjoined median and basal denticle configuration (Fig. 58). This is considered a derivation for this parvorder since it is consistently found in all known species (even though this same configuration was described by Kjellesvig-Waering for

genus *Palaeopisthacanthus*). The non-conjoined denticle pair is also seen, in part, in the euscorpium genus *Troglocormus* (Fig. 60) as well as in many superstitioniids such as *Troglotayosicus* (Lourenço, 1981: Fig. 44), *Alacran* (Francke, 1982a: Fig. 4), *Sotanochactas elliotti* (Mitchell, 1971: Figs. 6-7), *Typhlochactas cavicola* (Francke, 1986: Fig. 4) and *T. rhodesi* (Mitchell, 1968: Figs. 4-5). Again, the minute scorpion *T. mitchelli* exhibits the most radical departure, only equipped with three denticles (Sissom, 1988: Fig. 2), the basal denticle presumably is lost.

Ventral surface. Jeram (1994a) reports for *C. elegans*: "... fixed finger ... Inferior dentition consists of a row of five subequal teeth ..." In our Figure 56 (after Jeram, 1994a), we see that the ventral surface of the fixed finger is equipped with somewhat low-profile denticles adjacent to the subdistal, median, and basal dorsal denticles. Kjellesvig-Waering (1989) illustrates the fixed finger for *Palaeopisthacanthus schucherti* but does not show ventral dentition. However, it is not clear which view is being shown, and therefore, we do not know exactly whether these ventral accessory denticles

are present in this species. Consequently, we consider the condition illustrated and described by Jeram (1994a) for *C. elegans* as primitive.

The ventral surface of the cheliceral fixed finger is illustrated for all major Recent scorpion groups in Figures 57–63. In the primitive condition, based on Jeram's (1994a) description of *Compsoscorpheus elegans* (our Fig. 56), we see five small denticles on the ventral surface. In primitive Recent scorpion parvorders we also see denticles on this surface. For Pseudochactida (Fig. 57), four to five small denticles are present (variable within the same species, *Pseudochactas ovchinnikovi*), remarkably in the same configuration as that seen in the primitive condition. In Chaerilida (Fig. 58), we see a series of substantial denticles, six in our example of *Chaerilus variegatus* (Stockwell (1989: Fig. 53) illustrated eight small denticles for *C. granulatus*). In some *Chaerilus* species these denticles are less developed: in *C. tryznai*, we see six pigmented denticles of medium development; in species *C. chapmani* (a troglobitic species) and *C. tichyi*, five weakly developed and faintly pigmented denticles are present. We consider the ventral denticles present in these two parvorders plesiomorphic. In parvorder Buthida (represented by *Androctonus* in Fig. 59), we see two well-developed denticles, indicative, in general, of this large scorpion group. We consider this specialized variant of the ventral dentition of the fixed finger a derivation for the parvorder Buthida. However, there are some exceptions in the Buthida for this configuration. The following genera lack these denticles: *Karasbergia* (Lamoral, 1979: 555) and *Uroplectes* (Sissom, 1990: 94). Sissom (1990: 97) and Fet et al. (2001a: 184–185) also report that genera *Anomalobuthus*, *Hemibuthus*, *Isometroides*, *Liobuthus*, *Lychas*, *Pectinibuthus*, and *Psammobuthus* are equipped with only one ventral denticle. A single ventral denticle is also found in some species of New World genera *Alayotityus*, *Centruroides*, *Microtityus*, *Rhopalurus*, *Tityus*, and *Zabius* (R. Teruel, pers. comm., 2003). In parvorder Iurida, ventral dentition is essentially absent; where it does occur it is considered a localized derivation for that group. In family Euscorpiidae we see as many as five small ventral denticles in genus *Troglocormus* (Fig. 60). For the related vaejovid genera *Paruroctonus*, *Smeringurus* (Fig. 62), and *Vejovoidus* (Fig. 63), we see two to three small ventral denticles. Gertsch & Soleglad (1966: Fig. 42) illustrated three denticles for *Smeringurus mesaensis*. These ventral denticles are also found in some species of *Pseudouroctonus* (represented by *P. reddelli* in Fig. 61). Gertsch & Soleglad (1972: Fig. 31) illustrated three such denticles for species *P. cazieri*. These occurrences of ventral denticles are only of localized importance, maybe providing diagnostic characters at the genus level.

Trichobothria

Trichobothria, their fundamental orthobothriotaxic patterns, basic positional orientation within these patterns, and neobothriotaxy, all play an important role in this study. Fundamental orthobothriotaxic patterns provide major synapomorphies at the parvorder levels defined herein; basic trichobothria positional patterns are important at the superfamily level as well as lower levels such as families, subfamilies and tribes, discussed and/or defined in this study; neobothriotaxy is critical, in part, in differentiating the subfamilies within the family Chactidae. In this section we discuss relevant trichobothria characterizations involving all of these subjects.

Soleglad & Fet (2001) presented a formal cladistic procedure for evaluating the evolution of orthobothriotaxic patterns in Recent scorpions. In their analysis individual trichobothrium homologies were hypothesized spanning all defined orthobothriotaxic types including two fossil groups, the palaeopisthacanthids and the genus *Archaeobuthus*. Crucial to this approach was that each trichobothrium was treated as a separate cladistic character. This same technique currently is being applied to the complicated neobothriotaxy found in the euscorpiid genus *Euscorpheus* (Fet & Soleglad, in progress), thus establishing homology in key accessory trichobothria. Many of the observations presented in this paper concerning the trichobothrial positions and/or patterns of orthobothriotaxy found in the Vaejoidea and Chactidae(-V) families are based on preliminary results of an ongoing cladistic study of the Type C pattern (Soleglad, in progress). In this study all 48 trichobothria comprising the Type C pattern are mapped onto "positional grids", thus allowing the cladistic characterization of individual trichobothria positions.

Orthobothriotaxic patterns: In this current study the same set of existence criteria and corresponding homologies as established in Soleglad & Fet (2001), involving 62 existence characters, were incorporated with the other structural characterizations established in this paper. The resulting phylogeny deviated slightly from that derived in the other study which was based solely on orthobothriotaxy. The phylogeny in this study is formally contrasted in detail with that of Soleglad & Fet (2001) elsewhere in this paper, where differences in support and trichobothria derivations are presented.

In this study, the totality of all characterizations provides a basic topology outlining the parvorders established herein. As it turns out each Recent scorpion parvorder established in this study corresponds directly to a basic orthobothriotaxic pattern type, as formally defined by Vachon (1974), types A, B and C, and Soleglad & Fet (2001), types P, F1, and D:

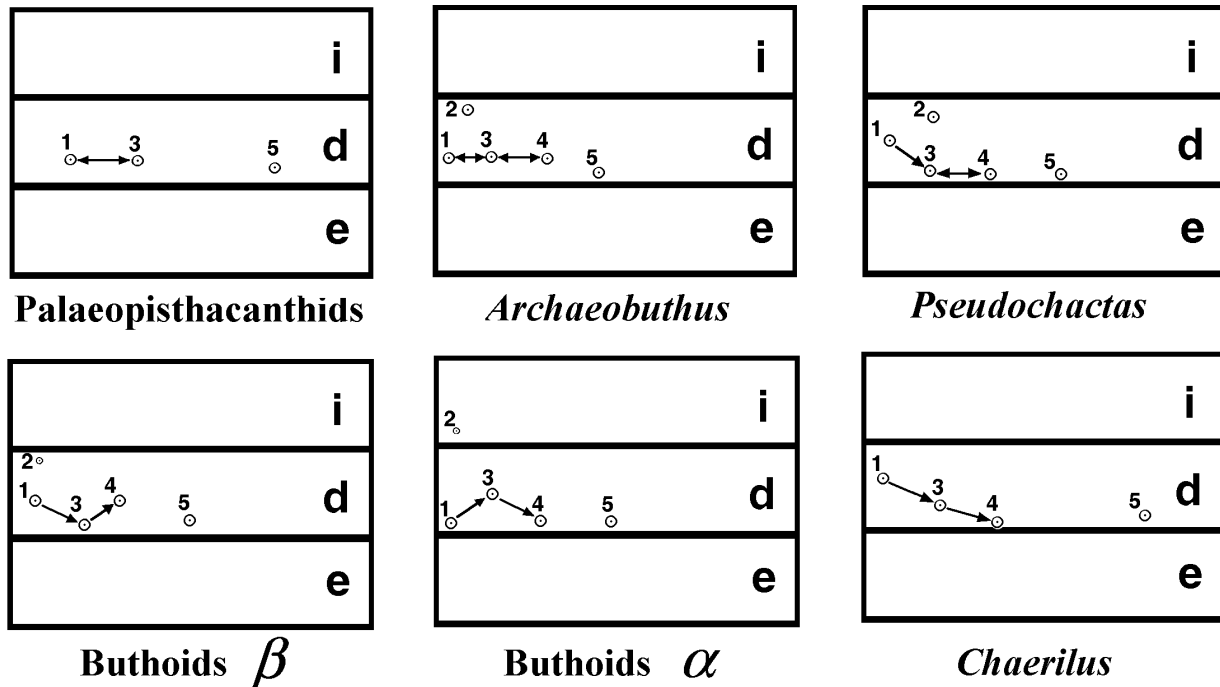


Figure 64: Femur *alpha/beta* trichobothria pattern of fossil and primitive Recent scorpions (after Soleglad & Fet (2001: Fig. 4), in part). Designations reflect three sub-patterns: trichobothria d_1 – d_3 alignment with respect to dorsoexternal carina, trichobothria d_3 – d_4 alignment with respect to dorsoexternal carina, and d_2 surface position (dorsal or internal). Arrowheads depict direction of alignment, double arrowheads depict parallel alignment. i = internal surface, d = dorsal surface, e = external surface.

Type P, family Palaeopisthacanthidae
 Type F1, family Archaeobuthidae
 Type D, parvorder Pseudochactida
 Type A, parvorder Buthida
 Type B, parvorder Chaerilida
 Type C, parvorder Iurida

Although we model orthobothriotaxy as a six-state ordered character, we also present the actual derivations on an individual trichobothrium basis for the four Recent scorpion parvorders (see **Appendix E**). These can be considered synapomorphies for each parvorder.

Trichobothria positions – femur: The *alpha/beta* pattern established by Vachon (1975) for the Type A configuration is an important character in the taxonomy of buthoid scorpions. Sissom (1990: 93) used it as his primary couplet in his extensive key to buthoid genera. Vachon (1975) identified the positional orientation of femoral dorsal trichobothria d_1 , d_3 and d_4 as well as the dorsal/internal position of d_2 . Soleglad & Fet (2001) discussed this basic pattern as it related to the fossil scorpion *Archaeobuthus* and Recent scorpion *Pseudochactas*. These two species did not comply specifically with either *alpha* or *beta* patterns as originally defined by Vachon. Soleglad & Fet (2001) hypothesized homology of all, or part, of the trichobothria involved in the *alpha/beta* pattern across all primitive Recent scorpions. In particular, *Arch-*

aeobuthus, *Pseudochactas* and the buthoids exhibit all four trichobothria and *Chaerilus* has three, lacking d_2 . Consequently, in this study, we have divided the original pattern as defined by Vachon into three separate characters. This further breakdown of the *alpha/beta* pattern is necessary in order to adequately place *Archaeobuthus*, *Pseudochactas* and *Chaerilus* within this scheme originally designed for the buthoids. Following is a breakdown of the *alpha/beta* pattern into three sub-patterns (Fig. 64):

- *Alpha/beta* sub-pattern: alignment of d_1 – d_3
 - parallel to dorsoexternal carina (primitive)
 - points toward dorsoexternal carina (β)
 - points away from dorsoexternal carina (α)
- *Alpha/beta* sub-pattern: alignment of d_3 – d_4
 - parallel to dorsoexternal carina (primitive)
 - points away from dorsoexternal carina (β)
 - points toward dorsoexternal carina (α)
- *Alpha/beta* sub-pattern: placement of d_2
 - on dorsal surface (primitive and β)
 - on internal surface (α)

In Vachon's (1975: Figs. α , β) original definition for the *alpha* pattern, d_1 – d_3 point away and d_3 – d_4 point

toward the dorsoexternal carina, and d_2 is located on the internal surface. In contrast, these conditions are reversed in the *beta* pattern. In *Archaeobuthus*, $d1-d3-d4$ trichobothria are in a straight line, thus both sub-pattern alignments are parallel to the dorsoexternal carina, and $d2$ is located on the dorsal surface, which we hypothesize here as primitive states. *Pseudochactas* exhibits the same pattern as *Archaeobuthus* except $d1-d3$ point toward the dorsoexternal carina, a *beta* pattern characteristic. Soleglad & Fet (2001: 24, 28) considered the pattern exhibited by *Pseudochactas* as intermediate between *Archaeobuthus* and *beta* pattern buthoids, thus exhibiting the most primitive femoral pattern found in Recent scorpions. As discussed in detail in the section concerning cladistics, this breakdown of the *alpha/beta* pattern provides more resolution in the topology of these primitive genera as well as possibly providing additional insight into the phylogeny of the buthoids. The effects of this modified *alpha/beta* model is discussed further in the section dealing with cladistic analysis.

Homologies – Caraboctoninae: For the iuroid subfamily Caraboctoninae, Stockwell (1989: 114, Figs. 175–176) proposed an important change to the trichobothria homology scheme as originally suggested by Vachon for genus *Caraboctonus* (Vachon, 1974: Figs. 154–156) and followed by Francke & Soleglad for two species of *Hadruroides* (1980: Figs. 9–12, 27–30). We accept these alternative homologies for several reasons. As stated by Stockwell, this interpretation is more parsimonious since it is less disruptive to trichobothria positions normally encountered within the Type C pattern. In particular, Vachon suggested that palm trichobothria *Db* and *Dt* occurred on the middle of the fixed finger, an essentially unprecedented position for these trichobothria (albeit, Vachon, 1974: Figs. 190–192, also made similar homologies for euscorpoid genus *Chactopsis*). In Stockwell's interpretation, these trichobothria are designated on the distal aspect of the palm. Although distally situated, their relative distance and positions are comparable to other configurations normally found on the proximal aspect of the palm; in addition, *Db* and *Dt* straddle the digital carina, also typical of Type C pattern scorpions, therefore, this new interpretation is a more intuitive designation. Finally, under this new interpretation, the pattern of the *db-dsb-dst-dt* series is now consistent with other Type C pattern scorpions, another reason to accept this new interpretation.

This new interpretation also establishes common patterns found within the superfamily Iuroidea as well as within the family Caraboctonidae. Stockwell's new scheme (see our Fig. 65) involves the following six changes to homology:

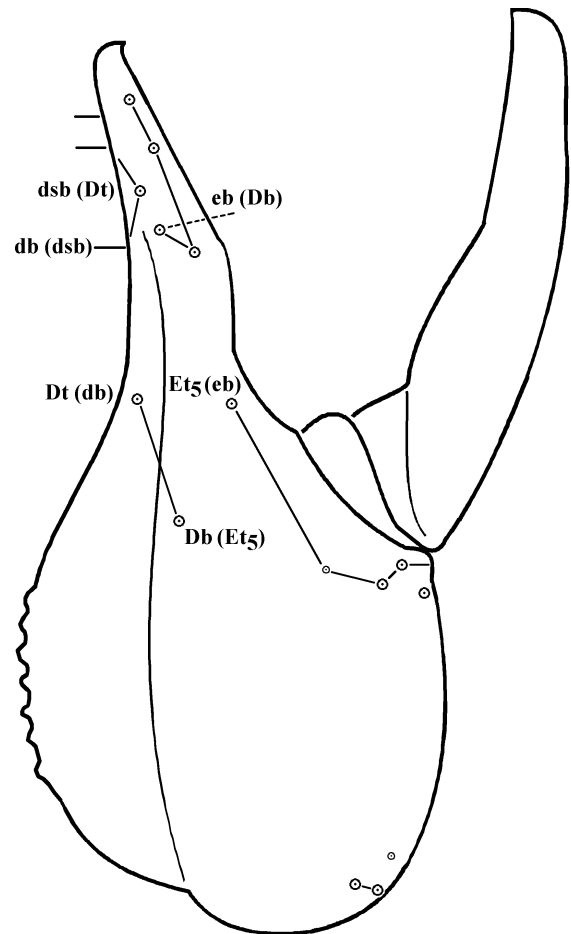


Figure 65: Diagrammatic pattern (external view) of *Hadruroides charcasus* showing alternative chelal trichobothria designations for subfamily Caraboctoninae based on Stockwell's (1989: Figs. 175–176) interpretation. Connected trichobothrial series depict new interpretations; trichobothria designations in parentheses depict Vachon's (1974: Figs. 154–156) original designations.

Db replaces *Et5*
Dt replaces *db*
Et5 replaces *eb*
db replaces *dsb*
eb replaces *Db*
dsb replaces *Dt*

Stockwell's interpretation of trichobothria *esb* and *eb* could also be reversed, but we accept these designations for overall completeness with his change. Based on these changes in homology we see that 1) the superfamily Iuroidea show chelal fixed finger trichobothria series *db-dt* and *eb-et* on the distal half to two-thirds of the finger (*Calchas*, due to its short fingers, exhibits *db* on the base, but otherwise complies with this position for the other seven trichobothria); 2) in family Caraboctonidae, palm trichobothrium *Et5* is found on the chelal fixed finger (as exhibited in genus *Hadrurus*

(Soleglad, 1976a)). These characters are reflected in the cladistic analysis presented elsewhere in this paper.

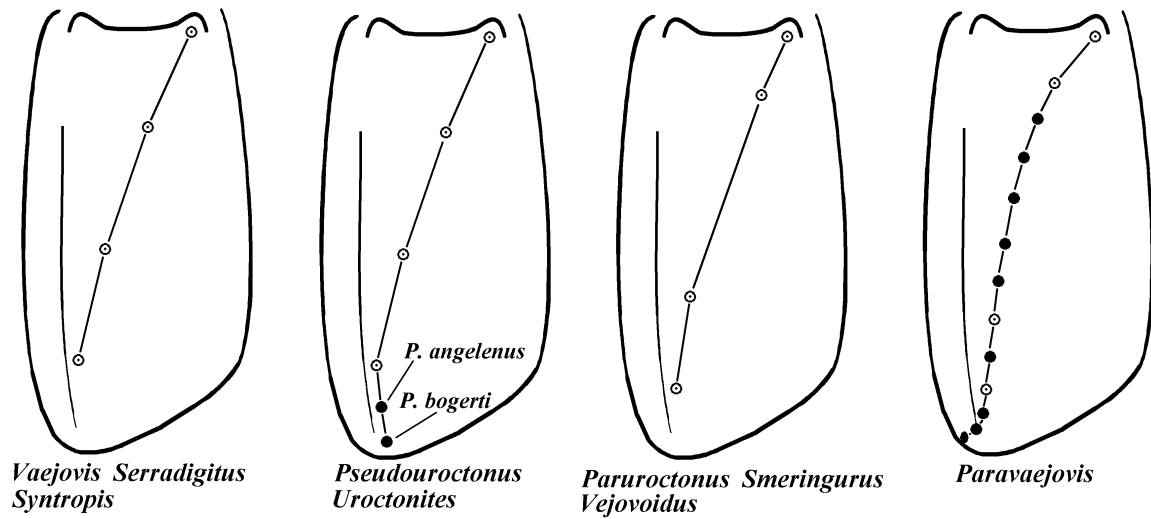
Chactoidae – orthobothriotaxy: There are a number of subtle but significant differences in the positions and overall patterns of orthobothriotaxy separating families Vaejoidea and Chactoidae(-V). These are found on both the pedipalp chela and patella.

Chela – V_1 – V_4 series: In the Vaejoidea the ventral trichobothrial series V_1 – V_4 is in general aligned in a straight line, V_1 positioned distally close to the internal articulation condyle of the movable finger and V_4 situated proximal on the palm, quite close to the ventroexternal carinae. The individual trichobothria are roughly evenly spaced. This pattern is quite consistent across all genera of Vaejoidea (Fig. 66). For *Paruroctonus* and related genera (*Smeringurus*, *Vaejovoidus*, and *Paravaejovis*) we see a small positional difference between trichobothria V_1 , V_2 and V_3 : distance between V_2 and V_3 is noticeably larger than that seen in other typical vaejoidea, due in part, to the slightly closer proximity of trichobothria V_1 and V_2 , and likewise more proximal positioning of V_3 . Since *Paravaejovis* is neobothriotaxic in this series, we have hypothesized the designation of orthobothriotaxic trichobothria based on this presumed relationship, thus the feature just described is also illustrated for this genus. For the Chactoidae(-V), we see that the V_1 – V_2 – V_3 juncture conspicuously angles toward the internal aspect of the palm. There is only one exception to this, which is exhibited by euscorpoid subfamilies Euscorpinae and Megacorminae. In this pattern, we see an exceptional short series, with V_4 being positioned on the external aspect of the palm. Soleglad & Sissom (2001) considered this a synapomorphy for the family Euscorpidae which reversed itself in the tribe Scorpipini, subfamily Scorpipinae. In addition, there is a general tendency in Chactoidae(-V) for the ventral trichobothria series to be shorter in length, V_4 not positioned as far proximally. Presumably this is caused, in part, by the internal angling of the V_1 – V_2 – V_3 juncture. The shortest ventral series is found in the Brotheinae subtribe Brotheina (Figs. 66, 89–90). ***ib*–*it* series:** For the vaejoidea, the internal trichobothrial series *ib*–*it* is positioned on the chelal fixed finger, never on the palm (Figs. 67–78), although *ib* in some species of the genera *Pseudouroctonus* and *Uroctonites* is situated quite close to the palm, located next to the extreme finger edge of the articular membrane (Fig. 73–74). In the vaejoidea, the *ib*–*it* series is situated more proximally in the “mexicanus” and “nitidulus” groups of *Vaejovis* (Figs. 71–72), the more distal positions exhibited on the genus *Serradigitus* and to some degree, *Vaejovis* groups “punctipalpi” and “eusthenura”. In *Paruroctonus* and related genera, the *ib*–*it* series is somewhat basal, especially species *P. stahnkei* and *P. gracilior* (Fig. 75), but never as basal as that seen in some *Pseudouroctonus* or *Uroctonites* species. In the Chactoidae(-V), the *ib*–*it*

series is essentially found on the chelal palm, next to the movable finger articular membrane (see Figs. 81–90). In the family Superstitioniidae, we see the basal positioning of this series limited to trichobothrium *ib*, although *it* is usually quite close to the membrane. In genus *Alacran*, trichobothrium *it* is situated midfinger, quite distant from *ib*, which is located basally. For the other families making up Chactoidae(-V), the *ib*–*it* series is located well on the chelal palm, adjacent to the fixed finger articulation membrane (Figs. 81–90). ***eb*–*et* series:** In Vaejoidea, the fixed finger trichobothrial series *eb*–*et* is arranged in an essentially straight line with basal trichobothrium *eb* angling towards the dorsal edge of the finger (Fig. 79). This basic pattern is constant throughout the family. Within the vaejoidea, the angle formed by trichobothria *esb* and *eb* is more exaggerated in the genera *Pseudouroctonus* and *Uroctonites*, and, to a degree, in genus *Paravaejovis* (Fig. 79). In Chactoidae(-V) the pattern exhibited by this series is variable, but, in general, not conforming to the pattern found in the vaejoidea (*Superstitionia* is the only exception). In the family Chactidae we see a radical angling of the trichobothria *est*–*esb*–*eb* juncture towards the dorsal edge of the fixed finger, *eb* situated quite close to the articular membrane, *esb* position more dorsally in the finger (Fig. 79). This same configuration is also found on the euscorpoid subfamilies Euscorpinae and Megacorminae. For the euscorpoid subfamily Scorpipinae, the superstitioniids, and chactid subtribe Brotheina, the *eb*–*et* series is arranged in a straight line, no angling whatsoever at the *est*–*esb*–*eb* trichobothria juncture. For the scorpipines and Brotheina, we consider this a derivation from the unique angling of the *est*–*esb*–*eb* juncture as seen in the other chactids. In the superstitioniids, we consider the variations exhibited derived from that seen in the vaejoidea.

Patella: In family Vaejoidea we see that ventral trichobothrium v_3 is situated on the external aspect of the patella, positioned somewhat distally on the segment, at least above trichobothrium *est* and sometimes *et_3*—this pattern is constant in the entire family (Fig. 80). Within the vaejoidea we see subtle positional differences in some of the genera. For example, in genera *Serradigitus* and *Syntropis*, v_3 is found above the *et_3* trichobothrium and in contrast, we see v_3 situated below *et_3* in *Paruroctonus* and related genera (Fig. 80). In Chactoidae(-V) we see the external placement of v_3 only in the superstitioniid genera *Superstitionia* and *Troglotayosicus*, subfamily Superstitioniinae (Fig. 80). In all other superstitioniids (subfamily Typhlochactinae), v_3 is situated on the ventral aspect. Interestingly, in genera *Typhlochactas* and *Sotanochactas*, we see that ventral trichobothrium v_2 is found on the external aspect of the patella, a condition only matched in the Old World iuroids. What is interesting about the external positioning of v_3 in genera *Superstitionia* and *Trog-*

Vaejoidea



Superstitioniidae + Euscorpidae + Chactidae

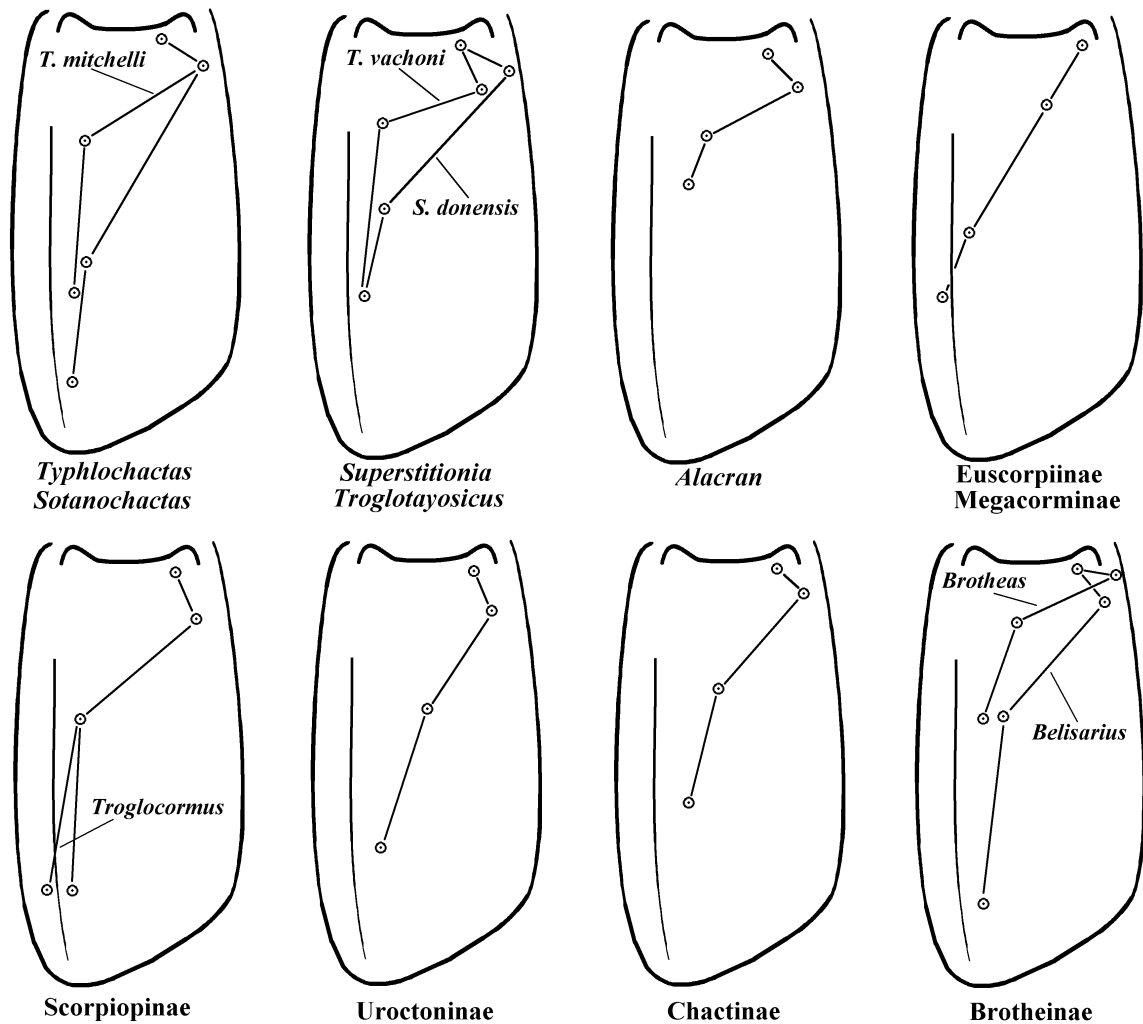
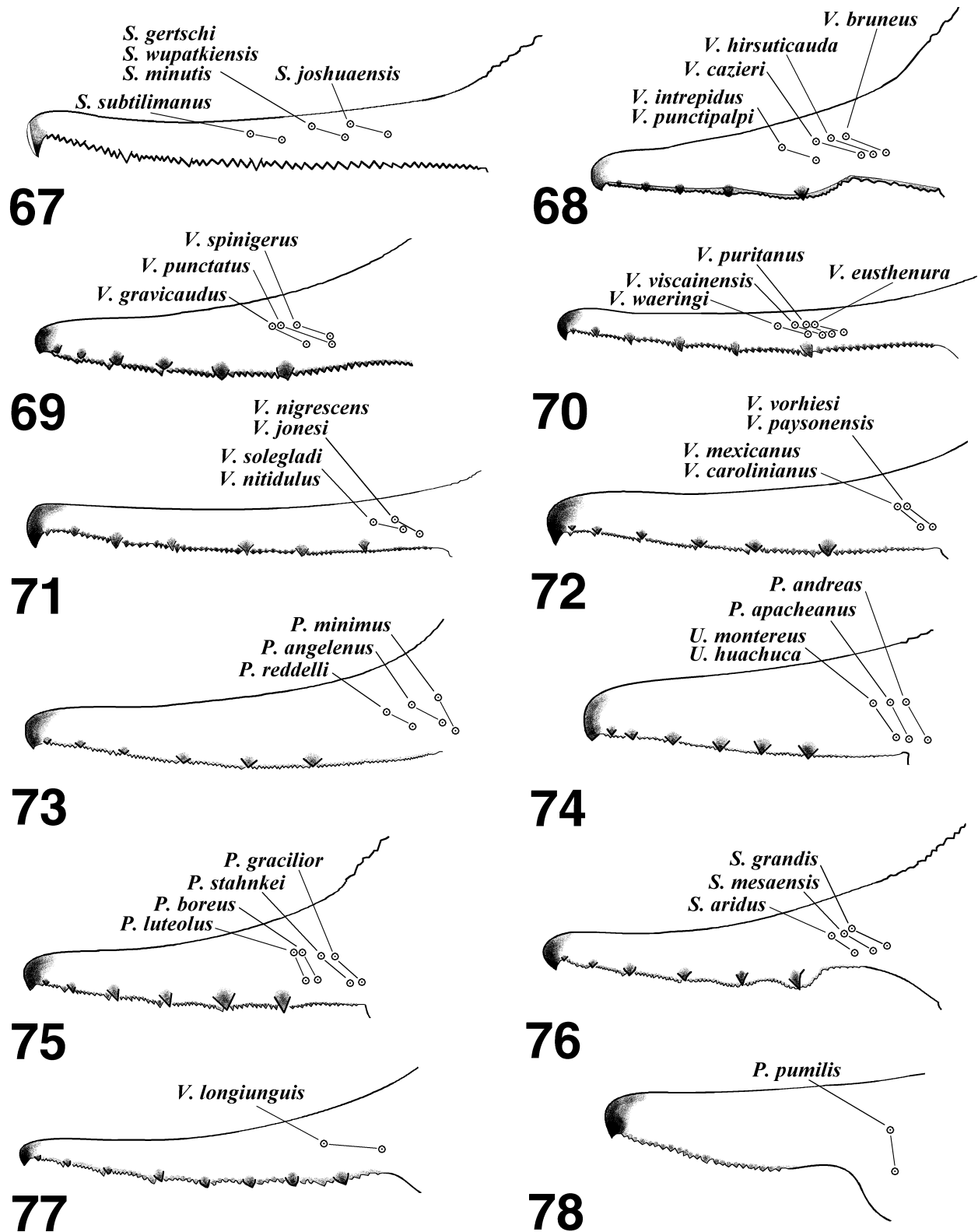
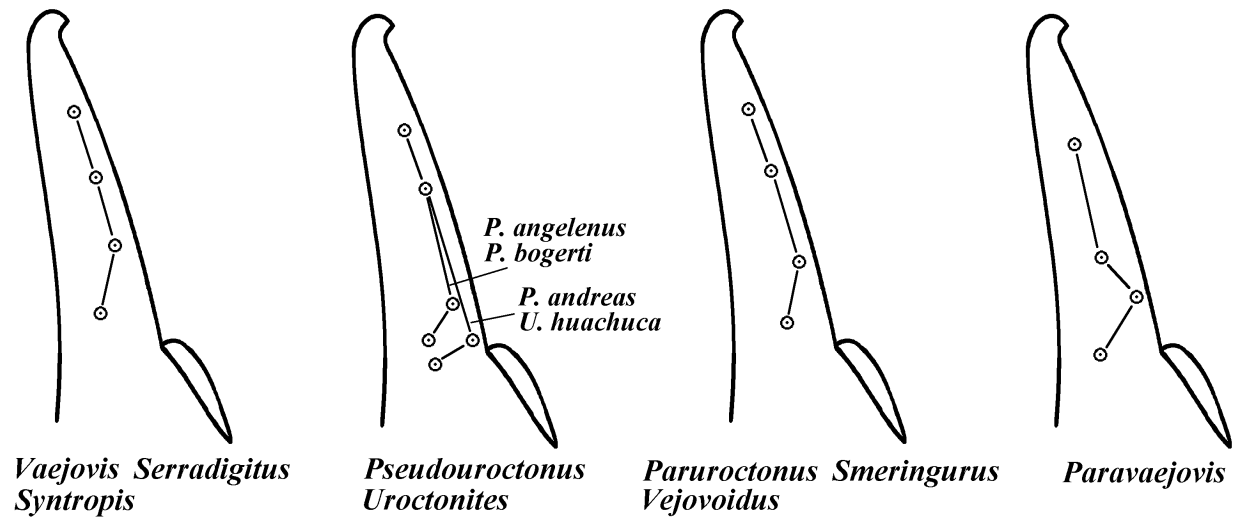


Figure 66: Diagrammatic trichobothrial patterns of ventral aspect of chela (partial) for superfamily Chactoidea. Distinctions within a pattern are identified by representative genera and/or species. Open circles depict the orthobothriotaxic series V_1-V_4 ; closed circles depict hypothesized accessory trichobothria.



Figures 67-78: Relative positions of chelal trichobothria series *ib-it* for major vaejoid genera showing representative species. 67. *Serradigitus*. 68. *Vaejovis*, ‘punctipalpi’ and ‘intrepidus’ (*V. intrepidus cristimanus*) groups. 69. *Vaejovis*, ‘eusthenura’ group. 70. *Vaejovis*, ‘eusthenura’ group. 71. *Vaejovis*, ‘nitidulus’ group. 72. *Vaejovis*, ‘mexicanus’ group. 73. *Pseudouroctonus* (*P. minimus castaneus*). 74. *Pseudouroctonus* and *Uroctonites*. 75. *Paruroctonus*. 76. *Smeringurus*. 77. *Vejovoides*. 78. *Paravaejovis*.

Vaejoidea



Superstitioniidae + Euscorpiidae + Chactidae

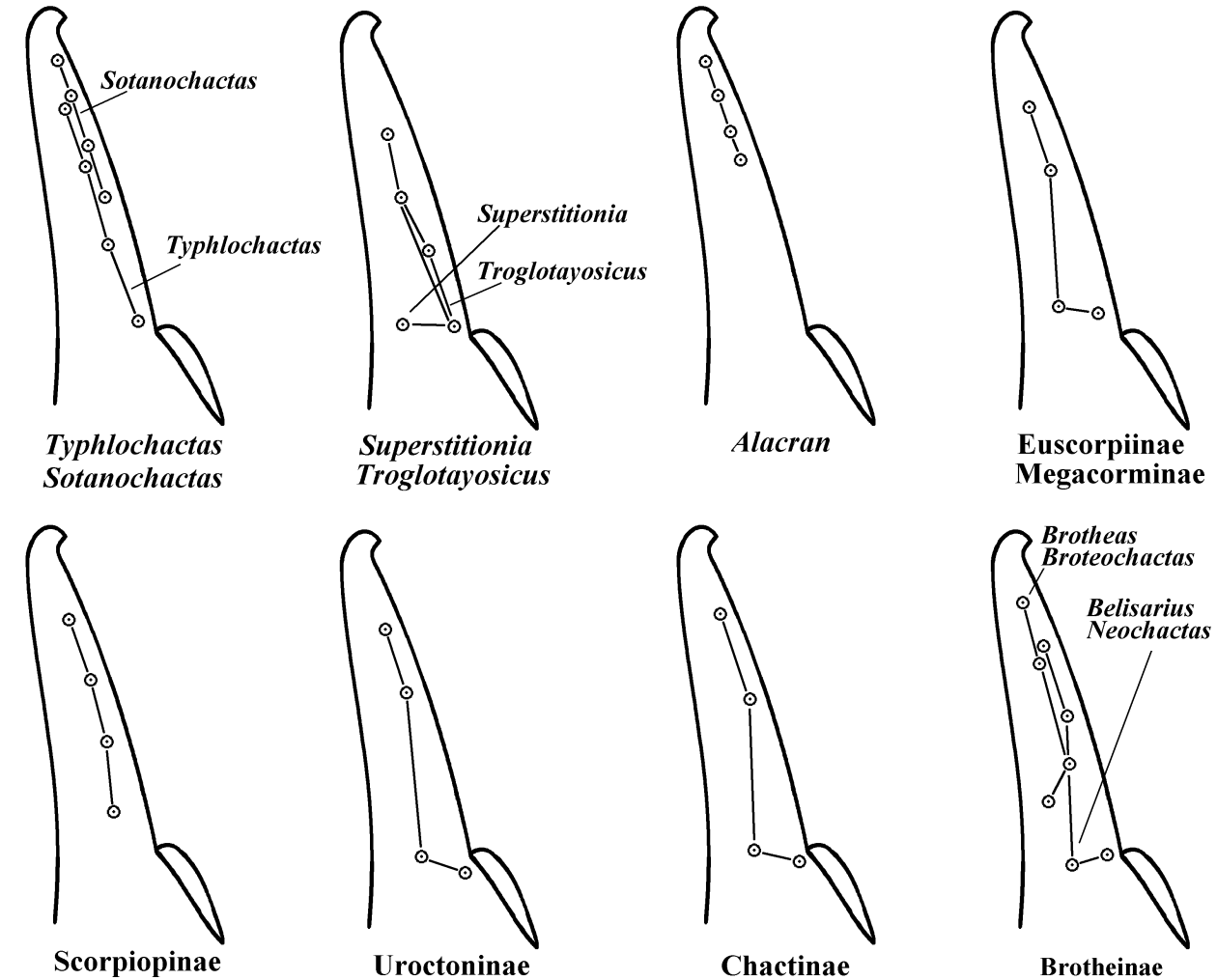
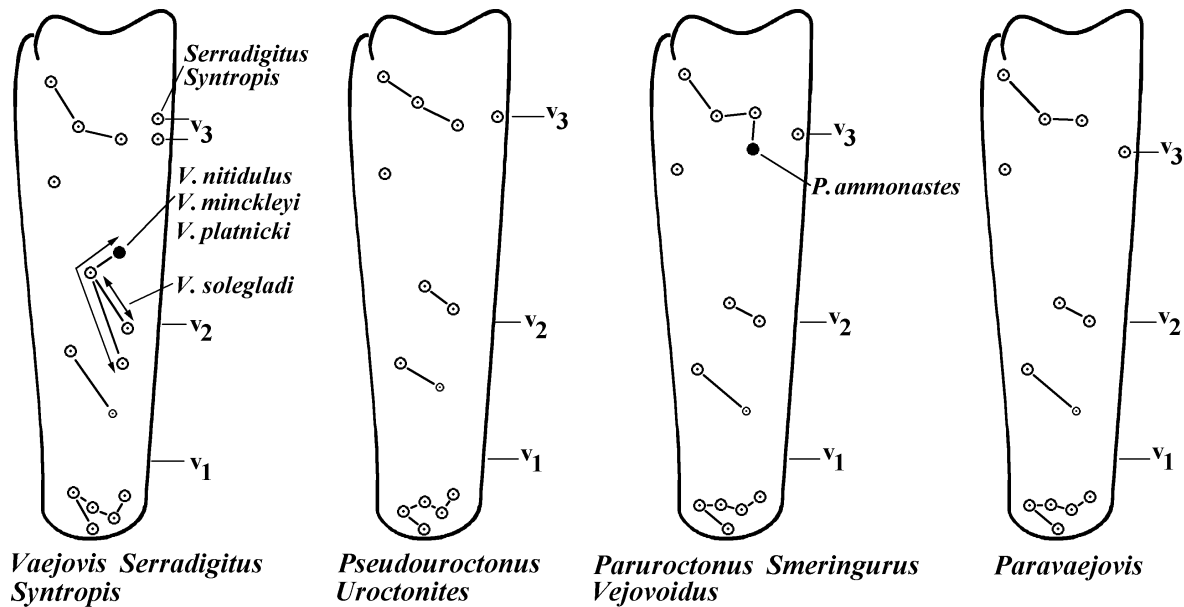


Figure 79: Diagrammatic trichobothrial patterns of chelal fixed finger (partial) showing *eb-et* series for superfamily Chactoidea. Distinctions within a pattern are identified by representative genera and/or species.

Vaejoidea



Superstitioniidae

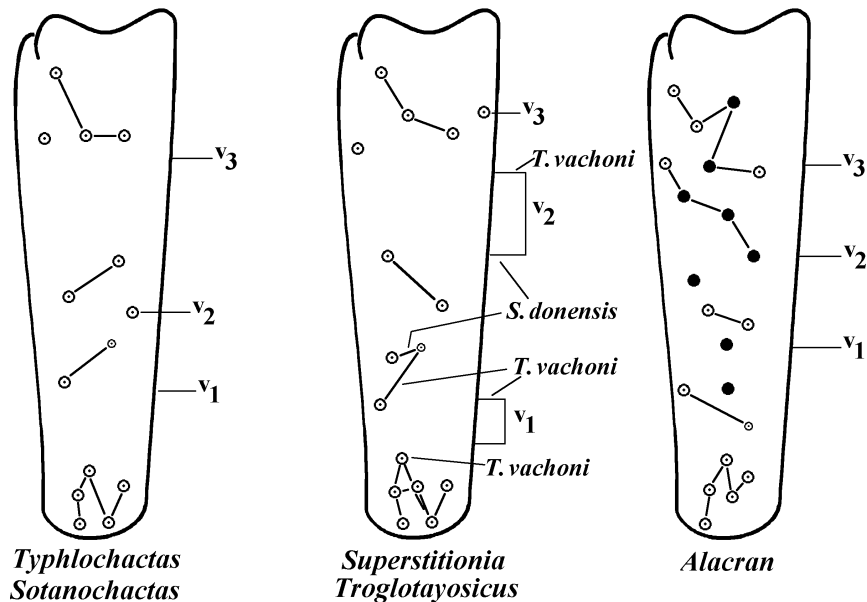


Figure 80: Diagrammatic trichobothrial patterns of external aspect of patella for chactoid families Vaejoidea and Superstitioniidae. Distinctions within a pattern are identified by representative species. Open circles depict orthobothriotaxic trichobothria; closed circles depict hypothesized *accessory* trichobothria.

lotayosicus is that it is found above *et*₃—a condition very similar to that found in many of the vaejooids. With the other chactoid families, Chactidae and Euscorpidae, which in general are highly neobothriotaxic on the patellar ventral surface, we find trichobothrium v₃ located on the ventral surface. Fortunately, within this

large assemblage of taxa we have two orthobothriotaxic genera (family Chactidae), *Uroctonus* and *Belisarius*, which we can use to hypothesize orthobothriotaxic trichobothria within this series in other genera (see below). In both *Belisarius* and *Uroctonus*, we see that v₃ is roughly midsegment to proximal on this surface,

definitely below trichobothria *est* and *et*₃, and the distance between trichobothria *v*₃ and *v*₂ is equal to or less than that between *v*₂ and *v*₁.

Vaejovidae – neobothriotaxy: Unlike Chactoidea(-V), the vaejovids are essentially void of any major neobothriotaxy (terms *major* and *minor* in this paper refer to the extent of additive neobothriotaxy). Only one species, *Paravaejovis pumilis*, exhibits major neobothriotaxy, this found on the ventral aspect of the chelal palm (Fig. 66). This neobothriotaxy is variable, providing a range (mean) of 11–14 (12.256), based on 117 samples (Soleglad & Sissom, 2001: Table 3). Except for *Paravaejovis*, we only find minor neobothriotaxy in a few scattered genera and/or species in the Vaejovidae: Soleglad & Gertsch (1972: Fig. 70) reported for species *Pseudouroctonus bogerti* two additional ventral trichobothria in the chelal ventral series. In this study we report one accessory trichobothrium in this same series for species *P. angelenus*. Based on very limited material it is not known to what extent variability is found with these additional accessory trichobothria in these two closely related species. Haradon (1984: Figs. 25–26) reported an additional trichobothrium in the patellar external *et* series for species *Paruroctonus ammonastes* Haradon (see our Fig. 80). Haradon (1984: 325, Table 2) states "... high incidence of 15 external trichobothria on brachium ...". Note, this count includes the externally placed *v*₃ trichobothrium. Since Haradon provided a range for this count (14–15), we must assume there is minor variability in the absence-presence of this accessory trichobothrium. Probably the most important occurrence of neobothriotaxy found in the vaejovids is that found in several species of the *Vaejovis* "nitidulus" group. This neobothriotaxy is represented by a single accessory trichobothrium found midsegment on the external aspect of the patella. Sissom & Francke (1985) reported this condition for species *V. nitidulus* and *V. minckleyi* Williams, and Sissom (1991) reported it for species *V. kochi* Sissom, *V. platnicki* Sissom, and *V. rubrimanus* Sissom. Sissom & Francke (1985) hypothesized that the accessory trichobothrium belonged to the *esb* series. However, based on the comparative alignment of the *em* series on species of this group which lack the accessory trichobothrium, *em*₁–*em*₂ slanting *downward*, we hypothesize here that the accessory trichobothrium belongs to the *em* series (Fig. 80). In order to realize Sissom & Francke's original interpretation, the *em*₁–*em*₂ series must slant upwards. Accompanying our interpretation is the longer distance between trichobothria *em*₁ and *em*₂. Since this condition is found in multiple species in the "nitidulus" group, spanning a somewhat large geographical area in Mexico (Coahuila, Nuevo León, San Luis Potosí, Querétaro, and Distrito Federal), it suggests a significant phylogenetic relationship between these species within this group.

Chactidae – neobothriotaxy: Within the family Chactidae, we hypothesize three independent instances of major neobothriotaxy: *Anuroctonus* in subfamily Uroctoninae; all genera in subfamily Chactinae, including tribes Nullibrotheini and Chactini; and all genera in tribe Brotheini in subfamily Brotheinae. It is interesting to point out here that only two genera in Chactidae exhibit orthobothriotaxy, *Belisarius* (Fig. 87), tribe Belisariini, subfamily Brotheinae, and *Uroctonus* (Fig. 81), subfamily Uroctoninae. These two genera are very important in the definition of Chactidae since they provide crucial information in the determination of orthobothriotaxic trichobothria in the other chactid genera where extensive neobothriotaxy exists. This, in turn, provides key characters in distinguishing Chactidae from the other Chactoidea(-V) families. By comparing the trichobothrial patterns of the chela and patella of these two genera, *Belisarius* and *Uroctonus*, we see that key trichobothrial series are very similar in position. **Chela:** *Db* and *Dt* located basally on the chela; *Eb*₁ is situated close to the ventroexternal carina or on the internal aspect of the palm; the *V*₁–*V*₂–*V*₃ juncture angles toward the internal aspect of the palm; *ib* and *it* are situated on the palm, adjacent to the articular membrane of the movable finger; *eb* is situated quite close to the movable finger articular membrane; *esb* found more mid-finger, so that *est*–*esb*–*eb* juncture angles outward towards the dorsal edge of the fixed finger. **Patella:** *v*₁–*v*₃ are situated on the ventral aspect of the patella; *v*₃ is located proximal to external trichobothria *est* and *et*₃ so that the distance between trichobothria *v*₃ and *v*₂ is less than or equal to the distance between *v*₂ and *v*₁; *esb*₁ is located midsegment; *esb*₂ is situated quite close to *eb* series.

Uroctoninae: *Anuroctonus* exhibits major variable neobothriotaxy. This neobothriotaxy is found on the ventral aspect of the chela as well as on the ventral and external surfaces of the patella (Fig. 82). Great variability in the number of accessory trichobothria are found in most of the series of these two pedipalp segments: chelal ventral series numbers range from as low as 12 to many as 26; patella ventral aspect, 10–19; and patella external aspect (which includes ventral accessory trichobothria extending from the ventral aspect), 23–34 (ranges based on over 800 samples for the chela and 150 for the patella). Of course, the external aspect of the patella exhibits several series, some of which do not reflect variability either because they are orthobothriotaxic, or have a fixed number of accessory trichobothria (see discussion below). It is important to note that we are currently revising the genus *Anuroctonus* (Soleglad & Fet, in progress) and can state here that the variability just stated in these series is due, in part, to speciation, therefore the stated ranges involve more than one species. We use the pattern found in *Uroctonus* to determine important orthobothriotaxic

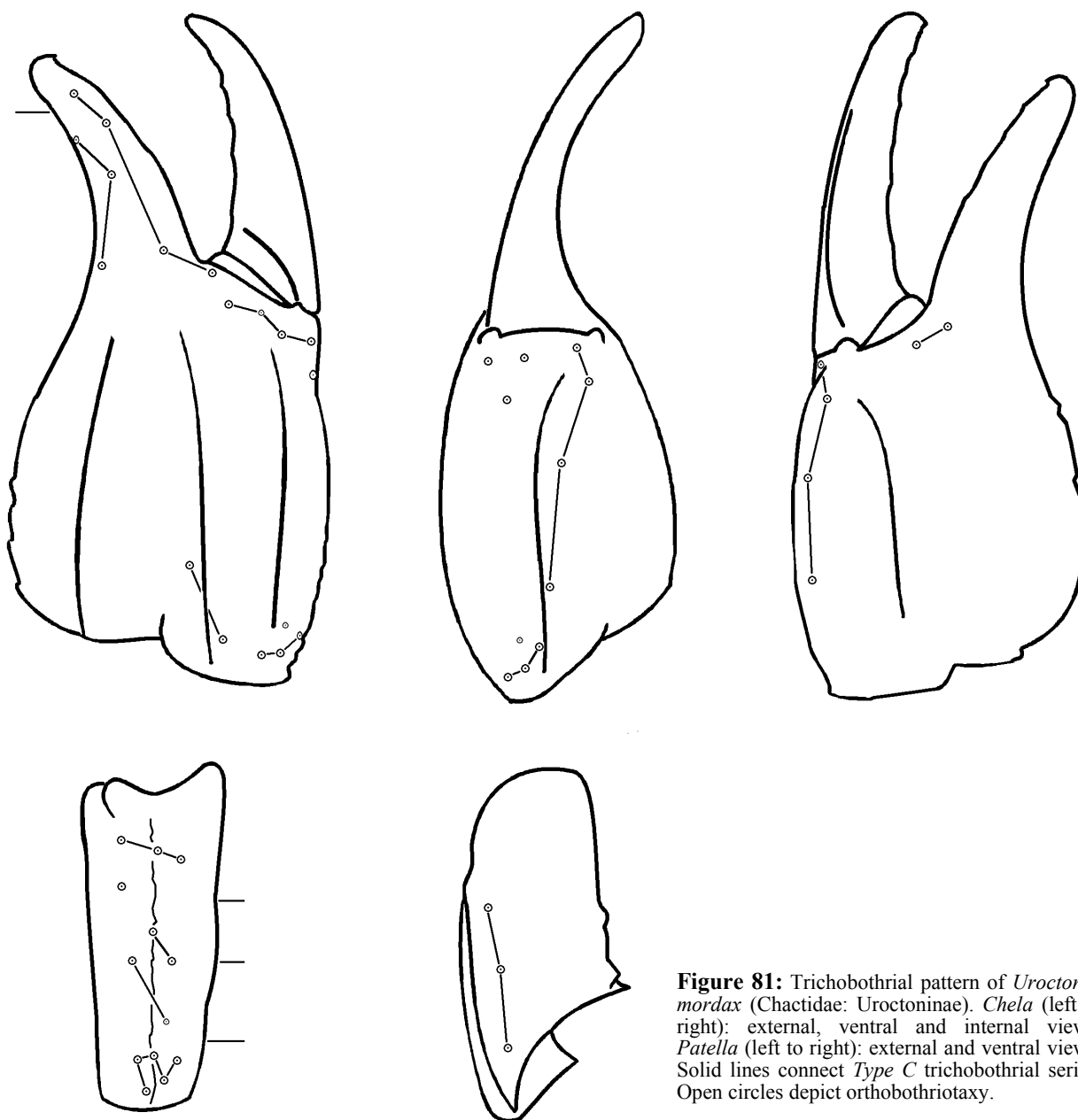


Figure 81: Trichobothrial pattern of *Uroctonus mordax* (Chactidae: Uroctoninae). *Chela* (left to right): external, ventral and internal views. *Patella* (left to right): external and ventral views. Solid lines connect Type C trichobothrial series. Open circles depict orthobothriotaxy.

trichobothria in the complicated pattern found in *Anuroctonus*. **Chela:** the ventral series in *Anuroctonus* continues onto the external surface extending into the Eb_1 – Eb_3 palm series. Using *Uroctonus* as a point of reference we see that the ventral accessory trichobothria split the Eb series, Eb_1 being situated on the ventroexternal carina. The designation of V_1 and V_2 reflects the Chactoidae(-V) characteristic of the V_1 – V_2 – V_3 juncture angling towards the internal aspect of the palm, the designations of V_3 and V_4 are more arbitrary, but do reflect the somewhat short length of the series as a whole as it extends down the palm. **Patella:** v_1 – v_3 are based on comparable positions of these trichobothria found in *Uroctonus*, also, the most proximal trichobothrium in *Anuroctonus* is clearly accessory as

indicated by its petite form; ventral accessory trichobothria extend onto the external aspect of this segment, mixing somewhat with the et series; we hypothesize that the eb series, which contains seven trichobothria (two accessory) and series est , which contains three accessory trichobothria, are static; the et , em and esb series show variability in numbers of accessory trichobothria. Similarities in trichobothrial series positions between *Uroctonus* and *Anuroctonus* are as follows: **Chela:** Db and Dt are situated basally on the chelal palm; ib and it are situated on the palm, adjacent to the articular membrane of the movable finger; est – esb – eb juncture angles toward the dorsal aspect of the fixed finger, eb is situated quite close to the articulation membrane of the movable finger. Based on established

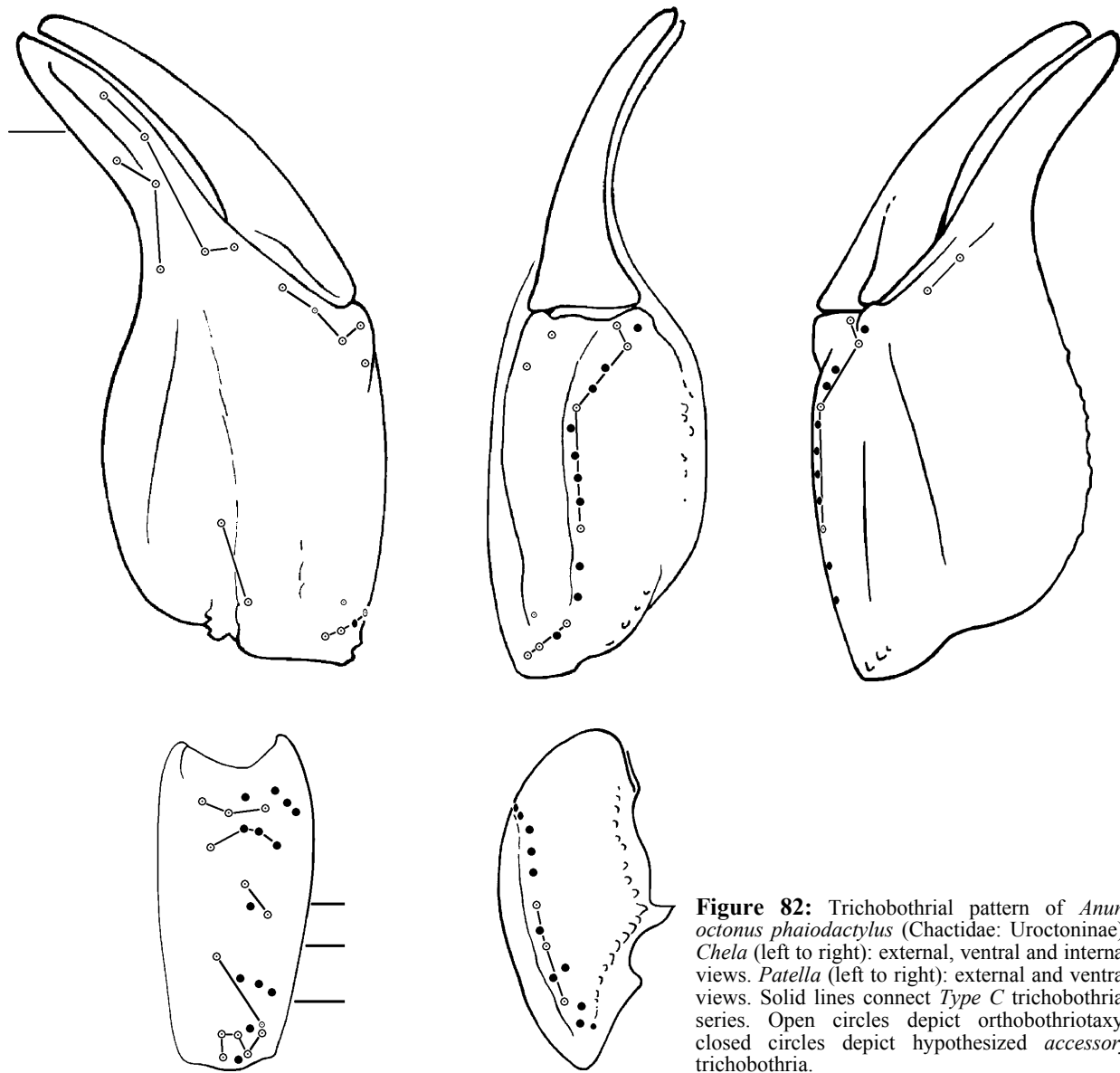


Figure 82: Trichobothrial pattern of *Anuroctonus phaiodactylus* (Chactidae: Uroctoninae). *Chela* (left to right): external, ventral and internal views. *Patella* (left to right): external and ventral views. Solid lines connect Type C trichobothrial series. Open circles depict orthobothriotaxy; closed circles depict hypothesized accessory trichobothria.

homologies using *Uroctonus*, Eb_1 is close to or on the internal aspect of the palm, $V_1-V_2-V_3$ juncture angles toward the internal face of the palm. **Patella:** distance between trichobothria esb_1 and esb_2 is extensive, esb_1 is positioned midsegment and esb_2 is situated close to the eb series; v_3 is found on the ventral surface proximal to external trichobothria est and et_3 . The neobothriotaxic pattern described and illustrated in this paper for *Anuroctonus* is consistent with that suggested by Vachon (1974: Fig. 143).

Chactinae: All genera in subfamily Chactinae exhibit major fixed neobothriotaxy. This complicated pattern shows little or no variability within tribes Chactini (genera *Chactas* (Fig. 83), *Teuthraustes* (Fig. 84), and *Vachoniochactas* (Fig. 85)) and Nullibrotheini (genus *Nullibrotheas* (Fig. 86)). Neobothriotaxy is restricted to the patella only, and exhibited both on the

ventral and external surfaces. This neobothriotaxy is represented by two distinct, yet very similar, patterns, representing Chactini and Nullibrotheini, respectively. **Chactini** (Figs. 83–85): the ventral aspect of the patella contains five trichobothria (two accessory); the external series eb , esb and em are orthobothriotaxic, accessory trichobothria being found in series est with three trichobothria (two accessory) and et with five trichobothria (two accessory). In this pattern we see that the em series is proximal of midsegment and the esb_1 is located proximally, consequently distance between trichobothria esb_1 and esb_2 is quite small. We consider these conditions to be diagnostic of this subfamily. The designation of orthobothriotaxic trichobothria v_1-v_3 is determined using *Belisarius* and *Uroctonus* as a basis as well as noting the petite size of the most proximal trichobothrium which we hypothesize is accessory.

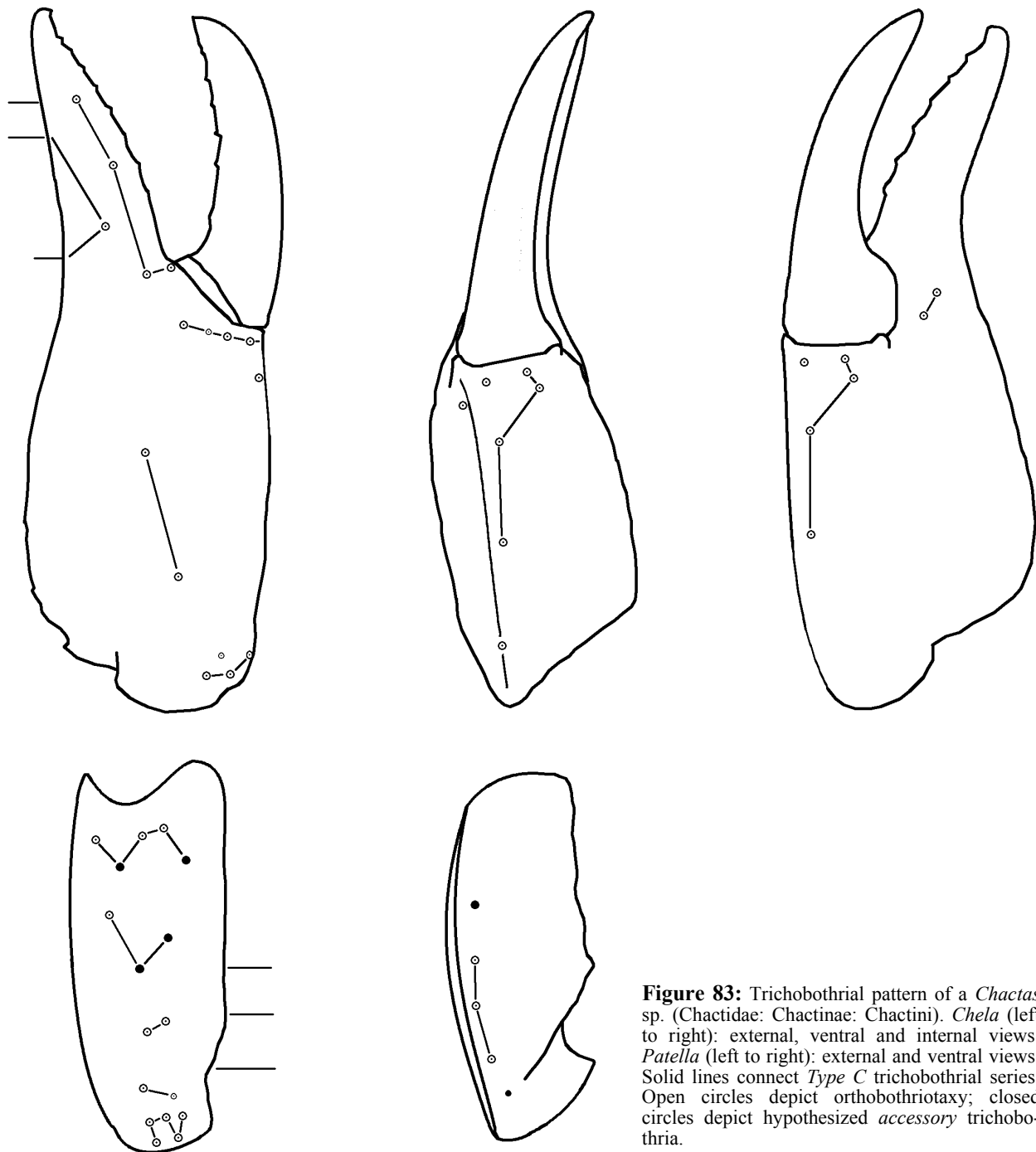


Figure 83: Trichobothrial pattern of a *Chactas* sp. (Chactidae: Chactinae: Chactini). *Chela* (left to right): external, ventral and internal views. *Patella* (left to right): external and ventral views. Solid lines connect *Type C* trichobothrial series. Open circles depict orthobothriotaxy; closed circles depict hypothesized *accessory* trichobothria.

Nullibrotheini (Fig. 86): the ventral aspect of the patella contains six trichobothria (three accessory); external series *eb*, *esb* and *em* are orthobothriotaxic, accessory trichobothria being found in series *est* with four trichobothria (two accessory) and *et* with five trichobothria (two accessory). Comparing the patterns in these two tribes we see that they only differ in the number of ventral and *est* series trichobothria (each by one trichobothrium). In addition, we see that the individual series are situated in similar positions, both with the *esb* series situated quite proximal on the

segment. On the chela, the two tribes also are quite similar, reflecting typical chactid characters: *ib* and *it* are situated on the palm, adjacent to the articular membrane; V_1 – V_2 – V_3 juncture angles towards the internal face; V_1 – V_4 series is situated on distal half of palm; Eb_1 is situated close to ventroexternal carina or found on internal aspect; *est*–*esb*–*eb* juncture angles toward the dorsal aspect of fixed finger, *eb* situated quite close to articular membrane; *Db*–*Dt* series is found on the proximal half of the palm, but never basally. The neobothriotaxic pattern described above and illustrated in this paper is

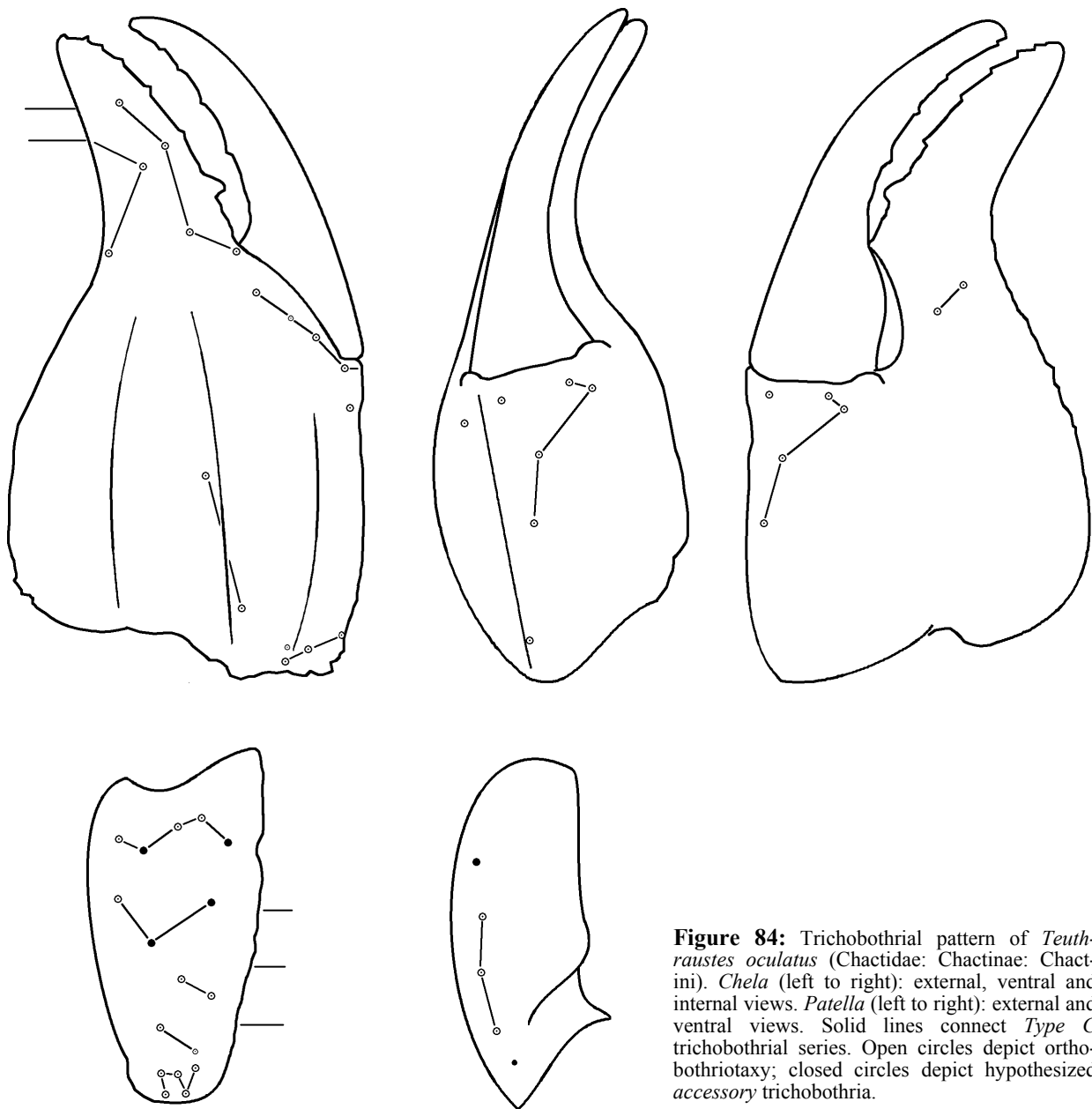


Figure 84: Trichobothrial pattern of *Teuthraustes oculatus* (Chactidae: Chactinae: Chactini). *Chela* (left to right): external, ventral and internal views. *Patella* (left to right): external and ventral views. Solid lines connect Type C trichobothrial series. Open circles depict orthobothriotaxy; closed circles depict hypothesized accessory trichobothria.

consistent with Vachon's (1974: Figs. 174–175) designations. Noted exceptions (these exceptions are based on existing literature and therefore are not necessarily complete or accurate) to this fixed neobothriotaxic pattern, which are as follows: Patella, ventral aspect: four (not five) trichobothria (one (not two) accessory), *Chactas barravierai* (Lourenço, 1997: Fig. 56); Patella, external aspect: series *et* with four (not five) trichobothria (one (not two) accessory), *Vachoniochactas ashleeae* (Lourenço, 1994: Fig. 8).

Brotheinae: The two tribes in subfamily Brotheinae are separated, in part, by the neobothriotaxy found in Brotheini but lacking in monotypic tribe Belisariini (genus *Belisarius* (Fig. 87)) which is orthobothriotaxic. As with subfamily Chactinae, this complicated neobothriotaxic pattern is in general fixed *within* and

between its genera, *Brotheas* (Fig. 89), *Broteochactas*, *Hadrurochactas* (Fig. 90), and *Neochactas* (Fig. 88). This neobothriotaxic pattern is present on the patella only, exhibiting accessory trichobothria on both the ventral and external segment surfaces: seven trichobothria (four accessory) are found on the ventral aspect of the patella; the designation of orthobothriotaxic trichobothria v_1 – v_3 are based on the comparison with sister tribe Belisariini (genus *Belisarius*), and the petite form of the most proximal trichobothrium which is clearly accessory. External series *eb* and *em* are orthobothriotaxic, series *esb* with six trichobothria (four accessory), *est* with five trichobothria (four accessory) and *et* with six trichobothria (three accessory). The two tribes in subfamily Brotheinae share many similarities in chelal trichobothria positions: *ib* and *it* are situated on

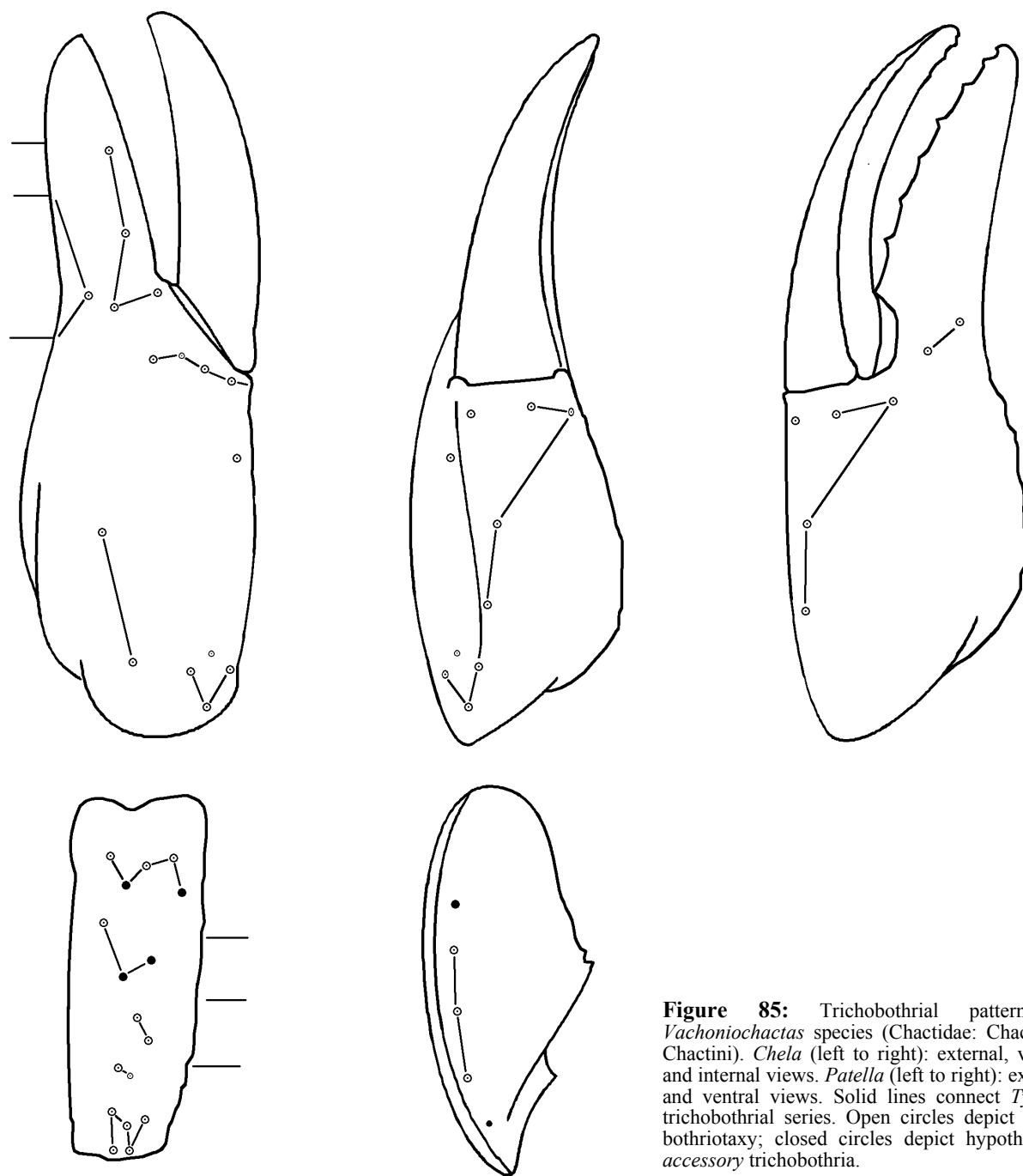


Figure 85: Trichobothrial pattern of *Vachoniochactas* species (Chactidae: Chactinae: Chactini). *Chela* (left to right): external, ventral and internal views. *Patella* (left to right): external and ventral views. Solid lines connect *Type C* trichobothrial series. Open circles depict orthobothriotaxy; closed circles depict hypothesized accessory trichobothria.

the palm, adjacent to the articular membrane; $V_1-V_2-V_3$ juncture angle towards the internal aspect of the palm, extremely exaggerated in Brotheini; Eb_1 is either situated on the ventroexternal carina or on the internal aspect of the palm. Other chelal trichobothria series positions are discussed below in section on subtribes. The neobothriotaxic pattern described and illustrated here deviates from Vachon's (1974: Fig. 176) original designations as follows: est_2 is changed to esb_1 , and esb_1 is designated as accessory. This change is more consistent with *Belisarius*, based on its position of esb_1 .

Exceptions to this fixed neobothriotaxic pattern are as follows (these exceptions are based on illustrations from existing literature and therefore it is not necessarily complete or accurate): Patella, ventral aspect: eight (not seven) trichobothria (five (not four) accessory), *Cayooca venezuelensis* (González-Sponga, 1996a: 4) (note, this increase in one trichobothrium is diagnostic, in part, for this monotypic genus); Patella, external aspect: series esb with five (not six) trichobothria (three (not four) accessory), *Neochactas neblinensis* (González-Sponga, 1991: Fig. 10).

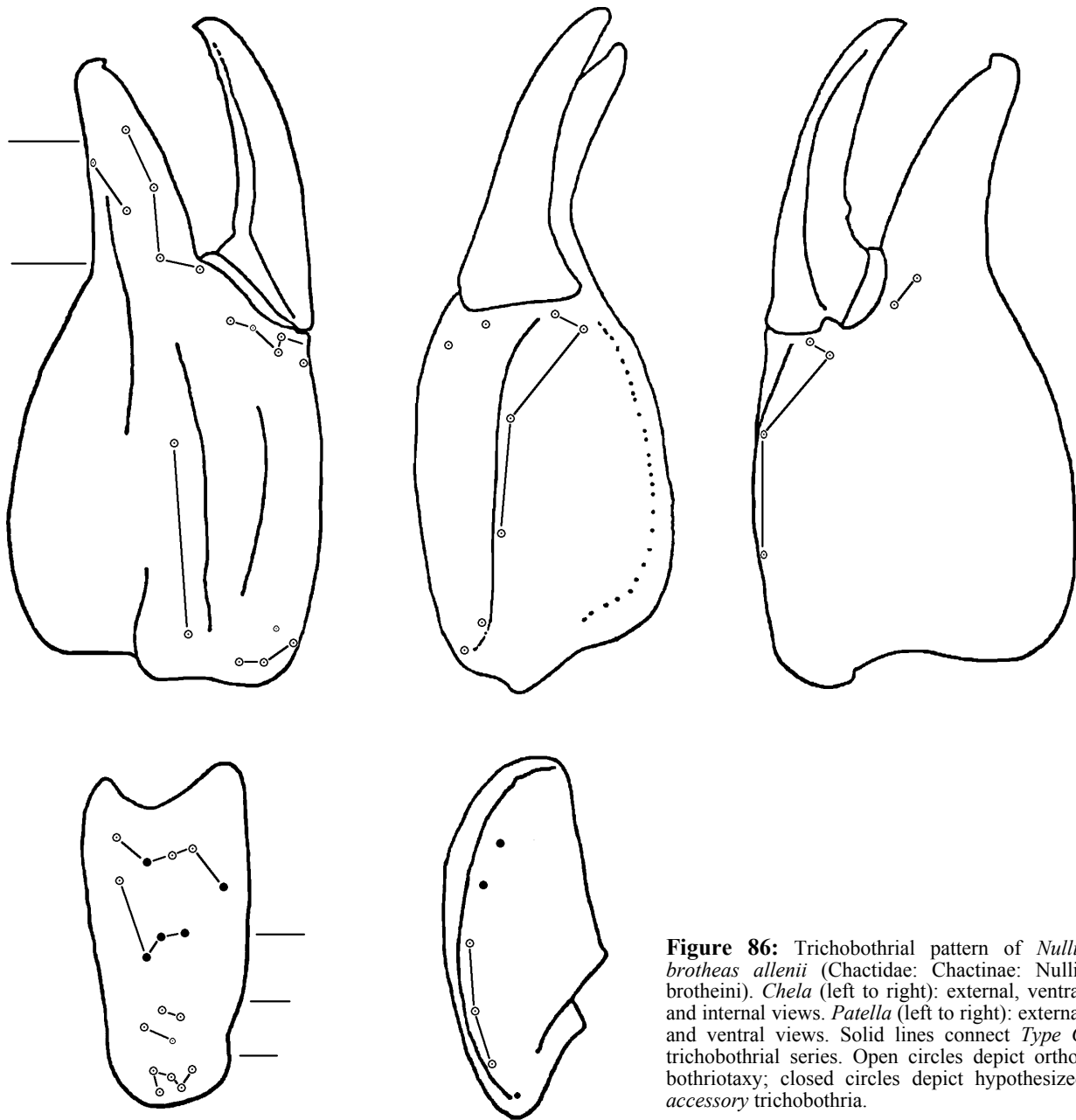


Figure 86: Trichobothrial pattern of *Nullibrotheas allenii* (Chactidae: Chactinae: Nullibrotheini). *Chela* (left to right): external, ventral and internal views. *Patella* (left to right): external and ventral views. Solid lines connect Type C trichobothrial series. Open circles depict orthobothriotaxy; closed circles depict hypothesized accessory trichobothria.

Brotheini – subtribes: Within the tribe Brotheini we isolate two subtribes, **Neochactina** and **Brotheina**. These two subtribes are delineated by unique trichobothria positional differences in three key chelal series. Subtribe Neochactina contains genus *Neochactas* (Fig. 88) and Brotheina contains three genera: *Brotheas* (Fig. 89), *Broteochactas*, and *Hadrurochactas* (Fig. 90). These subtribes are distinguished as follows: **subtribe Neochactina:** series *eb-et* is situated on the proximal two-thirds of the fixed finger, *est-esb-eb* juncture angles toward the dorsal aspect of the finger, *eb* situated quite close to the articular membrane; series *Et₃-Et₅* is situated on the distal aspect of the palm, never extending to the fixed finger; *Db* and *Dt* are located on the middle of the palm, *Dt* proximal of trichobothrium *Est*. **subtribe**

Brotheina: series *eb-et* is situated on the distal two-thirds of the fixed finger, *est-esb-eb* juncture angles toward the cutting edge of the finger, *eb* found on the finger midpoint, not close to the articular membrane; series *Et₃-Et₅* is located distally on the palm, *Et₅*, and sometimes *Et₄*, found on the fixed finger; *Db* and *Dt* are located on distal half of the palm, *Dt* usually distal of trichobothrium *Est*. It is important to note here that subtribe Neochactina complies with the other two chactid subfamilies as to the positional distinctions of these three trichobothria, and therefore it is clear that these positional differences defining subtribe Brotheina are *derived*. This distinction, in part, was illustrated by Vachon (1974: Figs. 224–225) for genera *Broteochactas* (= our *Neochactas*) and *Brotheas*. See the classification

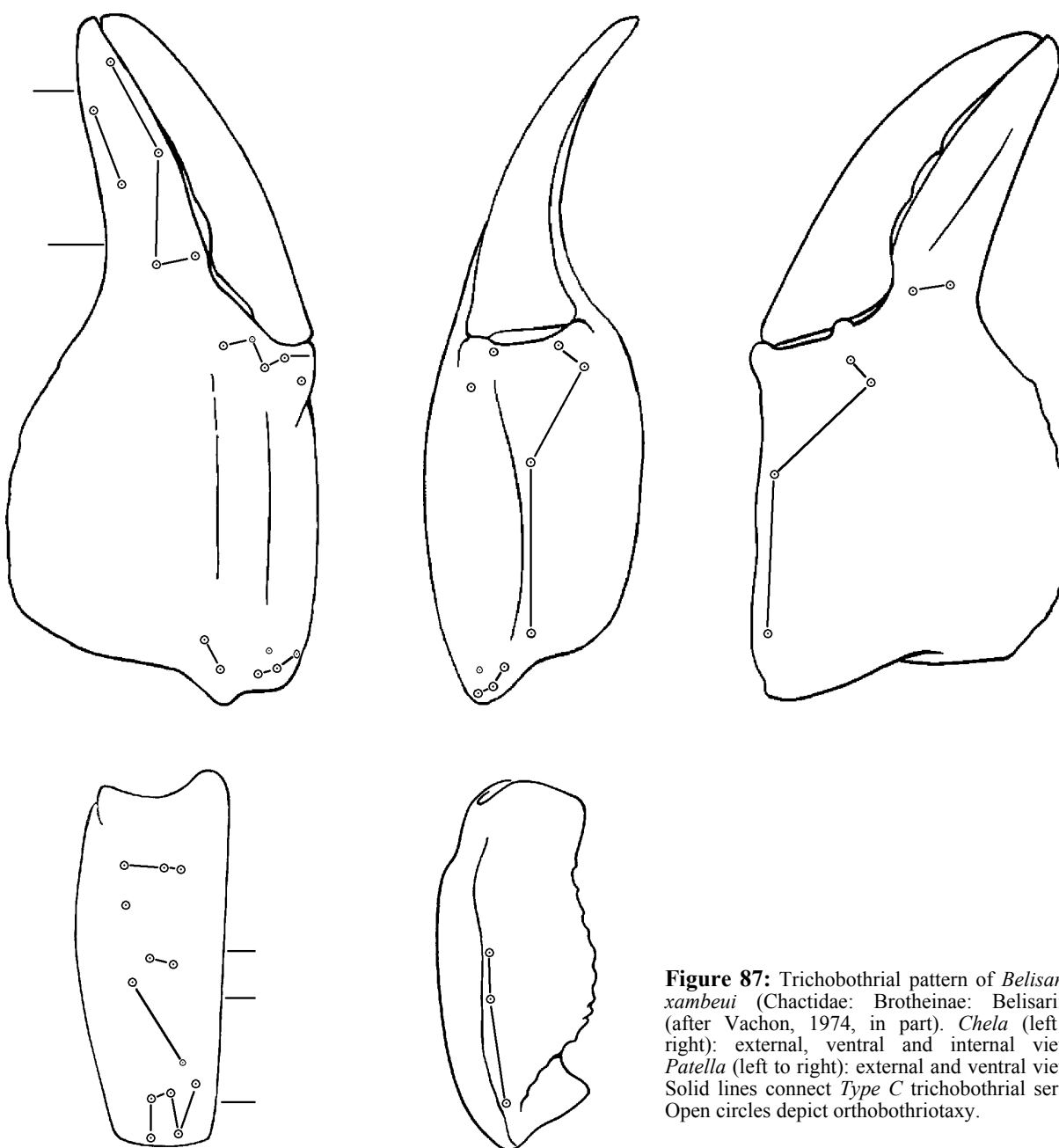


Figure 87: Trichobothrial pattern of *Belisarius xambeui* (Chactidae: Brotheinae: Belisariini) (after Vachon, 1974, in part). *Chela* (left to right): external, ventral and internal views. *Patella* (left to right): external and ventral views. Solid lines connect *Type C* trichobothrial series. Open circles depict orthobothriotaxy.

section below for more discussion and further refinement of these two subtribes.

Chactoid neobothriotaxy – formal definition of types: Above we described the three instances of neobothriotaxy found in the family Chactidae. Here, we formally state their definitions and type assignment for future reference. In addition, for completeness and reference in later sections, we also define the single neobothriotaxy pattern type found in family Superstitioniidae (i.e., *Alacran*) and the two neobothriotaxic pattern types for the family Euscorpidae (discussed in detail in Soleglad & Sissom, 2001: 45–55). The definition of these formal types implies that they

evolved separately within the families in which they occurred, a hypothesis of this paper.

It is important to mention here, that except for *Paravaejovis* (Vaejovidae) and *Hadrurus* (Caraboctonidae), the only other extant major neobothriotaxic patterns occur in superfamily Scorpionoidea. In the only two major cladistic analyses which considered the scorpionoids, Stockwell (1989) and Prendini (2000), neobothriotaxy was completely ignored by the former and the latter, in general, considered all individual instances of neobothriotaxy within the superfamily to have occurred in the *same evolutionary lineage*. We discuss the affects of this somewhat “conservative”

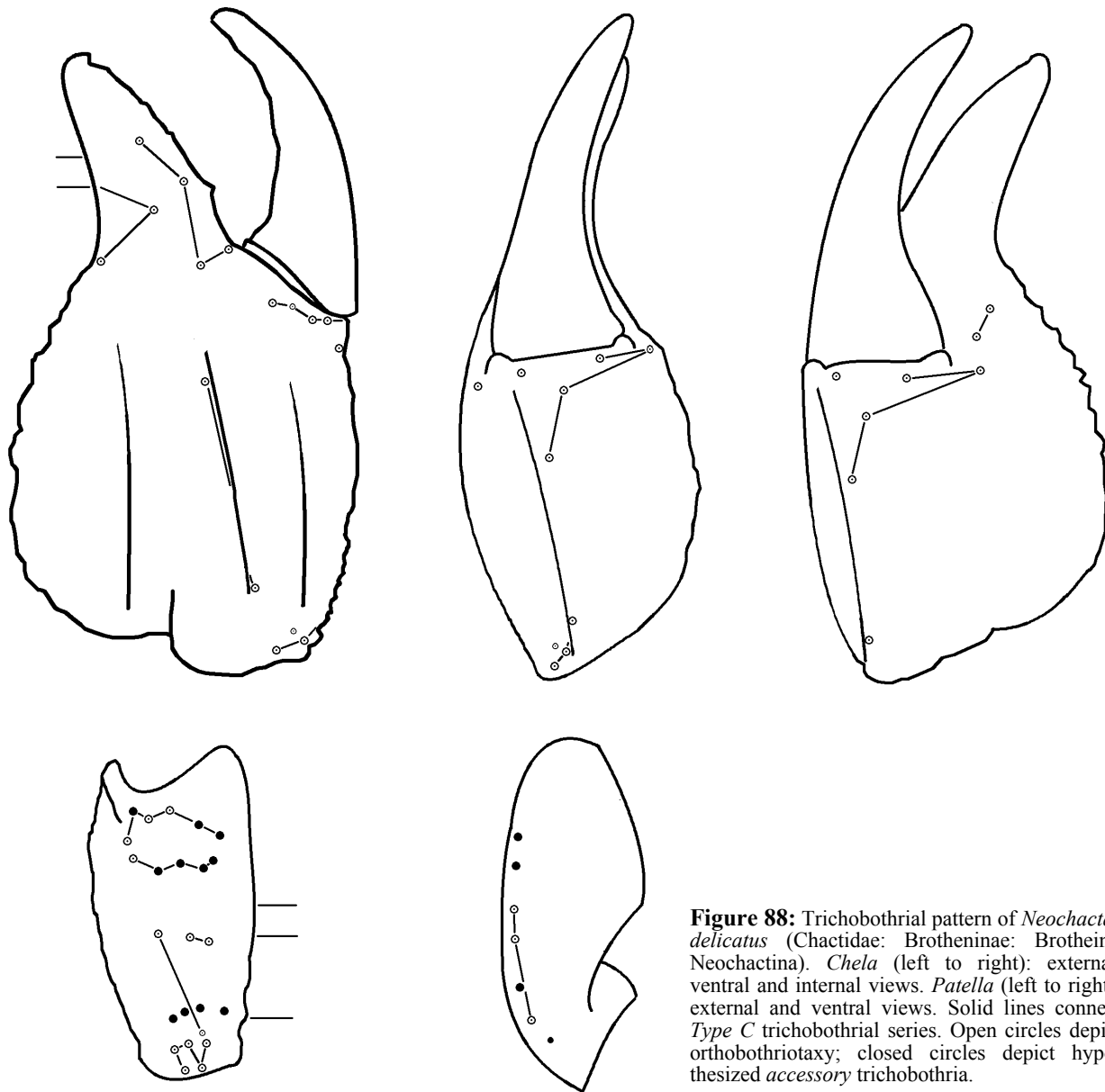


Figure 88: Trichobothrial pattern of *Neochactas delicatus* (Chactidae: Brotheninae: Brotheini: Neochactina). *Chela* (left to right): external, ventral and internal views. *Patella* (left to right): external and ventral views. Solid lines connect Type C trichobothrial series. Open circles depict orthobothriotaxy; closed circles depict hypothesized accessory trichobothria.

approach to the modeling of neobothriotaxy offered by Prendini in the sections dealing with cladistics and classification.

Chactid neobothriotaxic type Ch1: Neobothriotaxy is limited to the ventral and external aspects of the patella, and is fixed in general pattern and in number of accessory trichobothria. **Patella ventral surface:** 4–6 (5) trichobothria (1–3 (2) accessory), positioned in a linear line; most proximal trichobothrium (accessory) is petite in size. **Patella external surface:** 17–18 (17) trichobothria (4–5 (4) accessory) distributed by series as follows: $eb = 5$ (no accessory); $esb = 2$ (no accessory), located proximally, distance between esb_1 and esb_2 is minimal, approximating distance between em_1 and em_2 ; $em = 2$ (no accessory), located proximal of segment midpoint; $est = 3-4$ (3) (2–3 (2) accessory), $est_1-est_2-est_3$

form a V-like pattern; $et = 4-5$ (5) (1–2 (2) accessory). This neobothriotaxic type is found exclusively in subfamily Chactinae (Figs. 83–86).

Chactid neobothriotaxic type Ch2: Neobothriotaxy is limited to the ventral and external aspects of the patella, and is fixed in general pattern and in number of accessory trichobothria. **Patella ventral surface:** 7–8 (7) (4–5 (4) accessory), positioned in linear line; most proximal trichobothrium (accessory) is petite in size. **Patella external surface:** 23–24 (24) trichobothria (10–11 (11) accessory) distributed by series as follows: $eb = 5$ (no accessory); $esb = 5-6$ (6) (3–4 (4) accessory), esb_1 located midsegment, distance between esb_1 and esb_2 is considerably greater than distance between em_1 and em_2 ; $em = 2$ (no accessory), located midsegment; $est = 5$ (4 accessory), pattern irregular; $et = 6$ (3 accessory), pattern

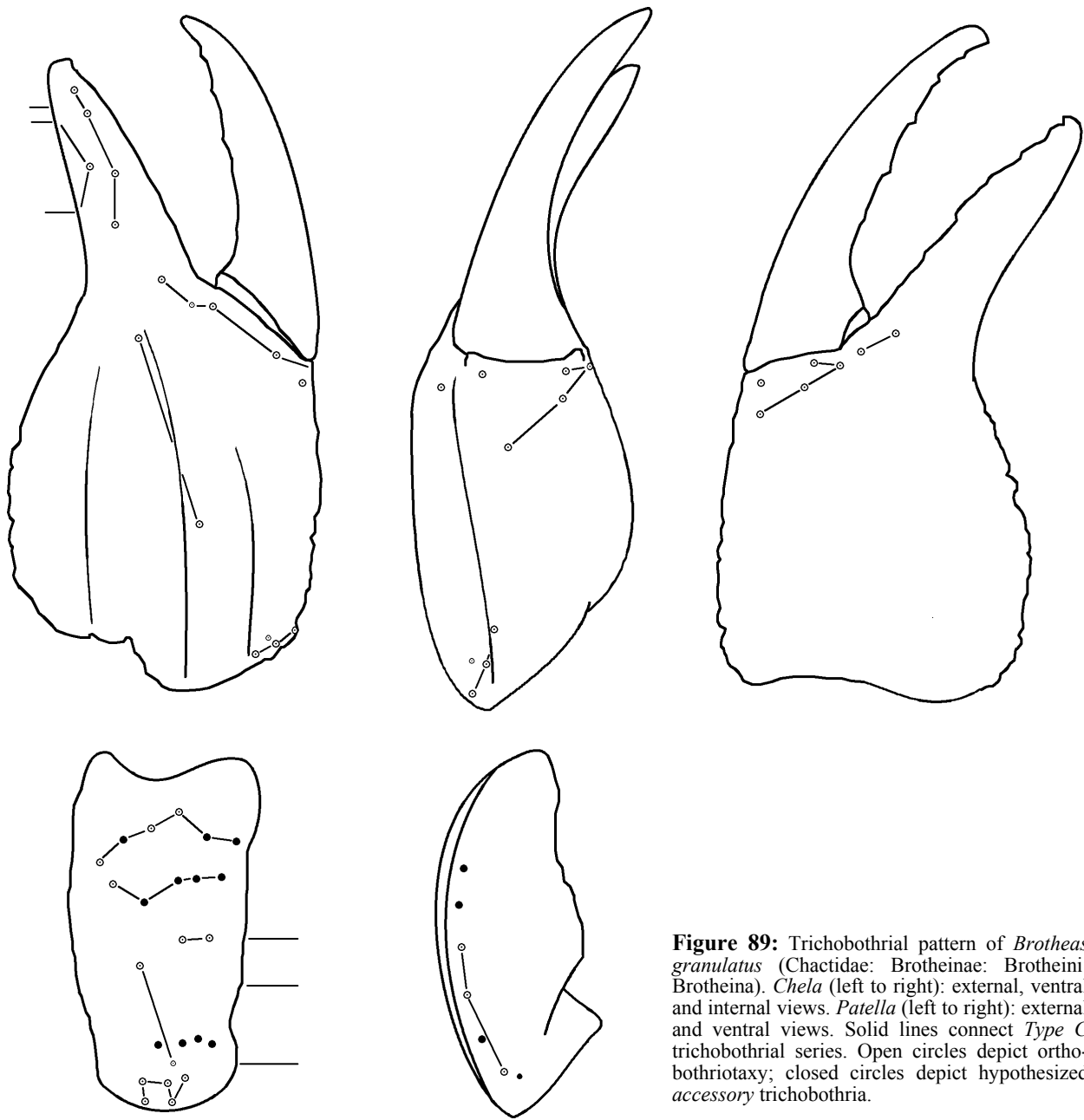


Figure 89: Trichobothrial pattern of *Brotheas granulatus* (Chactidae: Brotheinae: Brotheini: Brotheina). *Chela* (left to right): external, ventral and internal views. *Patella* (left to right): external and ventral views. Solid lines connect Type C trichobothrial series. Open circles depict orthobothriotaxy; closed circles depict hypothesized accessory trichobothria.

irregular. This neobothriotaxic type is found exclusively in subfamily Brotheinae, tribe Brotheini (Figs. 88–90).

Chactid neobothriotaxic type Ch3: Neobothriotaxy is found on the ventral aspect of the chela and the ventral and external aspects of the patella, and is variable, in part, in general pattern and in number of accessory trichobothria. **Chela ventral surface:** 12–26 (mean is species dependent) (8–22 accessory), extends to extreme proximal aspect of palm where it extends onto the external surface. **Patella ventral surface:** 10–19 (mean is species dependent) (7–16 accessory), extends to distal one-quarter and continues onto the external surface; these “wrap around” accessory trichobothria number 2–5 (mean is species dependent); total number of trichobothria attributed to ventral series, including both

ventral and external surfaces, is 12–24; trichobothria are sometimes doubled proximally into two rows, the most distal trichobothrium (accessory) is petite in size. **Patella external surface:** 18–25 (mean is species dependent) distributed by series as follows: $eb = 7$ (2 accessory); $esb = 2$, esb_1 located midsegment, distance between esb_1 and esb_2 is considerably greater than distance between em_1 and em_2 ; $em = 2-7$ (0–5 accessory); $est = 4$ (3 accessory); $et = 3-5$ (0–2 accessory). [Note, in this pattern the designation of accessory trichobothria for the em series is arbitrary, although they occur in regions occupying both the em and esb series.] This neobothriotaxic type is found exclusively in subfamily Uroctoninae, genus *Anuroctonus* (Fig. 82).

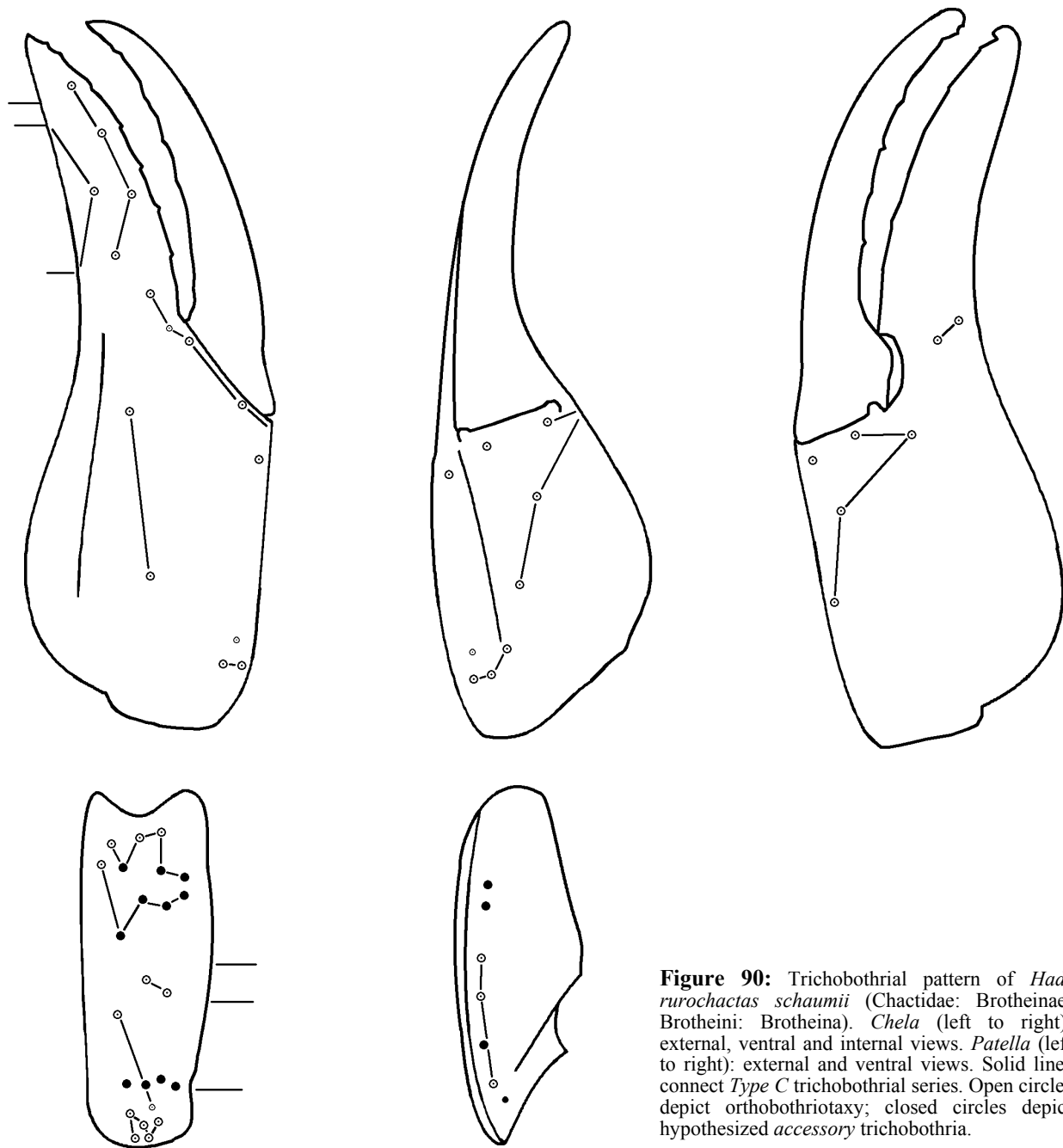


Figure 90: Trichobothrial pattern of *Hadrurochactas schaumii* (Chactidae: Brotheinae: Brotheini: Brotheina). *Chela* (left to right): external, ventral and internal views. *Patella* (left to right): external and ventral views. Solid lines connect Type C trichobothrial series. Open circles depict orthobothriotaxy; closed circles depict hypothesized accessory trichobothria.

Superstitioniid neobothriotaxic type Su1: Neobothriotaxy is found on the external aspects of the chela and the patella. Due to the lack of material, variability in pattern and number of accessory trichobothria is not well defined. **Chela external surface:** For the unique scorpion *Alacran*, we find minor neobothriotaxy on the chela, three external accessory trichobothria, two on the proximal half of the palm close to the ventroexternal carina and one on the inner base of the fixed finger. **Patella external surface:** 20–21 trichobothria distributed by series as follows: $eb = 5$ (no accessory), $esb = 2$ (no accessory), $em = 5$ (3 accessory), $est = 4$ (3 access-

ory), and $et = 5$ (2 accessory). The assignment of accessory trichobothria to a particular series is arbitrary. Francke (1982a: 52, Figs. 5–11) states "... tibia with 26–27 trichobothria ..." but did not specify where the variability occurred. We suspect that it is found presumably on the external aspect but exactly where on the surface is not known. This neobothriotaxic type is found exclusively in subfamily Typhlochactinae, genus *Alacran* (Fig. 80).

EuscorpIID neobothriotaxic type Eu1: Neobothriotaxy is found on the ventral aspect of the chela, in part, and the ventral and external aspects of the patella, and is

variable, in part, in general pattern and in number of accessory trichobothria. **Chela ventral surface:** Neobothriotaxy on this surface is only found on three species in the genus *Euscorpium*: *E. flavicaudis*, *E. italicus*, and *E. naupliensis*. In the first species (subgenus *Tetra-trichobothrius*) the number of accessory trichobothria (two, is fixed); for the other two species (subgenus *Polytrichobothrius*) the number is variable, 8–13 trichobothria (4–9 accessory). **Patella ventral surface:** 5–14 trichobothria (2–11 accessory), positioned in linear line (in genus *Chactopsis*, this series angles at trichobothria v_5 or v_6); most proximal trichobothrium (accessory) is petite in size. **Patella external surface:** 19–40+ trichobothria distributed by series as follows: $eb = 7-13$ (2–8 accessory), $esb = 2-3$ (0–1 accessory), esb_a (specific to subgenus *Polytrichobothrius*) = 0–11 (0–11 accessory), $em = 2-6$ (0–4 accessory), positioned midsegment, $est = 4-5$ (3–4 accessory), and $et = 3-10$ (0–7 accessory). This neobothriotaxic type is found in subfamilies Euscorpiinae and Megacorminae (see Soleglad & Sissom (2001: Figs. 88–92, 106–111).

Euscorpiid neobothriotaxic type Eu2: Neobothriotaxy is found on the ventral aspect of the chela, in part, and the ventral and external aspects of the patella, and is variable, in part, in general pattern and in number of accessory trichobothria. **Chela ventral surface:** Neobothriotaxy on this surface is only found on genus *Alloscorpions* where it numbers 9–15 (5–11 accessory). **Patella ventral surface:** 6–19 trichobothria (3–16 accessory), positioned in linear line; most proximal trichobothrium (accessory) is petite in size. **Patella external surface:** 17–26 trichobothria, distributed by series as follows: $eb = 5$ (0 accessory), $esb = 2$ (0 accessory), $em = 2$ (0 accessory), positioned proximally, $est = 4-10$ (3–9 accessory), and $et = 4-7$ (1–4 accessory). This neobothriotaxic type is found in subfamily Scorpiopinae. Note, the numbers above exclude genus *Dasyscorpions* which exhibits massive neobothriotaxy on the pedipalp patella, 23 ventral trichobothria (20 accessory) and well over fifty on the external surface. The topology resulting in Soleglad & Sissom's (2001) analysis implies that this derivation occurred after the major neobothriotaxy found throughout the subfamily Scorpiopinae, thus is autapomorphic for *Dasyscorpions*. See Soleglad & Sissom (2001: Figs. 93–99, 100–105) for illustrations of this neobothriotaxic pattern type.

Pedipalp ornamentation – patella

The patella carinal configurations have been analyzed for all taxa in our cladistic ingroup as well as several other species outside our study. The development of the patellar spurs, the number of carinae, their relationship to the patellar spurs, are all considered important diagnostic characters.

Nomenclature: Vachon (1952: 60–61, Figs. 66–68) illustrated the eight major carinae found on the pedipalp patella. Interestingly, these figures were based on a buthid, the major representative of his monumental study in scorpions. The terminology used by Vachon was also recommended by Stahnke (1970: 310: Table 1, Part 2). We follow this nomenclature as well, with a couple of exceptions involving the carinae that extend from the patellar spurs found on the internal surface of the patella. Figure 91, which illustrates a diagrammatic cross-section of the patella, depicts the nomenclature used in this paper for all eight carinae found on this pedipalp segment. The Dorsal Patellar Spur (DPS) and Ventral Patellar Spur (VPS) (terminology first introduced by Soleglad & Sissom (2001: 59–62)) may be optionally part of internal carinae, the spurs providing the proximal beginning of the individual carinae. We identify these carinae as the DPS_c and VPS_c carinae, replacing Vachon and Stahnke's terminology of *internal dorsal* and *internal ventral*, respectively. Alternatively, the spurs can be solitary, without an interconnecting carina. The identification of these spurs is dependent on the scorpion group in concern. Some groups, the euscorpiids for example, have very well developed spurs, the euscorpiines and megacormines with a strong DPS and the scorpiopines with both spurs showing medium to strong development. As reported by Soleglad & Sissom (2001), each patellar spur is accompanied by a somewhat stout seta at its base which makes for easy identification even if the spur is small or near obsolete. The internal surface of the patella, where the patellar spurs are situated, sometimes can be vaulted, providing a very pronounced projection from the segment. This projection is even more exaggerated if accompanied by well-developed patellar spurs.

Fossil development – the palaeopisthacanthids: Jeram (1994a: 535) provided detailed information on the patella carinal development for the Carboniferous scorpion *Compsoscorpium elegans*: "... The precise number of carinae cannot be established in the flattened fossil material, but at least seven were present. Two internal carinae bear particularly large tubercles, each carrying a single setal follicle ..." Clearly, Jeram was referring to both patellar spurs, each with a single seta. This fact implies that these spurs are not a recent development in the extant scorpions. Based on this partial data, we are hypothesizing this as the primitive state for the number of carinae (seven) for the pedipalp patella since it is the best information available to date. We also know that the DPS_c and VPS_c are present as well, thus establishing the primitiveness of these two internal carinae. In addition we are assuming here (as a hypothesis) that of the eight carinae identified in our Figure 91, DM_c is the only carina absent in the palaeopisthacanthids.

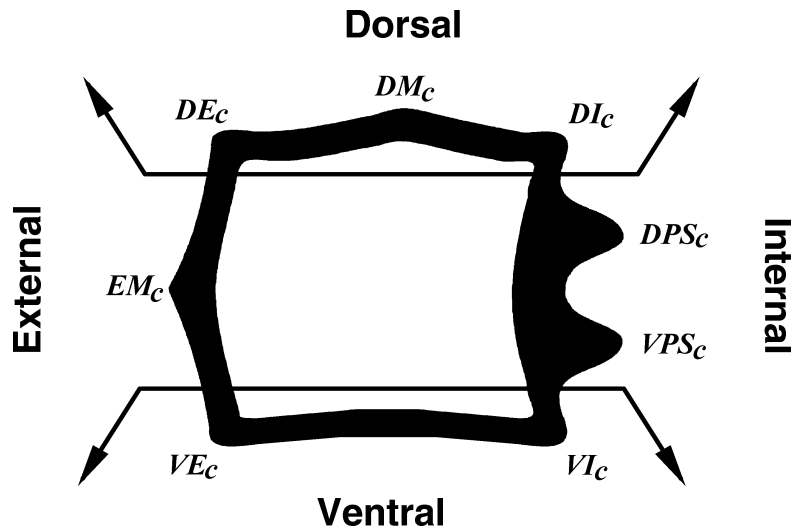


Figure 91: Diagrammatic cross-section of a pedipalp patella depicting carinal terminology. Dorsal carinae: DE_c = dorsoexternal carina, DM_c = dorsomedian carina, DI_c = dorsointernal carina. Ventral carinae: VE_c = ventroexternal carina, VI_c = ventrointernal carina; External carina: EM_c = exteromedian carina; Internal carinae: DPS_c = Dorsal Patellar Spur carina, VPS_c = Ventral Patellar Spur carina.

Lourenço (2001: 645, Fig. 13) writes for the Cretaceous scorpion *Archaeobuthus estephani* "... tibia with three dorsal carinae observable ..." This comment is interesting since it may imply that this species has DM_c , exclusively a buthoid carina (see below), although it is not clear exactly which carinae are actually present. Lourenço's figure may also imply this as well, since we see a weak line of granules situated between what are presumably DI_c and DE_c . Of course, we cannot definitely determine how many and/or which carinae occur in this species even though one could assume the granulated internal aspect shown in the figure is carina DPS_c .

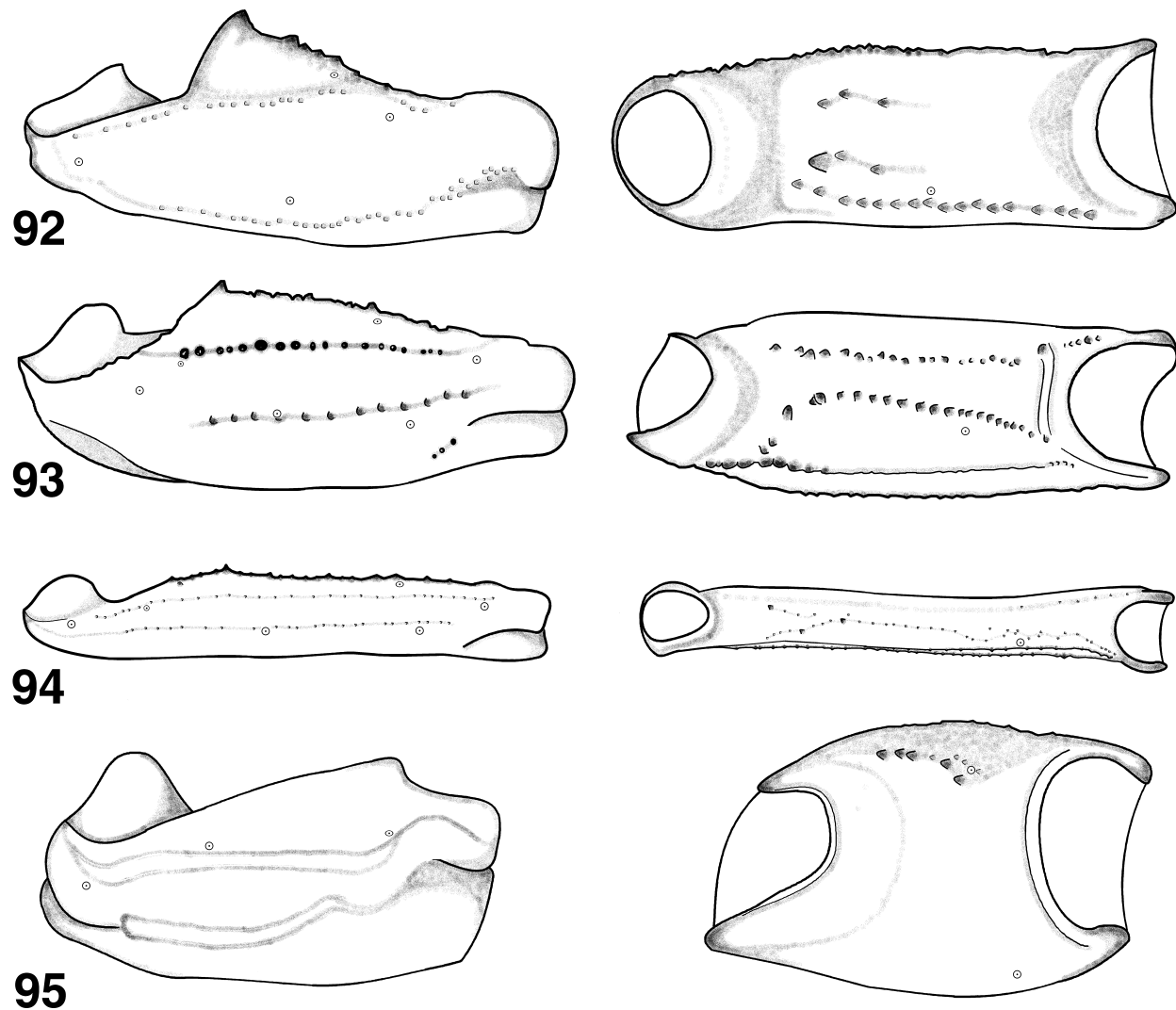
For the five "palaeo-buthid" genera (Baltic amber, 65–55 Ma), described by Lourenço and Weitschat (1996, 2000, 2001), we have sparse information on the patellar carina development, as follows: For genus *Palaeotityobuthus*, patella is unknown; for genera *Palaeoprotobuthus* and *Palaeolychas*, patella "... feebly carinate ..."; genus *Palaeoakentrobuthus*, "... with 5 keels: one internal, 3 dorsal and 1 external, other faces not visible ...", presumably DM_c is present on this genus based on the report of three dorsal carinae; and genus *Palaeoananteris*, "... tibia with 7 keels ...", Fig. 2-c shows the absence of DM_c , consistent with the number of carinae reported. Assuming this report is accurate, we have a buthoid without the DM_c carina (see below).

Recent scorpions: In Recent scorpions we see definitive patterns of patellar carinal configurations within its basic clades. Of particular diagnostic importance is the presence/absence of carinae DM_c , DPS_c , and VPS_c , these, in part, provide important distinctions within Recent scorpions. Also of importance is the development of the patellar spurs and, in general, to what degree the internal surface of the patella is vaulted. In general all Recent scorpions exhibit the fundamental minimal set of five carinae, two dorsal, DE_c

and DI_c , two ventral, VE_c and VI_c , and one external, EM_c , but there are many important exceptions. Below we characterize the patellar carinal configuration for each parvorder.

Pseudochactida: *Pseudochactas* exhibits seven carinae, including the patellar spur carinae DPS_c and VPS_c (Fig. 92). We consider this configuration plesiomorphic for this parvorder, since we have hypothesized the same configuration for the Carboniferous palaeopisthacanthids. In this unique scorpion species we see a well-developed vaulted internal projection from which the two patellar spurs are visible, DPS more developed than VPS . Carinae DPS_c and VPS_c are well-developed, but only extend to midsegment.

Buthida: In this analysis we find eight carinae (as illustrated in Fig. 91) present on all buthoid genera evaluated. This parvorder differs from the primitive state as exhibited in the palaeopisthacanthids and Pseudochactida with the presence of the DM_c carina. We consider this carina derived for the parvorder Buthida, thus a synapomorphy — it is not found in any other Recent scorpion. In Figures 93–94 we illustrate the patellar carinae for two buthoid genera, representing both the Old and New Worlds (*Mesobuthus* and *Tityus*). In both figures we can see a somewhat well-developed DM_c carina, extending most of the length of the segment. In Buthida, the patellar spur carinae, DPS_c and VPS_c , are also well-developed, again, extending most of the segments length, especially DPS_c . In *Tityus* (Fig. 94), in contrast to *Mesobuthus* (Fig. 93), we see a somewhat weak VPS_c , essentially merging into DPS_c . This weak VPS_c is also exhibited in genera *Isometrus*, *Lychas* and *Uroplectes* (based on limited number of species sampled). The patellar spurs themselves, DPS and VPS , are not particularly well developed in this parvorder as, for example, seen in some groups in parvorder Iurida. Stockwell (1989: 93–94) also mentioned the DPS_c carina

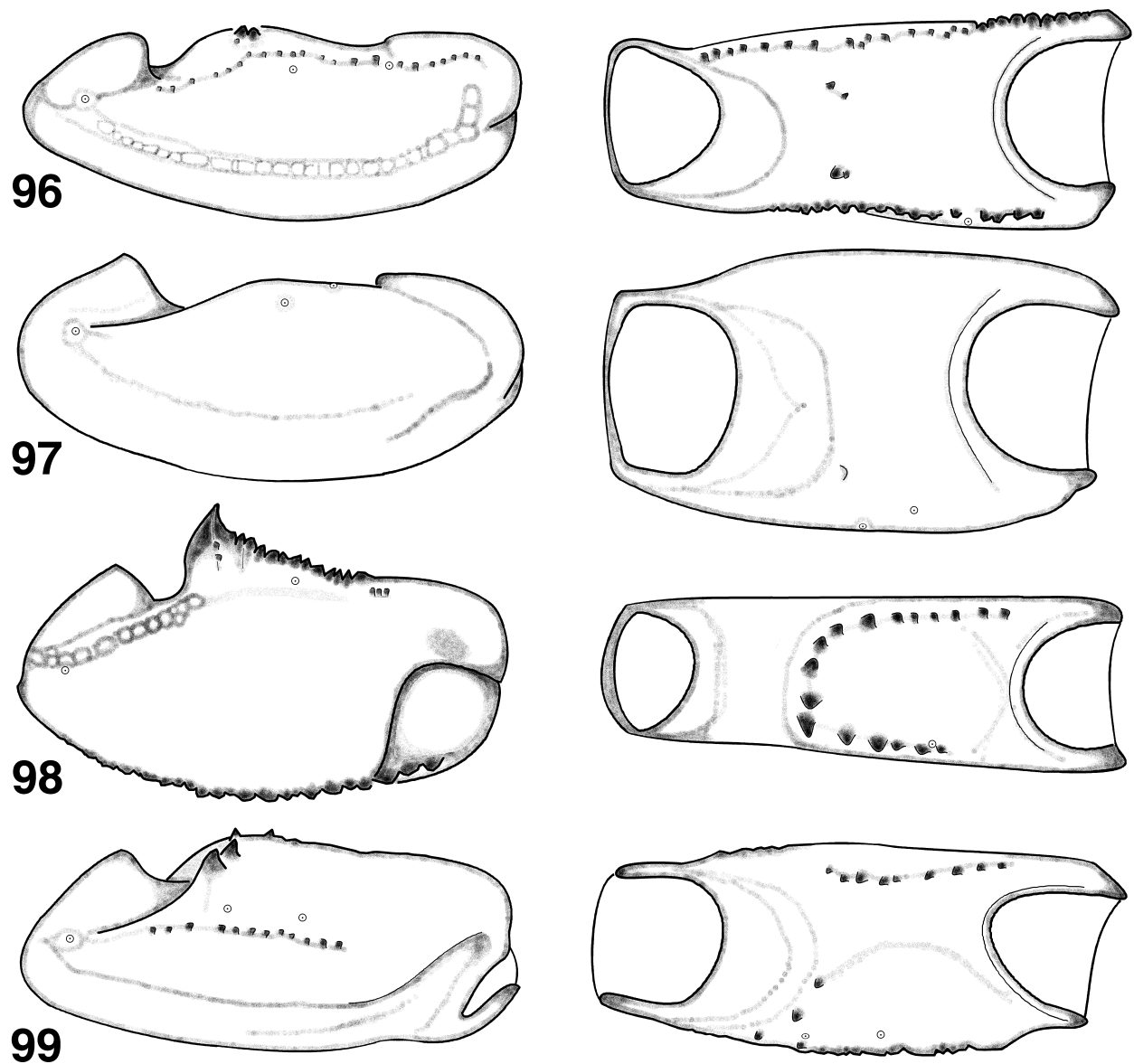


Figures 92-95: Pedipalp patella showing dorsal and internal carinae. Dorsal (left) and internal (right) views (note, in internal view, dorsal surface of patella is situated on bottom aspect of figure). **92.** *Pseudochactas ovchinnikovi*. **93.** *Mesobuthus caucasicus*. **94.** *Tityus nematochirus*. **95.** *Chaerilus variegatus*. Note presence of dorsomedian carinae, DM_c , in the two buthoid genera (Figs. 93-94).

considering it a separate derivation than that seen in the vaejovids (see below). He, however, did not mention the DM_c or VPS_c carinae.

Chaerilida: As noticed by Stockwell (1989), the patella of the chaerilids is quite exceptional, the dorsointernal aspect is somewhat concaved, providing a vaulted appearance to the ventrointernal edge. The DPS is not present, but the VPS is present along with an accompanying VPS_c carina. Thus, *Chaerilus* has six carinae on this segment, missing DPS_c and DM_c . As a possible connection to the unusual patellar shape, the trichobothrial patterns are also interesting on the chaerilid patella (Fig. 95). It is the only Recent scorpion that is equipped with two internal trichobothria, the unique trichobothrium i_2 (as identified in Soleglad & Fet (2001: Fig. 3)) being positioned quite close to the VI_c carina. In line with this additional trichobothrium, we

see that *Chaerilus* also is equipped with three ventral trichobothria, hypothesized by Soleglad & Fet (2001: 10) to be homologous to those found in Type C orthobothriotaxy. However, considering positional analysis, we see that trichobothria v_2 and v_3 are positioned quite close to the VI_c carina (as is i_2). One, therefore, could hypothesize that these trichobothria are connected to the i_2 trichobothrium based on their close proximity, thus these are totally new trichobothria (Stockwell (1989: 100), in part, also considered this as a possibility). If this is the case, then we only have one ventral trichobothrium homologous with Type C orthobothriotaxy, v_1 (their positions are essentially identical in both parvorders). Soleglad & Fet (2001), in general, did not incorporate positional considerations, instead maximizing the minimal number of trichobothria in all homology analyses. This alternative hypothesis

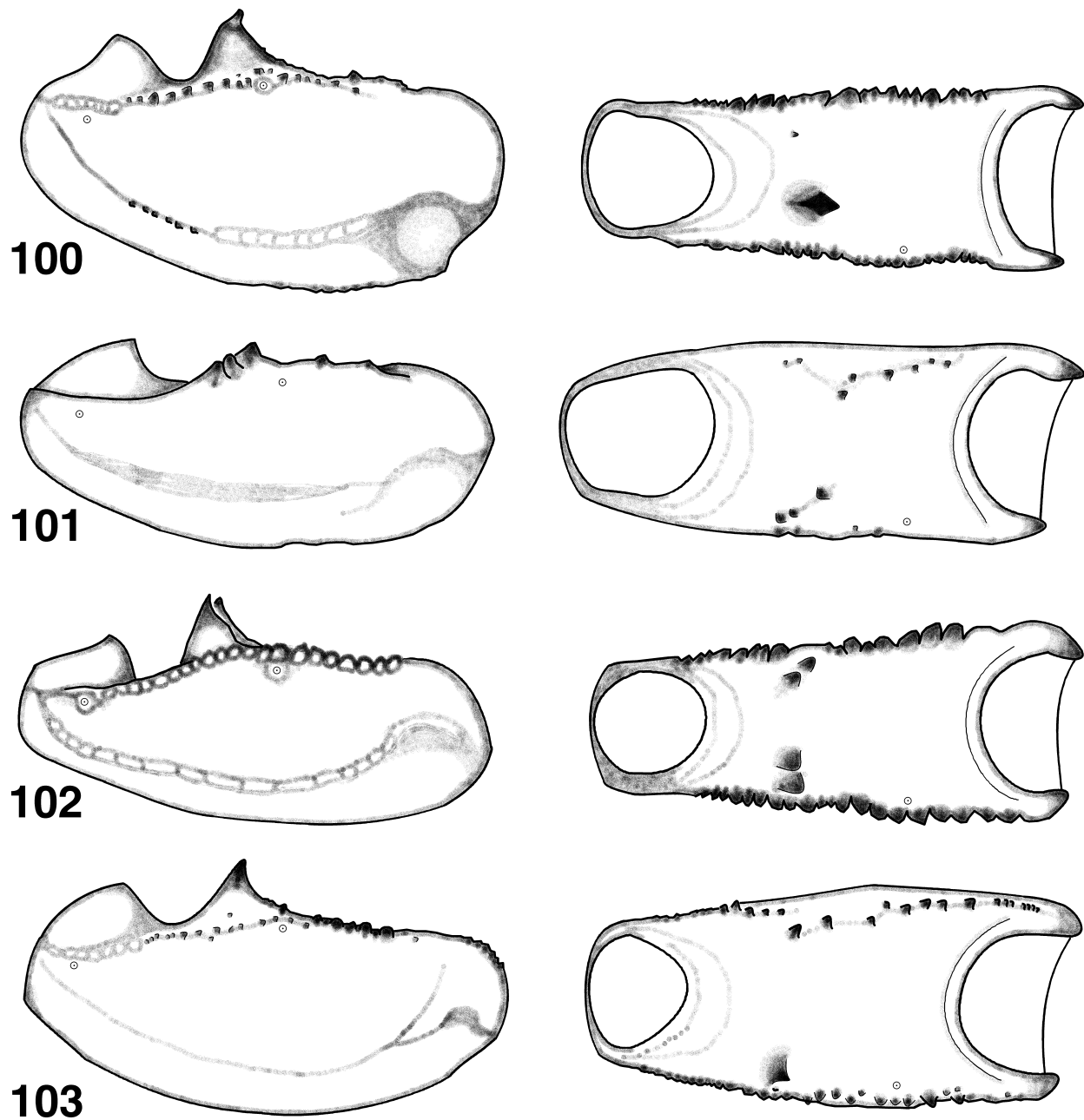


Figures 96-99: Pedipalp patella showing dorsal and internal carinae. Dorsal (left) and internal (right) views (note, in internal view, dorsal surface of patella is situated on bottom aspect of figure). **96.** *Calchas nordmanni*. **97.** *Bothriurus araguayae*. **98.** *Liocheles* sp. (Papua New Guinea) **99.** *Bioculus comondae*.

would weaken the taxonomic connection between the two parvorders, Chaerilida and Iurida, by establishing only one common ventral patellar trichobothrium (note that only these two parvorders exhibit any ventral trichobothria on the patella in Recent scorpions).

Iurida: Great diversity is present in the patellar carinal development in parvorder Iurida. In general, only the basic five carinae are present, but some superfamilies and families, exhibit an additional carinae. The DM_c carina is absent, being found exclusively in Buthida. The patellar spur development can be exceptional in this parvorder; the families Liochelidae, Euscorpidae, and chactid subfamily Uroctoninae exhibit significant development of at least one of the spurs.

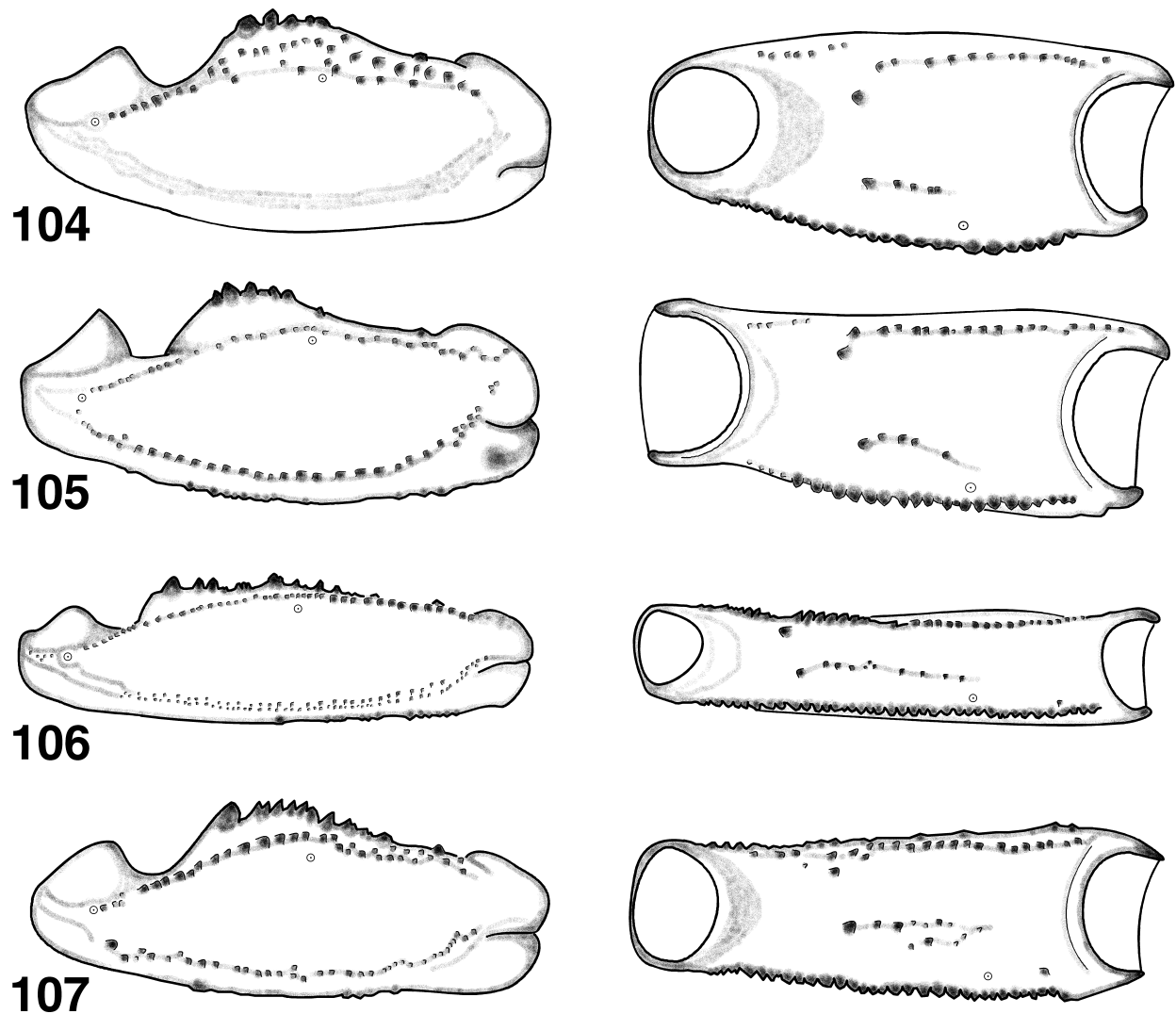
Iuroidea: In this small superfamily we see the basic configuration of the five patellar carinae. For the Old World family Iuridae, the internal aspect of the patella, which is slightly vaulted, is armed with small doubled patellar spurs (represented by *Calchas* in Fig. 96). In *Hadruioides* (Caraboctonidae), the internal aspect is more vaulted, also with small doubled patellar spurs. The North American genus *Hadrurus* has an exceptionally flat internal surface on this segment, exhibiting absolutely no vaulting. Both patellar spurs are absent and the internal surface is densely covered with long, stout setae, making the identification of patellar spur setae impossible.



Figures 100-103: Pedipalp patella showing dorsal and internal carinae. Dorsal (left) and internal (right) views (note, in internal view, dorsal surface of patella is situated on bottom aspect of figure). **100.** *Euscorpium naupliensis*. **101.** *Chactas* sp. **102.** *Uroctonus mordax mordax*. **103.** *Anuroctonus* sp.

Scorpionoidea: In the scorpionoids, we see that family Bothriuridae is essentially equipped with five basic carinae, missing both patellar spur carinae as well as exhibiting underdeveloped DPS and VPS (represented by *Bothriurus* in Fig. 97). The same is true for subfamily Scorpioninae (family Scorpionidae), which exhibits a very flat internal surface, showing little or no vaulting. In the diplocentrines, we see that dorsal carinae DI_c and DE_c are positioned in close proximity, caused, in part, by the lowering of the DI_c carina (represented by *Bioculus*

in Fig. 99). This interpretation is supported by the unusual position of dorsal trichobothrium d_2 which is found above carina DI_c , on the internal aspect of the patella. In the family Liochelidae, the internal surface of the patella is considerably vaulted, with a well-developed DPS (represented by *Liocheles* in Fig. 98) (*Cheloctonus* does not have the vaulted condition, which is presumably a reversal of this unusual character as suggested by Prendini (2000: 49)). The DI_c and VI_c carinae are disrupted from a proximal to anterior



Figures 104-107: Pedipalp patella showing dorsal and internal carinae. Dorsal (left) and internal (right) views (note, in internal view, dorsal surface of patella is situated on bottom aspect of figure). **104.** *Vaejovis punctatus*. **105.** *Vaejovis punctipalpi*. **106.** *Serradigitus subtilimanus*. **107.** *Paruroctonus silvestrii*. Note the presence of the DPS carina, DPS_c , in this family.

direction, but do continue along the edges of the vaulted surface. These conditions are the most exaggerated in genera *Liocheles*, *Hadogenes* and *Opisthacanthus*, with Hemiscorpiinae showing a similar configuration but with slightly less development. The vaulted condition is also reported for genus *Heteroscorpion*.

Chactoidea(-V): This assemblage contains some of the most developed patellar spurs in Recent scorpions. The DPS is exceptionally well-developed in the euscorpiones (Fig. 100) and megacormines. These are amply illustrated in Soleglad (1976b), Soleglad & Sissom (2001: Figs. 149–154), and Fet & Soleglad (2002: Figs. 11, 21, 33, 44, 56). In the latter reference, the relative length of the DPS was used, in part, to distinguish some of the species studied in that paper. In the scorpiones, we find a medium-developed DPS accompanied by a strongly developed VPS, providing a “fork-like” appearance to the internal surface of the patella

(Soleglad & Sissom, 2001: Figs. 155–160). The VPS exhibited in the scorpiones is the most developed in all Recent scorpions. For chactid subfamily Uroctoninae, the DPS is well-developed. On genus *Uroctonus*, we see both DPS and VPS development, both doubled forming a small “fork” at each spur, the dorsal showing considerably more development (Fig. 102). *Uroctonus*’s sister genus, *Anuroctonus*, also has a well-developed DPS but the VPS is weak to obsolete (Fig. 103). The other two chactid subfamilies, Chactinae and Brotheinae, as well as the family Superstitioniidae, have essentially obsolete patellar spurs. Interestingly, although the strong patellar spur development just discussed in some chactoids is considerable, no accompanying carinae, DPS_c and VPS_c , are present, nor is the internal surface vaulted to any degree. Thus all Chactoidea(-V) are restricted to the minimal five carinae configuration.

Vaejovidae: Stockwell (1989: 93–94) first pointed out the development of the DPS_c carina in the vaejovids (referred to as the *internal median carina*), considering it a synapomorphy. For the vaejovids, Stockwell considered the DPS_c carina obsolete in the genera *Pseudouroctonus* and *Uroctonites*, a suggested reversal of this character derivation. We agree that this carina is reduced on these genera but we do not believe it is obsolete. In general, the DPS_c carina does not extend as far distally on the segment as in the other vaejovid genera (Figs. 104–107), but is developed if viewed from the distal end of the patella. In these genera the DPS is well-developed, sometimes setting on a somewhat vaulted internal surface of the segment. Stockwell (1989: 149, Table 6) modeled this carina with two characters (his characters 41 and 42): all vaejovid genera, including the chactid genus *Uroctonus*, were hypothesized as having the DPS carina (character 41), having then been lost (character 42) in genera *Pseudouroctonus*, *Uroctonites*, and *Uroctonus*. As coded, these two characters form an additive binary complex forcing this ordering of DPS_c carinal gain/loss. Of course, based on the cladistic analysis presented in this study, we propose that the DPS_c carina was not lost in *Uroctonus* since it was never present in this genus in the first place.

Following is the comparative development of the DPS_c carinae of several species representing *Pseudouroctonus* and *Uroctonites*:

- Pseudouroctonus reddelli*, weak development, three denticles (including the DPS)
- P. andreas*, medium development, five denticles
- P. apacheanus*, medium to strong development, four denticles
- P. minimus castaneus*, medium to strong development, four denticles
- P. angelenus*, very strong development, nine denticles
- Uroctonites huachuca*, very weak development, three denticles
- U. montereus*, weak development, two denticles

Stockwell (1989) considered the relatively robust development of the chela to account for the subtle difference in DPS_c carinal development observed within the species of these two genera. The data above seems to support this hypothesis, in part, in the two *Uroctonites* species represented here, but is belied by the tiny species *P. andreas*, which has very stocky short-fingered chelae.

Venom glands and the female reproductive system - Pavlovsky

Venom glands: Pavlovsky (1912, 1913, 1924a, 1924b, 1925; also spelled Pawlowsky and Pavlovskij)

was among the first authors to survey important anatomical systems of scorpions across many scorpion genera and families, with an unusually representative selection of scorpion genera. He specifically paid attention to the phylogenetic importance of anatomical features, or, in his own words, "...apart from pursuing the morphological aims, I endeavoured in my work to obtain facts which would be of use to systematists who are continually pointing out the importance of the study of the comparative anatomy of scorpions for their purposes" (Pavlovsky, 1924b: 616). In his investigation of the venom glands, Pavlovsky (1913) was the first to discover two types of glands: one with simple, smooth epithelium (*Type I*), and another, with folded epithelium (*Type II*). *Type I* glands were found by Pavlovsky (1912, 1913, 1924b) in families Chactidae, Euscorpiidae, Iuridae (*Calchas*), and Liochelidae; actual taxa examined in these families are shown in Table 1 (given according to the current taxonomy accepted in the present paper). *Type II* glands were found in Bothriuridae, Buthidae, Caraboctonidae, Iuridae (*Iurus*), Liochelidae, Scorpionidae, and Urodacidae; see Table 1 for actual taxa examined in these families. *Type I* gland was considered by Pavlovsky (1912, 1913, 1924b) to be the primitive (or embryonic type) condition due to the fact that *Type II* folded gland is derived from *Type I* during embryogenesis in both *Scorpio maurus* (Scorpionidae) and *Androctonus crassicauda* (Buthidae); this developmental feature was later confirmed by Probst (1972). Further authors addressed venom gland morphology (Birula, 1917a, 1917b; Werner, 1934; Francke & Soleglad, 1981; Lourenço, 1985; Stockwell, 1989; Sissom, 1990; Farley, 1999). Birula (1917b: 36) confirmed, following Pavlovsky (1913) that Chactidae, Chaerilidae, Euscorpiidae, Vaejovidae, and some Liochelinae (*Liocheles*, *Iomachus*) have simple epithelium, but distinguished between intermediate folded epithelium in Bothriuridae, Caraboctonidae (*Hadruroides*), Urodacidae (*Urodacus*), some Liochelidae (*Opisthacanthus*, *Hemiscorpius*), and highly folded in Scorpionidae (*Heterometrus*, *Scorpio*, *Opisthophthalmus*, *Pandinus*). Francke & Soleglad (1981) reviewed this issue in Iuridae and Caraboctonidae, confirming that only one iurid genus (*Calchas*) has simple glands, while four other genera of Iuroidea have folded condition. Simple glands in some Liochelidae (=Ischnuridae) (Lourenço, 1985; Sissom, 1990) are considered a secondary derivation (Stockwell, 1989).

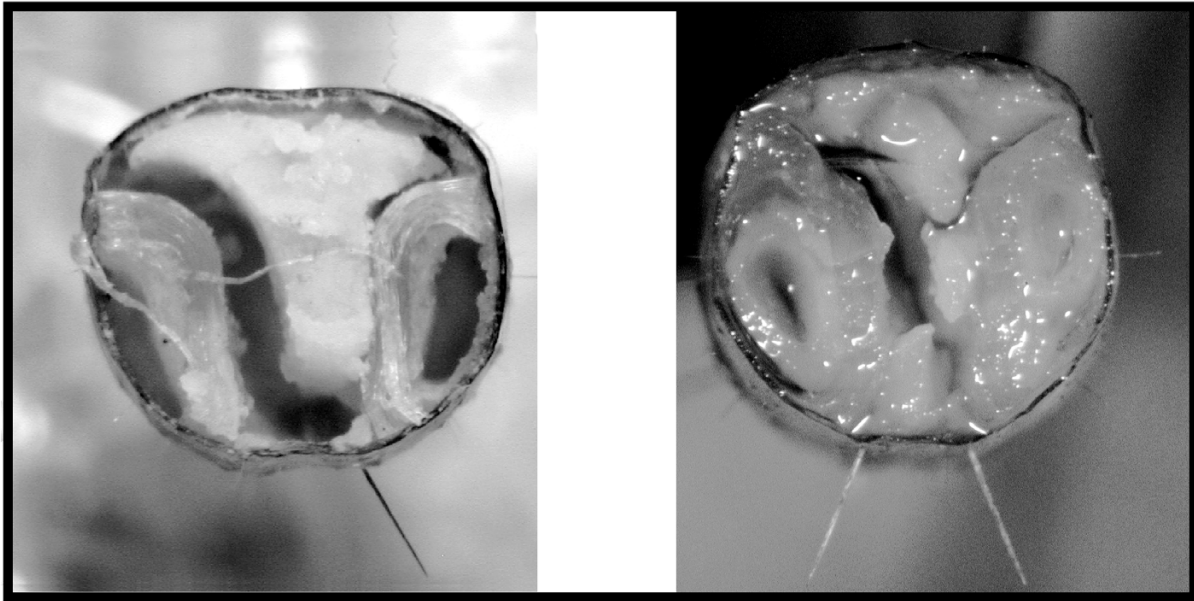
We studied the cladistic analyses presented by Stockwell (1989) and Prendini (2000) addressing the construction of the scorpion venom gland. Stockwell (1989) coded all taxa with *complex* glands except for the scorpionoid genera comprising family Liochelidae and subfamily Heteroscorpioninae which he coded as *simple*. Even genera *Calchas* and *Chaerilus* were coded as *complex* even though he discussed in the text that

Type I Venom Glands (simple)	
Iuridae	<i>Calchas nordmanni</i>
Liochelidae	<i>Opisthacanthus elatus</i> , <i>O. madagascariensis</i>
Chactidae	<i>Uroctonus mordax</i> (other unlisted genera?)
Euscorpiidae	<i>Euscorpius carpathicus</i> , <i>E. italicus</i> , <i>E. germanus</i> , <i>E. mingrelicus</i>
Type II Venom Glands (folded)	
Buthidae	<i>Androctonus australis</i> , <i>A. crassicauda</i> , <i>Buthus occitanus</i> , <i>Centruroides gracilis</i> , <i>Hottentotta judaicus</i> , <i>Mesobuthus caucasicus</i> , <i>M. eupeus</i> , <i>Orthochirus scrobiculosus</i>
Iuridae	<i>Iurus dufourei</i>
Caraboctonidae	<i>Caraboctonus keyserlingii</i> , <i>Hadruiroides lunatus</i> , <i>Hadrurus hirsutus</i>
Bothriuridae	<i>Bothriurus vittatus</i>
Liochelidae	<i>Hemiscorpius lepturus</i>
Scorpionidae	<i>Heterometrus cyaneus</i> , <i>Scorpio maurus</i>
Urodacidae	<i>Urodacus manicatus</i> , <i>U. yaschenkoi</i>

Table 1: Scorpion families and species evaluated by Pavlovsky (1912, 1913, 1924a, 1924b, 1925) in his analysis of the scorpion venom gland types.

Reticular Mesh of Six Cells	
Chaerilidae	<i>Chaerilus variegatus</i>
Iuridae	<i>Iurus dufourei</i>
Bothriuridae	<i>Brachistosternus intermedius</i> , <i>Bothriurus bonariensis</i>
Liochelidae	<i>Iomachus politus</i> , <i>Liocheles australasiae</i>
Scorpionidae	<i>Scorpio maurus</i> , <i>Heterometrus cyaneus</i>
Chactidae	<i>Broteas subgranosus</i> , <i>Broteochactas gollmeri</i> , <i>Teuthraustes witti</i> , <i>Uroctonus mordax</i>
Euscorpiidae	<i>Euscorpius flavicaudis</i> , <i>Scorpiops leptochirus</i> , <i>S. montanus</i>
Vaejovidae	<i>Vaejovis cristimanus</i> , <i>V. spinigerus</i>
Reticular Mesh of Eight Cells	
Buthidae	<i>Androctonus australis</i> , <i>Anomalobuthus rickmersi</i> , <i>Babycurus buttneri</i> , <i>Buthus occitanus</i> , <i>Centruroides elegans</i> , <i>C. margaritatus</i> , <i>Compsobuthus acutecarinatus</i> , <i>Grosphus madagascariensis</i> , <i>Hottentotta emini</i> , <i>H. hottentotta</i> , <i>H. judaicus</i> , <i>H. saulcyi</i> , <i>Isometrus maculatus</i> , <i>Leiurus quinquestriatus</i> , <i>Liobuthus kessleri</i> , <i>Lychas marmoreus</i> , <i>L. mucronatus</i> , <i>L. tricarinatus</i> , <i>L. variatus</i> , <i>Mesobuthus caucasicus</i> , <i>M. eupeus</i> , <i>Odonoturus dentatus</i> , <i>Orthochirus scrobiculosus</i> , <i>Parabuthus leiosoma</i> , <i>P. planicauda</i> , <i>Tityus bolivianus</i> , <i>T. cambridgei</i> , <i>Uroplectes fischeri</i> , <i>U. formosus</i> , <i>U. lineatus</i> , <i>U. triangulifer</i>

Table 2: Scorpion families and species evaluated by Pavlovsky (1924a, 1925) in his analysis of the female scorpion reproductive system.



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Figures 108-109: Cross-section of telson vesicle showing construction of venom glands. **108.** *Pseudochactas ovchinnikovi*, simple glands (no folding of epithelium walls). **109.** *Mesobuthus caucasicus*, complex glands (note folding of epithelium walls).

Calchas has simple glands. We suspect that this may be an omission in Stockwell's data matrix. In the text he considered complex as primitive (contrary to Pavlovsky's hypothesis) and the simple gland as a derivation from this state. Stockwell's modeling of the venom gland (his character 137) only included these mappings. Based on other modeling techniques used by Stockwell, we suspect that he should have created a character setting all taxa with complex glands, his proposed primitive state, and then create one or more additional characters to represent the secondary derivation to simple (e.g., one character for *Calchas* and another for the scorpionoids, assuming separate

evolution). Prendini (2000) followed Stockwell's assumption that complex is primitive and coded the same scorpionoid genera with simple glands (his character 113), but he did code *Chaerilus* with simple glands. Sissom (1990) stated that all iuroid genera have complex venom glands, ignoring Pavlovsky's report of simple glands for genus *Calchas*.

We dissected the telson vesicle of two *Pseudochactas ovchinnikovi* specimens, determining that the venom glands are simple (Fig. 108). We contrast these two venom gland dissections with that of a buthid, *Mesobuthus caucasicus* (Fig. 109) which illustrates the complex folding found in its venom gland.

Female reproductive system: Considering the anatomy of female reproductive system, Pavlovsky (1924a, 1925) discovered that Buthidae differ profoundly from all other families in structure of their ovariuterus: while in all other families, the ovariuterus formed a reticular mesh of six cells with four transverse ovarian tubes, in Buthidae it has eight cells with five transverse ovarian tubes (with exceptions in some species of *Tityus* which have two cells; Sissom, 1990). For his investigation of the anatomy of ovariuterus, Pavlovsky (1924a, 1925) studied the following families of scorpions: Buthidae, Bothriuridae, Chaerilidae, Chactidae, Euscorpiidae, Iuridae, Scorpionidae, Liochelidae, Vaejovidae; see Table 2 for the actual species examined in these families. The six- versus eight-cell structure of ovariuterus was confirmed by Francke (1982a), who considered eight-cell condition plesiomorphic; Stockwell (1989), however, considered the six-cell condition plesiomorphic, and eight-cell condition a buthid synapomorphy.

Pectinal development

Based on an extensive survey of scorpion descriptions spanning the families Vaejovidae and Chactoidae(-V), we discover that the pectines, in general, are considerably more developed in Vaejovidae than they are in Chactoidae(-V). By development we are specifically referring to the number of pectinal teeth (i.e., not their size or specific embellishments of the other pectinal plates). Although the number of pectinal teeth is usually considered a low-level character normally used in the diagnoses of species, the differences exhibited between these families, which are widespread throughout both, are considerable and therefore we consider this a valid differentiating character. Although these differences in pectinal development can be quantified in various ways, we concentrate here on the number of pectinal teeth, data that is readily available in scorpion literature. In order to further quantify and relate pectinal development to specific taxonomic groups within the superfamily, we constructed a ratio using the total length of an adult specimen and its mean pectinal tooth count (only the female gender is considered in this analysis). In Figures 110–111, we show the general distribution of pectinal tooth counts versus the length of an adult specimen for the families Chactoidae(-V) and Vaejovidae. In these charts, we also break down the data into families in Chactoidae(-V) (Fig. 110) and genera and groups within the Vaejovidae (Fig. 111). In these generalized charts, we see that the pectinal tooth counts are considerably lower in Chactoidae(-V), showing very little overlap with those found in the vaejovids. The highest mean pectinal tooth count value found in Chactoidae(-V) is 11.5, in contrast to 28.5 found in the vaejovids. The

lowest pectinal tooth count reported for Chactoidae(-V) is that by Lacroix (1992: Fig. 153), in his study of the chactid scorpion *Belisarius xambeui*. In this paper Lacroix illustrated the pectines of a female specimen which only had 2–3 pectinal teeth, which to our knowledge, is the lowest known number reported for a Chactoidae(-V) scorpion. In the typhlochactines, we find pectinal tooth counts as low as 4–5, males and females. Both *Superstitionia* and *Troglotayosicus* have 6–7 teeth. Interestingly, in *Superstitionia* the count is six for both female and male genders. For the rare megacormine species *Megacormus granosus* only three teeth have been reported (only the female is known for this species). In contrast, the lowest vaejovid pectinal tooth count is that of *Paravaejovis pumilis*, female, which has only 7–8 (7.5) pectinal tooth, in contrast to the male gender which exhibits a range of 12–16, almost twice as many as the female (Williams, 1980: 30). Except for this species, the lowest mean pectinal tooth count for the vaejovid female is 11.5, the average mean count being 16.5. The average mean ratio values (i.e., total length divided by pectinal tooth count) for the two family groups are 6.255 and 2.757, for Chactoidae(-V) and Vaejovidae, respectively. The Chactoidae(-V) value being more than twice that of the vaejovid. Figures 112–113 show scatter charts for all data samples used in this analysis for each family group, over 150 samples in all. See **Appendix D** for more details on the data, further breakdown into taxa groups within the two sets of families, and the assumptions used in conducting this analysis.

Absence of fulcra: In support of our thesis that pectinal development is more prevalent in the vaejovids than it is in Chactoidae(-V), we see that the absence (i.e., loss) of fulcra only occurs in Chactoidae(-V)—these pectinal plates are always present in the vaejovids. The importance of the presence or absence of these pectinal plates has been considered an important taxonomic character by many scorpion specialists (e.g., González-Sponga (1978) for the chactid genus *Taurepania* (= our *Broteochactas*) and Lourenço (1998a), for his family Troglotayosicidae). We do not believe that the absence of fulcra is necessarily that significant an event in Chactoidae(-V). We base this conclusion on the suggestion that this loss may be due to the reduced pectinal development in general, as established herein, and therefore is somewhat random within Chactoidae(-V). For example, Soleglad & Sissom (2001: 67) showed the great variability in the presence or absence of fulcra in the family Euscorpiidae. In Euscorpiidae, we find genera *Megacormus*, *Chactopsis*, *Parascorpiops*, *Dasyscorpiops*, and some species of *Plesiochactas*, *Scorpiops*, *Neoscorpiops* and *Euscorpiops* are lacking fulcra. In the genus *Euscorpius*, some species of the subgenus *Alpiscorpius* have essentially lost fulcra on the distal aspects of the pecten. These species are the smallest

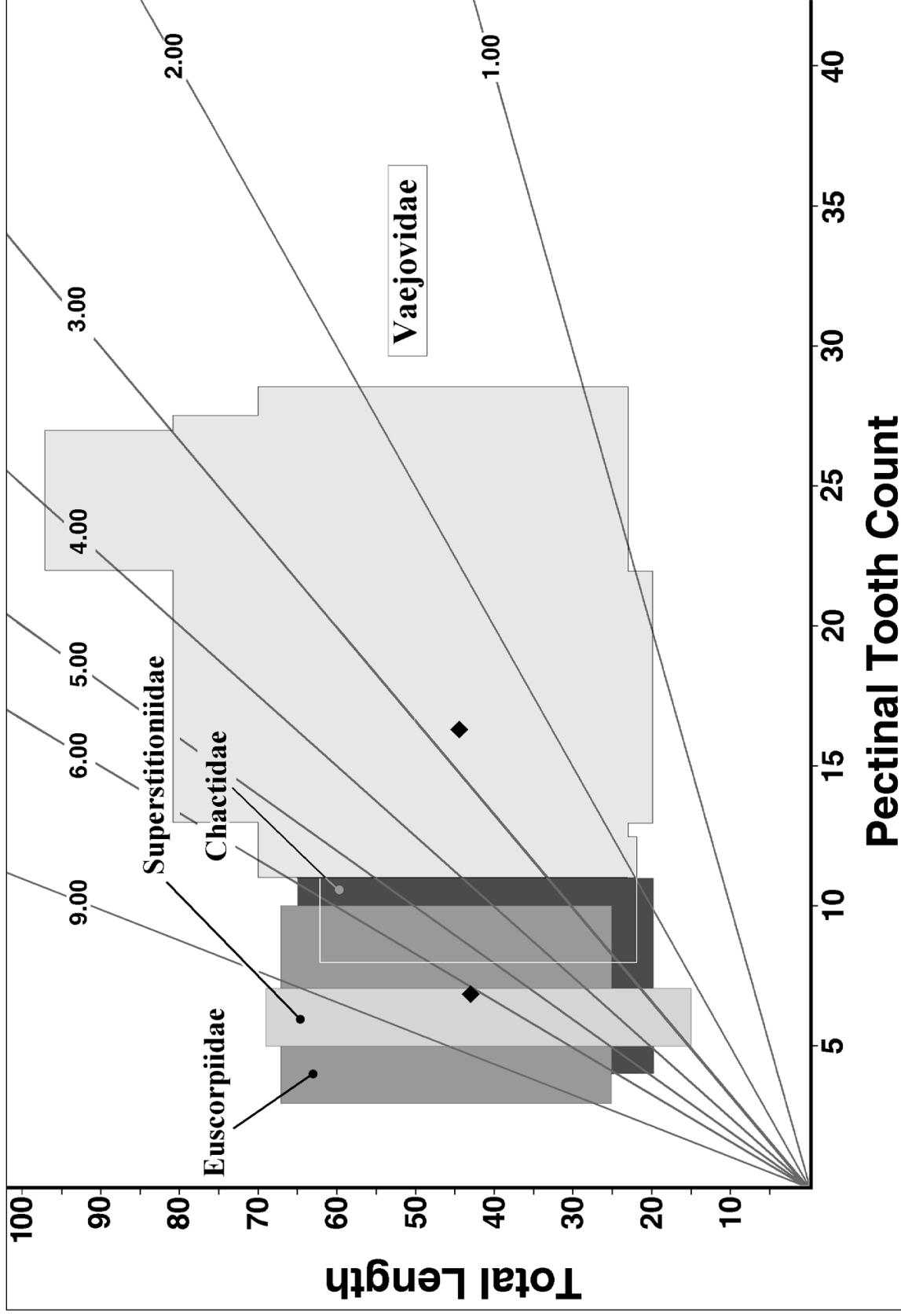


Figure 110: General distribution chart of *Total Length/Pectinal Tooth Count* ratio (female) for superfamily Chactioidea, showing breakdown of families Superstitioniidae, Euscorpidae and Chactidae. General distribution for family Vaejoividae is shown for contrast. Diagonal lines depict integer ratio values; closed diamonds indicate mean ratio values for both family sets.

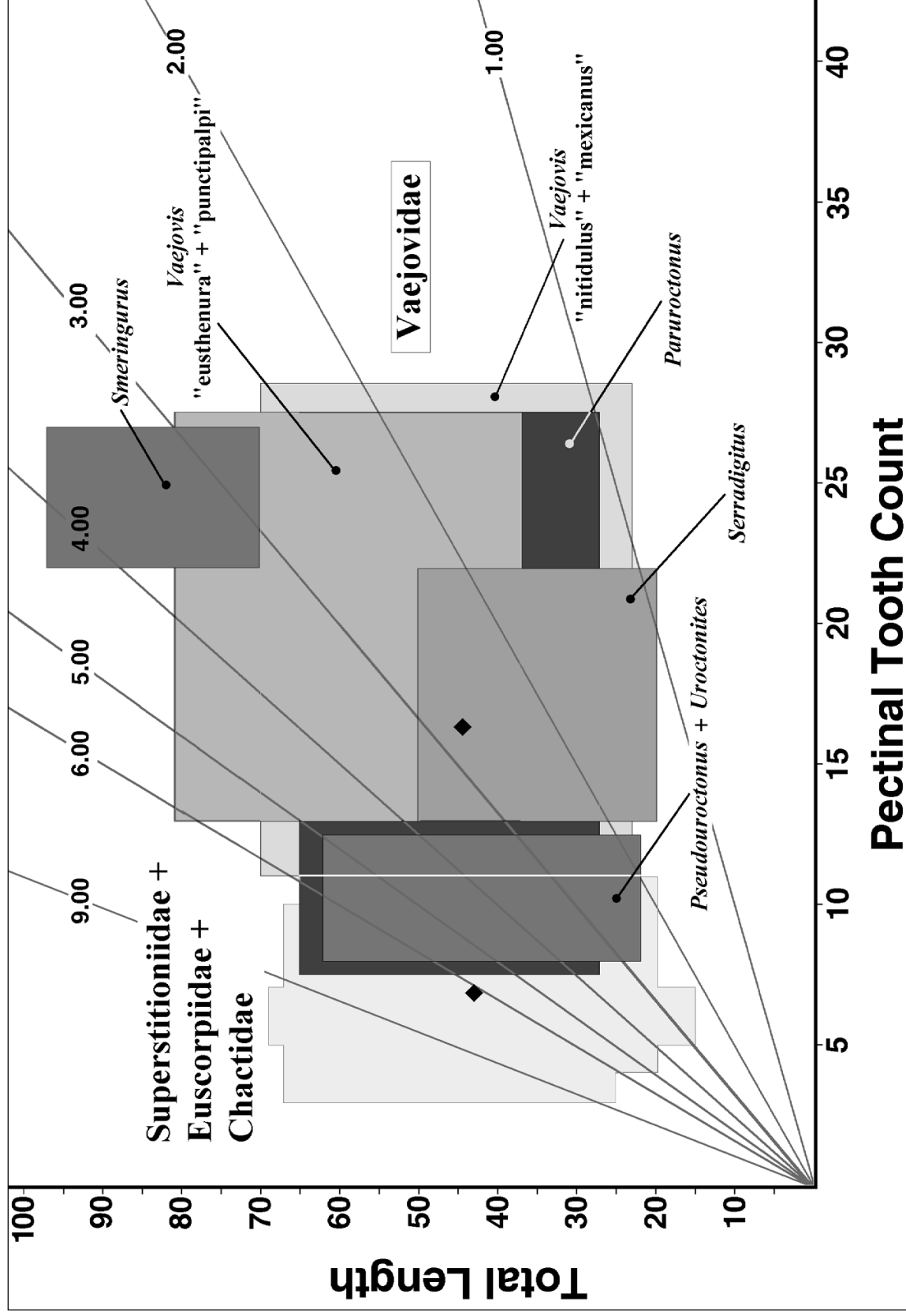


Figure 111: General distribution chart of Total Length/Pectinal Tooth Count ratio (female) for superfamily Chactioidea, showing vaejoivid genera *Smeringurus*, *Paruroctonus*, *Serradigitus*, *Pseudouroctonus* + *Uroctonites*, *Vaejois*, groups "nitidulus" + "mexicanus", and *Syntropis* + *Vaejois*, groups "eusthenura" + "punctipalpi". General distribution for families Chactidae, Euscorpiidae and Superstitioniidae are shown for contrast. Diagonal lines depict integer ratio values; closed diamonds indicate mean ratio values for both family sets.

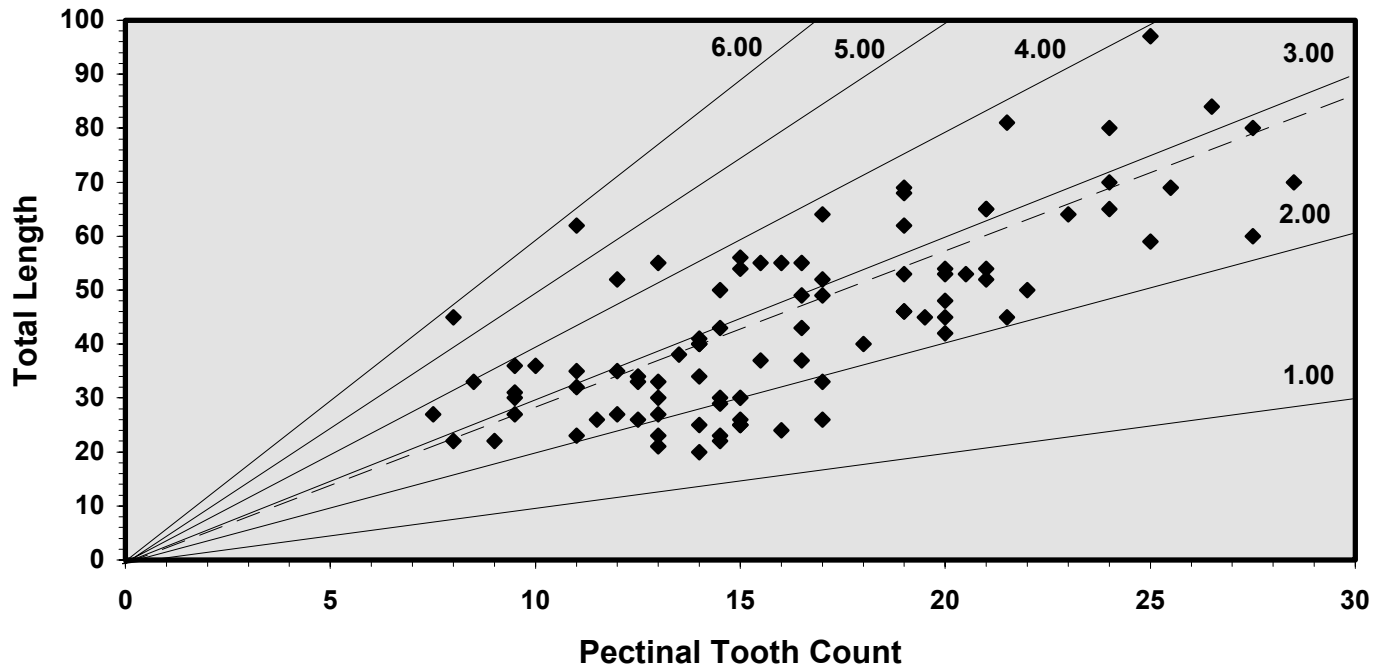


Figure 112: Scatter chart of *Total Length/Pectinal Tooth Count* ratio (female) for family Vaejovidae. Number of samples = 91; solid diagonal lines depict integer ratio values; *dashed line* depicts the mean ratio value.

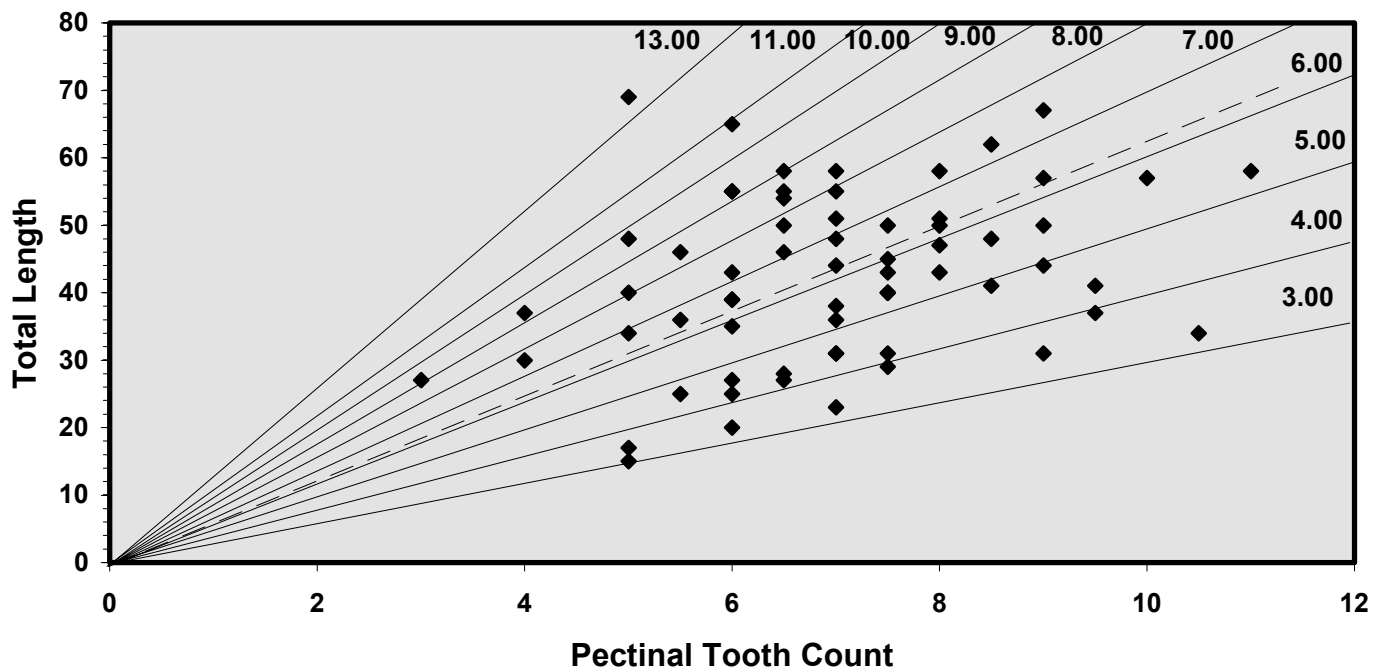


Figure 113: Scatter chart of *Total Length/Pectinal Tooth Count* ratio (female) for families Chactidae, Euscorpiidae, and Superstitioniidae. Number of samples = 65; solid diagonal lines depict integer ratio values; *dashed line* depicts the mean ratio value.

found in the genus as a whole, thus probably explaining, in part, their loss. In the chactoid family Superstitioniidae, all assigned species have lost fulcra except for *Superstitionia donensis*. In this case all are either cave adapted or occur in a litter microhabitat. Similarly, the cave/endogean scorpion *Belisarius xambeui* is also missing fulcra. We suggest here that the combination of microhabitat adaptation (i.e., litter, caves) and/or highly reduced pectines is the cause for the loss of fulcra in Chactoidea(-V), therefore, its importance can only be considered localized to the taxa that have lost these pectinal plates. The same may be true for Buthoidea, where loss of fulcra is common in small species (see e.g. Lourenço, 1996a, 1998b).

Cladistic Analysis

The cladistic analysis presented in this study has two goals: (1) the phylogenetic breakdown of the major upper-level taxa of Recent scorpions (which, in turn, allows us to determine the place of the genus *Pseudochactas*); and (2) the phylogenetic revision of the chactoid family Chactidae. The latter goal, as it turned out, due to the necessary inclusion and/or exclusion of certain taxa from other related families, also necessitated the analysis of families Superstitioniidae and Vaejovidae, and to a lesser extent, the superfamily Iuroidea. Only family Euscorpidae, which was recently investigated in detail by Soleglad & Sissom (2001), escaped any taxonomic alterations. Since it was necessary to evaluate families Superstitioniidae and Vaejovidae, as well as Iuroidea, all major genera from these groups were analyzed, including multiple species of the genus *Vaejovis*. For other superfamilies, such as Buthoidea and Scorpionoidea, the taxa set was not as extensive, though still containing a good representation of major subclades within these groups. In particular, for superfamily Buthoidea, we included representatives worldwide, since we believed that such a complete representation was necessary in order to adequately evaluate position of *Pseudochactas* within the Recent scorpions. Therefore, due to the somewhat large scope of this analysis, involving both high-level as well as lower level taxonomic issues, the taxa set chosen required ample representation across all major Recent scorpion groups. In addition, as stated elsewhere in this study, extensive use of the appropriate fossil record was deemed necessary to adequately investigate the clearly ancient lineages in the early evolution of Recent scorpions.

Since we were interested in two results from this study, we divided our cladistic analysis into two parts: the identification of characters whose applicability best addressed upper-level scorpion systematics (referred to

as *fundamental characters*), and those characters that were germane for the topological delineation of the family Chactidae. Of course, these two sets of characters overlapped in both sets of analyses, to one degree or another—the fundamental characters providing major relevance at the higher levels of Chactidae, and the more chactid-specific characters also providing relevance, in some situations, to the higher levels addressed in the first analysis. In both analyses, the complete taxa set was considered.

Tables 3 and 4 present the character state values assigned to the taxa set used in this cladistic analysis. Table 4 presents the orthobothriotaxy existence mappings, in part, originally described by Soleglad & Fet (2001). Table 3 presents all character mappings, excluding the existence mappings (which is replaced with a single ordered character, see below). **Appendix A** briefly describes all characters, their state assignments, and presents a brief discussion on the assumptions made in each character definition.

Taxa Set

Outgroup selection. The outgroup used in this analysis is the Carboniferous orthostern genus *Palaeopisthacanthus*. The definition of this genus has been expanded to incorporate information extracted from all species comprising its family Palaeopisthacanthidae, species *Palaeopisthacanthus schucherti*, *P. vogelandurdeni*, *Compsoscorpis elegans*, and *Cryptoscorpis americanus*. So, from the cladistic viewpoint, our concept of the genus “Palaeopisthacanthus” can be considered a composite of all the species in its family. This approach was necessary to maximize available information for hypothesized polarity argumentation. The Cretaceous orthostern species *Archaeobuthus estephani* was also included in our fossil taxa set, since we have good information on its trichobothrial pattern which is modeled in detail in this analysis. All these fossil data were extracted from three sources: Kjellesvig-Waering (1986), Jeram (1994a), and Lourenço (2001c).

Ingroup selection. One of the primary purposes of this analysis was to determine the phylogenetic position of the unique scorpion *Pseudochactas ovchinnikovi* within Recent scorpions. (This goal, in fact, precipitated our recent papers on the evolution of scorpion orthobothriotaxy (Soleglad & Fet, 2001) and the scorpion sternum (Soleglad & Fet, 2003), where this unique genus exhibited primitive characteristics in both of these structure types). To accomplish this goal it was necessary to include a large representation of all major Recent groups, as we believe that any demonstrated monophyly can be convincing only if the designated groups are well represented. We present the taxa group

used in the cladistic presented herein by scorpion family. Actual genera and species(s) used in the construction of the data matrix (Tables 3 and 4) are specified (see **Methods & Material** section for locality data of these species). The primary species (the species used for determining most character states) is listed first, followed by additional species, if used to actually construct the matrix or to enhance the definition of a character state for that genus. Of course, the overall character analysis presented elsewhere in this paper involved all the species listed in the **Methods & Material** section.

Pseudochactidae. This monotypic family is represented by genus *Pseudochactas*, species *P. ovchinnikovi*.

Chaerilidae. This monotypic family is represented by genus *Chaerilus*, the majority of characters are derived from *C. variegatus*, though *C. celebensis* and *C. petrzekai* also contributed.

Buthidae. Thirteen genera were considered in this analysis, representing both Old and New World faunas. New World: *Centruroides* (*C. sculpturatus*), *Microtityus* (*M. jaumei*), *Tityus* (*T. nematochirus*). Old World: *Androctonus* (*A. bicolor*), *Grosphus* (*G. hirtus*, *G. bistratus*), *Isometrus* (*I. maculatus*), *Karasbergia* (*K. methueni*), *Liobuthus* (*L. kessleri*), *Lychas* (*L. sp.*), *Mesobuthus* (*M. caucasicus*, *M. eupeus*), *Microbuthus* (*M. sp.*), *Orthochirus* (*O. scrobiculosus*), and *Uroplectes* (*U. vitatus*).

Microcharmidae. *Microcharmus hauseri*.

Iuridae. Both genera of this family are represented: *Calchas* (*C. nordmanni*) and *Iurus* (*I. dufourei*).

Caraboctonidae. Two out of three genera, belonging to both subfamilies are represented: *Hadruroides* (*H. maculatus*, *H. charcasus*) and *Hadrurus* (*H. obscurus*, *H. aztecus*, *H. hirsutus*).

Bothriuridae. Five genera are represented, both New and Old World: *Bothriurus* (*B. burmeisteri*, *B. araguayae*), *Brachistosternus* (*B. ehrenbergii*), *Centromachetes* (*C. pocockii*), *Cercophonius* (*C. squama*), and *Phoniocercus* (*P. pictus*).

Liochelidae. Three genera are represented, spanning both subfamilies: *Hadogenes* (*H. troglodytes*), *Liocheles* (*L. sp.*, *L. australasiae*), and *Hemiscorpius* (*H. maindroni*).

Scorpionidae. Two genera are considered, representing both subfamilies: *Scorpio* (*S. maurus*) and *Diplocentrus* (*D. ochoterenai*).

Urodacidae. This monotypic family is represented by its sole genus, *Urodacus* (*U. manicatus*).

Euscorpidae. All three subfamilies of this family are represented: *Euscorpium* (*E. italicus*, *E. tergestinus*, *E. mingrelicus*), *Megacormus* (*M. gertschi*), *Chactopsis* (*C. insignis*), *Scorpiops* (*S. tibetanus*), and *Troglocormus* (*T. willis*).

Chactidae. Eight genera are considered, representing all three subfamilies, four tribes, and two subtribes: *Chactas* (*C. sp.*), *Teuthraustes* (*T. oculatus*), *Nullibrotheas* (*N. allenii*), *Brotheas* (*B. granulatus*), *Neochactas* (*N. delicatus*), *Belisarius* (*B. xambeui*), *Uroctonus* (*U. mordax*), *Anuroctonus* (*A. phaiodactylus*, *A. sp.*).

Superstitionidae. Both subfamilies of this family were represented by the review of selected species, the other data is based on the available literature: *Superstitionia* (*S. donensis*), *Troglotayosicus* (*T. vachoni*, literature only), *Typhlochactas* (all species, literature only), and *Alacran* (*A. tartarus*).

Vaejovidae. All genera but one (*Uroctonites*) were represented for this family, including multiple species in genus *Vaejovis*, each representing major groups. *Paravaejovis* (*P. pumilis*), *Paruroctonus* (*P. silvestrii*), *Pseudouroctonus* (*P. reddelli*), *Serradigitus* (*S. subtilimanus*), *Syntropis* (*S. macrura*), *Vaejovis* (*V. nitidulus*, *V. punctipalpi*, *V. eusthenura*), and *Vejovoidus* (*V. longiunguis*).

Orthobothriotaxy analysis

Soleglad & Fet (2001) presented a formal cladistic procedure for evaluating orthobothriotaxy in Recent scorpions. In that analysis six orthobothriotaxic types were considered, the three original types defined by Vachon (1974), types A, B and C, a newly defined type for genus *Pseudochactas*, type D, and two fossil scorpion types, type P and F1, for the palaeopisthacanthids and genus *Archaeobuthus*, respectively. Based on these six types of orthobothriotaxy, 62 individual trichobothria were hypothesized for the pedipalp, each designated as a separate character in the cladistic analysis. When these 62 existence characters, representing all hypothesized orthobothriotaxic trichobothria, are combined with the other characters defined in this paper, the resulting topology differs from that derived in the original analysis. The topological differences are slight, however, the original analysis resulted in the topology (P, (F1, ((D, A), (B, (C))))), whereas the analysis based on all information presented herein resulted in (P, (F1, (D, (A, (B, (C))))). We analyzed the differences in support of the original result by constraining the topology to that derived in this present study. In the original results, we have 98 steps, CI and RI support of 0.6633 and 0.6333, and a G-fit of -26.707. In the present analysis the number of steps is 101 (3.1% increase), CI and RI support equals 0.6436 (3% decrease) and 0.6000 (5.3% decrease), and G-fit of -26.057 (2.4% decrease). Thus the overall support decrease is 2.4 – 5.3%.

Based on the distribution of trichobothrial gains and losses for the pedipalp in this new analysis, we find the following differences from that resulting in the original Soleglad & Fet (2001: Fig. 8) study. We show these

	Chela						Patella						Femur		
	ii	dddd	DD	eeee	EEEEEEEEEE	VVVV	ii	dddd	eeeeeeeeeeee	vvv	iiii	dddd	eeee		
	bt	bsst	bt	bsst	bbbssttttt	1234	12	12345	bbbbbsmmsttt	123	1234	12345	1234		
	bt	bt	bt	123bt12345				12345bb12t123							
								12							
<i>Palaeopisthacanthus</i>	00	0000	00	2022	2200220000	2222	00	20000	2000000000200	000	0000	22002	0020		
<i>Archaeobuthus</i>	00	2002	00	2222	2200220000	2000	20	22002	2000002022200	000	2200	22222	0020		
<i>Pseudochactas</i>	22	2002	00	2222	2200220000	2000	20	22200	2200020002220	000	2222	22222	2220		
<i>Chaerilus</i>	22	2002	00	2222	2202220000	2000	22	22000	2200020202220	222	2000	20222	2222		
<i>Centruroides</i>	02	2002	00	2122	2210220010	2200	20	22221	2200020202220	000	2211	21222	2200		
<i>Isometrus</i>	02	2002	00	2122	2210220010	2200	20	22221	2200020202220	000	2211	21222	2200		
<i>Tityus</i>	02	2002	00	2122	2210220010	2200	20	22221	2200020202220	000	2211	21222	2200		
<i>Microtityus</i>	02	2002	00	2122	2210220010	2200	20	22221	2200020202220	000	2211	21222	2200		
<i>Mesobuthus</i>	02	2002	00	2122	2210220010	2200	20	22221	2200020202220	000	2211	21222	2200		
<i>Androctonus</i>	02	2002	00	2122	2210220010	2200	20	22221	2200020202220	000	2211	21222	2200		
<i>Karasbergia</i>	02	2002	00	2122	2210220010	2200	20	22220	2200020202220	000	2211	20222	2200		
<i>Orthochirus</i>	02	2002	00	2122	2210220010	2200	20	22221	2200020202220	000	2211	20222	2200		
<i>Microbuthus</i>	02	2002	00	2122	2200220000	2200	20	22221	2200020202220	000	2211	20222	2200		
<i>Liobuthus</i>	02	2002	00	2122	2210220010	2200	20	22221	2200020202220	000	2211	21222	2200		
<i>Grosphus</i>	02	2002	00	2122	2210220010	2200	20	22221	2200020202220	000	2211	21222	2200		
<i>Lychas</i>	02	2002	00	2122	2210220010	2200	20	22221	2200020202220	000	2211	21222	2200		
<i>Uroplectes</i>	02	2002	00	2122	2210220010	2200	20	22221	2200020202220	000	2211	21222	2200		
<i>Microcharmus</i>	02	2002	00	2122	2210220010	2200	20	22221	2200020202220	000	2211	21222	2200		
<i>Iurus</i>	22	2222	22	2122	2221122212	2122	20	22221	2122221222212	222	2000	20000	2000		
<i>Calchas</i>	22	2222	22	2122	2221122212	2122	20	22000	2122221222212	222	2000	20000	2000		
<i>Hadrurides</i>	22	2222	22	2222	2221222212	2222	20	22000	2222212222222	222	2000	20000	2000		
<i>Hadrurus</i>	22	2222	22	2222	2221222212	2222	20	22000	2222212222222	222	2000	20000	2000		
<i>Bothriurus</i>	22	2222	22	2222	2221222212	2222	20	22000	2222212222222	222	2000	20000	2000		
<i>Brachistosternus</i>	22	2222	22	2222	2221222212	2222	20	22000	2222212222222	222	2000	20000	2000		
<i>Cercophonius</i>	22	2222	22	2222	2221222212	2222	20	22000	2222212222222	222	2000	20000	2000		
<i>Phonocereus</i>	22	2222	22	2222	2221222212	2222	20	22000	2222212222222	222	2000	20000	2000		
<i>Centromachetes</i>	22	2222	22	2222	2221222212	2222	20	22000	2222212222222	222	2000	20000	2000		
<i>Hadogenes</i>	22	2222	22	2222	2221222212	2222	20	22000	2222212222222	222	2000	20000	2000		
<i>Liocheles</i>	22	2222	22	2222	2221222212	2222	20	22000	2222212222222	222	2000	20000	2000		
<i>Hemiscorpius</i>	22	2222	22	2222	2221222212	2222	20	22000	2222212222222	222	2000	20000	2000		
<i>Scorpio</i>	22	2222	22	2222	2221222212	2222	20	22000	2222212222222	222	2000	20000	2000		
<i>Diplocentrus</i>	22	2222	22	2222	2221222212	2222	20	22000	2222212222222	222	2000	20000	2000		
<i>Urodacus</i>	22	2222	22	2222	2221222212	2222	20	22000	2222212222222	222	2000	20000	2000		
<i>Euscorpium</i>	22	2222	22	2222	2221222212	2222	20	22000	2222212222222	222	2000	20000	2000		
<i>Megacormus</i>	22	2222	22	2222	2221222212	2222	20	22000	2222212222222	222	2000	20000	2000		
<i>Chactopsis</i>	22	2222	22	2222	2221222212	2222	20	22000	2222212222222	222	2000	20000	2000		
<i>Scorpiops</i>	22	2222	22	2222	2221222212	2222	20	22000	2222212222222	222	2000	20000	2000		
<i>Troglocormus</i>	22	2222	22	2222	2221222212	2222	20	22000	2222212222222	222	2000	20000	2000		
<i>Belisarius</i>	22	2222	22	2222	2221222212	2222	20	22000	2222212222222	222	2000	20000	2000		
<i>Brotheas</i>	22	2222	22	2222	2221222212	2222	20	22000	2222212222222	222	2000	20000	2000		
<i>Neochactas</i>	22	2222	22	2222	2221222212	2222	20	22000	2222212222222	222	2000	20000	2000		
<i>Chactas</i>	22	2222	22	2222	2221222212	2222	20	22000	2222212222222	222	2000	20000	2000		
<i>Teuthraustes</i>	22	2222	22	2222	2221222212	2222	20	22000	2222212222222	222	2000	20000	2000		
<i>Nullibrotheas</i>	22	2222	22	2222	2221222212	2222	20	22000	2222212222222	222	2000	20000	2000		
<i>Anuroctonus</i>	22	2222	22	2222	2221222212	2222	20	22000	2222212222222	222	2000	20000	2000		
<i>Uroctonus</i>	22	2222	22	2222	2221222212	2222	20	22000	2222212222222	222	2000	20000	2000		
<i>Superstitionia</i>	22	2222	22	2222	2221222212	2222	20	22000	2222212222222	222	2000	20000	2000		
<i>Troglotayosicus</i>	22	2222	22	2222	2221222212	2222	20	22000	2222212222222	222	2000	20000	2000		
<i>Typhlochactas</i>	22	2222	22	2222	2221222212	2222	20	22000	2222212222222	222	2000	20000	2000		
<i>Alacran</i>	22	2222	22	2222	2221222212	2222	20	22000	2222212222222	222	2000	20000	2000		
<i>Vaejovis nitidulus</i>	22	2222	22	2222	2221222212	2222	20	22000	2222212222222	222	2000	20000	2000		
<i>V. eusthenura</i>	22	2222	22	2222	2221222212	2222	20	22000	2222212222222	222	2000	20000	2000		
<i>V. punctipalpi</i>	22	2222	22	2222	2221222212	2222	20	22000	2222212222222	222	2000	20000	2000		
<i>Smeringurus</i>	22	2222	22	2222	2221222212	2222	20	22000	2222212222222	222	2000	20000	2000		
<i>Paruroctonus</i>	22	2222	22	2222	2221222212	2222	20	22000	2222212222222	222	2000	20000	2000		
<i>Vejovoidus</i>	22	2222	22	2222	2221222212	2222	20	22000	2222212222222	222	2000	20000	2000		
<i>Paravaejovis</i>	22	2222	22	2222	2221222212	2222	20	22000	2222212222222	222	2000	20000	2000		
<i>Pseudouroctonus</i>	22	2222	22	2222	2221222212	2222	20	22000	2222212222222	222	2000	20000	2000		
<i>Serradigitus</i>	22	2222	22	2222	2221222212	2222	20	22000	2222212222222	222	2000	20000	2000		
<i>Syntropis</i>	22	2222	22	2222	2221222212	2222	20	22000	2222212222222	222	2000	20000	2000		

Table 4: Data matrix representing orthobothriotaxy. 62 trichobothria *existence* characters using a Sankoff schematic for weightings: *absent* ↔ *petite*, weight 1, *absent* ↔ *full*, weight 2, *petite* ↔ *full*, weight 1. State values: 0 = trichobothrium absent, 1 = trichobothrium present, petite in size, 2 = trichobothrium present, full size.

differences for three basic prototypic nodes, two intermediate nodes, and the six orthobothriotaxic types. The state derived in the original analysis is specified in parentheses:

Prototypic palaeopisthacanthid: no change in femur, patella, or chela.

Prototypic archaeobuthid: femur: i_2 absent (petite size); patella: em_1 petite (full size); chela: no change.

Prototypic recent: femur: i_3 petite (absent), i_4 petite (absent), e_2 full (petite); patella: d_3 petite (absent); chela: Eb_3 absent (petite).

(A+(B+C)) [new clade]: femur: e_3 lost; patella: em_1 full; chela: Eb_3 petite, Et_4 petite, V_2 petite.

(B+C): femur: i_3 lost (absent), i_4 lost (absent); patella: d_3 lost (absent); chela: no change.

Type P: no change in femur, patella, or chela.

Type F1: femur: i_2 absent (full size); patella: em_1 full (absent); chela: no change.

Type D: femur: no change; patella: d_3 full (absent); chela: Eb_3 absent, not lost (lost).

Type A: femur: e_3 absent, not lost (lost); patella: d_3 full (absent); chela: Et_4 absent (petite).

Type B: femur: e_3 full (absent); patella: no change; chela: Et_4 lost (absent), V_2 lost (absent).

Type C: femur: e_3 absent, not lost (lost); patella: no change; chela: Et_4 absent (petite).

Of particular interest is the absence of Eb_3 (petite) from the prototypic Recent scorpion node, removing homoplasy from this trichobothrium altogether. This further emphasizes importance of this trichobothrium; we now see that it is absent in both fossil representatives as well as in the primitive genus *Pseudochactas*, exists in petite form in the buthoids, and becomes a full trichobothrium in the chaerilids and type C scorpions. Also of interest and consistent with these observations, the Cretaceous fossil scorpion *Palaeburmesebuthus grimaldii* Lourenço is missing trichobothrium Eb_3 as well, Eb_1 and Eb_2 being present (Santiago-Blay et al., in press). See **Appendix E** for new derivation maps (which can be compared to maps presented in Soleglad & Fet (2001: Appendix B)).

Fundamental character analysis – parvorders and superfamilies

Here we present the resulting topology based on a set of fundamental characters, which, in our opinion, provide the most precise, clear delineation of upper-level divisions in Recent scorpions. These characters, 33 in number, are divided among the basic character types as follows:

- Trichobothria, existence and positional considerations – 12 characters (or 73 characters if full complement of existence characters are exercised) (out of 38)
- Cheliceral dentition – 4 characters (out of 8)
- Chelal dentition – 3 characters (out of 10)
- Leg spination and setation – 2 characters (out of 6)

- Sternum – 3 characters (out of 10)
- Hemispermatothore – 3 characters (out of 10)
- Metasomal carination – 1 character (out of 8)
- Pedipalp ornamentation – 4 characters (out of 8)
- Female reproductive system – 1 character (out of 7)

In many cases the choice of these characters was based on information being available in the fossil record, in particular the palaeopisthacanthids. In other cases, the characters were chosen because they provided basic diagnostic information within the superfamily Chactoidae, another area where much of our analysis concentrated. In this particular analysis, all 33 characters were assigned a weight of one (i.e., the default weight), three were assigned to partial ordering schematics as described below, and one character was completely ordered (also defined below). All characters were parsimony informative. Eight MPTs (Most Parsimonious Tree) were generated, based on two unresolved topologies within the buthoids, and four unresolved topologies within the scorpionoids. The overall length and support (Table 5) is 115, 0.8261, 0.9745, and -28.979 (tree length, consistency index (CI), retention index (RI), and G-fit, see Kitching et al. (1998) for definition of terms). The cladogram shown in Fig. 114 emphasizes parvorders, superfamilies, and families, therefore, most clades were collapsed at the subfamily and lower levels (i.e., no genera, except for the two fossils, are shown). All character distribution at these levels is shown. The cladogram illustrated in Fig. 115 shows a close-up of the effect of the three *alpha-beta* trichobothrial subpatterns on the primitive Recent scorpions, in this case the buthoid clade is not collapsed, showing all 14 genera. Although many of the clades are collapsed in Fig. 114, it must be stressed here that all 60 taxa were included in the analysis and therefore monophyly demonstrated in these high-level scorpion groups was based on the entire taxa set.

In the cladogram shown in Fig. 114 we see that the four parvorders of Recent scorpions are well defined with the minimal character set, even the two monotypic parvorders, *Pseudochactida* and *Chaerilida*. In addition, the three superfamilies comprising parvorder *Iurida*, are also well defined, namely *Iuroidea*, *Scorpionoidea*, and *Chactoidae*. Node support is indicated by the results of bootstrap and jackknife analyses. This cladogram clearly demonstrates that the support level involving the three primitive parvorders is somewhat reduced. Support for the three clades representing the topological positions of

Minimum Steps	Maximum Steps	Number of Steps	Number of MPTs	CI	RI	G-Fit (k = 2)
Fundamental Character Analysis						
95	880	115	8	0.8261	0.9745	-28.979
All Character Analysis						
343	2561	430	70123	0.7977	0.9608	-86.607

Table 5: Support data for fundamental and all character analyses. *CI* = consistency index, *RI* = retention index, *G-Fit* = Goloboff Fit (*k* = concavity constant which is set to 2 from of a range of 0–5).

Pseudochactida, Buthida, and Chaerilida ranged from 41 to 78%. In contrast, support for Iurida was 100%. This same reduction in support for the primitive parvorders is also demonstrated in our molecular (DNA) analysis presented in **Appendix B**. The reasons for this support reduction in morphology is caused, in part, by the incomplete knowledge of our fossil outgroup (i.e., missing information) and the primitive nature of Chaerilida, conflicting with the equally primitive by origin but at the same time highly derived parvorder Buthida.

As can be seen in Table 6, the level of homoplasy is at a minimum, a condition which, in our opinion, is crucial in establishing the correct homologies across these characters. The lowest character CI derived in this analysis is 0.500, as seen in four characters. We believe that at this level, where fundamental characters differentiate high-level Recent scorpion phylogeny, homoplasy should be kept to a minimum. Admittedly, some of this congruency is based on hypotheses assumed in this analysis, again, relying somewhat on the fossil record as described elsewhere in this paper.

Character specifics: We now describe the assumptions, support characteristics, and distribution of each fundamental character, grouped and ordered by its character type. For each character we describe the following: character number and its state values, what it represents, its characteristics (assumptions | CI | RI) (note, a CI of 1.000 implies nonhomoplasy), and its distribution across clades as illustrated in Fig. 114. Assumptions imply an *ordering*, which we categorized into three types: 1) a primary character and one or more secondary, tertiary, etc. characters; 2) fully ordered character states; and 3) partially ordered character states using PAUP's USERTREE schematic definition feature. The first ordering technique, which uses two or more characters, forces ordering by assigning a presumed primitive state to a taxa set and then defining one or more derivations from this state with additional characters. This approach of ordering is also referred to as an “additive” technique commonly used in “single-state” character definition schemes. Straight ordering allows a linear ordering between three or more states,

and partial ordering allows the definition of complex “ordered trees”. None of these ordering mechanisms forces polarity which is determined by the parsimony process.

Trichobothria (Figs. 64–90). Twelve fundamental characters deal with trichobothria existence and/or their relative positions as follows. Note in particular, that neobothriotaxy is not included in this character set. We assume that, in general, the evolutionary events which caused neobothriotaxy occurred *after* the derivation of major Recent scorpion families.

Character 1 (0, 1, 2, 3, 4, 5) – orthobothriotaxic types: characteristics = (ordered | 1.000 | 1.000); character ordering is defined as (0 = P, (1 = F1, (2 = D, (3 = A, (4 = B, (5 = C)))))). These states are based on orthobothriotaxic types defined by Vachon (1974) and Soleglad & Fet (2001); distribution: each orthobothriotaxic type is a synapomorphy for each Recent scorpion parvorder. The primitive state (0 = P) is mapped to the palaeopisthacanthids, state (1 = F1) is derived for the Cretaceous fossil scorpion *Archaeobuthus*, and states (2 = D), (3 = A), (4 = B), and (5 = C) are derived for parvorders Pseudochactida, Buthida, Chaerilida, and Iurida, respectively. A discussion is presented elsewhere in this paper on the actual orthobothriotaxic trichobothria derivations based on hypothesized existence statements for 62 trichobothria from which this single ordered character is modeled. It is important to stress here that our ordering of this character is based on the resulting topology when the 62 existence characters are in effect, which is identical to the topology presented in Fig. 114.

Character 2 (0, 1, 2), femoral alpha-beta sub-pattern-1 (alignment of trichobothria d_1 – d_3): characteristics = (no assumptions | 0.750 | 0.933); distribution: the character's primitive state, as exhibited in *Archaeobuthus*, is the parallel alignment of these two trichobothria to the dorsoexternal carina. The trichobothrial pair angles toward this carina (a *beta* characteristic) in the clade representing Recent scorpions (a synapomorphy); it reverses itself to the primitive state in genus *Liobuthus*; and it angles away from the

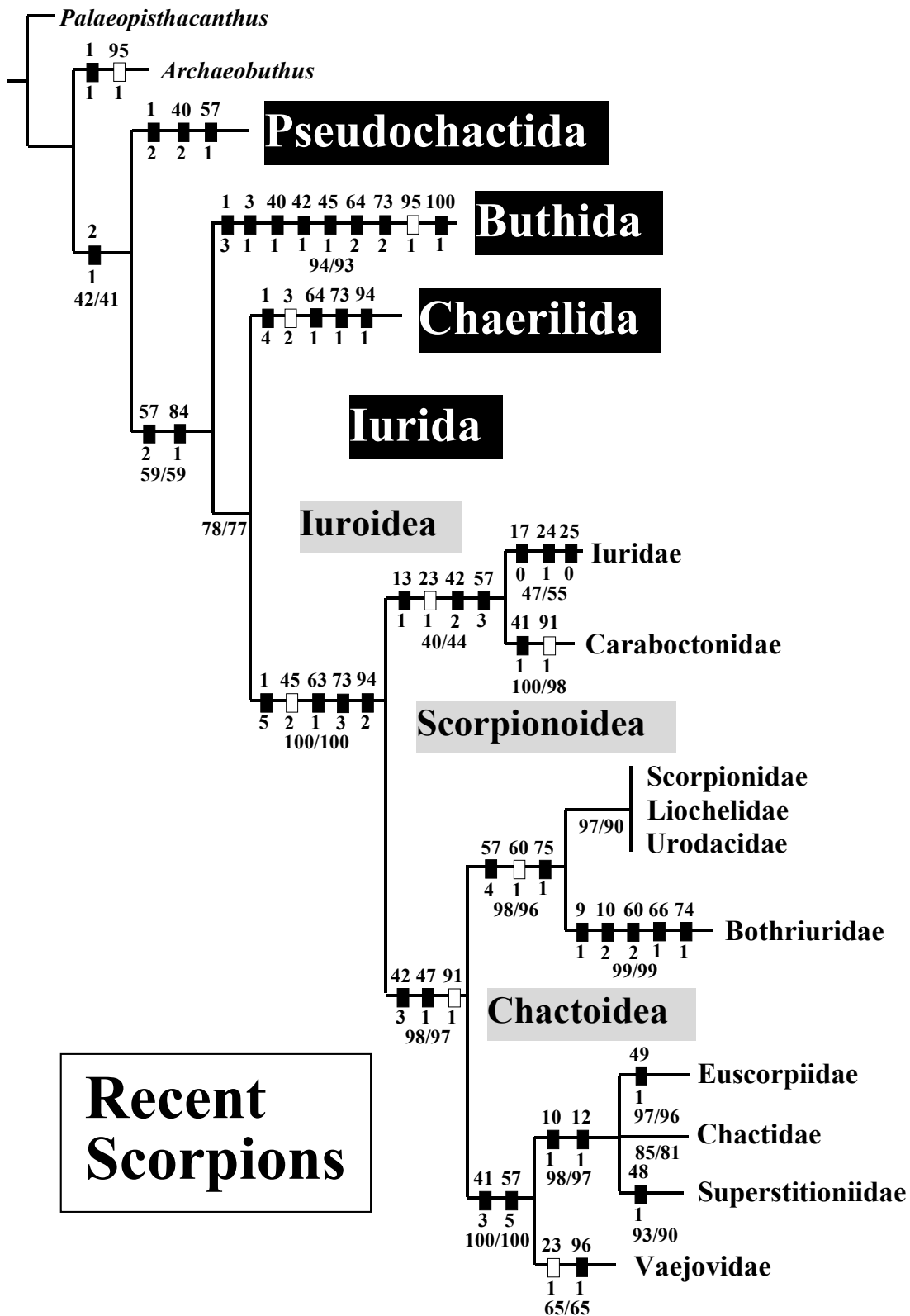


Figure 114: Cladogram showing phylogeny of Recent Scorpions based on *fundamental characters*: parvorders, superfamilies, and families. Bootstrap/jackknife values shown below branches (*mean* of five sequences of 1000 replicates, 5000 total each). White lettered, black background denotes parvorders; black lettered, gray background denotes superfamilies of parvorder Iuroidea; black lettered, white background denotes families of superfamily Iuroidea. *Open* rectangles indicate homoplasious characters. Character number on top, character state value on bottom.

dorsoexternal carina (an *alpha* characteristic) in the clade which includes New World bothoids, and African and Madagascar bothoid genera.

Character 3 (0, 1, 2), femoral *alpha-beta* sub-pattern-2 (alignment of trichobothria d_3-d_4): characteristics = (no assumptions | 0.600 | 0.857); distribution: this character's primitive state is the parallel alignment to the dorsoexternal carina, as exhibited in *Archaeobuthus* and *Pseudochactas*. The alignment angles away from the carina (a *beta* characteristic) on the bothoid clade (a synapomorphy); and, as in the previous character, it reverses itself to the primitive state in genus *Liobuthus*, and then the alignment angles towards the dorsoexternal carina (an *alpha* characteristic) in the same New World/African clade as discussed above for Character 2; finally the alignment angles toward the dorsoexternal carina which is independently developed in the chaerilids.

Character 4 (0, 1), femoral *alpha-beta* sub-pattern-3 (placement of trichobothria d_2): (this character is not shown in Fig. 114, see Fig. 115 for its distribution) characteristics = (no assumptions | 0.500 | 0.818); distribution: this character's primitive state is the dorsal placement of this trichobothrium, as exhibited in *Archaeobuthus*, *Pseudochactas*, and *beta* pattern bothoids; it moves to the internal aspect of the femur on *alpha* pattern bothoids. The homoplasy seen in this character's distribution is caused, in part, by the loss of this trichobothrium in genera such as *Karasbergia*, *Orthochirus*, and *Microbuthus* (considered to be subtractive neobothriotaxy as defined by Vachon (1974); also note that all are very small scorpions), and the loss seen in Chaerilida.

Character 9 (0, 1), chelal Et_2 position (Type C relevant): characteristics = (no assumptions | 1.000 | 1.000); distribution: the primitive state of Et_2 positioned on the external aspect of the chelal palm is present in all type C Recent scorpions except for the family Bothriuridae, where it is situated on the ventral aspect, a synapomorphy for the family.

Character 10 (0, 1, 2), chelal *ib* position (Type C relevant): characteristics = (no assumptions | 0.750 | 0.973); distribution: this character was modeled primarily for differentiations within superfamily Chactoidea, although it is also applicable to the scorpionoids where it appears to have some diagnostic benefit. The primitive state is trichobothrium *ib* positioned on the fixed finger; it is found on the palm, adjacent to the movable finger articular membrane in both the bothriurids and families Chactoidea(-V), each considered an independent derivation.

Character 12 (0, 1, 2), chelal V_1-V_4 orientation (Type C relevant): characteristics = (no assumptions | 0.750 | 0.971); distribution: the primitive state of this character is the orientation of the trichobothrial series V_1-V_4 in an essentially straight line, which continues for most of the

palm's length; a shortening of this trichobothrial series with the $V_1-V_2-V_3$ juncture usually angling internally, is considered derived, which has occurred in families Chactoidea(-V) and, independently, in some bothriurid genera.

Character 13 (0, 1, 2, 3), chelal finger *db-dt* and *eb-et* position (Type C relevant): characteristics = (no assumptions | 1.000 | 1.000); distribution: the primitive state of this character finds *db-dt* and *eb-et* trichobothrial series spaced throughout most of the finger; it is found on the distal half to two-thirds on superfamily Iuroidea, on the distal half in superstitioniid genus *Alacran*, and is located on the basal half in some scorpionoids. In particular, this character is considered a synapomorphy for superfamily Iuroidea, realized, in part, on the alternate interpretation of chelal trichobothria homology for Caraboctonidae proposed by Stockwell (1989). This is discussed in detail in the **Character Analysis** section.

Character 17 (0, 1), chelal *est*, *Est* and V_2 petite (Type C relevant): characteristics = (no assumptions | 1.000 | 1.000); distribution: the presence of these additional petite trichobothria is derived in family Iuridae, while presence of full trichobothria is considered the primitive state.

Character 23 (0, 1), patellar v_3 position (Type C relevant): characteristics = (no assumptions | 0.500 | 0.935); distribution: a ventral surface location of v_3 is the primitive condition, as found in the chaerilids, scorpionoids, and most Chactoidea(-V); it is located on the external patellar surface in the iuroids, the vaejovids and superstitioniid subfamily Superstitioniinae (not shown in Fig. 114).

Character 24 (0, 1, 2), patellar v_2 position (Type C relevant): characteristics = (no assumptions | 1.000 | 1.000); distribution: a ventral surface location of v_2 is considered the primitive condition, as found in most scorpions; it is found on the external patellar surface on the Old World iuroids (family Iuridae), and in the superstitioniid genera *Typhlochactas* and *Sotanochactas* (not shown in Fig. 114).

Character 25 (0, 1), patellar et_2 and eb_2 petite (Type C relevant): characteristics = (no assumptions | 1.000 | 1.000); distribution: the presence of these additional petite trichobothria is derived in family Iuridae, presence of full trichobothria is considered the primitive state.

Chelicerae (Figs. 40–63). Four characters depicting conditions of cheliceral dentition are included in the fundamental character set. It is important to mention here that we have excellent information from the sparse fossil record on this important taxonomic structure, especially in the palaeopisthacanthids, our outgroup.

Character 40 (0, 1, 2), dorsal edge of movable finger, basal (b) denticles: characteristics = (no assumptions | 1.000 | 1.000); distribution: the primitive state is the

Character	Range	Min Steps	Steps	Max Steps	CI	RI	G-Fit (k = 2)
Trichobothria							
1	5	5	5	41	1.000	1.000	1.000
2	3	3	4	18	0.750	0.933	0.750
3	3	3	5	17	0.600	0.857	0.600
4	2	2	4	13	0.500	0.818	0.600
9	2	2	2	23	1.000	1.000	1.000
10	3	3	4	40	0.750	0.973	0.750
12	3	3	4	38	0.750	0.971	0.750
13	4	4	4	25	1.000	1.000	1.000
17	2	2	2	20	1.000	1.000	1.000
23	2	2	4	33	0.500	0.935	0.600
24	3	3	3	21	1.000	1.000	1.000
25	2	2	2	20	1.000	1.000	1.000
Chelicerae							
40	2	2	2	15	1.000	1.000	1.000
41	11	11	14	73	0.786	0.952	0.500
42	10	10	11	123	0.909	0.991	0.750
45	2	2	3	16	0.667	0.929	0.750
Chelal Finger Dentition							
47	1	1	1	22	1.000	1.000	1.000
48	2	2	2	25	1.000	1.000	1.000
49	2	2	2	23	1.000	1.000	1.000
Leg Armament							
57	5	5	5	32	1.000	1.000	1.000
60	6	6	10	41	0.600	0.886	0.429
Sternum							
63	1	1	1	18	1.000	1.000	1.000
64	3	3	3	18	1.000	1.000	1.000
66	2	2	2	23	1.000	1.000	1.000
Hemispermatorphore							
73	3	3	3	16	1.000	1.000	1.000
74	2	2	2	23	1.000	1.000	1.000
75	1	1	1	11	1.000	1.000	1.000
Metasoma							
84	1	1	1	2	1.000	1.000	1.000
Pedipalp Ornamentation							
91	1	1	2	18	0.500	0.941	0.750
94	2	2	2	17	1.000	1.000	1.000
95	1	1	2	14	0.500	0.923	0.750
96	2	2	2	27	1.000	1.000	1.000
Female Reproductive System							
100	1	1	1	14	1.000	1.000	1.000

Table 6: Support data for *fundamental characters*; characters are grouped by their character structural type. See **Table 5** for definition of terms.

presence of a single basal denticle; it is lost in parvorder Pseudochactida, and is derived into two basal denticles in parvorder Buthida, both considered synapomorphies for these respective parvorders.

Character 41 (0, 1, 2, 3, 4), dorsal edge of movable finger, subdistal (sd) denticles: characteristics = (partially ordered | 0.786 | 0.952); partial ordering is defined as (0, (1, 2, (3, (4))))); distribution: the primitive state is a single subdistal denticle, where it is found in parvorders Pseudochactida, Chaerilida, and Buthida, as well as in superfamily Scorpionoidea and Old World iuroids (family Iuridae); the derivation of two subdistal denticles occurs independently (modeled, in part, as separate states) as follows: in the New World iuroids, family Caraboctonidae; in the bothriurids where it reverses itself in some genera (i.e., *Bothriurus*) (not shown in Fig. 114); and in superfamily Chactoidea. In the superstitioniid genera *Typhlochactas*, in part, and *Sotanochactas*, we see a single subdistal denticle, but it is not consistent in the former. We consider this a secondary loss from the two subdistal denticle state.

Character 42 (0, 1, 2, 3), ventral edge of movable finger: characteristics = (primary character, partially ordered | 0.909 | 0.991); partial ordering is defined as (0, (1, 2, 3)); distribution: the primitive state is a crenulated ventral edge, found in the palaeopisthacanthids, which is plesiomorphic to parvorders Pseudochactida and Chaerilida. From this crenulated edge we have three major derivations: two large denticles as seen in parvorder Buthida, a large proximal denticle as seen in superfamily Iuroidea, and a smooth edge as seen in superfamilies Scorpionoidea and Chactoidea. Secondary crenulation is found in chactoid families Euscorpidae, Chactidae, and Vaejovidae, all considered secondary derivations from a smooth state.

Character 45 (0, 1, 2), ventral surface of fixed finger: characteristics = (primary character | 0.667 | 0.929); distribution: the primitive state is a series of small but distinct denticles on the ventral surface, found on the palaeopisthacanthids, which we consider to be plesiomorphic for parvorders Pseudochactida and Chaerilida. For parvorder Buthida, we see two well-developed denticles on this surface, and for parvorder Iurida the denticles are absent (i.e., a smooth edge). We do see denticles present in some genera in family Vaejovidae and subfamily Scorpipinae, but we consider these conditions secondary derivations from a smooth surface.

Chelal finger dentition. The dentition of the chelal fingers is another important structure that impacts upper level scorpion systematics. As with most of the characters discussed in this section, the consistency in the fundamental median denticle (MD) row alignment as well as the absence or presence of accessory denticles is quite impressive. We only choose three characters for this particular analysis, those dealing with the overall

organization of the MD row and accessory denticles, the latter primarily for further delineation within the Chactoidea, in particular for the family Euscorpidae.

Character 47 (0, 1), MD denticle group alignment (primary): characteristics = (primary character | 1.000 | 1.000); distribution: the primitive state is the oblique orientation of the median denticle (MD) row groups. This primitive form is described very succinctly by Jeram (1994a: 529) for Carboniferous species *Palaeopisthacanthus vogelandurdeni* Jeram: "... dentition of fixed finger consists of slightly oblique non-imbricated primary sub-rows. ... twelve to fourteen denticles are present in each sub-row, the basal denticle in each being the largest. An internal accessory denticle lies just proximally to the basal denticle of each sub-row. There are no supernumerary denticles". We consider this oblique form of MD denticle groups to be plesiomorphic in the three primitive Recent scorpion parvorders, Pseudochactida, Buthida, and Chaerilida. We also considered it primitive for superfamily Iuroidea of the parvorder Iurida. This superfamily consistently exhibits oblique denticle group alignment across all five genera, New World as well as Old World. For clade Scorpionoidea + Chactoidea we see the only derivation from the primitive form, MD denticle groups aligned in a straight row (chactoid family Superstitioniidae is an exception, see next character below). The MD alignment as seen in Pseudochactida is the closest to that described by Jeram for the palaeopisthacanthid. The denticle groups do not overlap (i.e., are non-imbricating) and there are no accessory denticles. In Chaerilida, the MD denticle groups overlap, as they do also in some buthoids (*Tityus* and *Zabius* are good examples), which also may exhibit accessory dentition (e.g., *Centruroides*). Within superfamily Iuroidea, we see overlapping MD denticle groups in the Old World members (family Iuridae), and they are non-overlapping in New World genera (family Caraboctonidae).

Character 48 (0, 1, -), MD denticle group alignment (secondary): characteristics = (secondary character | 1.000 | 1.000); distribution: the primitive state of this character is a non-oblique alignment of the MD denticle groups, state 1 of Character 47. Derivation from this straight alignment to oblique is exhibited in chactoid family Superstitioniidae, hypothesized here as a secondary derivation of this condition. Inapplicable state applies to those taxa that exhibit the primitive state of Character 47, oblique orientation of MD denticle groups, a primary derivation.

Character 49 (0, 1, -), Inner accessory denticle (IAD): characteristics = (no assumptions | 1.000 | 1.000); distribution: the absence of IAD is considered the primitive state; they are absent in the palaeopisthacanthids, the primitive parvorders Pseudochactida, Chaerilida, and in most genera of Buthida. The presence of IAD is considered a synapomorphy for the chactoid

family Euscorpidae where they are present in all eleven genera (Soleglad & Sissom, 2001: 33–40).

Leg Armament (Figs. 10–39). We offer two fundamental characters involving the scorpion leg: the setal and spinule configurations of the ventral surface of the tarsus, and the presence or absence of pedal spurs (= tarsal spines). In addition, the tibial spur is considered important in scorpion systematics; however, it exhibited considerable homoplasy in our analysis (see Table 7), CI/RI = 0.286/0.500. Although the tibial spur is present in many fossil scorpions (e.g., *Compsoscorpium* (Jeram, 1994a: Text-Fig. 5-D), *Palaeoburmesebuthus* (Santiago-Blay et al. (in press)), *Pulmonoscorpium* (Jeram, 1994b)), there is a great variability seen in Recent scorpions. In the primitive parvorders, we see tibial spurs on legs III–IV in Pseudochactida (presumably plesiomorphic), absent in Chaerilida, and variable in Buthida. In Buthida, tibial spurs are absent in New World genera, and variable within the Old World members, although showing consistency across many genera. However, in certain Old World psammophilic genera (e.g., *Apistobuthus*, *Liobuthus*, etc.) we see either a reduction or the complete absence of these spurs, presumably a factor of microhabitat adaptation. In addition, the tibial spur appears to be a vestigial structure in Recent scorpions, since it exhibits little or no structure within the membrane from which it extends (personal observation of Graeme Lowe on *Apistobuthus*). Thus, one may assume that due to its vestigial nature it is highly susceptible to loss or near loss due to microhabitat pressures. Finally, we find tibial spurs on legs III–IV in the iuroid genus *Calchas*. We consider the iuroids by far the most primitive of the three superfamilies comprising parvorder Iurida; *Calchas* in particular, is quite interesting in this context.

Character 57 (0, 1, 2, 3, 4, 5), leg tarsus ventral surface armature, setae and spinules: characteristics = (primary character | 1.000 | 1.000); distribution: we have no data on the palaeopisthacanthids as to the armature of the tarsus. Consequently, we declare a null-state as primitive, which we assign to the palaeopisthacanthids. We recognize *five* distinct setal/spinule configurations in Recent scorpions, each configuration corresponding to specific superfamilies. The unique scorpion *Pseudochactas* (superfamily Pseudochactoidea) is equipped with an unprecedented dual row of short spinules. Superfamilies Buthoidea and Chaeriloidea are assigned the same state, exhibiting well-developed, irregular rows of socketed setae. In Chaeriloidea we see a small median row of spinules, which are lacking in Buthoidea. The superfamily Iuroidea has an unique median row of grouped spinule clusters. Superfamily Scorpionoidea is characterized with well-developed setal pairs, most groups with exaggerated limbated sockets. Spinules are optional in this superfamily. The superfamily Chactoidea

has a combination of moderately developed setal pairs and a median ventral row of spinules. Any derivations from these five basic configurations are considered secondary developments within the superfamily, as modeled in a secondary character (see **Appendix A**). Any structural relationship between these configurations as ordered in the cladogram in Fig. 114, is speculative. The connection between the dual rows of spinules found in *Pseudochactas* to the well-socketed setae found in the buthoids and chaeriloids is puzzling since we have no information on this structure in our outgroup, the palaeopisthacanthids. Consequently, the condition found in *Pseudochactas* is considered derived from an unknown primitive condition, and the condition exhibited in Buthoidea and Chaeriloidea is considered derived at the node defining Buthoidea + Chaeriloidea + Iurida. The differences between Buthoidea to Chaeriloidea, each equipped with large socketed setae, is quite subtle, as only the small median row of spinules in the latter hints at a difference. In the Iuroidea, we see the unique condition of spinule clusters formed in a median row. However, in the presumed most primitive member of Iuroidea, genus *Calchas*, we see that in the adults the same large-socketed setal pairs, as seen in *Chaerilus*, are prevalent. Only in juveniles and subadults are the spinule clusters evident, being dispersed within the larger setal pairs. The connection between *Chaerilus* and *Calchas* is appealing since the former also exhibits a small median spinule row. The relationship between the condition seen in Buthoidea and Chaeriloidea and superfamily Scorpionoidea is also somewhat straightforward, since the primary dominant armament in all three superfamilies is represented by the heavily socketed setal pairs, the differences only seen in the relative development of sockets. The same observation can be stated for superfamily Chactoidea; here, however, we have a reduction in the size of setal pairs and their sockets, appearing in many families, with an emphasis on the median spinule row.

Character 60 (0, 1, 2, 3), number of pedal spurs: characteristics = (partially ordered | 0.667 | 0.857); partial ordering is defined as (0, (1, (2)), 3); distribution: the presence of two pedal spurs is the primitive state for this character, being found in the three primitive parvorders of Pseudochactida, Buthida, and Chaerilida. Although the pedal spurs are not visible in the available fossil material for the palaeopisthacanthids, they are reported for fossil *Archaeobuthus* (Lourenço, 2001: 646, Fig. 9), *Palaeoburmesebuthus* (Santiago-Blay et al., in press), and also in a Carboniferous scorpion *Pulmonoscorpium kirktonensis* (Jeram, 1994b: 293). The derivation to one pedal spur (the loss of the retrolateral spur) is consistently found in scorpionoid families Scorpionidae, Liochelidae, and Urodacidae. It is also found in some genera of family Bothriuridae (*Phonocercus* in our ingroup), which accounts for a minor

homoplasy exhibited in our analysis. Prendini (2000, 2003a) reports a single pedal spur in bothriurid genera *Brandbergia*, *Lisposoma*, *Thestylus*, *Phonioecercus*, and *Vachonia*, the first four appearing as basal genera in his analysis. Following Prendini's results we also propose that the two pedal spurs seen in most bothriurids (our state '2') are derived from a single pedal spur configuration. For the chactoid family Superstitioniidae, we see in subfamily Typhlochactinae that the number of pedal spurs is variable: *Sotanochactas elliotii*, *Typhlochactas cavicola*, *T. granulatus*, and *T. rhodesi* are lacking both pedal spurs, and *T. mitchelli*, *T. reddelli*, *T. sylvestris*, and *Alacran tartarus* are lacking the retrolateral pedal spur. Since all of these scorpions are troglotic, one must wonder to what effect this loss of pedal spurs is related to microhabitat adaptation. The same suspicion can be made for the subterranean chactid species *Broteochactas trezzii* (Vignoli & Kovářik, 2003), **comb. n.** (described as *Taurepania trezzii*; see classification of Chactidae below), where both pedal spurs are missing. The condition of missing pedal spurs in the superstitioniids is given its own state ('3'), and is considered a different derivation from that seen in the scorpionoids.

Sternum. The sternum is considered an important structure in the taxonomy of upper-level scorpion groups. In this analysis, three characters are applicable at these higher levels: the basic sternum type, and distinctions within these types as to degrees of exhibited compression. The definitions of fundamental sternum types and compression within these types can be found in Sologlad & Fet (2003).

Character 63 (0, 1), sternum basic type: characteristics = (no assumptions | 1.000 | 1.000); distribution: The primitive condition is sternum type 1 which is present in the palaeopisthacanthids. The type 1 sternum is also found in all primitive parvorders: Pseudochactida, Chaerilida, and Buthida. Sternum type 2 is found in parvorder Iurida.

Character 64 (0, 1, 2, -), horizontal compression in sternum type 1: characteristics = (no assumptions | 1.000 | 1.000); distribution: the primitive state for this character is the absence of compression, which is indicated in the palaeopisthacanthids as well as in the Recent scorpion parvorder Pseudochactida. A specific shallow but wide compression is found in parvorder Chaerilida and a more exaggerated, though highly variable, form of horizontal compression is exhibited in Buthida.

Character 66 (0, 1, -), vertical compression in sternum type 2: characteristics = (no assumptions | 1.000 | 1.000); distribution: the primitive state for this character is the absence of compression, which is indicated in the primitive superfamily Iuroidea. Vertical compression is only found in the scorpionoid family

Bothriuridae, excluding, possibly, its two most basal genera, *Brandbergia* and *Lisposoma*.

Hemispermatothore and paraxial organ. We use three characters from the male reproductive system that apply to the upper-level systematics of Recent scorpions. In particular, the fundamental hemispermatothore type is important in these distinctions. Two other characters are considered as well which delineate the superfamily Scorpionoidea.

Character 73 (0, 1, 2, 3), hemispermatothore, basic type: characteristics = (no assumptions | 1.000 | 1.000); distribution: We do not know the ancestral form of this structure, since it is unknown in the fossil record. We also do not yet know the structure of the hemispermatothore for parvorder Pseudochactida, presumably the most primitive of all Recent scorpions. Repeated attempts by us and others (personal communications of David Sissom and Graeme Lowe) to find and remove such a structure have failed. The reason for this failure may have several possible reasons: since all male specimens examined were collected at the same time of the year (early May), possibly the structure is not developed in adult males at this season; or the structure as we know it in other scorpions may be so different in *Pseudochactas*, it was unrecognizable as a hemispermatothore; or *Pseudochactas* employs altogether a totally different mechanism for mating. Consequently, we have defined a "null state" for the primitive condition which we assign to our outgroup, the palaeopisthacanthids. From this unknown primitive state we recognize three derivations, the *fusiform* state, which was defined by Stockwell (1989) for parvorder Chaerilida, the *flagelliform* state as uniquely exhibited in parvorder Buthida, and the *lamelliform* state found in parvorder Iurida. The *fusiform* state described and illustrated by Stockwell (1989: Fig. 202) for species *Chaerilus granulatus*, has also been verified and illustrated for another unnamed species, *Chaerilus* sp., by Lourenço (2002b: Figs. 19–21).

Character 74 (0, 1, -), hemispermatothore lamina terminus: characteristics = (no assumptions | 1.000 | 1.000); distribution: this character is applicable for scorpions with *lamelliform* hemispermatothores. The primitive state for this character is a lamina terminus without a groove-like crest. The presence of a crest on the lamina terminus is considered a synapomorphy for the scorpionoid family Bothriuridae.

Character 75 (0, 1), paraxial organ with internobasal reflection of sperm duct: characteristics = (no assumptions | 1.000 | 1.000); distribution: this character is adopted directly from Stockwell (1989), his character 120, and Prendini (2000), his character 84, and is considered a synapomorphy for the superfamily Scorpionoidea of the parvorder Iurida.

Metasomal carination (Figs. 1–9). Metasomal carinae are considered important in diagnosing many scorpion groups. We use one character here which addresses the number of ventral median carinae found on segment V.

Character 84 (0, 1), number of ventral median carinae, segment V: characteristics = (no assumptions | 1.000 | 1.000); distribution: the primitive state for this character is the presence of two ventral median carinae on metasomal segment V. This primitive state has been established for the palaeopisthacanthids as well as for parvorder Pseudochactida. All other Recent scorpions have a single ventral median carina on this segment.

Pedipalp ornamentation (Figs. 91–107). The carinal structures of the pedipalp chelae and patellae exhibit important taxonomic characters for the diagnoses of high-level scorpion groups. For fundamental characters we include four, two of which identify basic carinal configurations for the two segments, and two which identify specific carinae on the patella.

Character 91 (0, 1), basic chela carinal configuration: characteristics = (no assumptions | 0.500 | 0.941); distribution: We do not have information on the carinal configuration of the chela for the palaeopisthacanthids, and therefore this data is missing for both of our fossil representatives. For parvorder Pseudochactida we see a reduced arrangement from the “8-carinae” configuration originally defined for the Buthida and Chaerilida by Prendini (2000). In Pseudochactida, we see five distinct carinae: digital (*D1*), dorsomarginal (*D4*), dorsointernal (*D5*), ventroexternal (*V1*), and ventrointernal (*V3*). The external and internal surfaces of the chelal palm are rounded and therefore the presence or absence of the external (*E*) or internal (*I*) carinae is obscured. However, there is no trace of the ventromedian (*V2*), subdigital (*D2*), or dorsosecondary (*D3*) carinae. Due to the absence of *D2* and *V2* and the strong development of *V3* we assign Pseudochactida to the “8-carinae” configuration. In addition to the three primitive parvorders, the Old World iuroids, family Iuridae, also conform to this primitive configuration (first described by Soleglad & Sissom (2001: Fig. 47)). The New World iuroids, family Caraboctonidae, conform to the “10-carinae” configuration, as do the two remaining superfamilies in Iurida.

Character 94 (0, 1, 2), basic patella carinal configuration: characteristics = (primary character | 1.000 | 1.000); distribution: the primitive state for this character is a seven carinae configuration, as seen in the palaeopisthacanthids. The seven carinae configuration is also seen in primitive parvorder Pseudochactida. It is also hypothesized for parvorder Buthida as well, which exhibits the basic seven carinae plus an additional eighth carina (see below). We propose that this condition is derived from the seven carinae configuration. Parvorder Chaerilida exhibits six carinae and parvorder Iurida is

hypothesized with five carinae, with any additional carinae being secondary derivations within this configuration.

Character 95 (0, 1), presence of the dorsal median (DM_c) carina on patella: characteristics = (secondary character | 0.500 | 0.923); distribution: the absence of the DM_c carina is considered the primitive state. It exists in parvorder Buthida, considered a synapomorphy, and possibly in the fossil *Archaeobuthus*. As stated above we propose that this carina is derived from the seven carinae configuration.

Character 96 (0, 1, -), presence of the dorsal patellar spur (DPS_c) carina: characteristics = (secondary character | 1.000 | 1.000); distribution: the absence of the DPS_c carina is considered a relatively primitive state. This carina exists only in the chactoid family Vaejovidae, which we hypothesize as a synapomorphy. As stated above, we propose that this carina is derived from the five carinae configuration.

Female reproductive system. We consider the number of “cells” in the scorpion ovariterus an important high-level character.

Character 100 (0, 1), number of cells in scorpion ovariterus: characteristics = (no assumptions | 1.000 | 1.000); distribution: we have no information on this character for any fossil scorpion, nor for the primitive scorpion *Pseudochactas*. Consequently, we follow Stockwell (1989) in proposing a reticulate mesh of six cells, found in parvorders Chaerilida and Iurida, to be primitive, and therefore, consider the eight cell configuration as seen exclusively in parvorder Buthida to be derived.

Character distribution by node. In this section we briefly discuss each node illustrated in the cladogram in Fig. 114, the fundamental characters and their states occurring on that node. The following statements can be considered definitions of these nodes in context of these 33 fundamental characters. The complete node definitions involving all characters are presented further below.

Archaeobuthus. Orthobothriotaxy type F1; pedipalp patellar DM_c carina present.

(Pseudochactida + (Buthida + (Chaerilida + (Iurida)))) (= Recent scorpions). Pedipalp femoral $d_1 \rightarrow d_3$ trichobothria configuration points toward the dorso-external carina.

Pseudochactida. Orthobothriotaxy type D; dorsal edge of cheliceral movable finger without basal denticle; ventral surface of leg tarsus with two submedian rows of spinules.

(Buthida + (Chaerilida + (Iurida))). Ventral surface of leg tarsus armed with numerous irregularly positioned setae; ventral median carina of metasomal segment V is single.

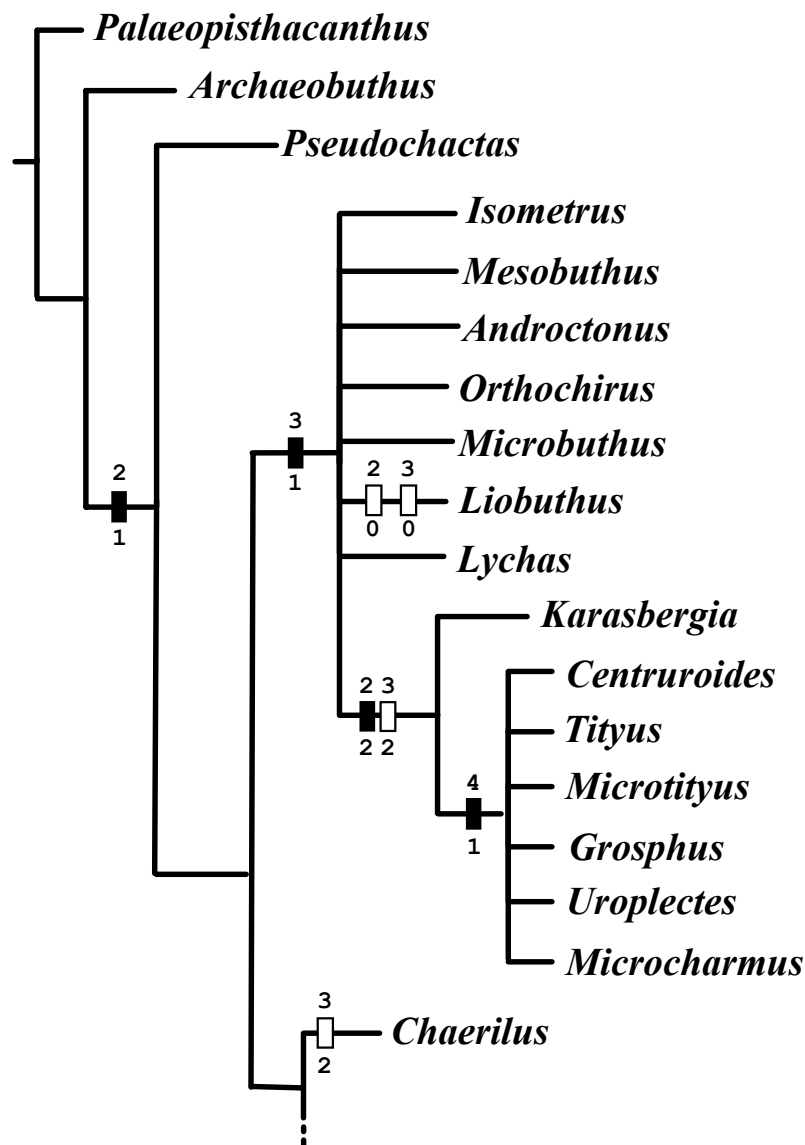


Figure 115: Partial cladogram showing effects of the pedipalp femoral *alpha/beta* trichobothria pattern in primitive Recent scorpions. *Alpha/beta* pattern is broken down into three characters: **2** = alignment of trichobothria d_1 – d_3 , **3** = alignment of d_3 – d_4 , **4** = placement of d_2 . States for characters 2 and 3: 0 = primitive, 1 = *beta* pattern, 2 = *alpha* pattern; states for character 4: 0 = dorsal surface, primitive/*beta* pattern; 1 = internal surface, *alpha* pattern. Open rectangles indicate homoplasious character states.

Buthida. Orthobothriotaxy type A; pedipalp femoral $d_3 \rightarrow d_4$ trichobothria configuration points away from dorsoexternal carina (*beta*); dorsal edge of cheliceral movable finger with two basal denticles; ventral edge of cheliceral movable finger with two large denticles; ventral surface of cheliceral fixed finger with two major denticles (protuberances); sternum, type 1, exhibits medium to exaggerated horizontal compression; hemispermatophore is *flagelliform*; pedipalp patellar DM_c carina present; ovariterus exhibits a reticulate mesh of eight cells.

Chaerilida. Orthobothriotaxy type B; pedipalp femoral $d_3 \rightarrow d_4$ trichobothria configuration points toward dorsoexternal carina; sternum, type 1, exhibits subtle wide horizontal compression; hemispermatophore is *fusiform*; pedipalp patella with six carinae configuration.

Iurida. Orthobothriotaxy type C; ventral surface of cheliceral fixed finger without denticles; sternum type 2; hemispermatophore is *lamelliform*; pedipalp patella with five carinae configuration.

Iuroidea. Chela trichobothrial series *db–dt* and *eb–et* found on distal half of fixed finger; patellar ventral trichobothrium v_3 found on external surface; ventral edge of cheliceral movable finger with one large denticle; ventral surface of leg tarsus with a median row of grouped spinule clusters.

Iuridae. Presence of additional petite trichobothria on the pedipalp chela; pedipalp patella ventral trichobothrium v_2 found on external surface; presence of additional petite trichobothria on the pedipalp patella.

Caraboctonidae. Cheliceral movable finger dorsal edge with two subdistal denticles; pedipalp chela with “10-carinae” configuration.

(Scorpionoidea + Chactoidea). Ventral edge of cheliceral movable finger smooth; denticle groups in median denticle (MD) row of pedipalp fixed finger are aligned in a straight line; pedipalp chela with “10-carinae” configuration.

Scorpionoidea. Ventral surface of leg tarsus with pairs of large socketed setae; legs with one pedal spur (pro-lateral); paraxial organ with internobasal reflection of sperm duct.

Bothriuridae. Pedipalp chelal trichobothrium Et_2 is situated on ventral surface; chelal trichobothrium ib is situated at the extreme base of fixed finger or on palm; legs with two pedal spurs; sternum, type 2, exhibiting vertical compression; hemispermatophore lamina terminus with a crest.

Chactoidea. Dorsal edge of cheliceral movable finger with two subdistal denticles; ventral surface of leg tarsus with moderately developed setal pairs and a median spinule row.

Vaejovidae. Pedipalp patella trichobothrium v_3 is situated on the external surface; patellar carina DPS_c present.

(Euscorpiidae + Chactidae + Superstitioniidae). Pedipalp chelal trichobothrium ib is situated at the extreme base of fixed finger or on palm; chelal trichobothria series V_1-V_4 is shortened, with $V_1-V_2-V_3$ juncture usually angled toward internal aspect.

Euscorpiidae. Pedipalp chelal fingers with inner accessory denticles (IAD).

Superstitioniidae. Denticle groups of the median denticle (MD) row on the pedipalp fixed finger aligned obliquely.

Alpha-beta pattern analysis. In the cladogram presented in Fig. 115, we show the effect on all primitive taxa of the three characters representing the *alpha-beta* trichobothrial pattern on pedipalp femur, which was originally defined by Vachon (1975). Even with this somewhat sparse character set, we can see a definite topology taking shape. As discussed elsewhere in this paper, the *alpha-beta* pattern defined by Vachon is divided here into three sub-patterns in order to incorporate the positions and/or alignments of the femoral dorsal trichobothria d_1-d_4 , as exhibited in the fossil scorpion *Archaeobuthus* and Recent scorpion genera *Pseudochactas* and *Chaerilus*. It has been generally accepted that the *beta* pattern, which is only found in Old World buthoids, represents the primitive configuration, while the *alpha* pattern found in New World and some Afrotropical buthoid genera is considered derived. Using *Archaeobuthus* and *Pseudochactas*, and to a lesser degree *Chaerilus*, we test this hypothesis of the primitive nature of the *beta* pattern. We can see directly from the cladogram in Fig. 115 that the *beta* pattern is indeed more primitive than the *alpha* pattern, since it itself is derived from the primitive

pattern exhibited in the fossil genus *Archaeobuthus*, and the *alpha* pattern, in turn, is derived from the *beta* pattern. In this cladogram we begin with the primitive state found in *Archaeobuthus*, where $d_1 \rightarrow d_3$ and $d_3 \rightarrow d_4$ are parallel to the dorsoexternal carina and d_2 is positioned on the dorsal surface (our three characters). At the node representing all Recent scorpions we see that trichobothria $d_1 \rightarrow d_3$ points toward the dorsoexternal carina, which is a *beta* pattern characteristic. *Pseudochactas* inherits this derived state as well as the primitive states of $d_3 \rightarrow d_4$ parallel to the dorsoexternal carina and the dorsal position of d_2 . At the parvorder Buthida node we see that the second part of the *beta* pattern, $d_3 \rightarrow d_4$, pointing away from the dorsoexternal carina, is a derived condition. At this point we have the original *beta* pattern as that defined by Vachon (1975), i.e. $d_1 \rightarrow d_3$ pointing towards and $d_3 \rightarrow d_4$ pointing away from the dorsoexternal carina, and inherited from the original state as seen in *Archaeobuthus*, d_2 is positioned on the dorsal surface. Within the buthoid clade we observe the following: genus *Liobuthus*, though considered *beta* by Vachon (1975), has trichobothria d_1 , d_3 and d_4 in a straight line, parallel to the dorsoexternal carina, the primitive condition. This is illustrated by Vachon (1974: Fig. 44) and also verified in this study. However, we consider this condition derived in this ultrapsammophilic species, which also exhibits other unusual departures from the “norm” in trichobothrial development (neobothriotaxy) and other morphological characters. In the clade (*Karasbergia* + (New World + *Grosphus* + *Uroplectes* + *Microcharmus*)) we see the beginnings of the *alpha* pattern, $d_1 \rightarrow d_3$ pointing away and $d_3 \rightarrow d_4$ pointing toward the dorsoexternal carina. The position of d_2 is unknown in *Karasbergia* since this trichobothrium is absent in this genus (it is also missing in genus *Microbuthus*, and, usually, in *Orthochirus*; both of these genera are included in our study). Finally, at the clade (New World + *Grosphus* + *Uroplectes* + *Microcharmus*) we have the complete *alpha* pattern, d_2 having migrated to the internal surface of the femur. To complete this discussion of the *alpha-beta* pattern, we see that genus *Chaerilus* (parvorder Chaerilida) exhibits the *alpha* pattern with respect to $d_3 \rightarrow d_4$ pointing towards the dorsoexternal carina, proposed here as an independent derivation. Otherwise *Chaerilus* inherits the *beta* pattern with respect to $d_1 \rightarrow d_3$ pointing towards the dorsoexternal carina. Trichobothrium d_2 position is undetermined since it is absent in *Chaerilus*.

Cladistic analysis, all characters – superfamily Chactoidea

Above, we described a fundamental set of characters (33 in number) that define the upper-level systematics of Recent scorpions, primarily at the parvorder

and superfamily levels. Predictively, this character set exhibited less resolution at the family, subfamily, and lower levels. The second goal of this study was the revision of the upper- to middle systematic levels of the superfamily Chactoidea, in particular the families Chactidae and Superstitioniidae. Many of the characters defined here are aimed specifically at these chactoid families, but also have relevance, in part, to other Recent scorpion groups covered in this paper. Consequently, at the end of this discussion we address all resolved nodes as discussed above in the fundamental character analysis, considering character distribution of all characters.

Figure 116 illustrates the cladogram for superfamily Chactoidea with *all characters* distributed. The nodes representing families Vaejoividae and Euscorpiidae are collapsed; otherwise, all genera used in the cladistic analysis are shown. Although we studied all vaejoivid genera (spanning over 50 species), our goal was only to adequately differentiate Vaejoividae from the other families in Chactoidea, in particular from Superstitioniidae and Chactidae. The family Euscorpiidae was studied in great detail by Soleglad & Sissom (2001) and therefore was represented here, as was the case with Vaejoividae, only to show its relationship with other families within Chactoidea. It is important to note here that ample taxa representation from all major scorpion groups is necessary in order to convincingly show monophyly of groups of interest. Using a token (“exemplar”) species here or there does not meet this requirement.

Out of 105 characters, three were uninformative and consequently were suppressed during the cladistic analysis. These characters, however, are discussed below and included in **Appendix A** where their state values are provided. All characters were assigned a weight of one (the default), two were ordered, and six were partially ordered. Table 5 shows the overall support statistics for this analysis, 430 steps, a CI, RI, and G-Fit of 0.7977, 0.9608, and -86.607 respectively. Due to the many unresolved topologies occurring within the buthoids, scorpionoids, vaejoivids, and euscorpiids, the number of MPTs was quite large, 70123 to be exact. Consequently the partial cladogram illustrated in Fig. 116 is based on a majority-rule consensus. The important clades of this topology, however, are well resolved, those showing the breakdown of families Superstitioniidae and Chactidae. The bootstrap/jackknife support values for these clades depicted in Fig. 116 are based on five separate sequences of 1000 pseudoreplicates each (i.e., the values shown in Fig. 116 are the mean of these sequences). As can be seen in the cladogram, all clades are well-supported, spanning 65/65% to 100/100%: 100/100% for superfamily Chactoidea, 65/65% for family Vaejoividae, 98/97% for clade ((Euscorpiidae + Chactidae) + Superstitioniidae), families Euscorpiidae, Chactidae, and Superstitioniidae with 97/96%, 85/81%, and 93/90% support, respectively.

Table 7 shows the character support for all homoplasious characters in this analysis. Three characters exhibit homoplasy under 0.500: the presence/absence of the leg tibial spur, CI = 0.286; the distal termination of pedipalp chelal carina V1, CI = 0.286; and the structure of the venom gland, CI = 0.333. The tibial spur was discussed above; it is probably an important character at the higher systematic levels, but due to its vestigial condition it is susceptible of being lost. The termination of chelal carina V1 is important in lower level systematics; it is clear, based on the high level of homoplasy exhibited in our analysis, that its distal termination should be modeled separately within a taxonomic group where it is variable, but not as a single derivation as modeled in the present study. The venom gland structure is another character that seems to be important systematically; however, considerable homoplasy is present based on the current modeling of the folding of the epithelial walls of these glands. Originally, we had included this character in the set of fundamental characters, but the significant homoplasy implied a superficial aspect to the current modeling. We believe that, as a minimum, the notion of “simple folding” must be modeled as separate evolutionary occurrences.

Character distribution for Chactoidea. We list the characters and their states for all nodes for superfamily Chactoidea as illustrated in Fig. 116.

Chactoidea. Dorsal edge of cheliceral movable finger with *two* subdistal denticles; ventral surface of leg tarsus with moderately developed setal pairs and a median spinule row; hemispermatophore capsule present, weakly to significantly developed; genital papillae of male visible at posterior edge of genital operculum.

Vaejoividae. Patellar trichobothrium v_3 is situated on the external surface; laminar “hook” present on hemispermatophore lamina base; dorsal lateral carinae of metasomal segment IV terminate in a conspicuous flared projection; overall shape of pedipalp chela is rounded; patellar carina DPS_c present; pectinal tooth numbers are relatively high.

(Supersitioniidae + (Euscorpiidae + Chactidae)). Chelal trichobothrium *ib* situated at the extreme base of fixed finger or on palm; chelal trichobothria series V_1-V_4 is shortened, with $V_1-V_2-V_3$ juncture usually angled toward internal aspect; sclerites of genital operculum of the female loosely connected; overall shape of pedipalp chela is rounded; stigma small and oval in shape; number of lateral eyes 0–2.

Superstitioniidae. Chelal trichobothrium *it* positioned at the extreme base of fixed finger; chelal trichobothria series $Db-Dt$ has *Db* basal and *Dt* situated at the base of fixed finger; denticle rows in median denticle (MD) row of chelal finger aligned obliquely; lateral carinae of metasomal segment V absent.

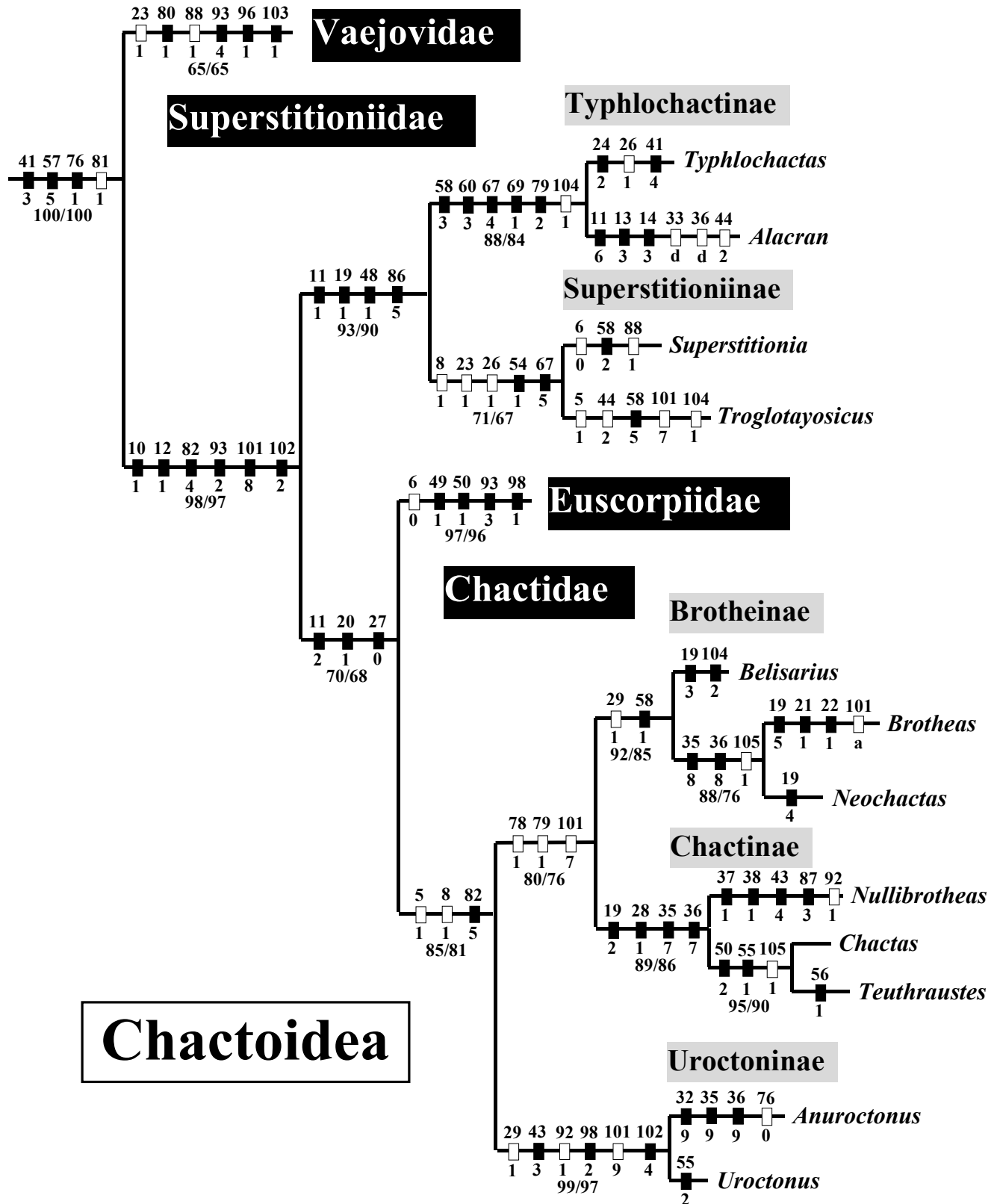


Figure 116: Cladogram showing phylogeny of superfamily Chactoidea. Bootstrap and jackknife values shown below branches (mean of five sequences of 1000 replicates, 5000 total each). White lettered, black background name captions denote families; black lettered, gray background captions denote subfamilies; and black lettered, white background captions denote genera. Nodes representing families Vaejoidea and Euscorpiidae are collapsed (i.e., taxa below family level are not shown). *Open* rectangles indicate homoplasious characters. Character number is on top, character state value is on bottom.

Typhlochactinae. Ventral surface of leg tarsus armed with setal pairs, ventral spinules are minimal or obsolete; number of leg pedal spurs variable, ranging from zero to two; sternum length equal to or longer than its width; sternum apex rounded, with minimal depression, lateral lobes flat; lamina terminus of hemispermatophore spatulate in shape; pectinal fulcra absent.

Typhlochactas (and Sotanochactas). Patellar trichobothrium v_2 positioned on external surface; patella trichobothria series esb_1 – esb_2 is aligned horizontally or slants “upward”; dorsal edge of cheliceral movable finger with variable number of subdistal denticles.

Alacran. Chelal trichobothrium it situated on distal half of fixed finger; chela trichobothria series db – dt and eb – et situated on distal half of fixed finger; chelal trichobothria series ib – it not adjacent, ib basal and it on distal half of fixed finger; neobothriotaxy Sul found on external aspect of chelal palm; neobothriotaxy Sul found on external aspect of patella; cheliceral fixed finger with median and basal denticles situated flush on finger surface, not conjoined on common trunk.

Superstitioniinae. Chelal trichobothrium Eb_1 on ventral surface or on VI carina; patella trichobothrium v_3 positioned on external surface; patella trichobothria series esb_1 – esb_2 is aligned horizontally or slants “upward”; chelal finger internal denticle (ID) are significantly larger than other denticles; sternum is wider than its length.

Superstitionia. Femur trichobothrium d is positioned midsegment horizontally, not close to the dorsoexternal carina; ventral surface of leg tarsus equipped with a median row of continuous elongated spinule clusters; dorsal lateral carinae terminus of metasomal segment IV flared.

Troglotayosicus. Femur trichobothrium d is considerably distal of i ; median and basal denticles of cheliceral fixed finger flush on edge, not conjoined on a common trunk; leg tarsus ventral surface found with elongated clusters of setae and/or spinules; stigma small and circular in shape; pectinal fulcra absent.

(Euscorpidae + Chactidae). Chelal trichobothrium it positioned on palm, next to articular membrane of movable finger; chelal trichobothrial series eb – et , eb closest to the fixed finger, esb angling towards the dorsal edge; patellar trichobothrium v_3 just proximal of, or at the midpoint of segment, and definitely proximal of trichobothria est and et_3 .

Euscorpidae. Femur trichobothrium d is situated horizontally midsegment, not next to dorsoexternal carina; chelal fingers with inner accessory denticles (IAD); chelal finger outer denticles (OD) removed from median denticle (MD) row; overall shape of pedipalp chelal palm is flat; patellar spurs DPS and/or VPS well-developed.

Chactidae. Femur trichobothrium d is positioned at the same level as, or distal to i ; chelal trichobothrium Eb_1 situated on ventral surface or on VI carina; sclerites of

genital operculum of female separated for most of its length.

(Brotheinae + Chactinae). Hemispermatophore truncal flexure absent; hemispermatophore lamina terminus tenuous, thin, highly tapered; stigma small and circular.

Brotheinae. Patellar trichobothria distance between esb_1 and esb_2 is much greater than distance between em_1 and em_2 ; ventral surface of leg tarsus dominated with setal pair configuration, median row of spinules essentially obsolete.

Belisarius (and Belisariini). Chelal trichobothrial series Db – Dt is located very basally, distance between Db and Dt quite small; pectinal fulcra absent.

Brotheini. Neobothriotaxy Ch_2 present on ventral surface of patella; neobothriotaxy Ch_2 present on external surface of patella; pectinal middle lamellae composed of a single plate or two, semi-fused with anterior lamellae, fulcra if present, are quite reduced.

Brotheas (and Brotheina). Chelal trichobothria Db is distal to base and Dt well pass palm midpoint; chelal trichobothrial series eb – et positioned on distal two-thirds of fixed finger, either in a straight line or est – esb – eb juncture angling toward fixed finger edge; chelal trichobothrium Et_5 situated on fixed finger; stigma large and slit-like in shape.

Neochactas (and Neochactina). Chelal trichobothria Db situated proximal of palm midpoint and Dt proximal of trichobothrium Est .

Chactinae. Chelal trichobothria Db basal, Dt situated at palm midpoint; patellar trichobothria em_1 – em_2 and esb_1 proximal of segment midpoint; neobothriotaxy Ch_1 present on ventral surface of patella; neobothriotaxy Ch_1 present on external surface of patella.

Nullibrotheas (and Nullibrotheini). An additional accessory trichobothrium found in est series of neobothriotaxy Ch_1 for external surface of patella; an additional accessory trichobothrium found in neobothriotaxy Ch_1 for ventral surface of patella; ventral edge of cheliceral movable finger with dentition; lateral carinae of metasomal segment IV present; distal termination of chelal VI carina curves towards the internal finger condyle.

(Chactas + Teuthraustes) (= tribe Chactini). Chelal finger outer denticles (OD) removed outward from the MD row; median denticle (MD) row of chelal finger divided into 7–9 groups; pectinal middle lamellae composed of a single plate or two, semi-fused with anterior lamellae, fulcra if present, quite reduced.

Uroctoninae. Distance between patellar trichobothria esb_1 and esb_2 considerably greater than distance between em_1 and em_2 ; ventral edge of cheliceral movable finger with dentition; chelal carina VI distally curves internal towards internal condyle of finger; patella patellar spurs DPS and/or VPS well-developed; stigma medium to long, oval in shape; 3–4 lateral eyes present.

Anuroctonus. Neobothriotaxy Ch_3 found on ventral surface of chela; neobothriotaxy Ch_3 found on ventral

Character	Range	Min Steps	Steps	Max Steps	CI	RI	G-Fit (k = 2)
Trichobothria							
2	3	3	4	18	0.750	0.933	0.750
3	3	3	5	17	0.600	0.857	0.600
4	2	2	4	13	0.500	0.818	0.600
5	2	2	4	28	0.500	0.923	0.600
6	2	2	3	17	0.667	0.933	0.750
7	2	2	3	22	0.667	0.950	0.750
8	2	2	4	30	0.500	0.929	0.600
10	3	3	4	40	0.750	0.973	0.750
12	3	3	4	38	0.750	0.971	0.750
13	4	4	5	25	0.800	0.952	0.750
15	2	2	3	21	0.667	0.947	0.750
19	9	9	12	63	0.750	0.944	0.500
23	2	2	4	33	0.500	0.935	0.600
26	2	2	3	27	0.667	0.960	0.750
27	2	2	3	41	0.667	0.974	0.750
29	2	2	3	17	0.667	0.933	0.750
Chelicerae							
39	6	6	7	34	0.857	0.964	0.750
41	11	11	14	73	0.786	0.952	0.500
42	10	10	11	123	0.909	0.991	0.750
44	3	3	4	4	0.750	0.000	0.750
45	2	2	3	16	0.667	0.929	0.750
Chelal Finger Dentition							
50	4	4	5	35	0.800	0.968	0.750
53	3	3	6	11	0.500	0.625	0.500
Leg Armament							
59	2	2	7	12	0.286	0.500	0.375
60	6	6	10	41	0.600	0.886	0.429
61	1	1	2	3	0.500	0.500	0.750
62	3	3	6	19	0.500	0.812	0.500
Hemispermatothore							
76	3	3	4	34	0.750	0.968	0.750
78	2	2	3	26	0.667	0.958	0.750
79	3	3	4	24	0.750	0.952	0.750
81	4	4	5	20	0.800	0.938	0.750
82	10	10	14	124	0.714	0.965	0.429
Metasoma							
85	5	5	6	6	0.833	0.000	0.750
88	2	2	4	27	0.500	0.920	0.600
90	2	2	3	7	0.667	0.800	0.750
Pedipalp Ornamentation							
91	1	1	2	18	0.500	0.941	0.750
92	2	2	7	18	0.286	0.688	0.375
95	1	1	2	14	0.500	0.923	0.750
98	3	3	4	17	0.750	0.929	0.750
Venom Glands, Miscellaneous							
99	1	1	3	5	0.333	0.500	0.600
101	10	10	17	47	0.588	0.811	0.300
102	11	11	20	117	0.550	0.915	0.250
104	5	5	6	27	0.833	0.955	0.750
105	3	3	4	23	0.750	0.950	0.750

Table 7: Support data for *all characters* exhibiting homoplasy; characters are grouped by their character structural type. See **Table 5** for definition of terms.

aspect of patella; neobothriotaxy *Ch3* found on external surface of patella; hemispermatophore capsule absent.

Uroctonus. Chelal finger median denticle (MD) row divided into 7–8 groups.

Character distribution by nodes for upper level clades. We now present the entire set of character distribution for the other upper-level clades, parvorders and superfamilies. For completeness, the fundamental characters discussed above are included.

(Archaeobuthus + (Pseudochactida + (Buthida + (Chaerilida + (Iurida))))). Distal denticles of cheliceral movable finger approximately equal in size.

Archaeobuthus. Orthobothriotaxy type F1; cheliceral fixed finger with median and basal denticles fused together; leg tibial spurs absent; pedipalp patellar DM_c carina present.

(Pseudochactida + (Buthida + (Chaerilida + (Iurida)))) (= Recent scorpions). Pedipalp femoral $d_1 \rightarrow d_3$ trichobothria configuration points toward the dorsoexternal carina; dorsal carinae of metasomal segment V absent; lateral carinae of metasomal segment V present on anterior half; lateral carinae of metasomal segment IV absent.

Pseudochactida. Orthobothriotaxy type D; dorsal edge of cheliceral movable finger without basal denticle; ventral surface of leg tarsus with two submedian row of spinules; transverse anterior carinae developed on metasomal segments I–III; stigma small and oval in shape.

(Buthida + (Chaerilida + (Iurida))). Ventral surface of leg tarsus armed with numerous irregularly positioned setae; ventral median carinae of metasomal segment V is single; transverse anterior carinae absent on metasomal segments I–III; venom glands are folded (complex).

Buthida. Orthobothriotaxy type A; pedipalp femoral $d_3 \rightarrow d_4$ trichobothria configuration points away from dorsoexternal carina (*beta*); dorsal edge of cheliceral movable finger with two basal denticles; ventral edge of cheliceral movable finger with two large denticles; ventral surface of cheliceral fixed finger with two major denticles (protuberances); sternum type 1, exhibits medium to exaggerated horizontal compression; leg coxae IV elongated; hemispermatophore is *flagelliform*; lateral carinae of metasomal segment V absent; DM_c carina of pedipalp patellar present; ovariuiterus exhibits a reticulate mesh of eight cells; stigma small to long, slit-like in shape.

(Chaerilida + (Iurida)). Leg tibial spurs absent.

Chaerilida. Orthobothriotaxy type B; pedipalp femoral $d_3 \rightarrow d_4$ trichobothria configuration points toward dorsoexternal carina; median and basal denticles of cheliceral fixed finger flush on surface, not conjoined on common trunk; sternum type 1, exhibits subtle wide horizontal compression; maxillary lobes I spatulate;

hemispermatophore is *fusiform*; pedipalp patella with six carinae configuration.

Iurida. Orthobothriotaxy type C; ventral surface of cheliceral fixed finger without denticles; sternum type 2; hemispermatophore is *lamelliform*; pedipalp patella with five carinae configuration; three lateral eyes present.

Iuroidea. Chela trichobothrial series *db–dt* and *eb–et* found on distal half of finger; patella ventral trichobothrium v_3 found on external surface; ventral edge of cheliceral movable finger with one large denticle; ventral surface of leg tarsus with median row of spinule clusters; stigma oval in shape.

Iuridae. Chelal trichobothrium Eb_1 on ventral surface or ventroexternal carina; chelal trichobothrium *it* on distal aspect of fixed finger; chelal trichobothria series *ib–it*, *ib* and *it* not adjacent; chelal trichobothrium Et_1 positioned on external surface of palm; additional petite trichobothria present on the chela; patella ventral trichobothrium v_2 found on external surface; additional petite trichobothria present on the patella.

Caraboctonidae. Chelal trichobothrium Et_5 positioned on fixed finger; neobothriotaxy present on external surface of patella; dorsal edge of cheliceral movable finger with *two* subdistal denticles; leg coxae IV elongated; lateral carinae partially present on metasomal segment IV; chela with “10-carinae” configuration.

(Scorpionoidea + Chactioidea). Ventral edge of cheliceral movable finger smooth; median denticle (MD) row of chelal finger aligned in straight line; sclerites of genital operculum of female generally fused; chela with “10-carinae” configuration.

Scorpionoidea. Ventral denticle of cheliceral movable finger considerably longer than dorsal denticle; outer denticles (OD) of chelal finger removed outward from median denticle (MD) row; ventral surface of leg tarsus with pairs of large socketed setae; legs with one pedal spur (prolateral); paraxial organ with a reflection of internobasal sperm duct; hemispermatophore capsule extremely well developed.

(Scorpionidae + Liochelidae + Urodacidae). Spacing between chelal trichobothria V_2 and V_3 much greater than V_3 and V_4 ; sternum length less than or equal to width; distal aspect of chelal ventroexternal (VI) carina curves internally; stigma slit-like in shape.

Bothriuridae. Chelal trichobothrium Et_2 situation on ventral surface of palm; chelal trichobothrium *ib* situated on extreme fixed finger base or on palm; chelal trichobothrium *it* positioned on extreme base of fixed finger; neobothriotaxy found on ventral surface of chelae; legs with two pedal spurs; sternum type 2, exhibiting vertical compression; hemispermatophore lamina terminus with crest; sclerites of genital operculum of female loosely connected; chelal ventroexternal (VI) carina placed on ventral surface, situated between external and internal condyles of the finger; stigma oval in shape.

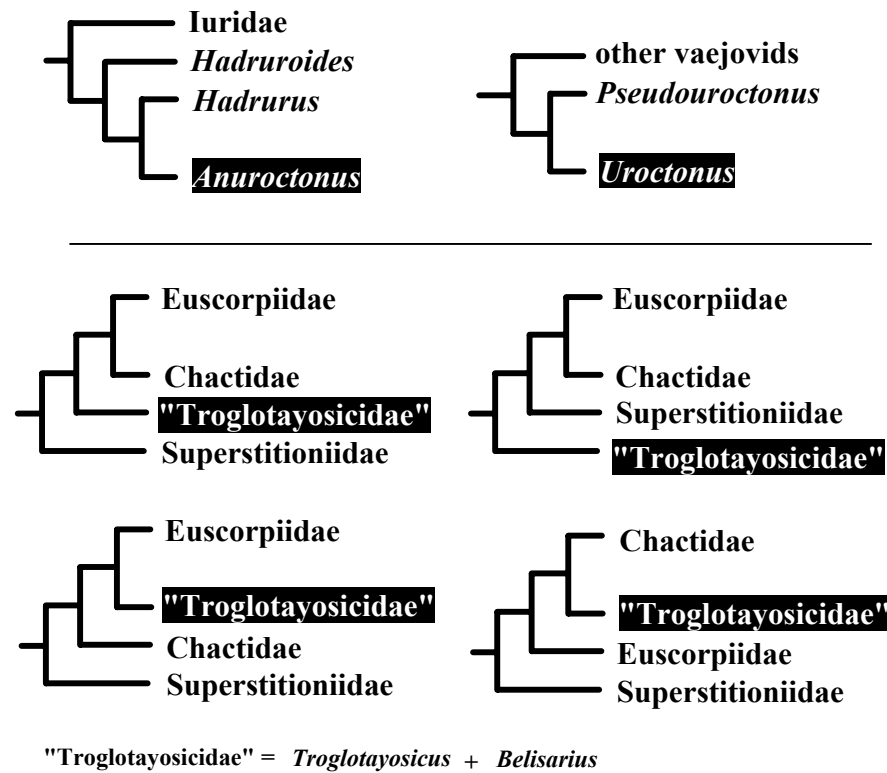


Figure 117: Constrained topologies (partial) showing previously accepted taxonomical groupings. *Anuroctonus* included in Iuroidea, sister genus to *Hadrurus*; *Uroctonus* included in Vaejovidae, sister genus to *Pseudouroctonus*; Lourenço's family Troglotayosicidae (= *Troglotayosicus* + *Belisarius*) forming four different arrangements with families Euscorpiidae, Chactidae, and Superstitioniidae.

Constrained topology analysis

We present here the results of our investigation into the overall reduction in support when certain original taxonomic topologies are imposed on our current data set. In particular, we are interested in the support differences involving chactid genera *Anuroctonus* and *Uroctonus*, and the family Troglotayosicidae (synonymized in this study). We examine the effects of these topology changes of *Anuroctonus* and *Uroctonus*, both when considered separately, and when considered together, since they are now included in the subfamily Uroctoninae. For Troglotayosicidae, we test several topological arrangements within the chactoids, involving families Euscorpiidae, Chactidae, and Superstitioniidae. Fig. 117 shows partial cladograms illustrating these constrained topologies.

Anuroctonus. Stockwell (1992) placed genus *Anuroctonus* in family Iuridae, subfamily Caraboctoninae (in this study superfamily Iuroidea, family Caraboctonidae) as the sister genus to *Hadrurus*. Our results place *Anuroctonus* in family Chactidae, subfamily Uroctoninae. We constrained our current topology by moving *Anuroctonus* from Uroctoninae to superfamily Iuroidea, binding with *Hadrurus* in family Caraboctonidae (Fig. 117). The number of tree steps increased by 59, an increase in steps of 13.7%; the CI, RI, and G-Fit character support decreased 2.8–12.1% (see Table 8). This result exhibits a significant reduction in support, especially considering it only involved the movement of one taxon

out of a group of 60. Of course, much of this reduction is caused by the somewhat basal placement of Iuroidea, shown in this present study to be the most primitive subfamily of the parvorder Iurida.

Uroctonus. Stockwell (1989: Fig. 257), in his cladistic analysis, considered *Pseudouroctonus*, *Uroctonus*, and *Uroctonites* as a well defined clade within Vaejovidae. This is the only cladistic treatment, to date, of this small assemblage of genera. In our present study, it is shown that *Uroctonus* is a member of the family Chactidae. We constrained our current topology by moving *Uroctonus* to family Vaejovidae, and coupling it with *Pseudouroctonus* (Fig. 117). The resulting increase in tree steps is 30, a 7% reduction in tree support, and the CI, RI, and G-Fit character support decreased 1.4–6.5% (Table 8). This decrease in overall support is considerably less than that seen in the constrained topology for *Anuroctonus*. This is easily explained however, since the movement of *Uroctonus* to Vaejovidae involves the same superfamily, Chactoidea, whereas *Anuroctonus* was moved across considerable "phylogenetic distance" to Iuroidea.

Anuroctonus and Uroctonus. Since newly created subfamily Uroctoninae includes both (and only) *Uroctonus* and *Anuroctonus*, we also tested the differences in support when both topological constraints discussed above are combined. This resulted in an increase of 80 tree steps, a 18.6% decrease in tree support. The CI, RI, and G-Step ranged 3.8–15.7% reduction in character support.

Constrained Topology	Tree Steps (% increase)	CI (% reduction)	RI (% reduction)	G-Fit (k = 2) (% reduction)
<i>Hadrurus</i> + <i>Anuroctonus</i>	489 (13.7)	0.7014 (12.1)	0.9342 (2.8)	-79.070 (8.7)
<i>Pseudouroctonus</i> + <i>Uroctonus</i>	460 (7.0)	0.7457 (6.5)	0.9472 (1.4)	-82.550 (4.7)
<i>Hadrurus</i> + <i>Anuroctonus</i> & <i>Pseudouroctonus</i> + <i>Uroctonus</i>	510 (18.6)	0.6725 (15.7)	0.9247 (3.8)	-76.857 (11.3)
S + (Troglotayosicidae + (E + C))	449 (4.4)	0.7639 (4.2)	0.9522 (0.9)	-83.437 (3.7)
Troglotayosicidae + (S + (E + C))	449 (4.4)	0.7639 (4.2)	0.9522 (0.9)	-83.437 (3.7)
S + (C + (Troglotayosicidae + E))	450 (4.7)	0.7622 (4.5)	0.9518 (0.9)	-83.365 (3.7)
S + (E + (Troglotayosicidae + C))	445 (3.5)	0.7708 (3.4)	0.9540 (0.7)	-83.744 (3.3)
Original Topology	430	0.7977	0.9608	-86.607

Table 8: Topological constraint analysis showing reductions in overall support based on increase of number of tree steps and the decrease in character support. See Fig. 117 for details on topologies. E = Euscorpiidae, C = Chactidae, S = Superstitioniidae. See Table 5 for definition of terms.

Troglotayosicidae. The family Troglotayosicidae, recently created by Lourenço (1998a), includes two genera, *Troglotayosicus* and *Belisarius*. Previously, cladistic results of Stockwell (1989, 1992) placed both of these genera in family Superstitioniidae. In a recent cladistic revision of family Euscorpiidae (Soleglad & Sissom, 2001), it was demonstrated that *Belisarius* showed a close affinity to the South American chactids. Both of these genera were treated in our current study, which demonstrates that *Belisarius* is a member of Chactidae, as suggested by Soleglad & Sissom (2001), subfamily Brotheinae, and *Troglotayosicus* is a member of family Superstitioniidae, showing a close affinity to the North American genus *Superstitionia*, as originally determined by Stockwell (1989, 1992). Based on all of these analyses, we tested four constrained topologies for the original family Troglotayosicidae, combining it with different chactoid families (Fig. 117). Only family Vaejovidae was excluded. As can be seen in Table 8 the reduction in support was minimal, increase in steps ranged 15–20 (3.5–4.7%) and character support decreased 0.7–4.5%. The topology combining Troglotayosicidae with Chactidae exhibited the less reduction in support, and the joining of Troglotayosicidae with Euscorpiidae showed the most reduction. This low reduction in support is not surprising since the relocation of the two genera involved clades that are phylogenetically close.

Classification of the Orthostern Scorpions

Below, we list the proposed classification of all above-genus taxa (parvorder, superfamily, family, subfamily, tribe, and subtribe), which we recognize among orthostern scorpions, with brief taxonomic

history of each taxon. Full list of extant genera included under each taxon can be found in Table 9. Details on taxonomy, species composition, and geographic distribution of most scorpion genera can be found in Fet et al. (2000).

Our treatment of the entire taxonomic diversity of scorpions compels us to approach the family-group ranks with a degree of balance and proportionality. Thus, while we accept topology of Prendini (2000), we downgrade three of his families in Scorpionoidea (Diplocentrinae, Hemiscorpiidae, and Heteroscorpionidae) to subfamily rank (under, respectively, Scorpionidae, Liochelidae, and Urodacidae). At the same time, in an opposite move, we elevate Caraboctoninae to the family rank in Iuroidea. These taxonomic acts, in our opinion, are justified by the required proportionality of cladistically defined family-level distinctions. While family-group ranks are somewhat arbitrary, the taxonomic balance within superfamilies Iuroidea, Chactoidea, and Scorpionoidea is best achieved by assigning family level only to primary clades (two in Iuroidea, four in Chactoidea, and four in Scorpionoidea). From our viewpoint, retaining Hemiscorpiidae, Heteroscorpionidae, or even a traditional Diplocentrinae as families would create an unnecessary emphasis on family diversity of Scorpionoidea—in fact, subfamilies in Chactoidea (i.e. Chactinae and Brotheinae) present deeper evolutionary differences than, say, those between Scorpioninae and Diplocentrinae. Since Prendini (2000) addressed almost exclusively scorpionoid taxa (his outgroups included only a *Centruroides* and a *Chaerilus*), his assignment of family or subfamily ranks was inevitably biased toward Scorpionoidea. It is not the “splitting” or “lumping” but the proportionality issue which is important here. Indeed, the same type of a perspective bias led Kjellesvig-

Waering (1986) to suggest lumping all extant scorpions into three families; or led Lamoral (1980) to suggest that Chactidae and Vaejovidae should be lumped into one family; or prevented, for many decades, a well-deserved recognition of Iuridae family rank.

Order Scorpiones C. L. Koch, 1837
Suborder Neoscorpiones Thorell & Lindström,
1885
Infraorder Orthosterni Pocock, 1911

This infraorder, as suggested by Stockwell (1989), included all Recent scorpion families as well as the Tertiary genus *Mioscorpio* and the Carboniferous family Palaeopisthacanthidae. Stockwell (1989) did not discuss the Cretaceous genus *Araripescorpius* (Campos, 1986) and Tertiary genera *Sinoscorpius* and *Uintsorpio* (Hong, 1983; Perry, 1985), probably due to a very fragmentary nature of these fossils. A number of additional fossil orthostern taxa have been described or recorded since 1989, both within Recent families (Lourenço & Weitschat, 1996, 2000, 2001; Santiago-Blay & Craig, 1998; Santiago-Blay et al., 2001) and outside of them (Jeram, 1994a, 1994b; Carvalho & Lourenço, 2001; Lourenço, 2001c, 2002a, 2003; Santiago-Blay et al., in press).

To accommodate all Recent families, we establish four *parvorders* (the order-group taxonomic category subordinate to infraorder): Pseudochactida, Buthida, Chaerilida, and Iurida. Some extinct species, genera, and families are also included under these four parvorders as specified below.

Diversity content of extant taxa in four parvorders is unequal. Parvorders Pseudochactida and Chaerilida each include a single monotypic family; parvorder Buthida includes two families and 82 genera; and parvorder Iurida includes 10 families and 83 genera (Table 9). Phylogenetic relationship between four extant parvorders as established in our analysis is a “ladderized” phylogeny (Pseudochactida, (Buthida, (Chaerilida, (Iurida))) (Fig. 114).

Characters used to distinguish the four parvorders of Recent scorpions are the fundamental orthobothriotaxic pattern types, setal and spinule armament of the leg tarsus, fundamental sternum types, cheliceral dentition, and basic hemispermatophore types.

Key to the parvorders of Recent scorpions

1. Orthobothriotaxic pattern type D; ventral aspect of leg tarsus with two rows of submedian spinules (*configuration 1*); metasomal segment V with paired ventral median carinae; dorsal edge of cheliceral movable *without* basal denticles
Pseudochactida

Orthobothriotaxic pattern type A, B, or C; ventral aspect of leg tarsus without two rows of submedian spinules, but equipped with multiple irregular rows of setae and/or ventral median row of spinules; metasomal segment V with single ventral median carina; dorsal edge of the cheliceral movable finger with basal denticles **2**

2. Orthobothriotaxic pattern type A; ventral aspect of leg tarsus with multiple irregular rows of setae, no trace of spinules (*configuration 2*); dorsal edge of cheliceral movable finger with *two* basal denticles; hemispermatophore is *flagelliform* **Buthida**

Orthobothriotaxic pattern type B or C; ventral aspect of leg tarsus with or without irregular setal rows, spinules present medially; dorsal edge of cheliceral movable finger with a *single* basal denticle; hemispermatophore is either *fusiform* or *lamelliform* **3**

3. Orthobothriotaxic pattern type B; sternum is *type 1*; hemispermatophore is *fusiform* **Chaerilida**

Orthobothriotaxic pattern type C; sternum is *type 2*; hemispermatophore is *lamelliform* **Iurida**

Parvorder Pseudochactida Soleglad & Fet, new parvorder

Composition. This monotypic parvorder, established here, includes the monotypic superfamily Pseudochactoida. It corresponds to orthobothriotaxy “Type D” (Soleglad & Fet, 2001).

Distribution. Central Asia. No fossil taxa are known.

Biogeographic history. The parvorder and superfamily could have been established in Permian/Triassic, judging from their ancestral position in scorpion phylogeny. We cannot speculate on whether this lineage was localized or widespread since there are no fossils belonging to Pseudochactida, and the parvorder is represented by a single monotypic genus.

Diagnosis. Scorpions in the parvorder Pseudochactida can be distinguished by the following characters: Synapomorphies. Orthobothriotaxy type D; dorsal edge of cheliceral movable finger without basal denticle; ventral surface of leg tarsus with two submedian rows of spinules; transverse anterior carinae developed on metasomal segments I–III; stigma small and oval in shape. Important Sympleiomorphies. Two ventral median carinae of metasomal segment V; sternum of *type 1*, lacking horizontal compression; median denticle row (MD) of pedipalp chelal finger arranged in *oblique* groups; pedipalp chela exhibits “8-carinae” configuration; pedipalp patella exhibits “7-carinae” configuration; ventral edge of cheliceral movable finger crenu-

Parvorder	Superfamily	Family	Subfamily	Tribe	Genus	
Pseudochactida Buthida	Pseudochactoidea Buthoidea	Pseudochactidae			<i>Pseudochactas</i>	
		Buthidae			<i>Afghanorhachirus</i> , <i>Afroisometrus</i> , <i>Akentrobuthus</i> , <i>Alayotiyus</i> , <i>Ananteris</i> , <i>Androctonus</i> , <i>Anomalobuthus</i> , <i>Apistobuthus</i> , <i>Australobuthus</i> , <i>Babycurus</i> , <i>Baloorthochirus</i> , <i>Birulattus</i> , <i>Buthacus</i> , <i>Buthaeoloides</i> , <i>Buthaeolus</i> , <i>Buthiscus</i> , <i>Buthoscorpio</i> , <i>Buthus</i> , <i>Caribetiyus</i> , <i>Centruroides</i> , <i>Charmus</i> , <i>Cicileus</i> , <i>Compsobuthus</i> , <i>Congobuthus</i> , <i>Darchenia</i> , <i>Egyptobuthus</i> , <i>Grosphus</i> , <i>Hemibuthus</i> , <i>Hemilychus</i> , <i>Himalayotiyobuthus</i> , <i>Hottentotta</i> , <i>Iranobuthus</i> , <i>Isometroides</i> , <i>Isometrus</i> , <i>Karasbergia</i> , <i>Kraepelina</i> , <i>Lanzatus</i> , <i>Leiturus</i> , <i>Liobuthus</i> , <i>Lissothus</i> , <i>Lychas</i> , <i>Lychasioides</i> , <i>Mesobuthus</i> , <i>Mesotiyus</i> , <i>Microbuthus</i> , <i>Microtiyus</i> , <i>Nanobuthus</i> , <i>Neobuthus</i> , <i>Neogrosphus</i> , <i>Odontobuthus</i> , <i>Odonturus</i> , <i>Orthochirooides</i> , <i>Orthochirus</i> , <i>Pakistanorthochirus</i> , <i>Parabuthus</i> , <i>Paraorthochirus</i> , <i>Pectinibuthus</i> , <i>Plesioibuthus</i> , <i>Polisius</i> , <i>Psammobuthus</i> , <i>Pseudolissothus</i> , <i>Pseudolychus</i> , <i>Pseudouroplectes</i> , <i>Raztanius</i> , <i>Rhopalurus</i> , <i>Sabinebuthus</i> , <i>Sassanidothus</i> , <i>Simonoidea</i> , <i>Somalibuthus</i> , <i>Somalicharmus</i> , <i>Thaicharmus</i> , <i>Tityobuthus</i> , <i>Tityopsis</i> , <i>Tiyus</i> , <i>Troglotiyobuthus</i> , <i>Uroplectes</i> , <i>Uroplectoidea</i> , <i>Vachoniolus</i> , <i>Vachonus</i> , <i>Zabius</i>	
Chaerilida Iurida	Chaeriloidea Iuroidea	Microchamidae			<i>Microcharmus</i> , <i>Neoprotoibuthus</i>	
		Chaerilidae			<i>Chaerilus</i>	
		Iuridae			<i>Caltchas</i> , <i>Iurus</i>	
		Caraboctomidae	Caraboctominae Hadruirinae		<i>Caraboctonus</i> , <i>Hadruroides</i> <i>Hadruirus</i>	
		Scorpionidae	Scorpioninae Diplocentrinae	Diplocentrini Nebini	<i>Heterometrus</i> , <i>Opisthophthalmus</i> , <i>Pandinus</i> , <i>Scorpio</i> <i>Bioctulus</i> , <i>Cazierius</i> , <i>Dichymocentrus</i> , <i>Diplocentrus</i> , <i>Heteronebo</i> , <i>Oiclus</i> , <i>Tarsoporosus</i> <i>Nebo</i>	
		Urodacidae	Urodacinae		<i>Urodacus</i>	
		Liochelidae	Heteroscorpioninae Liochelinae		<i>Heteroscorpion</i>	
		Bothriuridae	Liochelidae		<i>Cheloctonus</i> , <i>Chirromachetes</i> , <i>Chromachus</i> , <i>Hadogenes</i> , <i>Iomachus</i> , <i>Liocheles</i> , <i>Monodopisthacanthus</i> , <i>Opisthacanthus</i> , <i>Palaeocheloctonus</i> <i>Habibiella</i> , <i>Hemiscorpius</i>	
		Chactidae	Bothriuridae	Hemiscorpiinae		<i>Bothriurus</i> , <i>Brachistosternus</i> , <i>Brandbergia</i> , <i>Brazilobothriurus</i> , <i>Centromachetes</i> , <i>Cercophonius</i> , <i>Lisposoma</i> , <i>Orobothriurus</i> , <i>Phonioecercus</i> , <i>Tehuanka</i> , <i>Thesylus</i> , <i>Timogenes</i> , <i>Urophonius</i> , <i>Vachonia</i> <i>Chactas</i> , <i>Teuthraustes</i> , <i>Vachoniochactas</i>
			Chactidae	Chactinae	Chactini Nullibrotheini Brotheini Belisarini	<i>Nullibrotheina</i> : <i>Broteochoactas</i> , <i>Brotheas</i> , <i>Hadrurochactas</i> <u>Subtribe Neochactina</u> : <i>Neochactas</i> <i>Belisarius</i> <i>Anuroctonus</i> , <i>Uroctonus</i>
			Euscorpidae	Euscorpinae Megacorminae	Megacormini Chactopsini Scorpiopini Troglocormini	<i>Euscorpis</i> <i>Megacormus</i> , <i>Plesiochactas</i> <i>Chactopsis</i> <i>Alloscorpiops</i> , <i>Dasyrscorpiops</i> , <i>Euscorpis</i> , <i>Neoscorpis</i> , <i>Parascorpiops</i> , <i>Scorpiops</i> <i>Troglocormus</i>
			Supersitionidae	Supersitioninae Typhlochactinae		<i>Supersitionia</i> , <i>Troglatoyosicus</i> <i>Alacran</i> , <i>Sotanochactas</i> , <i>Typhlochactas</i>
	Vaejovidae			<i>Paravaejovis</i> , <i>Paruroctonus</i> , <i>Pseudouroctonus</i> , <i>Serradigitus</i> , <i>Smeringurus</i> , <i>Syntropis</i> , <i>Uroctonites</i> , <i>Vaejovis</i> , <i>Vejovoidis</i>		

Table 9: Taxonomy of Recent Scorpions (Order = Scorpiones, Suborder = Neoscorpiones, Infraorder = Orthosterni)

lated; dorsal edge of cheliceral movable finger with single subdistal denticle; ventral surface of cheliceral fixed finger with denticles.

Superfamily Pseudochactoidea Gromov, 1998, new rank

Type Genus. *Pseudochactas* Gromov, 1998.

Composition. This monotypic superfamily, established here, includes the monotypic family Pseudochactidae.

Distribution. Central Asia.

Taxonomic history. Lourenço (2000a) placed Pseudochactidae in his superfamily Chaeriloidea, without any justification.

Diagnosis. As in parvorder Pseudochactida.

Family Pseudochactidae Gromov, 1998.

Type Genus. *Pseudochactas* Gromov, 1998.

Composition. This monotypic family includes a single monotypic genus *Pseudochactas* (Gromov, 1998; Fet, 2000f).

Distribution. Central Asia (southeastern Uzbekistan, southwestern Tajikistan).

Biogeographic history. Unclear. The single genus *Pseudochactas* is found only in a restricted location in the mountains of Central Asia. The relict character of *Pseudochactas* could be due to its preservation in mild-climate, low-mountain depressions of Babatag and Gandzhino ranges (Gromov, 1998), with desert surroundings at lower altitudes. Ecologically, this is not a desert scorpion; it actively forages on wet mud along the temporary waterways, and likely spends most of dry season in hibernation (V. Fet & A. Gromov, pers. observation, 2002). It could represent one of the few faunal remnants of littoral fauna of the receded Tethys Ocean (Kryzhanovskiy, 1965), elevated by Tertiary mountain uplift. Many such important floral elements of littoral origin are found in low mountains of Uzbekistan and Tajikistan (Kamelin, 1979).

Diagnosis. As in parvorder Pseudochactida.

Discussion. Gromov (1998: 1003) keenly observed that “It is possible that the representative of this new family (Pseudochactidae) stands close to the common ancestor of all these families [the Recent scorpions]”. As Soleglad & Fet (2001) demonstrated based on trichobothrial patterns, *Pseudochactas* is certainly a basal member of Recent scorpions, and also shows significant affinity in some characters with the Carboniferous fossil scorpion family Palaeopisthacanthidae. This veritable “platypus of a scorpion” deserves further study in all aspects.

Parvorder Buthida Soleglad & Fet, new parvorder

Composition. This monotypic parvorder, established here, includes the monotypic superfamily Buthoidea. It corresponds to orthobothriotaxy “Type A” (Vachon,

1974; Soleglad & Fet, 2001). The geographic range of this parvorder covers both the Old and the New World. The oldest known fossils of Buthida are Tertiary (see below).

Distribution. All continents except Antarctica.

Diagnosis. Scorpions in the parvorder Buthida can be distinguished by the following characters: Synapomorphies. Orthobothriotaxy type A; pedipalp femoral d_3 – d_4 trichobothria configuration points away from dorsoexternal carina (*beta*); dorsal edge of cheliceral movable finger with *two* basal denticles; ventral edge of cheliceral movable finger with two large denticles; ventral surface of cheliceral fixed finger with two major denticles; sternum, *type 1*, exhibits medium to exaggerated horizontal compression; leg coxae IV elongated; hemispermatophore is *flagelliform*; lateral carinae of metasomal segment V absent; pedipalp patellar DM_c carina present; ovariterus exhibits a reticulate mesh of eight cells; stigma small to long, slit-like in shape. Important Sympleiomorphies. Ventral surface of leg tarsus ventral surface armed with numerous irregularly positioned setae; ventral median carinae of metasomal segment V is single; transverse anterior carinae absent on metasomal segments I–III; venom glands are folded (complex); median denticle row (MD) of pedipalp chelal finger arranged in *oblique* groups; pedipalp chela exhibits “8-carinae” configuration; dorsal edge of cheliceral movable finger with single subdistal denticle.

Superfamily Buthoidea C. L. Koch, 1837

Type Genus. *Buthus* Leach, 1815.

Composition. Following Lourenço (2000a), we include in the superfamily Buthoidea two families: Buthidae and Microcharmidae.

Distribution. All continents except Antarctica.

Taxonomic history. Stockwell (1989) included Buthidae as well as Chaerilidae in his Buthoidea, noting that these two taxa were treated as subfamilies of Buthidae by Laurie (1896a). Here, we establish a separate parvorder and superfamily for Chaerilidae.

Diagnosis. See parvorder Buthida.

Discussion. Monophyly of the extant Buthoidea is well-confirmed. We do not include in Buthoidea the Cretaceous fossil taxa: family Archaeobuthidae (genus *Archaeobuthus*) and genus *Palaeoburmesebuthus* (not assigned to any family), which were placed in Buthoidea by Lourenço (2002a, 2003); see below for further discussion. The oldest known fossils of Buthoidea, in our opinion, are Tertiary (Eocene/Paleocene; 65–55 Mya) genera of Buthidae from Baltic amber. The relationship between Buthidae and Microcharmidae is not clear.

Family Buthidae C.L. Koch, 1837

Type Genus. *Buthus* Leach, 1815.

Synonyms.

Androctonides C.L. Koch, 1837; type genus *Androctonus* Ehrenberg, 1828.

Available names of family-level groups. (STATUS UNCLEAR):

Isometrini Kraepelin, 1891; type genus *Isometrus* Ehrenberg, 1828 (see also Fet & Messing (in press) on a junior homonym Isometrinae, Crinoidea, Echinodermata).

Babycurini Pocock, 1896; type genus *Babycurus* Karsch, 1886.

Ananterinae Pocock, 1900; type genus *Ananteris* Thorell, 1891.

Tityinae Kraepelin, 1905; type genus *Tityus* C.L. Koch, 1836.

Orthochirinae Birula, 1917; type genus *Orthochirus* Karsch, 1892.

Charminae Birula, 1917; type genus *Charmus* Karsch, 1879.

Uroplectaria Pavlovsky, 1924; type genus *Uroplectes* Peters, 1861.

Rhopalurusinae Bücherl, 1969 (original spelling Rhopalurinae, a junior homonym of Rhopaluridae, Mesozoa; see Fet et al., 2003b); type genus *Rhopalurus* Thorell, 1876.

Akentrobuthinae Lamoral, 1976; type genus *Akentrobuthus* Lamoral, 1976 (see comments under family Microcharmidae).

Composition. The family Buthidae includes 80 extant genera (Table 9; Fet & Lowe, 2000; for additional genera described and synonymies made since 1998, see Lourenço, 1999a, 1999b, 2000b, 2000c, 2001a, 2001d; Fet et al., 2001a; Kovařík, 2001; Gantenbein et al., 2003).

Distribution. All continents except Antarctica. Some of the New World genera include extinct Tertiary species (amber of the Dominican Republic and Mexico). In addition, five fossil Tertiary genera of Buthidae (all from the Eocene/Oligocene Baltic amber, ca. 65 Mya) have been described: *Palaeolychas*, *Palaeotityobuthus*, *Palaeoprotobuthus*, *Palaeoakentrobuthus*, and *Palaeoananteris* (Lourenço & Weitschat, 1996, 2000, 2001); and a subfossil genus *Palaeogrosphus* was described from the copal of Madagascar (Lourenço, 2000c).

Taxonomic history. This family was early recognized as a separate lineage from all other extant scorpions (Peters, 1861); this division was maintained by all later taxonomists (Thorell, 1876a; Pocock, 1893; Kraepelin, 1899, 1905; Birula, 1917a, 1917b). Buthidae were considered a sister group of all other extant families by Lamoral (1980) and Sissom (1990). It is the only family of scorpions that has medical importance due to its potent, mammal-specific neurotoxins, and many aspects of buthid biology have been extensively studied. However, the comment by Stockwell (1989: 182) that the family Buthidae “is surprisingly poorly studied with

regard to suprageneric phylogenetic relationships” is still valid.

Biogeographic history. This extremely diverse family could have been established in Permian/Triassic within Pangea, judging from its modern worldwide distribution. Sissom (1990) followed Lamoral (1980) in assuming Laurasian origin of “protobuthoids”, spreading to Gondwanaland in Pangean times before the two masses split. However, there is certainly no evidence that buthid ancestors originated in the northern part of Pangea; this notion is probably a remnant of simplistic views of early scorpion geographers, including Kraepelin (1905) and Birula (1917a, 1917b) who derived buthids from non-orthostern Carboniferous taxa, which they superficially resemble. Statement by Lourenço & Sissom (2000: 122) that “during Pangean times...the protobuthids were the dominant fauna” certainly is not based on any known facts.

There are a number of widespread buthid genera as well as genera endemic to certain biogeographic regions. While extensive radiation is currently exhibited by buthids on all continents (especially in deserts and tropics of Asia, Africa, and the Americas), there is number of endemic genera. It could be possible to trace Gondwanaland relationships between African, Asian, and South American genera of Buthidae. For example, *Grosphus* and *Tityobuthus* are endemic to Madagascar (Lourenço, 1996a, 1996d), and *Ananteris* is found in both Africa and South America (Lourenço, 1993, 1996d), suggesting a Gondwanaland connection; Lourenço (1996b) considered *Ananteris* a close relative of *Tityobuthus*. The preliminary phylogeny (see discussion below) suggests that the New World Buthidae could form a separate lineage together with certain Old World genera; especially intriguing in our preliminary DNA phylogeny (Fet et al., 2003a) is connection between the Madagascan *Grosphus* and the New World Buthidae (*Centruroides* and *Rhopalurus*), which again could indicate Gondwanaland relationships. Fet et al. (2003a) emphasized that the extensive radiation of Buthidae could parallel evolution of unique mammal-specific neurotoxic venom in this family.

Diagnosis. See parvorder Buthida.

Discussion. Subfamilies are currently not recognized in Buthidae; for detailed taxonomic history of this issue see Fet & Lowe (2000: 54–55). Analysis of subfamilial and tribal division of Buthidae is beyond the scope of our present paper. The complexity of this family clearly requires further division, and already early authors introduced subfamilies (Kraepelin, 1905; Birula, 1917a, 1917b) and even tribes (Pavlovsky, 1924). Most of subfamily names have not been formally synonymized, and the issue has been controversial (Froy, 2002) but not yet approached with modern methods of classification. There are indications that at least two major groups exist within this family, which might correspond

to two trichobothrial configurations—"alpha" and "beta" patterns on the pedipalp femur discovered by Vachon (1975), and discussed further in this paper. The most recent key of buthid genera (Sissom, 1990: 93–100) suggested that the "beta" pattern is present almost exclusively in the Old World genera. At the same time, "alpha" pattern is found in all other New World genera (all of which also share a loss of tibial spurs; Sissom, 1990: 89) and a number of the Old World genera (mainly Afrotropical). Toxicologists routinely discuss profound differences in venom structure and function between Buthidae of the Old World (such as *Androctonus*, *Leiurus* and *Mesobuthus*; all "beta" pattern), and the New World (*Centruroides*, *Tityus*; all "alpha" pattern) (Loret & Hammock, 2001; Froy & Gurevitz, 2003). The preliminary DNA phylogeny (Fet et al., 2003a) appears to agree with a possible division into at least two subfamilies; in addition, tribal division could become necessary. If subfamilies will be introduced, the nominotypical subfamily Buthinae will likely incorporate most Old World genera with "beta" configuration. We should also note that the current genus-level diversity in Buthidae is much higher in the Old World (71 genera) than in the New World (10 genera), although species-level diversity is in fact higher in the New World. To some extent it could be an artifact of "splitting" tendencies of buthid taxonomists who worked in the Old World (Fet & Lowe, 2000; Fet et al., 2003a), and to the absence of modern revisions of the largest New World buthid genera such as *Centruroides* (ca. 50 species) and *Tityus* (ca. 120 species). On the other hand, it is clear that evolutionary radiation of Buthidae in the deserts of Asia and Africa is unrivalled by that in the New World where most desert niches are occupied by Vaejovidae or Bothriuridae (Nenilin & Fet, 1992).

Family Microcharmidae Lourenço, 1996

Type Genus. *Microcharmus* Lourenço, 1995.

Composition. The family includes two genera, *Microcharmus* and *Neoprotobuthus* (Fet, 2000d).

Distribution. Madagascar.

Taxonomic history. This family was first introduced as a monotypic subfamily of Buthidae (Lourenço, 1996a), and later elevated to the family rank (Lourenço, 1998a), with only a preliminary justification. Lourenço (1998b) also included in Microcharmidae the subfamily Akentrobuthinae (with a single African genus, *Akentrobuthus*) (Fet, 2000d). Later, however, Lourenço (2000b) transferred *Akentrobuthus* back to Buthidae. Since subfamilies in Buthidae are currently not defined, the status of Akentrobuthinae remains undetermined. An additional genus, *Neoprotobuthus*, was described in Microcharmidae by Lourenço (2002b).

Biogeographic history. Lourenço (1996a) discussed in detail scorpion taxa endemic to Madagascar, which

generally are related to the African fauna and diverged with the split of Gondwanaland.

Diagnosis. A diagnosis cannot be provided as justifying a separate family. Microcharmidae were defined as a subfamily of Buthidae by Lourenço (1996a: 27), and further as a family (Lourenço, 1998a: 845–847), but the given features are not diagnostic even at subfamily level.

Discussion. Lourenço (1996b, 1996d) suggested that the genus *Microcharmus* is closely related to the Indian genus *Charmus* (Buthidae), which would correspond to the Gondwanaland origin of the group but violates the monophyly of Buthidae. The relationship between Microcharmidae and Buthidae is also unclear since there was no combined phylogenetic analysis of these families.

R. Teruel (pers. comm., 1999; Fet, 2000d: 421) noticed that Akentrobuthinae Lamoral, 1976 had a priority over Microcharmidae Lourenço, 1996; therefore when Lourenço (1998b) decided to include Akentrobuthinae in Microcharmidae, the combined family name should have been changed to Akentrobuthidae. However, since Akentrobuthinae was transferred back to Buthidae by Lourenço (2000b), no such change is required.

Parvorder Chaerilida Soleglad & Fet, new parvorder

Composition. This monotypic parvorder, established here, includes the monotypic superfamily Chaeriloidea. It corresponds to orthobothriotaxy "Type B" (Vachon, 1974; Soleglad & Fet, 2001).

Distribution. South and Southeast Asia. No fossil taxa are known.

Biogeographic history. The parvorder and superfamily could have been established in Permian/Triassic, judging from their ancestral position in scorpion phylogeny. We cannot speculate on whether this lineage was localized or widespread since there are no fossils belonging to Chaerilida, and the parvorder is represented by a single monotypic genus.

Diagnosis. Scorpions in the parvorder Chaerilida can be distinguished by the following characters: **Synapomorphies.** Orthobothriotaxy type B; pedipalp femoral d_3 – d_4 trichobothria configuration points toward dorsoexternal carina; cheliceral fixed finger with median and basal denticles flush on surface, not conjoined on common trunk; sternum, *type 1*, exhibits subtle wide horizontal compression; maxillary lobes I spatulate; hemispermaphore is *fusiform*; pedipalp patella with "6-carinae" configuration. **Important Symplesiomorphies.** Median denticle row (MD) of pedipalp chelal finger arranged in *oblique* groups; pedipalp chela exhibits "8-carinae" configuration; ventral edge of cheliceral movable finger crenulated; dorsal edge of cheliceral movable finger with a single subdistal denticle; ventral surface of cheliceral fixed finger with denticles; leg tibial spurs absent.

Superfamily Chaeriloidea Pocock, 1893

Type Genus. *Chaerilus* Simon, 1877.

Composition. The superfamily is monotypic and includes only family Chaerilidae.

Distribution. South and Southeast Asia.

Taxonomic history. This superfamily name was first used by Lourenço (2000a) who included under it two families, Chaerilidae and Pseudochactidae. We restrict the content of Chaeriloidea to Chaerilidae, and establish a separate parvorder and superfamily for Pseudochactidae.

Diagnosis. As in parvorder Chaerilida.

Discussion. Contrary to the opinion of Stockwell (1989: 180), Lamoral (1980) was not the first to use the name Chaeriloidea since he only used a vernacular name “chaeriloids”.

Family Chaerilidae Pocock, 1893

Type Genus. *Chaerilus* Simon, 1877.

Composition. This monotypic family includes a single genus, *Chaerilus* (Fet, 2000a; Kovařík, 2000b)

Distribution. South and Southeast Asia.

Taxonomic history. This taxon was established early by Pocock (1893) as a subfamily of Chactidae, and first elevated to the family rank by Kraepelin (1899). Interestingly, Laurie (1896b) placed it as a subfamily under Buthidae, and cladistic analysis of Stockwell (1989) also showed that Chaerilidae are a sister group of Buthidae. Some authors considered *Chaerilus* to be related to the genus *Calchas* (now in Iuridae) (Birula, 1917a, 1917b; Werner, 1934). The rank and placement of this taxon remained ambiguous until Vachon (1956, 1963, 1971) demonstrated a very distinct cheliceral dentition and trichobothrial pattern for the genus *Chaerilus*. The work of Vachon (1974) firmly reestablished Chaerilidae as a separate family with the unique trichobothrial “Type B”. Stockwell (1989) placed Chaerilidae in his superfamily Buthoidea together with Buthidae. A revision of Chaerilidae was published by Kovařík (2000b).

Biogeographic history. Unclear. Modern species of *Chaerilus* are limited to tropical areas of South And Southeast Asia, although they reach considerable altitudes in Kashmir, Nepal, and Tibet (Kovařík, 2000b), which indicates their ecological plasticity and tolerance of cold climate. Lamoral (1980) suggested that Chaerilidae originated in Pangaen times as an eastern Laurasian relict, and then moved into the Oriental region after the Indian plate connected with Eurasia; and then became isolated in the Oriental region as the Himalayas formed. This is only a plausible speculation based exclusively on modern distribution of *Chaerilus*. Lourenço (1996a, 1996d) noted that their Laurasian origin would explain absence of Chaerilidae in Madagascar.

Diagnosis. As in parvorder Chaerilida.

Parvorder Iurida Soleglad & Fet, new parvorder

Composition. This parvorder, established here, includes three superfamilies (Chactoidea, Iuroidea, and Scorpionoidea) and 10 families. It corresponds to orthobothriotaxy “Type C” (Vachon, 1974; Soleglad & Fet, 2001).

Distribution. All continents except Antarctica.

Biogeographic history. Our phylogenetic analysis demonstrates the relationship between three superfamilies of this parvorder as (Iuroidea, (Scorpionoidea, Chactoidea)). Since already the oldest of superfamilies, Iuroidea, has a disjunct modern distribution between the New World and the Mediterranean, representatives of the parvorder Iurida should clearly have been present in the times of Pangea, which marks the possible upper age (Triassic) of the youngest node in the phylogeny of extant scorpions at the parvorder level (split of parvorder Iurida, the most derived of four scorpion parvorders). The oldest known fossils of Iurida are Cretaceous (families Protoischnuridae and Palaeoeuscorpiidae). All three superfamilies of Iurida exhibit worldwide distribution, variously disjunct at the level of families, tribes, and sometimes even genera.

Diagnosis. Scorpions in the parvorder Iurida can be distinguished by the following characters: Synapomorphies. Orthobothriotaxy type C; ventral surface of cheliceral fixed finger without denticles; sternum *type 2*; hemispermatophore is *lamelliform*; pedipalp patella with “5-carinae” configuration; three lateral eyes present. Important Symplesiomorphies. None.

Discussion. The phylogeny of the parvorder Iurida, as established here, supports the topology (Iuroidea, (Scorpionoidea, Chactoidea)). This conflicts with the interpretation of Stockwell (1989) who included Iuridae (=current Iuroidea) in his Vaejovoidea.

Characters used to define the superfamilies of parvorder Iurida are cheliceral dentition, leg pedal spurs, leg tarsus armature, and the paraxial organ.

Key to the superfamilies of parvorder Iurida

1. Ventral edge of cheliceral movable finger with large basal denticle; ventral aspect of leg tarsus equipped medially with separated spinule clusters (*configuration 3*)..... **Iuroidea**

Ventral edge of cheliceral movable finger without large basal denticle, edge either smooth or with irregular crenulations; ventral aspect of leg tarsus without medial spinule clusters, spinules either absent altogether, or present as a contiguous row (*configurations 4 or 5*) **2**

2. Legs with one pedal spur (retrolateral spur absent, though this character is reversed in some bothriurid genera); ventral aspect of leg tarsus equipped with pairs of large limbated socketed setae, median spinule row optional (*configuration 4*); paraxial organ with reflection of internobasal sperm duct **Scorpionoidea**

Legs with two pedal spurs (though one or more pedal spurs are lost in many troglotic species); ventral aspect of leg tarsus equipped with moderately developed setal pairs and/or median row of spinules (*configuration 5*); paraxial organ without reflection of internobasal sperm duct

Chactoidea

Superfamily Chactoidea Pocock, 1893

Type Genus. *Chactas* Gervais, 1844.

Synonyms.

Vaejovoidea Thorell, 1876, **new synonymy** (valid as family name).

Composition. We include under Chactoidea four families: Chactidae, Euscorpiidae, Superstitioniidae, and Vaejovidae. The content of Chactoidea is changed here compared to that of Lourenço (2000a): we include here family Vaejovidae, and the superfamily Vaejovoidea is synonymized with Chactoidea. Family Iuridae is placed in superfamily Iuroidea, with the exception of genus *Anuroctonus*, which is transferred from Iuridae to Chactidae. The following new changes are also enforced within Chactoidea: family Troglotayosicidae is synonymized with Superstitioniidae, and its two genera are transferred to Superstitioniidae (*Troglotayosicus*) and Chactidae (*Belisarius*); genus *Uroctonus* is moved from Vaejovidae to Chactidae; and a new arrangement of subfamilies, tribes, and subtribes is established in Chactidae.

Distribution. Europe, Asia, Africa (*Euscorpius*; Mediterranean Sea coast), North America, Central and South America.

Taxonomic history. The taxonomic history of this superfamily is complicated and confusing; see Sissom (2000a) for details. The name was used first by Birula (1917a, 1917b), and embraced Chactidae (which also then included taxa currently assigned to Euscorpiidae and Chaerilidae), Vaejovidae (which also then included taxa currently assigned to Euscorpiidae and Iuridae), and, in addition, Bothriuridae. The separate status of Bothriuridae was soon recognized, and this family was excluded from Chactoidea by Mello-Leitão (1945). Placement of Chaerilidae in Chactoidea persisted until Vachon (1956, 1963, 1974) demonstrated a separate trichobothrial “Type B” for Chaerilidae. Lamoral (1980: 443) suggested that Chactidae and Vaejovidae should be lumped further together into one family. Relationships

among these families remained unclear until recently; Sissom (1990) treated Chactidae (in broad sense, including current Euscorpiidae and Superstitioniidae) and Vaejovidae together in his key, for practical purposes designed without familial distinctions. Stockwell (1989) recognized Chactoidea as including Chactidae, Euscorpiidae, and Scorpiopsidae, but listed Superstitioniidae under Vaejovoidea, which also included Iuridae. Stockwell (1992) formally established Euscorpiidae, Scorpiopsidae, and Superstitioniidae as separate families. Lourenço (2000a), who followed unpublished classification of Stockwell (1989), listed five families in Chactoidea (Chactidae, Euscorpiidae, Scorpiopsidae, Superstitioniidae, and Troglotayosicidae) and two families in Vaejovoidea (Iuridae and Vaejovidae). Until recently, many authors indicated that separation of Vaejovidae from Chactidae and related families was problematic (Sissom, 2000a).

Biogeographic history. Our phylogenetic analysis demonstrates the relationship between chactoid families as ((Euscorpiidae, Chactidae), Superstitioniidae), Vaejovidae). Two of these families (Chactidae and Euscorpiidae) incorporate both New World and Old World taxa, while Superstitioniidae and Vaejovidae are found only in the New World. However, this modern distribution is not sufficient to suggest New World origin of Chactoidea. Significant disjunctions between Old World and New World taxa of Chactidae and Euscorpiidae, sometimes at the subfamily level (Brotheinae and Scorpiopinae), cannot be explained by the Gondwanaland breakup or by dispersal, and suggest that these ancient lineages existed already in the Pangean times. The only known fossil chactoid is a presumably Oligocene vaejovid from Mexico (Santiago-Blay et al., 2001). The Cretaceous family Palaeoeuscorpiidae, included in Chactoidea by Lourenço (2003), is treated here as parvorder Iurida *incertae sedis* (see below). A complete absence of Afrotropical and Australian taxa is peculiar for Chactoidea.

Diagnosis. Synapomorphies. Dorsal edge of cheliceral movable finger with *two* subdistal denticles; ventral surface of leg tarsus configured with moderately developed setal pairs and a median spinule row; hemispermaphore capsule present, weak to moderate development; genital papillae of male visible at posterior edge of genital operculum. *Important Sympletiomorphies.* Ventral edge of cheliceral movable finger smooth; median denticle (MD) row of chelal finger aligned in straight line; sclerites of genital operculum of female generally fused; chela with “10-carinae” configuration.

Discussion. An interesting but not generally known fact is that the generic name *Chactas* was given after the literary character, a Native American youth of Natchez tribe in a famous romantic novel *Atala* by the French writer Chateaubriand, published in 1801.

Characters used to delineate the four chactoid families involve positions of trichobothria on the pedipalp chelae and patellae, the fundamental configuration of the chelal finger median denticle (MD) row, presence or absence of accessory denticles on the chelal fingers, neobothriotaxy, and the overall carinal development and shape of the chelal palm.

Key to the families of superfamily Chactoidea

1. Chelal trichobothrial series *ib-it* positioned on fixed finger, never on palm; chelal trichobothrial series V_1-V_4 distributed for most of palm length, $V_1-V_2-V_3$ juncture does not angle internally; patellar trichobothrium v_3 located on external surface of segment; patellar DPS_c carina found on internal surface **Vaejovidae**

Chelal trichobothrial series *ib-it* positioned on palm (*it* sometimes found on extreme base of finger); chelal trichobothrial series V_1-V_4 does not extend entire length of palm, and/or, $V_1-V_2-V_3$ juncture angles internally; patellar trichobothria v_3 located on ventral surface of segment (only found on external surface in subfamily Superstitioniinae, two species); patellar DPS_c carina absent on internal surface **2**

2. Median denticle (MD) row of chelal finger broken up into *oblique* non-overlapping denticle groups **Superstitioniidae**

Median denticle (MD) row of chelal finger arranged in a contiguous straight line **3**

3. Chelal fingers equipped with inner accessory denticles (IAD), outer denticles (OD) situated outside of median denticle (MD) row; major variable neobothriotaxy present, types *Eu1* and *Eu2*; chelal palm is flat in appearance, carinae $D3$ and $V2$ essentially obsolete, angle formed by carinae $D3:D4:D5$ greater than 90° **Euscorpiidae**

Chelal finger without IAD, OD situated in median denticle (MD) row; either orthobothriotaxic or major neobothriotaxy present, types *Ch1*, *Ch2*, *Ch3*; chelal palm not flat, more round in appearance, carinae $D3$ and $V2$ development variable, angle formed by carinae $D3:D4:D5$ less than or equal to 90° **Chactidae**

Family Chactidae Pocock, 1893

Type Genus. *Chactas* Gervais, 1844.

Composition. As a result of a considerable revision presented in this paper, the family Chactidae now includes three subfamilies (Chactinae, Brotheinae, and Uroctoninae) and 11 genera. The content of Chactidae is

changed here compared to Sissom (2000a). We introduce here the subfamilial division as well as establish tribes and subtribes in Chactinae and Brotheinae. Two new family-group taxa are described: tribe Nullibrotheini and subtribe Neochactina, with a new genus *Neochactas*. The subfamily Uroctoninae (with genus *Uroctonus*) is restored from synonymy and transferred to Chactidae from Vaejovidae, and the genus *Anuroctonus* is transferred to Uroctoninae from Iuridae (subfamily Hadrurinae). The genus *Belisarius* is transferred from Troglotayosicidae to Chactidae (subfamily Brotheinae), and the subfamily Belisariinae is downgraded to the tribe rank. We also reestablish the nominotypic subfamily Chactinae.

Distribution. Europe, North America, Central and South America.

Taxonomic history. Taxonomic history of Chactidae is given in detail by Sissom (2000a). When first introduced, this family included also *Euscorpis* (now in Euscorpiidae), and later incorporated a variety of genera currently placed in Chaerilidae, Euscorpiidae, Iuridae, and Superstitioniidae. The important (but largely unpublished) revision of Stockwell (1989, 1992) elevated Euscorpiidae and Superstitioniidae to family rank, and restricted Chactidae to 10 genera. Sissom (2000a) did not recognize any subfamilies in Chactidae. Soleglad & Sissom (2001) transferred genus *Chactopsis* from Chactidae to Euscorpiidae.

Biogeographic history. The chactids are predominantly a tropical South American group (see distribution of genera and species in Table 10) However, this family also incorporates four genera, which give it a peculiar disjunct distribution: *Nullibrotheas*, *Anuroctonus* and *Uroctonus* in North America, and *Belisarius* in Europe (!). These four taxa split the family into a phylogeny, which exhibits a dazzling European-South American disjunction within subfamily Brotheinae. Existence of Belisariini in Europe, and of Nullibrotheini and Uroctoninae in North America indicate an ancient, possibly Pangean age of Chactidae. Monod & Lourenço (2001) note that, with the exception of *Chactas keyserlingi* (which inhabits dry non-forested mountains in Colombia), all South American chactids are restricted to tropical forests. Disjunct distribution of some South American genera can be attributed to the recent (Pleistocene) fluctuations of tropical rainforest (Lourenço, 1988, 1994, 1996b). In South America, prevalence of the taxa of subfamily Chactinae is observed in northwestern to central areas and those of Brotheinae, in north-central to eastern areas, both overlapping and concentrating in Venezuela, which accounts for over 50% of species (see Table 10). This concentration, however, could be an artifact due to the detailed research of M. A. González-Sponga (1996a, etc.) in Venezuela.

Diagnosis. Synapomorphies. Femur trichobothrium *d* is positioned equal or distal to *i*; chelal trichobothrium

*Eb*₁ situated on ventral surface or on *VI* carina; genital operculum of female separated for most of its length. Important Sympletiomorphies. Chela trichobothrium *it* positioned on palm, next to articular membrane of movable finger; chelal trichobothrium *eb* closest to fixed finger, *esb* angling toward dorsal edge; patellar trichobothrium *v*₃ positioned just proximal of or at midpoint of segment and definitely proximal of trichobothria *est* and *et*₃; chelal trichobothrium *ib* situated on extreme fixed finger base or on palm; chelal trichobothria series *V*₁–*V*₄ shorten, *V*₁–*V*₂–*V*₃ juncture usually angled toward internal aspect; overall shape of pedipalp chela is rounded; stigma small and oval in shape; number of lateral eyes 0–2.

Characters key to delineating the subfamilies, tribes and subtribes of family Chactidae involve major neobothriotaxy, positions of orthobothriotaxic trichobothria on the chela and patella, the armature of the cheliceral movable finger ventral edge, development of the patella dorsal and ventral spurs (DPS and VPS), and position of the ventroexternal carina of the chela.

Key to the subfamilies, tribes and subtribes of family Chactidae

1. Major neobothriotaxy, type *Ch1*; patella external trichobothrial series *esb*₁–*esb*₂ and *em*₁–*em*₂ situated on proximal aspect, distance between *esb*₁ and *esb*₂ is small, approximating distance between *em*₁ and *em*₂ (Subfamily **Chactinae**) 2

Orthobothriotaxic or exhibiting major neobothriotaxy types *Ch2* or *Ch3*; patella external trichobothrial series *esb*₁ and *em*₁–*em*₂ situated on midsegment, distance between *esb*₁ and *esb*₂ is much greater than distance between *em*₁ and *em*₂ 3

2. Patellar trichobothria ventral series with five (5) trichobothria and external series *est* with three (3) trichobothria; chelal ventroexternal (*VI*) carina extends to external finger condyle; ventral edge of cheliceral movable finger is smooth
Tribe **Chactini**

Patellar trichobothria ventral series with six (6) trichobothria and external series *est* with four (4) trichobothria; chelal ventroexternal (*VI*) carina does not meet external finger condyle, curving internally on distal aspect; ventral edge of cheliceral movable finger is dentated distally
Tribe **Nullibrotheini**

3. Ventral surface of leg tarsus predominantly equipped with lateral paired setae, ventral median

row of spinules essentially obsolete; ventral surface of cheliceral movable finger smooth; dorsal and ventral patellar spurs (DPS and VPS) underdeveloped or obsolete; chelal ventroexternal (*VI*) carina extends to external finger condyle
(Subfamily **Brotheinae**) 4

Ventral surface of leg tarsus equipped with ventral median row of spinules and lateral paired setae; ventral surface of cheliceral movable finger with dentition, basally or on entire edge; DPS and/or VPS well-developed; chelal ventroexternal (*VI*) carina does not meet external finger condyle, curving internally on distal aspect
Subfamily **Uroctoninae**

4. Major neobothriotaxy, type *Ch2*; chelal trichobothria series *Db* and *Dt* found on mid-segment to distal aspects of palm, distance between *Db* and *Dt* at least one-half the length of palm (Tribe **Brotheini**) 5

Orthobothriotaxic; chelal trichobothria series *Db* and *Dt* found on extreme proximal aspect of palm, distance between *Db* and *Dt* considerably less than one-third length of palm Tribe **Belisariini**

5. Chelal fixed finger trichobothrial series *eb*–*et* found on proximal two-thirds of finger; *est*–*esb*–*eb* juncture angles away from finger edge, *eb* situated quite close to articular member of movable finger, *esb* situated more toward dorsal aspect; chelal trichobothria *Et*₃–*Et*₅ situated on distal-middle aspect of palm, *Et*₅ not on fixed finger; chelal trichobothrial series *Db*–*Dt* situated on proximal to midsegment of palm, *Db* situated proximally on palm Subtribe **Neochactina**

Chelal fixed finger trichobothrial series *eb*–*et* found on distal two-thirds of finger; *est*–*esb*–*eb* juncture angles toward finger edge, *eb* removed from articular member of movable finger, *esb* situated more toward finger edge; chelal trichobothria *Et*₃–*Et*₅ situated on distal-dorsal aspect of palm, *Et*₅ situated on or at base of fixed finger; chelal trichobothrial series *Db*–*Dt* situated on midsegment to distal aspect of palm, *Db* situated proximal to midsegment on palm Subtribe **Brotheina**

Subfamily Chactinae Pocock, 1893

Type Genus. *Chactas* Gervais, 1844.

Composition. This subfamily includes two tribes: Chactini (Central and South America; three genera) and Nullibrotheini (Mexico, one genus). This taxonomic arrangement of four chactid genera, as opposed to subfamily Brotheinae, is proposed here for the first time.

Distribution. North America (Mexico), Central America (Panama, Costa Rica), South America.

Biogeographic history. Chactini are found only in the tropical Central and South America (Table 10), while the tribe Nullibrotheini includes a monotypic desert genus. It is unlikely that Nullibrotheini has a recent South American origin, and therefore it could be a relict of much earlier (Pangean?) distribution of Chactinae. Disjunct distribution of some South American genera of Chactini can be attributed to the recent (Pleistocene) fluctuations of tropical rainforest (Lourenço, 1988, 1994, 1996b).

Diagnosis. Synapomorphies. Chelal trichobothria *Db* basal, *Dt* situated at palm midpoint; patellar trichobothria series *em₁-em₂* and *esb₁* proximal of segment midpoint; neobothriotaxy *Ch1* present on patellar ventral surface; neobothriotaxy *Ch1* present on patellar external surface. Important Sympletiomorphies. Hemispermatophore truncal flexure absent; hemispermatophore lamina terminus tenuous, thin, highly tapered; stigma shape small and circular.

Tribe Chactini Pocock, 1893

Type Genus. *Chactas* Gervais, 1844.

Composition. The tribe is established here. It includes three genera (*Chactas*, *Teuthraustes*, *Vachonichactas*).

Distribution. Central and South America.

Taxonomic history. Sissom (2000a) retained the division of *Chactas* into five subgenera.

Biogeographic history. Chactini mainly inhabit the tropical South America, where they exhibit a high diversity (Table 10). A single species, *Chactas exsul*, is found in Central America (Panama, Costa Rica).

Diagnosis. Synapomorphies. Chelal finger outer denticles (OD) removed outward from the MD row; chelal finger median denticle (MD) row divided into 7–9 groups; pectinal middle lamellae composed of a single plate or two, semi-fused with anterior lamellae, fulcra quite reduced. Important Sympletiomorphies. Chelal trichobothria *Db* basal, *Dt* situated at palm midpoint; patellar trichobothria series *em₁-em₂* and *esb₁* proximal of segment midpoint; neobothriotaxy *Ch1* present on patellar ventral surface; neobothriotaxy *Ch1* present on patellar external surface.

Tribe Nullibrotheini Sologlad & Fet, new tribe

Type Genus. *Nullibrotheas* Williams, 1974.

Composition. This new monotypic tribe is described here. It includes a single monotypic genus *Nullibrotheas*.

Distribution. Mexico (southern Baja California).

Taxonomic history. The single known species of the genus *Nullibrotheas* has been originally assigned to Chactidae as “*Broteas*” or *Broteochactas* by earlier authors. Williams (1974, 1980), who described this genus, placed it in Vaejovidae. Stockwell (1989, 1992)

transferred *Nullibrotheas* back to Chactidae; see Sissom (2000a, 2000c).

Biogeographic history. Baja California Peninsula separated from the Mexican mainland ca. 5.5 Ma ago. The Cape region of Baja California Sur, where genus *Nullibrotheas* is found (Williams, 1974, 1980), has been isolated in Pliocene, which led to formation of cryptic species (Grismer, 2000; Riddle et al., 2000; Gantenbein et al., 2001a). Such an isolation could facilitate the survival of a relict lineage which led to *Nullibrotheas*.

Diagnosis. Synapomorphies. Patella external *est* series with additional accessory trichobothrium; patella ventral surface with additional accessory trichobothrium; ventral edge of cheliceral movable finger with dentition; lateral carinae of metasomal segment IV present; chelal *VI* carina distal termination curves towards the internal finger condyle. Important Sympletiomorphies. Chelal trichobothria *Db* basal, *Dt* situated at palm midpoint; patellar trichobothria series *em₁-em₂* and *esb₁* proximal of segment midpoint; neobothriotaxy *Ch1* present on patellar ventral surface; neobothriotaxy *Ch1* present on patellar external surface.

Discussion. *Nullibrotheas* shows a close affinity to its sister tribe Chactini. In particular, the unique major fixed neobothriotaxic patterns for the pedipalp patella exhibited in both, type *Ch1*, are quite distinct. All patellar external series match in position and pattern, though in *Nullibrotheas* we see an additional accessory trichobothrium in the *est* series (Fig. 86). The patellar ventral series also exhibits an additional accessory trichobothrium (six total trichobothria in the ventral series in Nullibrotheini and five in Chactini). Only one species is defined in this genus, *N. allenii*, but its range in Baja California Sur is quite extensive, extending from Mulege in central Baja to Cabo San Lucas at the Cape (Williams, 1974: Fig. 5). Within this geographical range considerable overall size differences are exhibited, populations in the La Paz area reach sizes of 60 mm, whereas adults in most other areas range from 30–45 mm. In addition, color populations are present over this distributional range. These observations (Williams, 1974) are based on the examination of over 280 specimens. Williams decided this variability best be attributed to a single variable species. In support of this conclusion, based on the limited number of specimens examined by us, we detect no variability in the number of accessory trichobothria, showing consistency to the fixed neobothriotaxic pattern exhibited in this chactid subfamily. In scorpion groups that exhibit variability in neobothriotaxy, this variability can be useful in determining phylogenetic relationships within the group (e.g., *Euscorpium*, *Anuroctonus*, *Hadrurus*).

Subfamily Brotheinae Simon, 1879, new rank

Type Genus. *Brotheas* C. L. Koch, 1837.

Synonyms.

	Panama & Costa Rica	Columbia	Ecuador	Peru	Venezuela	Brazil	Guyana	Suriname	French Guiana	Trinidad & Tobago
<i>Chactas</i>	1	11	3		14					2
<i>Teuthraustes</i>		1	11	2	6	1				
<i>Vachoniochactas</i>					2	1				
<i>Broteochactas</i>					8	2			1	1
<i>Brotheas</i>		1			14	7	2	1	2	
<i>Hadrurochactas</i>					3	3			1	
<i>Neochactas</i>		2			27	4	1		5	1
Chactinae	1	12	14	2	22	2				2
Brotheinae		3			52	16	3	1	9	2

Table 10: Distribution of chactid subfamilies Chactinae and Brotheinae in Central and South America. Data based primarily on species listed in Sissom (2000a), with addition of new data (González-Sponga, 1993, 1996a, 1997; Kovařík, 1999; Lourenço, 1999d; Lourenço & Pinto-da-Rocha, 2000; Lourenço & Dastych, 2001; Monod & Lourenço, 2001; Pinto-da-Rocha et al., 2002; Vignoli & Kovařík, 2003). Entries denote the *number* of species for each genus. Note the dominant distribution of Chactinae in northwestern to central areas and Brotheinae in north-central to eastern areas, both overlapping and concentrating in Venezuela (shaded area), which accounts for over fifty percent of the species. This concentration, however, could be an artifact due to the detailed research of M. A. González-Sponga (1996a, etc.) in Venezuela for many decades.

Belisariinae Lourenço, 1998, **new synonymy** (valid as tribe name).

Composition. This subfamily is established here. It includes two tribes, Brotheini (four genera) and Belisariini (one genus).

Distribution. Europe, South America.

Taxonomic history. The name Brotheidae, based on the type genus *Brotheas* C.L. Koch, 1837, is here taken out of synonymy (Sissom, 2000a: 288). It was never used as a valid family-group name since suggested by Simon (1879: 92) as a family Broteidae (incorrect original spelling), but remained an available synonym. Its establishment as a subfamily does not enable priority of Brotheidae Simon, 1879 over Chactidae Pocock, 1893 and Chactoidea Pocock, 1893; this situation is specifically addressed by the Article 35 of the Code (ICZN, 1999): “After 1999, if a family group name is older than a prevailing name for a higher family group rank, it does not displace the junior name”.

Biogeographic history. Disjunct range of Brotheinae is a remarkable relict feature, paralleled in scorpions at the subfamily level only in Scorpiopinae and Diplocentrinae. Both the European Belisariini (a single monotypic genus *Belisarius*) and the South American Brotheini could be relicts of much earlier (Pangean?) distribution of Chactidae. Disjunct distribution of some South American genera of Brotheini can be attributed to the recent (Pleistocene) fluctuations of tropical rainforest (Lourenço, 1988, 1994, 1996b; Monod & Lourenço, 2001).

Diagnosis. Synapomorphies. Patellar trichobothria distance between *esb*₁ and *esb*₂ is much greater than distance between *em*₁ and *em*₂; ventral surface of leg

tarsus dominated with setal pair configuration, median row of spinules essentially obsolete. Important Sympletiomorphies. Hemispermatophore truncal flexure absent; hemispermatophore lamina terminus tenuous, thin, highly tapered; stigma shape small and circular.

Tribe Brotheini Simon, 1879, new rank

Type Genus. *Brotheas* C. L. Koch, 1837.

Composition. The tribe is established here, embracing four genera from tropical South America. It is divided into two subtribes (the category not used before in scorpion systematics): Brotheina and Neochactina, established here.

Distribution. South America.

Taxonomic history. Sissom (2000a: 313) outlined an important taxonomic problem connected with the South American genera now included in the tribe Brotheini. The genus *Hadrurochactas* has often been considered a synonym of *Broteochactas*. Lourenço (1986, 1988) placed *Hadrurochactas*, along with *Auyantepuia*, *Taurepania* and *Vachoniochactas* as “species groups” in *Broteochactas*; later, however, he resurrected *Vachoniochactas* as a valid genus (Lourenço, 1994a). González-Sponga (1996a) continued to recognize *Hadrurochactas* and *Taurepania*, and these two genera therefore were listed as valid genera by Sissom (2000a), while *Auyantepuia* was listed as a synonym of *Broteochactas*. Sissom (2000a) listed only two species of *Hadrurochactas* (*H. odoardi* and *H. schaumii*). Monod & Lourenço (2001: 195–196) discussed these issues, and again considered *Hadrurochactas* a species-group of *Broteochactas* (“schaumii” group), commenting that this decision “is, however, only preliminary”. In

addition to *Broteochactas odoardo* González-Sponga, 1985 and *Broteochactas schaumii* (Karsch, 1880), Monod & Lourenço (2001) also listed in the “schaumii” group the species *Broteochactas brejo*, *Broteochactas mapuera*, and a new species, *Broteochactas polisi* Monod & Lourenço, 2001.

Diagnosis. Synapomorphies. Neobothriotaxy *Ch2* present on ventral surface of patella; neobothriotaxy *Ch2* present on external surface of patella; pectinal middle lamellae composed of one or two plates, semi-fused with anterior lamellae, fulcra if present, quite reduced. Important Sympletiomorphies. Patellar trichobothria distance between *esb*₁ and *esb*₂ is much greater than distance between *em*₁ and *em*₂; ventral surface of leg tarsus dominated with setal pair configuration, median row of spinules essentially obsolete.

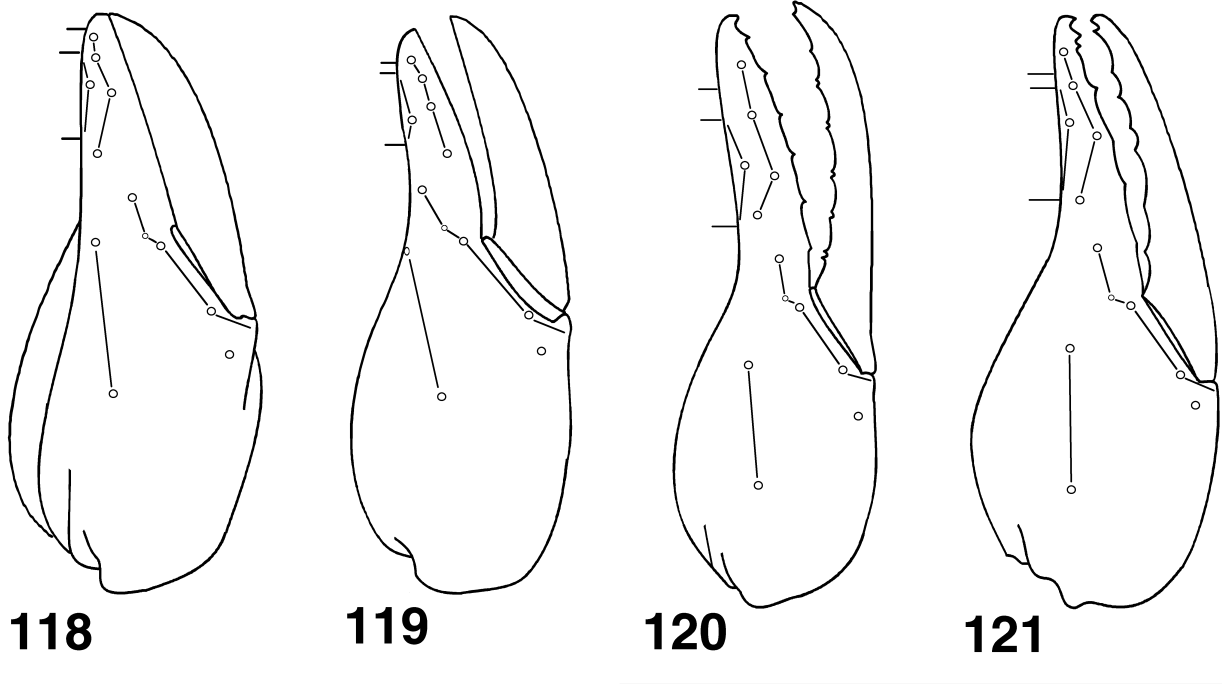
Discussion. This tribe is well-defined within the chactids by its distinct neobothriotaxy *Ch2* found on both the ventral and external surfaces of the patella. As with subfamily Chactinae, this neobothriotaxy is essentially fixed as to its number of accessory trichobothria and overall pattern distribution. Within this tribe, we can distinguish two subtribes based entirely on relative positions and configurations of key trichobothrial series of the chela. Although these diagnostic characters were briefly described in the **Character Analysis** section, we discuss them here in detail, quantifying the variability seen across the species of these two subtribes.

The primary character distinguishing two subtribes within Brotheini is the orientation of the *eb* and *esb* trichobothria. In subtribe Neochactina, the *est-esb-eb* juncture angles away from the fixed finger edge (Figs. 124–125); trichobothrium *eb* is located at the base of the fixed finger, and positioned very close to the articular membrane at the fixed/movable finger juncture; and trichobothrium *esb* is located closer to the dorsal edge of the fixed finger, removed from the finger edge. In general, the *eb-et* series is positioned on the basal two-thirds of the fixed finger. In subtribe Brotheina, the *est-esb-eb* juncture, if not straight, angles toward the fixed finger edge (Figs. 118–123); trichobothrium *eb* is removed from the finger edge, located more towards the dorsal edge of the fixed finger, never close to the articular membrane; and trichobothrium *esb* is located closer to the finger edge. In general, the *et-eb* series is located on the distal two-thirds of the fixed finger, but this is variable depending on the morphometric proportions of the chelal fingers. Vachon (1974: Figs. 224–225) first identified these differences for species *Brotheas gervaisi* (his Fig. 224) and *Neochactas delicatus* (identified by Vachon as *Broteochactas delicatus*, his Fig. 225). We follow Vachon’s designations of the *eb* and *esb* trichobothria (note that, in many of the trichobothria illustrated by González-Sponga (1996a), this author reverses the designations of *eb* and *esb*). It is important to note here that the *eb-esb* positional orientations exhibited in sub-

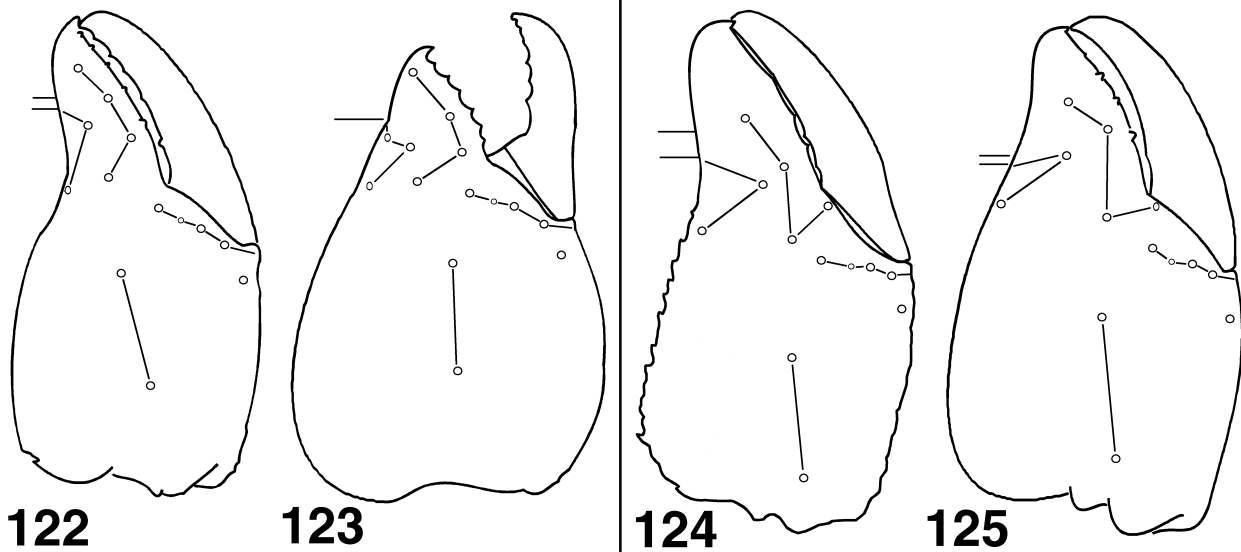
tribe Neochactina are the same as that found in the brotheine tribe Belisariini, chactid subfamilies Chactinae and Uroctoninae, and in euscorpoid subfamilies Euscorpinae and Megacorminae. Clearly this condition is relatively primitive within the clade “Euscorpidae + Chactidae” and therefore, the *eb-esb* pattern exhibited in subtribe Brotheina is *derived*. In concert with the relative positions of the *eb-et* series distinguishing the two subtribes, the *db-dt* series also reflects these distinctions; i.e., *db-dt* series is situated on the basal two-thirds of the fixed finger in Neochactina and, in contrast, is located on the midfinger to distal two-thirds in Brotheina. The second character used to diagnose these subtribes is the relative positions of the *Et*₃–*Et*₅ trichobothria. In subtribe Neochactina, these trichobothria are located on the distal aspect of the palm, below the articular membrane of the movable finger, between the fixed/movable finger juncture and the external condyle, and are never found on the fixed finger. In subtribe Brotheina, depending on the attenuation of the fingers, at least *Et*₅ is located adjacent to or dorsal of the fixed/movable finger juncture. In genus *Brotheas* and those species of *Broteochactas* that exhibit somewhat elongated fingers, *Et*₅, *Et*₄ and sometimes *Et*₃, are located dorsal of the fixed/movable finger juncture, *Et*₅ and *Et*₄ actually located on the fixed finger (Figs. 118–121). The third character distinguishing these two subtribes is the location of the *Db-Dt* series. In subtribe Neochactina, *Db* is always located considerably proximal of the midpoint of the chelal palm and *Dt* is always located proximal of the movable finger external condyle and usually proximal of trichobothrium *Est*. In Brotheina, *Db* is located close to or distal of the palm midpoint and *Dt* is usually located distal of trichobothrium *Est* and many times, on species with longer fingers, is found on the fixed finger base. Figures 118–125 illustrate these three characters showing the complete spectrum of relative locations as seen in subtribe Brotheina. Except for the very short-fingered species, *Broteochactas nitidus* (Fig. 122) and *B. scorzai* (Fig. 123), we see consistency with all diagnostic characters described above. In these short-fingered species, only the primary character, the position of trichobothria *eb* and *esb*, is the most apparent. However, by closely comparing these two species with *Neochactas sarisarinamensis* (Fig. 124) and *N. laui* (Fig. 125), the subtle differences between the relative positions of *Et*₅–*Et*₃ and *Db-Dt* series are evident.

It is interesting to point out here that, when González-Sponga (1978) created genus *Auyanteputia* to distinguish species *Broteochactas scorzai* from other species of *Broteochactas*, he used, in part, the primary diagnostic character presented here to distinguish the two Brotheini subtribes. In particular, González-Sponga attributed the pattern we define, in part, for subtribe Brotheina, to his new genus *Auyanteputia*. Francke & Boos (1986) discussed González-Sponga’s result and

Brotheina



Neochactina



Figures 118-125: Diagrammatic trichobothrial pattern of chela external surface (partial) of Brotheinae tribe Brotheini showing relative positions of trichobothrial series *eb-et*, *db-dt*, *Et₂-Et₅*, *Est*, and *Db-Dt* for subtribes Brotheina and Neochactina. **118.** *Brotheas cunucunumensis* González-Sponga, 1984 (after González-Sponga (1996a), in part). **119.** *Broteochactas venezuelensis* (González-Sponga, 1996) (after González-Sponga (1996b), in part). **120.** *Hadrurochactas odoardo* González-Sponga, 1985 (after González-Sponga (1996a), in part). **121.** *Broteochactas porosa* Pocock, 1900 (after González-Sponga (1996a), in part). **122.** *Broteochactas nitidus* Pocock, 1893 (after Francke & Boos, 1986, in part). **123.** *Broteochactas scorzai* Dagert, 1957 (after González-Sponga (1996a), in part). **124.** *Neochactas sarisarinamensis* (González-Sponga, 1985) (after González-Sponga (1996a), in part). **125.** *Neochactas laui* (Kjellesvig-Waering, 1966) (after Francke & Boos, 1986, in part).

dismissed it because the character was not consistent within species of *Broteochactas* (i.e., they examined species which exhibited both the Neochactina and Brotheina *eb-esb* patterns described in this paper).

Francke & Boos's logic for rejecting *Auyantepuia* is not particularly sound here, since González-Sponga created the new genus to accommodate these distinctions. However, whether or not one accepts Francke & Boos's reason for rejecting *Auyantepuia*, the point becomes mute. This is because Francke & Boos (1986) redescribed *Broteochactas nitidus*, based on a lectotype designated by them, thus confirming it as the type species of *Broteochactas*. Since this type species exhibits the same pattern as attributed to *Auyantepuia* by González-Sponga, and our subtribe Brotheina, *Auyantepuia*, in our opinion, remains a synonym of *Broteochactas*. This, in turn, requires that those species of *Broteochactas* González-Sponga contrasted with *Auyantepuia* must be placed in a different genus. We do this here by establishing the new genus *Neochactas*, which becomes the type genus for subtribe Neochactina. We discuss below in the appropriate subtribe sections the reallocation of species of the tribe Brotheini necessitated by this change.

Subtribe Brotheina Simon, 1879, new rank

Type Genus. *Brotheas* C. L. Koch, 1837

Composition. This new subtribe is established here. It includes three genera: *Brotheas* C. L. Koch, 1837; *Broteochactas* Pocock, 1893 (= *Auyantepuia* González-Sponga, 1978; = *Taurepania* González-Sponga, 1978, **syn. n.**; = *Cayooca* González-Sponga, 1996, **syn. n.**; = *Guyanochactas* Lourenço, 1998, **syn. n.**); and *Hadrurochactas* González-Sponga, 1978. The genera *Cayooca*, *Guyanochactas*, and *Taurepania* are here synonymized with *Broteochactas* for the reasons given below. The genus *Brotheas* remains as originally defined, and there are no changes to its species content. The content of the genus *Broteochactas* is changed here, as a large number of species are transferred from *Broteochactas* to the new genus *Neochactas* (subtribe Neochactina), and at the same time all species formerly assigned to genera *Cayooca*, *Guyanochactas*, and *Taurepania* are transferred to *Broteochactas*. The following species are transferred to *Broteochactas*: from *Cayooca*: *Broteochactas venezuelensis* (González-Sponga, 1996), **comb. nov.** (type species of *Cayooca*); from *Guyanochactas*: *Broteochactas gonzalezspongai* (Lourenço, 1988), **comb. nov.** (type species of *Guyanochactas*); *B. gougei* Vellard, 1932, **comb. nov.**; *B. mascarenhasi* (Lourenço, 1988), **comb. nov.**; from *Taurepania*: *Broteochactas manisapanensis* (González-Sponga, 1992), **comb. nov.**; *B. porosus* Pocock, 1900, **comb. nov.** (type species of *Taurepania*); *B. trezzii* (Vignoli & Kovařík, 2003), **comb. nov.**; *B. verneti* (González-Sponga, 1992), **comb. nov.**; *B. vestigialis* (González-Sponga, 1978), **comb. nov.** The following three species remain in *Broteochactas*: *Broteochactas nitidus* Pocock, 1893 (type species), *B. gollmeri* (Karsch, 1879), and *B. scorzai* Dagert, 1957. Since we consider *Hadrurochactas* a valid genus (see

below), we transfer to this genus three Brazilian species from *Broteochactas*: *Hadrurochactas brejo* (Lourenço, 1988), **comb. nov.**; *H. mapuera* (Lourenço, 1988), **comb. nov.**; and *H. polisi* (Monod & Lourenço, 2001), **comb. nov.** In addition, one more species not listed in González-Sponga (1996a) and Sissom (2000a), *H. machadoi* González-Sponga, 1993, belongs to *Hadrurochactas*.

Distribution. South America.

Diagnosis. Synapomorphies. Chela trichobothria *Db* situated close to palm midpoint, *Dt* well past palm midpoint, distal of trichobothrium *Est*; chelal trichobothrial series *eb-et* positioned on finger distal two-thirds; *est-esb-eb* juncture angles toward fixed finger edge, *eb* removed from finger edge; chelal *Et₅* situated at base or on fixed finger. Important Sympletiomorphies. Neobothriotaxy *Ch2* present on ventral surface of patella; neobothriotaxy *Ch2* present on external surface of patella; pectinal middle lamellae composed of one or two plates, semi-fused with anterior lamellae, fulcra if present, quite reduced.

Discussion. The genus-level taxonomy of tribe Brotheini is uncertain due to the dubious definition of several genera, which attempt to organize the many species described in the last 25 years. To exasperate this situation, many of these species were defined from few specimens and few localities (Sissom, 2000a). Although we are not in a position to determine the validity of the 75+ species comprising this subtribe, we do evaluate here the current characters now used to define the various genera comprising this subtribe. We briefly list the diagnostic characters currently used to identify these genera, most of which are derived from keys and diagnoses presented by González-Sponga (1996a), Lourenço (1998d), and Monod & Lourenço (2001).

Genus *Brotheas* C.L. Koch, 1837: distinguished by its large, elongated stigmata (González-Sponga, 1996a and Lourenço, 1998d); carapace surface convex, covered with dense granulation and punctation (González-Sponga, 1996a); ventral surface of leg tarsus with well-developed, evenly positioned setal pairs (Lourenço, 1998d).

Genus *Broteochactas* Pocock, 1893: distinguished by small, oval to round stigmata (González-Sponga, 1996a and Lourenço, 1998d); carapace surface flat, smooth and shiny (González-Sponga, 1996a); ventral surface of leg tarsus with numerous bristle-like, irregularly positioned setae (González-Sponga, 1996a and Lourenço, 1998d); pectinal teeth number 9–11 (González-Sponga, 1996a).

Genus *Cayooca* González-Sponga, 1996: distinguished by eight trichobothria on the patella ventral surface (all characters from González-Sponga, 1996b); carapace broad and flat; ventral surface of leg tarsus with well-developed, evenly positioned setal pairs; stigmata small and oval.

Genus *Guyanochactas* Lourenço, 1998: distinguished by oval to round stigmata (all characters from Lourenço, 1998d); ventral surface of leg tarsus with well-developed, evenly positioned setal pairs; 45–65 mm. in length.

Genus *Hadrurochactas* Pocock, 1893: distinguished by a subaculear tooth on the telson vesicle (González-Sponga, 1996a and Monod & Lourenço, 2001); telson vesicle very flat laterally (Monod & Lourenço, 2001); adults not exceeding 24 mm (González-Sponga, 1996a).

Genus *Taurepania* González-Sponga, 1978: distinguished by absence of pectinal fulcra (all characters from González-Sponga, 1996a); carapace surface flat, smooth and shiny; ventral surface of leg tarsus with numerous bristle-like, irregularly positioned setae; pectinal teeth number 5–8.

By studying the diagnostic characters listed above, we see that *Brotheas* is unique with its large slit-like stigmata, a character unprecedented in the families Chactidae, Euscorpiidae, and Superstitioniidae, and only found elsewhere in the chactoids in family Vaejovidae. Therefore, within this special context, the slit-like stigma is an important character. Otherwise, the stigma shape of small, oval to round, cannot be used to separate other genera. Secondary characters distinguishing *Brotheas* are the granulated and convex carapace surface, and the well-developed evenly positioned setal pairs of the ventral surface of the leg tarsus. However, these two characters are also found in the genus *Guyanochactas*. *Broteochactas* is distinguished from *Brotheas* and *Guyanochactas* by its bristle-like, irregularly positioned setal pairs of the ventral surface of the leg tarsus, but this condition is also matched in genera *Taurepania* and *Hadrurochactas*. *Taurepania* is stated to have pectinal tooth counts ranging from 5–8, but in the individual species descriptions (González-Sponga, 1996a; Vignoli & Kovářik, 2003), we see a range from 4 to 12 (includes both genders). Also, all five species of *Taurepania* are lacking pectinal fulcra, potentially a good diagnostic character. However, González-Sponga (1996a) states that fulcra are optionally present in genera *Brotheas* and *Broteochactas* thus this cannot be used as a reliable character for *Taurepania*, especially between it and *Broteochactas*. Genus *Cayooca* is defined from a single species based on a single specimen, and its only distinguishable character is an extra accessory trichobothrium on the ventral surface of the patella. Considering its leg tarsus armature, *Cayooca* is indistinguishable from *Guyanochactas*, except for this extra trichobothrium. It appears that smaller species in this subtribe have a tendency for more numerous, thinner bristle-like, and irregularly positioned tarsal setae. In the larger species, exemplified by *Brotheas*, we see a lower number of stouter, more regularly positioned setal pairs. This same trend is also present in the subfamily Chactinae, where

the setal pairs are very numerous and elongated in the small genus *Vachoniochactas*, which also exhibits a reduced to obsolete median spinule row. Genus *Hadrurochactas* is diagnosed by González-Sponga (1996a) by its small size and “subaculear tooth”. Yet in González-Sponga’s (1996a) figures, we see that *H. odoardo* is lacking this structure. However, Monod & Lourenço (2001), referring to this genus as the “schaumii” group within genus *Broteochactas*, considered it a legitimate taxonomic group. They included five species, *Broteochactas polisi*, *B. schaumii*, *B. brejo*, *B. mapuera*, and *B. odoardo*. Their depiction of the “subaculear tooth” (their Figs. 5–8) is a much better description of this structure, where they define it as a granulated carina. In our specimen of *H. schaumii*, we see five delicate irregular granulated carinae extending along the ventral surface of the telson vesicle, the median carina with slightly elongated spines, extending to the vesicle/aculeus juncture, the so-called “subaculear tooth”. In addition to these granulated carinae, the vesicle of these species is quite flat when viewed laterally. Interestingly, we see an analogous situation with the equally small chactine genus *Vachoniochactas* which also exhibits a median carina on the ventral surface of the vesicle, terminating in a series of 1–2 pointed granules at the vesicle/aculeus juncture, also termed a “subaculear tooth” by González-Sponga (1978).

Based on the consistency within these unique characters across several species, we consider *Hadrurochactas* a valid genus as originally recognized by Pocock (1893) and listed in Sissom (2000a). In addition, we also recognize *Brotheas* and *Broteochactas* as valid, comprising the stem genera of this subtribe. However, we do not believe *Guyanochactas* (which is nothing but a large *Broteochactas* with well-developed tarsal setal pairs), *Taurepania* (which is not adequately separable from *Broteochactas*), and *Cayooca* (which is based on a single specimen) are valid genera, and therefore synonymize all three with genus *Broteochactas*.

Subtribe Neochactina Soleglad & Fet, new subtribe

Type Genus. *Neochactas* Soleglad & Fet, new genus.

Composition. This new monotypic subtribe is described here.

Distribution. South America.

Diagnosis. Synapomorphies. Chelal trichobothrium *Db* situated proximally on palm base, trichobothrium *Dt* distal of midpoint but proximal of trichobothrium *Est*. Important Sympleiomorphies. Neobothriotaxy *Ch2* present on ventral surface of patella; neobothriotaxy *Ch2* present on external surface of patella; pectinal middle lamellae composed of a one or two plates, semi-fused with anterior lamellae, fulcra if present, quite reduced; chelal trichobothrial *est-esb-eb* configuration angles away from fixed finger edge, *eb* close to finger edge.

Discussion. This subtribe is the most primitive component in tribe Brotheini, where the juncture of trichobothria *est-esb-eb* angles away from the fixed finger edge, a condition commonly found in many of the chactoids. This orientation of *est-esb-eb*, plus the more basal positioning of the *Db-Dt* and *Et₃-Et₅* trichobothrial series, separate *Neochactina* from its sister subtribe *Brotheina*.

***Neochactas* Soleglad & Fet, gen. nov.**

Type species. *Broteochactas laui* Kjellesvig-Waering, 1966

Composition. Based on the trichobothrial patterns reported in literature (Lourenço, 1983; Francke & Boos, 1986; González-Sponga, 1996a, 1997; Lourenço & Pinto-da-Rocha, 2000), as well as analysis of some type material, the majority of species formerly included in *Broteochactas* belong to *Neochactas*. The following 36 species are transferred from *Broteochactas* to *Neochactas* (species whose trichobothria patterns have not been verified are indicated with an asterisk): *Neochactas bariensis* (González-Sponga, 1991), **comb. nov.**; *N. bilbaoi* (González-Sponga, 1978), **comb. nov.**; *N. bruzuali* (González-Sponga, 1980), **comb. nov.**; *N. caroniensis* (González-Sponga, 1996), **comb. nov.**; *N. colombiensis* (González-Sponga, 1976), **comb. nov.**; *N. delicatus* (Karsch, 1879), **comb. nov.**; *N. efeni* (González-Sponga, 1978), **comb. nov.**; *N. eliasilvai* (González-Sponga, 1980), **comb. nov.**; *N. fei* (Pinto-da-Rocha et al., 2002), **comb. nov.**; *N. fravalae* (Lourenço, 1983), **comb. nov.**; *N. gaillardii* (Lourenço, 1983), **comb. nov.**; *N. garciai* (González-Sponga, 1978), **comb. nov.**; *N. granosus* (Pocock, 1900), **comb. nov.**; *N. guaiquinimensis* (González-Sponga, 1997), **comb. nov.**; **N. jaspei* (González-Sponga, 1993), **comb. nov.**; *N. josemanueli* (González-Sponga, 1992), **comb. nov.**; *N. kelleri* (Lourenço, 1997), **comb. nov.**; *N. kjellesvigi* (González-Sponga, 1992), **comb. nov.**; *N. laui* (Kjellesvig-Waering, 1966), **comb. nov.**; *N. leoneli* (González-Sponga, 1978), **comb. nov.**; *N. neblinensis* (González-Sponga, 1991), **comb. nov.**; *N. orinocensis* (Scorza, 1954), **comb. nov.**; *N. panarei* (González-Sponga, 1980), **comb. nov.**; *N. paoensis* (González-Sponga, 1996), **comb. nov.**; *N. parvulus* (Pocock, 1897), **comb. nov.**; *N. racenisi* (González-Sponga, 1975), **comb. nov.**; *N. riopinensis* (González-Sponga, 1992), **comb. nov.**; **N. ruizpittoli* (González-Sponga, 1993), **comb. nov.**; *N. sanmartini* (González-Sponga, 1974), **comb. nov.**; *N. santanai* (González-Sponga, 1978), **comb. nov.**; *N. sarisarinamensis* (González-Sponga, 1985), **comb. nov.**; *N. simarawochensis* (González-Sponga, 1980), **comb. nov.**; *N. sissomi* (Lourenço, 1983), **comb. nov.**; *N. skuki* (Lourenço & Pinto-da-Rocha, 2000), **comb. nov.**; **N. verai* (González-Sponga, 1993), **comb. nov.**; *N. yekuanai* (González-Sponga, 1984), **comb. nov.**

Diagnosis. Same as subtribe *Neochactina*.

Tribe Belisariini Lourenço, 1998, new status

Type Genus. *Belisarius* Simon, 1879.

Composition. This new monotypic tribe includes monotypic genus *Belisarius*. The former subfamily *Belisariinae* is downgraded here to the tribe rank under the subfamily *Brotheinae*.

Distribution. Europe (France, Spain).

Taxonomic history. Tribe *Belisariini* corresponds to the subfamily *Belisariinae* introduced by Lourenço (1998a; incorrect original spelling *Belisariinae*) who followed unpublished classification of Stockwell (1989). *Belisariinae* was originally placed in the family *Troglo-tayosicidae* (Fet & Sissom, 2000b).

Biogeographic history. This unique, relict genus is the only Old World taxon belonging to the family *Chactidae*. This remarkable blind scorpion, which lives in litter and caves in the Pyrenees, has not been sufficiently studied; accounts of distribution and biology were given by Vachon (1945), Auber (1961), and Lacroix (1992).

Diagnosis. Synapomorphies. Chelal trichobothrial series *Db-Dt* very basal, distance between *Db* and *Dt* quite small; pectinal fulcra absent. **Important Sympleiomorphies.** Patellar trichobothria distance between *esb₁* and *esb₂* much greater than distance between *em₁* and *em₂*; ventral surface of leg tarsus dominated with setal pair configuration, median row of spinules essentially obsolete; orthobothriotaxic.

Discussion. Taxonomic position of this genus has recently been influenced by its cave adaptations, i.e. the loss of eyes and pectinal fulcra. Both Stockwell (1989) and Lourenço (1998a) placed *Belisarius* in groups that were dominated by these suspect characters. It is important that *Belisarius*, along with genus *Uroctonus*, are the only members of *Chactidae* that exhibit orthobothriotaxy. The trichobothrial patterns of these two genera are remarkably similar (see Figs. 81 and 87). Moreover, the trichobothrial patterns found in these two scorpion genera play the key role in determining homologous orthobothriotaxic trichobothria in the other chactid genera which exhibit major neobothriotaxy. Of particular importance is the somewhat basal positioning of the patellar ventral trichobothria, *v₁-v₃*, and the overall position and orientation of external series *esb₁-esb₂*. See discussion under subfamily *Superstitioniinae* for more details on the previous taxonomic position of *Belisarius*.

Subfamily Uroctoninae Mello-Leitão, 1934

Type Genus. *Uroctonus* Thorell, 1876.

Composition. This subfamily, as defined here, includes two genera, *Anuroctonus* and *Uroctonus*. The subfamily name is here taken out of synonymy, where it was available under the family *Vaejovidae* (Sissom, 2000c: 504), and transferred to *Chactidae*. We transfer to *Uroctoninae* genus *Anuroctonus*, which was previously listed in *Iuridae* (Sissom & Fet, 2000b).

Distribution. North America (Mexico, USA).

Taxonomic history. Stockwell (1989) used this name as a tribe rank in Vaejovidae but this change remained unpublished. Two genera, which are included here, are transferred from Iuridae (*Anuroctonus*) and Vaejovidae (*Uroctonus*). Placement of *Anuroctonus* was uncertain for many years: it was placed in Hadrurinae by Stahnke (1974; under Vaejovidae) and Stockwell (1989, 1992; under Iuridae), and treated as a genus *incertae sedis* by Francke & Soleglad (1981) and Sissom (1990). The genus was listed under Iuridae (subfamily Hadrurinae) by Sissom & Fet (2000b). Here, we follow Werner (1934) in placing *Anuroctonus* under Uroctoninae.

Biogeographic history. The two North American genera of Chactidae, *Anuroctonus* and *Uroctonus*, are sister taxa, ecologically divergent. *Anuroctonus* is a typical desert borrowing scorpion, found in California, Nevada, Utah, and Idaho (USA), and also in Mexico (Baja California Norte). *Uroctonus* is a less xeric species, found in western states of USA (California, Oregon) from sea coast to 2400 m in the montane forests (Gertsch & Soleglad, 1972; Williams, 1986; Sissom, 2000c). Interestingly, the two genera are essentially allopatric in coastal California, *Anuroctonus* replacing *Uroctonus* south of the Monterey Peninsula (Hjelle, 1972: Figs. 49–50), extending south into Baja California and east into the Great Basin. In central-eastern California, their ranges somewhat overlap, especially in Kern, Los Angeles, and Inyo counties. Interestingly, the isolated species *Uroctonus franckei* Williams, only reported at altitudes 2133 m or higher, occurs in the same area as *Anuroctonus phaiodactylus*, in the high eastern Sierra Nevada (Williams, 1986). We have examined specimens of *A. phaiodactylus* from the general type locality of *U. franckei*, but from a somewhat lower altitude (1244 m).

Relationship between Uroctoninae and the other two chactid subfamilies is unclear. It is unlikely that Uroctoninae has a recent South American origin, and therefore it could be a relict of much earlier distribution of Chactidae. The separation and isolation of chactid subfamilies between South America and North America could result from the decoupling of the North American and South American plates, which played a prominent role in formation of the Caribbean region in late Mesozoic–early Tertiary (Rosen, 1976; Francke & Soleglad, 1981).

Diagnosis. Synapomorphies. Patellar trichobothria distance between esb_1 and esb_2 considerably greater than distance between em_1 and em_2 ; ventral edge of cheliceral movable finger with dentition; chelal carina VI distally curves internal towards internal condyle of finger; patellar spurs DPS and/or VPS well-developed; stigma medium to long in size, oval in shape; 3–4 lateral eyes present. Important Sympleisiomorphies. Femur trichobothrium d positioned equal or distal to i ; chelal trichobothrium Eb_1 situated on ventral surface or on VI

carina; genital operculum of female separated for most of its length.

Discussion. Establishment of this subfamily in Chactidae involved the transfer of two genera from other families, *Uroctonus* from Vaejovidae, and notably, *Anuroctonus*, from a different superfamily, Iuroidea.

Uroctonus. *Uroctonus* has long been a member of family Vaejovidae. Interestingly, the two genera now comprising Uroctoninae were considered related by earlier workers, having shared the same vaejovid subfamily Uroctoninae (old definition, as recognized by Mello-Leitão (1934: 81)) with genera *Uroctonoides* Chamberlin (= *Teuthraustes*, synonymized by Soleglad, 1973), and *Physoactonus* Mello-Leitão (= *Rhopalurus*, fam. Buthidae, synonymized by Francke, 1977). These genera were separated from Vaejovinae, in part, by their reduced number of pectinal middle lamellae, a somewhat minor and superficial character for subfamilial distinctions. Gertsch & Soleglad (1972) named several new species which they placed in genus *Uroctonus*. The primary character used for this placement was the crenulation found on the ventral edge of the cheliceral movable finger; in addition, secondary characters included the robust pedipalp chelae, the indentation on the anterior edge of the carapace, and reduced pectinal tooth counts. In general, these characters taken together, which were shared with *Uroctonus*, were unprecedented in the vaejovids. Issues involving trichobothria positions were not considered at that time since the use of trichobothriotaxy was new to the North American systematists (albeit Gertsch & Soleglad (1972) illustrated some of the first trichobothrial patterns of North American scorpion genera.). Based on other characters, Stahnke (1974) rejected the inclusion of most of these species in *Uroctonus* (he, correctly, only accepted *U. grahmi*), placing them in genus *Vaejovis*. Stockwell (1992) then moved most of these species into *Pseudouroctonus*, a genus originally created by Stahnke (1974) for species *P. reddelli*. Williams & Savary (1991) created *Uroctonites* for three of these species placed in *Pseudouroctonus* as well as naming a new fourth species. Stockwell (1989) offered the only cladistic treatment of these genera, considering the clade “*Pseudouroctonus* + (*Uroctonites* + *Uroctonus*)” monophyletic in Vaejovidae. Therefore, whether one agreed or not to which species belonged in *Uroctonus*, there seemed to be general agreement that they were all closely related. In this present study, we disagree with this conclusion, transferring *Uroctonus* to the family Chactidae. This transfer is based on several key positions of orthobothriotaxic trichobothria, involving both the chela (the *ib–it*, *eb–et*, and $V_1–V_4$ series) and the patella (the ventral location of trichobothrium v_3). Secondary characters such as the completely separated genital operculum of the female and the termination of the dorsal lateral carinae of metasomal segment IV coinciding with the articulation condyle, are exhibited in

Uroctonus and other chactids but are not found in the vaejovids.

Anuroctonus. Although Stockwell (1992) formally transferred *Anuroctonus* to the family Iuridae (now superfamily Iuroidea), much of the foundation for this move was established earlier in his unpublished dissertation (Stockwell, 1989), where he hypothesized that *Anuroctonus* is the sister genus to *Hadrurus*. It is of interest here to note that, out of 137 single state characters defined by Stockwell (1989), *only one* differed across the genera *Hadrurus* and *Anuroctonus*, that dealing with the arrangement of the chelal median denticle (MD) row (we discuss this below). In 1992, Stockwell presented his rationale for moving *Anuroctonus* to the iuroids. First, Stockwell limited his choices for *Anuroctonus* placement (it was *incertae sedis* at the time) to either Vaejovidae or Iuroidea, completely dismissing Chactidae. Chactidae was not considered as an alternative because all pedipalp patellar ventral trichobothria were restricted to the ventral surface in this family, and therefore, it was noticed in contrast that one or more ventral trichobothria are found on the external surface in Vaejovidae and Iuroidea. Although we consider the displacement of patellar ventral trichobothria to the external surface an important derivation *if they are orthobothriotaxic*, we do not necessarily think it is important if the trichobothrium in question is *accessory* (i.e., unlike the orthobothriotaxic trichobothrium, the accessory trichobothrium did not move to the external surface—it originated there). *Anuroctonus* and *Hadrurus* both exhibit major neobothriotaxy and both share the unusual feature of the patellar ventral series “wrapping” around distally to the external surface. We agree with Stockwell that some of these displaced trichobothria in *Hadrurus* probably do involve trichobothrium v_3 because this trichobothrium is also found on the external surface in all other members of Iuroidea. However, we cannot make this same assumption with *Anuroctonus*. The trichobothria extending to the external surface are located on the extreme distal aspect of the segment (Fig. 82). If *Anuroctonus* belongs to Chactidae, an option Stockwell should have considered as well, then we can equally conclude that these trichobothria are much too distal to include v_3 —thus this important derivation is absent in this genus, therefore eliminating any connection with *Hadrurus*. This alternative conclusion is based on two orthobothriotaxic chactid genera (*Belisarius* (Fig. 87) and *Uroctonus* (Fig. 81)), where we see that v_3 is located more midsegment. Therefore, in Stockwell’s argument, he *must assume Anuroctonus* belongs to either Vaejovidae or Iuridae in order to conclude that v_3 indeed is one of these trichobothria found on the external surface—clearly a circular argument. Chactidae is an equally valid alternative. In our argument we use positions of important orthobothriotaxic trichobothria of the

chela to form a connection between *Anuroctonus* and the chactids and then, based on this connection, can conclude that v_3 is indeed located on the ventral surface, not on the external surface as assumed by Stockwell. Stockwell also considered major neobothriotaxy as a common character between these two genera, which is true, but it certainly is not unique and he did not present arguments for establishing that they had the same derivation (i.e., major neobothriotaxy is quite common in the chactoids and scorpionoids). For example, in genera *Paravaejovis* and *Anuroctonus*, the ventral trichobothria of the chela extend to the external surface of the palm (Figs. 66 and 82), but they do not extend to the external surface in *Hadrurus*. The somewhat unique fully separated genital operculum found in the females of *Hadrurus* and *Anuroctonus* is another character Stockwell thought important; again, however, this same condition is also found in the chactids. Finally, more important than any of these characters offered by Stockwell (1992), are the dentition of ventral edge of the cheliceral movable finger, the alignment of the median denticle (MD) row of the chelal finger, and the unique spinule configuration of ventral surface of the leg tarsus. Stockwell (1989) considered the small denticle(s) found on the base of the ventral edge of the cheliceral movable finger of *Anuroctonus* to be homologous to the large single denticle found in Iuroidea. We refute this homology for two reasons: 1) small denticle(s) are not homologous to a large single denticle, which is consistently found in, and only in, the iuroids; 2) the presence of minor crenulation on the ventral edge of the cheliceral movable finger is not unusual in the chactoids, so the necessity to consider the minor dentition found in *Anuroctonus* and not other similar crenulations found in some vaejovids (e.g., *Paruroctonus gracilior*, *P. stahnkei*, etc.), homologous to the substantial tooth found in Iuroidea, is clearly arbitrary and therefore unfounded. All iuroids have their median denticle (MD) groups of the chelal finger aligned obliquely; the MD row is straight in *Anuroctonus*, as it is in most chactoids. We have demonstrated in this paper that the oblique MD groups exhibited in the iuroids are directly inherited from the primitive condition as found in the primitive parvorders Pseudochactida, Buthida, and Chaerilida (which those parvorders, in turn, inherited from the fossil orthosterns such as palaeopisthacanthids). *Anuroctonus* inherited the straight MD row from an earlier derivation which occurred at the node “Scorpionoidea + Chactoidea”. [Note: the obliquely arranged MD row found in the chactoid family Superstitioniidae is considered a “recent” secondary derivation from a straight MD row]. It was established in this paper (see **Character Analysis** section) that the ventral armature of the leg tarsus found in all five iuroid genera is based on a unique spinule cluster configuration. In genus *Hadrurus* the spinule clusters, which are quite exaggerated in its sister subfamily Caraboctoninae, are fused

into a solid “spinule-looking” structure. In *Anuroctonus* we see the conventional spinule row common to chactid subfamilies Chactinae and Uroctoninae. Of course, Stockwell (1989, 1992) was not aware of this unique development of the iuroid leg tarsus median spinule row.

Family Euscorpiidae Laurie, 1896

Type Genus. *Euscorpius* Thorell, 1876.

Synonyms.

Scorpiopidae Kraepelin, 1905 (valid as subfamily name).

Composition. The family includes three subfamilies (Euscorpiinae, Megacorminae, Scorpiopinae) and 11 genera (Soleglad & Sissom, 2001).

Distribution. Europe, Asia, Africa (Mediterranean Sea coast), North America, South America.

Taxonomic history. This taxon was originally introduced as a subfamily of Chactidae. It was formally elevated to the family level by Stockwell (1992), and listed as a family in Fet & Sissom (2000a). Recently, Soleglad & Sissom (2001) conducted a detailed phylogenetic analysis of Euscorpiidae, and introduced a number of sweeping taxonomic changes. They included in Euscorpiidae the former family Scorpiopidae, transferred the genus *Chactopsis* from Chactidae, and introduced subfamilies and tribes. Soleglad & Sissom (2001) demonstrated the relationship of euscorpiid subfamilies as (Euscorpiinae, (Megacorminae, Scorpiopinae)).

Biogeographic history. The euscorpiids cover a remarkable disjunct range, which includes Europe and West Asia (Euscorpiinae), South and Southeast Asia (Scorpiopini), South America (Chactopsini), and North America (Troglocormini, Megacorminae). Such a disjunction could indicate an ancient (Mesozoic?) age of Euscorpiidae, and could be explained by its Laurasian origin and subsequent differential extinction (Nenilin & Fet, 1992), with migration of Chactopsini to South America. Absence of xeric taxa is notable in this family.

Diagnosis. See Soleglad & Sissom (2001) for details.

Subfamily Euscorpiinae Laurie, 1896

Type Genus. *Euscorpius* Thorell, 1876.

Composition. This monotypic subfamily includes a single genus, *Euscorpius* (Soleglad & Sissom, 2001).

Distribution. Europe, Asia (Turkey, Caucasus), Africa (Mediterranean Sea coast). Introduced to England, Yemen, Uruguay (Fet & Sissom, 2000a).

Taxonomic history. For a long time, the genus *Belisarius* (now in Chactidae) was placed here (largely due to geographic proximity) until it was transferred to Superstitioniidae by Stockwell (1992). The genus *Euscorpius* includes four subgenera (Fet & Sissom, 2000a; Gantenbein et al., 1999); our ongoing revision (Fet & Soleglad, in progress) is likely to justify a genus rank for some if not all of them.

Biogeographic history. Representatives of *Euscorpius* inhabit a wide variety of habitats from sea level to high mountains (over 2000 m in the Alps, Balkans and Taurus). A complex taxonomy of this genus follows its ancient history around the changing Mediterranean Sea (Birula, 1917a, 1917b) and only recently became a subject of a detailed study using rich morphological data and modern DNA techniques (Gantenbein et al., 1999, 2000, 2001b, 2002; Fet, 2003; Fet et al., 2002, 2003c; Fet & Soleglad, 2002).

Diagnosis. See Soleglad & Sissom (2001) for details.

Subfamily Megacorminae Kraepelin, 1905

Type Genus. *Megacormus* Karsch, 1881.

Composition. The subfamily includes two tribes, Chactopsini and Megacormini, introduced by Soleglad & Sissom (2001).

Distribution. North America (Mexico), South America.

Taxonomic history. This taxon was originally introduced as a subfamily of Chactidae. Soleglad (1976b) and Francke (1979) suggested that megacormines are closely related to euscorpiines. It was listed in Chactidae by Sissom (1990), and considered a synonym of Euscorpiidae by Fet & Sissom (2000a).

Biogeographic history. The megacormines are a New World subfamily with a disjunct distribution of tribes Chactopsini (South America) and Megacormini (Mexico).

Diagnosis. See Soleglad & Sissom (2001) for details.

Tribe Chactopsini Soleglad & Sissom, 2001

Type Genus. *Chactopsis* Kraepelin, 1912.

Composition. This monotypic tribe includes a single genus, *Chactopsis* (Soleglad & Sissom, 2001).

Distribution. South America (Brazil, Peru, Venezuela).

Taxonomic history. *Chactopsis* was transferred from Chactidae to Euscorpiidae by Soleglad & Sissom (2001) who established a separate tribe for this genus.

Diagnosis. See Soleglad & Sissom (2001) for details.

Tribe Megacormini Kraepelin, 1905

Type Genus. *Megacormus* Karsch, 1881.

Composition. This tribe includes two genera: *Megacormus* and *Plesiochactas* (Soleglad & Sissom, 2001).

Distribution. North America (Mexico).

Taxonomic history. The tribe was established by Soleglad & Sissom (2001).

Diagnosis. See Soleglad & Sissom (2001) for details.

Subfamily Scorpiopinae Kraepelin, 1905

Type Genus. *Scorpiops* Peters, 1861.

Composition. The subfamily includes two tribes, Scorpiopini and Troglacormini, and seven genera (Soleglad & Sissom, 2001).

Distribution. North America (Mexico), Asia (south and southeast).

Taxonomic history. This taxon was originally introduced as a subfamily of Vaejovidae (under Scorpiopinae, incorrect original spelling) where it persisted for a long time (Stahnke, 1974), although this placement was considered not satisfactory (Sissom, 1990). The subfamily Scorpiopinae was formally elevated to the family level by Stockwell (1992), confirmed by Lourenço (1998c), and listed as a family in Fet (2000h) who corrected the name spelling to Scorpiopidae. A revision of this family was published by Kovařík (2000a). Most recently, Scorpiopidae was downgraded to a subfamily of Euscorpiidae by Soleglad & Sissom (2001), who also introduced two tribes, so that the content of family Scorpiopidae as given in Fet (2000h) and Kovařík (2000a) now corresponds to the tribe Scorpiopini.

Biogeographic history. The scorpiopines exhibit a spectacular disjunction between their main range in tropical Asia (a diverse tribe Scorpiopini), and the New World (Mexico) range of the tribe Troglacormini (which survives only as a cave genus *Troglacormus*). Such a disjunction could indicate an ancient age of Scorpiopinae, and could be explained by the Laurasian origin of both groups and subsequent differential extinction.

Diagnosis. See Soleglad & Sissom (2001) for details.

Tribe Scorpiopini Kraepelin, 1905

Type Genus. *Scorpiops* Peters, 1861.

Composition. The tribe includes six genera.

Distribution. South and Southeast Asia.

Taxonomic history. This tribe was established by Soleglad & Sissom (2001).

Biogeographic history. The Scorpiopini are distributed mainly in the tropics of Asia, but also reach high altitudes in the Himalayas. Their origin does not appear to be connected with Gondwanaland fragmentation, and they could be considered an ancient Laurasian relict group. The genus *Parascorpiops* represents a peculiar island form from the mountains of Indonesia.

Diagnosis. See Soleglad & Sissom (2001) for details.

Tribe Troglacormini Soleglad & Sissom, 2001

Type Genus. *Troglacormus* Francke, 1981.

Composition. This monotypic tribe includes a single genus, *Troglacormus*.

Distribution. North America (Mexico).

Taxonomic history. *Troglacormus* was previously included in subfamily Megacorminae of Chactidae (Sis-

som, 1990), or in Euscorpiidae without distinguishing a subfamily (Fet & Sissom, 2000a). This tribe was established by Soleglad & Sissom (2001) who demonstrated its affinity to the Asian scorpiopines.

Biogeographic history. Two species of *Troglacormus* are found only in the caves of north-central and northeastern Mexico (Fet & Sissom, 2000a), and clearly represent an ancient, relict lineage.

Diagnosis. See Soleglad & Sissom (2001) for details.

Family Superstitioniidae Stahnke, 1940

Type Genus. *Superstitionia* Stahnke, 1940.

Synonyms.

Troglotayosicidae Lourenço, 1998, **new synonymy**; type genus *Troglotayosicus* Lourenço, 1981.

Composition. This family includes two subfamilies (Superstitioniinae and Typhlochactinae) and five genera. The content of Superstitioniidae is changed here as we return the genus *Troglotayosicus* to this family, as suggested by Stockwell (1989, 1992). The family Troglotayosicidae is abolished here and synonymized with Superstitioniidae; the genus *Belisarius* is transferred to Chactidae (subfamily Brotheinae).

Distribution. North America (Mexico, USA), South America (Ecuador).

Taxonomic history. This taxon was created as a monotypic subfamily of Chactidae (Stahnke, 1940) (incorrect original spelling Superstitioninae). Subfamily Superstitioniinae was formally elevated to the family rank by Stockwell (1992) who also included here genera *Troglotayosicus* and *Belisarius*. The unpublished division of Superstitioniidae by Stockwell (1989) included four subfamilies: Superstitioninae, Troglotayosinae, Belisariinae, and Typhlochactinae. Later, Lourenço (1998a) placed *Troglotayosicus* and *Belisarius* in a separate family, Troglotayosicidae (incorrect original spelling Troglotayosidae). For the detailed taxonomic history see Sissom (2000b) and Fet & Sissom (2000b).

Biogeographic history. Presence of *Troglotayosicus* in Ecuador, and all other taxa of Superstitioniidae in North America (Mexico, USA) could indicate an ancient age of Superstitioniidae; see similar patterns in Chactidae and Caraboctonidae. Its taxa have a clearly expressed relict character: this family is notable for having cave and/or blind species (genera *Alacran*, *Sotanochactas*, *Typhlochactas*, *Troglotayosicus*).

Diagnosis. Synapomorphies. Median denticle (MD) row groups of chelal finger aligned obliquely; chelal trichobothrium *it* positioned at extreme base of fixed finger; chelal trichobothria *Db* basal and *Dt* situated at base of fixed finger; lateral carinae of metasomal segment V absent. Important Sympleiomorphies. Chelal trichobothrium *ib* situated on extreme fixed finger base or on palm; chelal trichobothria series V_1-V_4 does not extend entire length of palm, $V_1-V_2-V_3$ juncture usually

angles towards internal aspect; sclerites of genital operculum of female loosely connected; overall shape of pedipalp chela rounded; stigma small and oval in shape; number of lateral eyes 0–2.

Discussion. The phylogenetic position of this family is interesting since we see it exhibiting intermediate characteristics between the vaejovids and the clade “Euscorpidae + Chactidae”. It is a small family, but many of its members are quite unique, only the subfamily Typhlochactinae contains a genus, *Typhlochactas*, with multiple species—a group (along with *Sotanochoctas*) of closely related, highly derived scorpions. The trichobothrial pattern of the patella of this group is quite unusual where ventral trichobothrium v_2 is located on the external surface. The only other scorpion group with an externally located v_2 is the Old World iuroids. *Alacran*, the only member of this family exhibiting major neobothriotaxy, *Sul*, in many ways is quite unlike the other members of its family. Of course, it is the only large member of the family, exceeding 70 mm in length; this size along with its beautiful mahogany color and audacious appendage proportions make it a totally different looking scorpion. It is the only member of Superstitioniidae where all three patellar ventral trichobothria are located on the ventral surface. In subfamily Superstitioniinae, we have two monotypic genera, both with ventral trichobothrium v_3 located on the external surface. The somewhat distal position of v_3 is identical to that seen in the vaejovids, making these two groups the only Recent scorpions with this configuration. Except for *Alacran*, we see an unusual arrangement of the patellar external trichobothria series esb_1 – esb_2 . This series is either horizontally parallel to the segment’s width (*Superstitionia*) or slants upward from esb_1 to esb_2 . In *Alacran*, this series, as in most chactoid scorpions, slants downward. Except for *Superstitionia*, the members of this family lack at least the median eyes and pectinal fulcra, the latter all troglobitic. However, due to possible confusion caused by severe adaptation to troglobitic conditions, we have purposely ignored the absence or presence of eyes in our cladistic analysis. Even the loss of pectinal fulcra, another character often associated with cave adaptation, is treated locally within groups in our analysis.

Characters used to distinguish the subfamilies and genera of family Superstitioniidae are: the position of the pedipalp patellar trichobothria, neobothriotaxy, leg tarsus armament, pedipalp chelal finger dentition, sternum construction, and the structure of the hemispermaphore.

Key to subfamilies and genera of family Superstitioniidae

1. Patellar trichobothrium v_3 located on external surface of segment; ventral surface of leg tarsus

with numerous irregular medially positioned spinules and/or setae; internal denticles (ID) of chelal fingers considerably enlarged; hemispermaphore lamina terminus narrower than its base, not spatulate; sternum wider than long, apex not rounded exhibiting typical depression and convex lateral lobes (subfamily **Superstitioniinae**) 2

Patellar trichobothrium v_3 located on ventral surface of segment; ventral surface of leg tarsus with lateral setal pairs, little or no median spination present; internal denticles (ID) of chelal fingers not considerably enlarged; hemispermaphore lamina terminus wider than its base, spatulate; sternum longer or equal than wide, apex rounded, exhibiting little depression, lateral lobes not convex (subfamily **Typhlochactinae**) 3

2. Femoral trichobothrium d positioned considerably distal to i ; chelal trichobothrial series eb – et aligned in straight line; fulcra of pectines absent genus **Troglotayosicus**

Femoral trichobothrium d not positioned considerably distal to i , essentially proximal or adjacent in position; chelal trichobothrial series eb – et not aligned in straight line, trichobothrium eb angles considerably toward dorsal edge of fixed finger; fulcra of pectines present genus **Superstitionia**

3. Major neobothriotaxy, type *Sul*, found on pedipalpal chelae and patellae; patellar trichobothrial series v_1 – v_3 located on ventral surface of segment; patellar trichobothrial series esb_1 – esb_2 angles downward genus **Alacran**

Orthobothriotaxic; patellar trichobothrium v_2 located on external surface of segment; patellar trichobothrial series esb_1 – esb_2 angles upward 4

4. Chela trichobothrial series ib – it located on base of fixed finger/palm, ib and it closely grouped; chela trichobothrial series eb – et located on basal two-thirds of fixed finger genus **Typhlochactas**

Chela trichobothrial series ib – it located on basal half of finger, ib and it exhibiting considerable separation; chela trichobothrial series eb – et located on distal half of fixed finger genus **Sotanochoctas**

Subfamily Superstitioniinae Stahnke, 1940

Type Genus. *Superstitionia* Stahnke, 1940.

Synonyms.

Troglotayosicinae Lourenço, 1998, **new synonymy**.

Composition. The subfamily includes two monotypic genera: *Superstitionia* (North America: USA, Mexico), and *Troglotayosicus* (South America: Ecuador). The content of Superstitioniinae is changed here as we include the genus *Troglotayosicus*.

Distribution. North America, South America.

Taxonomic history. This taxon was originally introduced as a subfamily of Chactidae. It corresponds to the tribe Superstitionini of Francke (1982a).

Diagnosis. Synapomorphies. Chelal trichobothrium Eb_1 on ventral surface or on VI carina; patella trichobothrium v_3 on external surface; patella trichobothria series esb_1 – esb_2 aligned parallel or slants “upward”; chelal finger internal denticle (ID) significantly larger than other denticles; sternum wider than long. Important Sympleisiomorphies. Median denticle (MD) row of chelal finger aligned obliquely; chelal trichobothrium it positioned at extreme base of fixed finger; chelal trichobothria Db basal and Dt situated at base of fixed finger; lateral carinae of metasomal segment V absent.

Discussion. The combination of “*Superstitionia* + *Troglotayosicus*” is not new, in fact, Stockwell (1989: Fig. 255) showed this relationship in ladderized form, and except for his inclusion of genus *Belisarius*, his topology is quite similar to that derived in this study: Stockwell topology (without *Belisarius* and *Sotanochactas*) = (*Superstitionia*, (*Troglotayosicus*, (*Alacran*, *Typhlochactas*))), versus the resulting topology of this study = ((*Superstitionia*, *Troglotayosicus*), (*Alacran*, *Typhlochactas*)). Unfortunately, Stockwell used the presence or absence of eyes, both median (his character 24) and lateral (character 25), as characters in his analysis, both distributed as synapomorphies in his Fig. 255. These two characters, in part, were the cause for *Belisarius* binding within this clade. It is clear that the loss of eyes is almost entirely due to adaptation to troglobitic conditions. This trend is commonly seen throughout Recent scorpions: at least the median eyes and tubercle are reduced or absent altogether, the loss of lateral eyes is more unusual (e.g., *Troglocormus* in the euscorpids, *Chaerilus chapmani* in the chaerilids, *Belisarius* and *Taurepania trezzii* in the brotheines, all the typhlochactines, *Diplocentrus mitchelli* Francke in the diplocentrines). Since as a result in this current study, as well as in the euscorpoid revision by Soleglad & Sissom (2001), it is clear that *Belisarius* is a member of Chactidae, its move to Superstitioniidae as proposed by Stockwell (1989) could have easily been caused by this emphasis on the lack of eyes.

Lourenço (1998a) placed genera *Troglotayosicus* and *Belisarius* into a new family Troglotayosicidae, based on a set of highly unusual and creative characters for familial diagnoses: 1) total length of scorpion 25 to

32 mm; 2) two pairs of lateral eyes, median eyes absent; 3) sternum pentagonal; 4) stigmata small and round; 5) median plates and distal denticles of pectines are round; 6) legs with two pedal spurs; 7) cheliceral movable finger with *significant* serrulae; 8) trichobothria orthobothriotaxic, Type C; 9) leg tarsus with a number of “spinule” series, or two rows of “spinules”. Clearly, these diagnostic characters were carefully crafted to eliminate other troglobitic scorpions. None of these diagnostic characters qualify as a serious candidate for family distinction, since they are either much too low-level in nature (e.g., the character referring to the scorpion size), or are characters which apply to large aggregates of scorpion groups (e.g., sternum, orthobothriotaxy Type C, presence of pedal spurs on the legs). Again, as with Stockwell (1989), Lourenço (1998a) emphasized characters that are commonly found in cave adapted species (which includes both *Belisarius* and *Troglotayosicus*), the loss of the median eyes and tubercle, and the loss of pectinal fulcra. The loss of fulcra, in general, is not that unusual in the chactoids. The presence of serrulae is quite common in the chactoids (including *Superstitionia*, *Typhlochactas*, many vaejovids) and also is known in the Old World iuroid, *Calchas*. (Of course this character is qualified as “significant” which presumably distinguished it from “insignificant” serrulae).

The primary synapomorphy for the superstitioniids is the secondary derivation of the oblique median denticle (MD) row of the chelal finger. After repeated attempts to borrow the type of *Troglotayosicus vachoni*, we were not able to gain access to this specimen. Although the original description by Lourenço (1981) is in general very thorough and well-illustrated, we still had specific questions dealing with the chelal finger dentition and the exact armament of the leg tarsus. We have in our possession two drawings of *Troglotayosicus vachoni* by Lourenço (supplied indirectly to us by David Sissom) of the chelal movable finger of *Troglotayosicus* (one of which is published in Lourenço (1998a: Fig. 18)). Both of these drawings are depicted from an outer angle, obscuring the exact alignment of the MD row (this was also discussed by Soleglad & Sissom (2001: 40)). From both of these drawings we see extraordinarily large denticles, which, depending on the drawing, are either internal denticles (ID) or outer denticles (OD). Based on the equally large distal denticles which clearly are internal, we presume the midfinger denticles are internal as well (which may mean this species is lacking outer denticles (OD)?). The MD row, which is obscured by some large denticles, appears to be composed of extremely small denticles. Consequently, in our cladistic analysis we assign *Troglotayosicus* an “unknown” state for the alignment of the finger MD row. However, we assigned the enlarged ID denticles found in *Troglotayosicus* to the same state as the genus

Superstitionia which also has highly enlarged ID denticles. This is considered a synapomorphy for this small subfamily. The leg tarsus armature is another area in which we needed more resolution. In Lourenço's (1981: Fig. 43, 1998a: Fig. 15) illustration we see a large number of irregularly positioned elongated setae and/or spinules. The figure clearly shows socketed bristles, but the sockets are so small, that we are not sure whether all of these are setae or an artifact of an artist's rendering (i.e., some may be spinules). To add to the confusion, Lourenço (1981, 1998a) refers to setae/spinules as "spiniformes". The distinction between this configuration and that found in *Superstitionia* is discussed in the **Character Analysis** section.

Subfamily Typhlochactinae Mitchell, 1971

Type Genus. *Typhlochactas* Mitchell, 1971.

Composition. This subfamily includes three genera (*Alacran*, *Sotanochoactas*, and *Typhlochactas*).

Distribution. North America (Mexico).

Taxonomic history. This taxon was originally introduced as a subfamily of Chactidae. It corresponds to the tribe Typhlochactini of Francke (1982a).

Diagnosis. Synapomorphies. Ventral surface of leg tarsus with setal pairs, ventral spinules minimal or obsolete; number of leg pedal spurs varies from zero to two; sternum length equal to or greater than width; sternum apex rounded, with minimal depression, lateral lobes flat; hemispermatophore lamina terminus spatulate in shape; pectinal fulcra absent. Important Sympleosio-morphies. Chelal finger median denticle (MD) row groups aligned obliquely; chelal trichobothrium *it* positioned at extreme base of fixed finger; chelal trichobothria *Db* basal and *Dt* situated at base of fixed finger; lateral carinae of metasomal segment V absent.

Family Vaejovidae Thorell, 1876

Type Genus. *Vaejovis* C.L. Koch, 1836.

Synonyms.

Syntropinae Kraepelin, 1905.

Composition. The family includes nine genera, which are outlined in detail by Sissom (2000c). No subfamilies or tribes are currently recognized. The content of Vaejovidae is changed here as the genus *Uroctonus* (North America) is moved to Chactidae (under the reestablished subfamily Uroctoninae).

Distribution. North America (Mexico, USA).

Taxonomic history. The taxonomic history of Vaejovidae is traced in detail by Sissom (2000c). For a long time, subfamilies Iurinae and Scorpiopinae (=Scorpiopsinae) were included here (Stahnke, 1974). Later, both Iurinae (including what is now Caraboctonidae) and Scorpiopinae were elevated to the family rank (Francke & Soleglad, 1981; Sissom, 1990; Stockwell, 1992). The subfamily Scorpiopinae later was placed as a subfamily in Euscorpiidae (Soleglad & Sissom, 2001). Stockwell

(1989) introduced two subfamilies, four tribes, and three new genera, but all these changes remain unpublished.

Biogeographic history. Vaejovidae are a predominantly arid group found in the desert regions of Mexico and the USA, exhibiting a number of xeric adaptations. It is reasonable to assume that at least recent (late Tertiary) radiation of this family is connected to aridization on the North American continent (Morafka et al., 1994). Santiago-Blay et al. (2001) reported a presumably vaejovid Oligocene fossil from Mexico (Puebla). Lourenço & Sissom (2000) considered vaejovids a group of Laurasian origin, based on their modern distribution.

Diagnosis. Synapomorphies. Patella trichobothrium *v₃* situated on external surface; single ventral distal spinule (VDS) pair found on leg tarsus; laminar "hook" present on hemispermatophore lamina base; dorsal lateral carinae of metasomal segment IV terminates in conspicuous flared projection; overall shape of pedipalp chela rounded; patellar carina *DPS_c* present; pectinal tooth numbers relatively large. Important Sympleosio-morphies. Dorsal edge of cheliceral movable finger with *two* subdistal denticles; ventral surface of leg tarsus configured with moderately developed setal pairs and median spinule row; hemispermatophore capsule present, weak to significant; genital papillae of male visible at posterior edge of genital operculum.

Discussion. Further taxonomic division of this family is contingent on a revision of the large (ca. 70 species) genus *Vaejovis*, which is not monophyletic (Stockwell, 1989, 1992; Sissom, 2000c). Stockwell (1989) separated *Vaejovis* into three genera but this decision was never published. Ponce & Beutelspacher (2001: 88) presented unpublished diagnoses and names for Stockwell's genera "*Sissomius*" and "*Lissovaejovis*"; these names, however, cannot be considered published by Ponce & Beutelspacher according to ICZN (1999) since these diagnoses neither list type species nor fix type specimens.

Superfamily Iuroidea Thorell, 1876, new rank

Type Genus. *Iurus* Thorell, 1876.

Composition. This superfamily is established here. It includes two families: Iuridae and Caraboctonidae (the latter is elevated here to family rank). Our Iuroidea corresponds to the family Iuridae as treated by Sissom & Fet (2000b), excluding the genus *Anuroctonus*, which is transferred to Chactidae.

Distribution. Europe, Asia, North America, South America.

Taxonomic history. The taxonomic history of Iuroidea is complicated (see Sissom & Fet, 2000b). Iurinae and Caraboctoninae were treated as subfamilies of Vaejovidae by Kraepelin (1905), then as subfamilies of Iuridae by Francke & Soleglad (1981). Stahnke (1974) created the subfamily Hadrurinae (under Vaejovidae), which included *Hadrurus* and *Anuroctonus*. Stockwell

(1992) recognized family Iuridae with three subfamilies (Iurinae, Caraboctoninae, and Hadrurinae). Stockwell (1989) and Lourenço (2000a) included Iuridae in the superfamily Vaejovoidea.

Biogeographic history. A significant range disjunction between Old World iuroids (Iuridae) and New World ones (Caraboctonidae, both Nearctic and Neotropical), suggests that this ancient lineage probably existed already in the Pangean times. Francke & Soleglad (1981) indicated that its modern vicariance could be created by a series of events starting from the Jurassic opening of the North Atlantic. The separation and isolation of Caraboctonidae subfamilies between South America and North America could result from the decoupling of the North American and South American plates, which played a prominent role in formation of the Caribbean region in late Mesozoic–early Tertiary (Rosen, 1976; Francke & Soleglad, 1981).

Diagnosis. Synapomorphies. Ventral edge of cheliceral movable finger with one large denticle; ventral surface of leg tarsus with median row of spinule clusters; stigma oval in shape; chela trichobothrial series *db–dt* and *eb–et* found on distal half of finger; patella ventral trichobothrium v_3 found on external surface; **Important Sympleiomorphies.** Median denticle row (MD) of pedipalp chelal finger arranged in *oblique* groups; pedipalp chelae exhibits “8-carinae” configuration; dorsal edge of cheliceral movable finger with single subdistal denticle.

Family Iuridae Thorell, 1876

Type Genus. *Iurus* Thorell, 1876.

Synonyms.

Calchinae Birula, 1917; type genus *Calchas* Birula, 1899.

Composition. The family Iuridae includes two monotypic genera from the Mediterranean region (Greece and Turkey), *Calchas* and *Iurus*. Subfamilies are not recognized in Iuridae. The content of Iuridae is restricted here since the former subfamily Caraboctoninae is elevated to family rank. The subfamily Hadrurinae is transferred to Caraboctonidae, and the genus *Anuroctonus* is transferred to Chactidae (subfamily Uroctoninae).

Distribution. Europe (Greece), Asia (Turkey).

Taxonomic history. This taxon was first established as a subfamily Iurini in Thorell’s Pandinoidea, and included genera *Iurus* and *Uroctonus* (the latter now in Chactidae). Pocock (1893) first recognized Iuridae as a family but expanded it to include also current Chactidae, Chaerilidae, Euscorpiidae, and Vaejovidae. Kraepelin (1905) treated iurids as a monotypic subfamily under Vaejovidae.

The genus *Calchas* Birula, 1899 was for a long time included in Chactidae. To accommodate it, Birula (1917a, 1917b) established a special subfamily Calchi-

nae (under Chactidae). Vachon (1971, 1974) demonstrated that *Calchas* is very close to *Iurus* but did not propose taxonomic changes. Francke & Soleglad (1981) reestablished Iuridae as a family, with two subfamilies (Iurinae and Caraboctoninae); they moved *Calchas* to Iurinae. Their Caraboctoninae (formerly in Vaejovidae) included tribe Caraboctonini (genera *Caraboctonus* and *Hadruioides*) and tribe Hadrurini (genus *Hadrurus*). Later, Stockwell (1992) reestablished the subfamily Hadrurinae, which included *Hadrurus* and *Anuroctonus* as first introduced (under Vaejovidae) by Stahnke (1974). Sissom & Fet (2000b) listed three subfamilies (Caraboctoninae, Hadrurinae, and Iurinae) and six genera in Iuridae.

Biogeographic history. Details on a possible relict history of *Iurus*, which ranges from southern Greece to Anatolia, were given in Vachon (1953) and Kinzelbach (1975). The other, vicariant genus *Calchas*, also seems to be a relict; an account of its ecology and distribution is found in Birula (1917a, 1917b) and Kinzelbach (1980).

Diagnosis. Synapomorphies. Chelal trichobothrium *Eb₁* on ventral surface or ventroexternal carina; chelal trichobothrium *it* on distal aspect of fixed finger; chelal trichobothria *ib* and *it* not adjacent; chelal trichobothrium *Et₁* positioned on external surface of palm; presence of additional petite trichobothria on the chela; patellar ventral trichobothrium v_2 found on external surface; presence of additional petite trichobothria on patella. **Important Sympleiomorphies.** Ventral edge of cheliceral movable finger with one large denticle; ventral surface of leg tarsus with median row of spinule clusters; stigma oval in shape; chelal trichobothrial series *db–dt* and *eb–et* found on distal half of finger; patella ventral trichobothrium v_3 found on external surface.

Discussion. See discussion under subfamily Uroctoninae for the reasons for removing *Anuroctonus* from Iuroidea.

Family Caraboctonidae Kraepelin, 1905, new rank

Type Genus. *Caraboctonus* Pocock, 1893.

Composition. This new family is established here. It includes two subfamilies: Caraboctoninae and Hadrurinae. Tribes are not recognized.

Distribution. North America, South America.

Biogeographic history. The family Caraboctonidae has a disjunct range, with subfamily Caraboctoninae in South America (with two disjunct genera), and subfamily Hadrurinae with disjunct range in Mexico and North America.

Diagnosis. Synapomorphies. Chelal trichobothrium *Et₅* positioned on fixed finger; neobothriotaxy present on external surface of patella; dorsal edge of cheliceral movable finger with *two* subdistal denticles; leg coxae IV elongated; lateral carinae partially present on

metasomal segment IV; chela with “10-carinae” configuration. Important Sympletiomorphies. Ventral edge of cheliceral movable finger with one large denticle; ventral surface of leg tarsus with median row of spinule clusters; stigma oval in shape; chelal trichobothrial series *db–dt* and *eb–et* found on distal half of finger; patellar ventral trichobothrium *v*₃ found on external surface.

Subfamily Caraboctoninae Kraepelin, 1905

Type Genus. *Caraboctonus* Pocock, 1893.

Synonyms.

Hadruridae Mello-Leitão, 1934; type genus *Hadruridae* Pocock, 1893.

Composition. This subfamily includes two genera, *Caraboctonus* and *Hadruridae*.

Distribution. South America (Bolivia, Ecuador, Galapagos Islands, Chile, Peru).

Biogeographic history. Of two genera of Caraboctoninae, *Caraboctonus* has clear adaptations to arid habitats, and is found only in the deserts of Chile and southern Peru (Lourenço, 1995).

Diagnosis. Synapomorphies. Ventral surface of leg tarsus with heavily populated spinule cluster groups; leg tarsus unguicular spur blunted; genital papillae of male visible from genital operculum posterior edge; accessory trichobothrium found in patellar external *em* series. Important Sympletiomorphies. Chelal trichobothrium *Et*₅ positioned on fixed finger; dorsal edge of cheliceral movable finger with *two* subdistal denticles; leg coxae IV elongated; lateral carinae partially present on metasomal segment IV; chela with “10-carinae” configuration.

Subfamily Hadrurinae Stahnke, 1974

Type Genus. *Hadrurus* Thorell, 1876.

Composition. This monotypic subfamily includes a single genus *Hadrurus*.

Distribution. North America (USA and Mexico).

Taxonomic history. The content of Hadrurinae is changed here since we transfer the genus *Anuroctonus* to Chactidae (subfamily Uroctoninae), so that the subfamily is now monotypic.

Biogeographic history. Species of *Hadrurus* are the largest desert scorpions in North America, and their evolution clearly is connected to aridization of this continent (Morafka et al., 1994). DNA phylogeny of this genus (Fet et al., 2001) agrees with its Mexican origin as suggested earlier (Soleglad, 1976a).

Diagnosis. Synapomorphies. Major neobothriotaxy present on ventral aspect of pedipalpal chela, and on ventral and external aspects of patella; ventral surface of leg tarsus with fused spinule cluster groups; leg tarsus unguicular spur well-developed; genital papillae of male absent. Important Sympletiomorphies. Chelal trichobothrium *Et*₅ positioned on fixed finger; dorsal edge of

cheliceral movable finger with *two* subdistal denticles; leg coxae IV elongated; lateral carinae partially present on metasomal segment IV; chela with “10-carinae” configuration.

Discussion. See discussion above under subfamily Uroctoninae for the reasons for removing *Anuroctonus* from Iuroidea.

Superfamily Scorpionoidea Latreille, 1802

Type Genus. *Scorpio* Linnaeus, 1758.

Synonyms.

Bothriuroidea Simon, 1880, **new synonymy** (valid as family name).

Composition. This superfamily includes four extant families: Bothriuridae, Liochelidae, Scorpionidae, and Urodacidae. We do not recognize a separate superfamily Bothriuroidea as proposed by Mello-Leitão (1945) and Lourenço (2000a); it is synonymized here with Scorpionoidea. With changes in rank of some taxa, our content of extant Scorpionoidea is the same as that of Stockwell (1989) and Prendini (2000). We also include here the fossil family Protoischnuridae following Carvalho & Lourenço (2001).

Distribution. Asia, Africa, Australia, Oceania, North America, Central and South America.

Taxonomic history. Stockwell (1989) included five families in Scorpionoidea: Bothriuridae, Diplocentridae, Ischnuridae, Scorpionidae, and Urodacidae; his analysis clearly defined the basal position of Bothriuridae. Prendini (2000) provided a detailed morphological phylogenetic analysis of this superfamily, and justified existence of seven families (Bothriuridae, Diplocentridae, Hemiscorpiidae, Heteroscorpionidae, Ischnuridae, Scorpionidae, and Urodacidae).

Biogeographic history. The scorpionoids are found both in the New and the Old World. Our placement of Protoischnuridae (South America) (Carvalho & Lourenço, 2001) in this superfamily marks the oldest scorpionoid taxon as Lower Cretaceous (ca. 110 Mya). Final vicariant separation of South America and Africa took place 100 to 120 Mya (Hay et al., 1999). By this time, a scorpionoid family Protoischnuridae already existed in South America so it is conceivable that other scorpionoid families (Bothriuridae, Liochelidae, Scorpionidae, and Urodacidae) also already have diverged. All other available scorpionoid fossils (family Scorpionidae) are Tertiary. One could interpret scorpionoids as a group which originated in Gondwanaland since its few representatives in the northern continents (North America, North Africa, Middle East) could be Tertiary migrants. Presence of *Mioscorpio* in Miocene of Europe sets the possible age bracket for such migrants. Further, the current distribution of scorpionoids could be due to differential extinction of a formerly widespread group (Nenilin & Fet, 1992), and then one does not have to evoke Gondwanaland disjunctions with subsequent south-to-

north migrations to explain disjunct ranges of such groups as Diplocentrinae.

Diagnosis. Synapomorphies. Ventral surface of leg tarsus with pairs of large socketed setae; legs with one pedal spur (prolateral); paraxial organ with reflection of internobasal sperm duct; hemispermatophore capsule extremely well-developed; ventral denticle of cheliceral movable finger considerably longer than dorsal denticle; chelal finger outer denticles (OD) removed outward from median denticle (MD) row. Important Sympleiomorphies. Ventral edge of cheliceral movable finger smooth; median denticle (MD) row of chelal finger aligned in straight line; genital operculum of female generally fused; chela with “10-carinae” configuration.

Discussion. We confirm the phylogeny of Scorpionoidea as recently established by Prendini (2000) in his extensive cladistic analysis. The family Bothriuridae is a sister group to three other scorpionoid families. With the nomenclatural changes introduced here, the family Urodacidae (Urodacinae + Heteroscorpionidae) is the sister group to the clade including Liochelidae (Liochelinae + Hemiscorpiinae) and Scorpionidae (Scorpioninae + Diplocentrinae).

Family Bothriuridae Simon, 1880

Type Genus. *Bothriurus* Peters, 1861.

Synonyms.

Telegonini Peters, 1861; type genus *Telegonus* C. L. Koch, 1837 (= *Thestylus* Simon, 1880), a junior homonym of *Telegonus* Hübner, 1816 (Lepidoptera).

Acanthochiroidae Karsch, 1880 (incorrect original spelling; should be Acanthochiridae); type genus *Acanthochirus* Peters, 1861 (= *Cercophonius* Peters, 1861).

Lisposominae Lawrence, 1928; type genus *Lisposoma* Lawrence, 1928.

Brachistosterninae Maury, 1973; type genus *Brachistosternus* Pocock, 1893.

Vachoniinae Maury, 1973 (incorrect original spelling Vachonianinae; see Fet & Braunwalder, 2000); type genus *Vachonia* Abalos, 1954.

Composition. The bothriurids include 14 genera; subfamilies are not recognized. The validity of the genus *Brazilbothriurus* was doubted by Prendini (2003a).

Distribution. Asia, Africa, Australia, South America.

Taxonomic history. This distinct family was recognized early by scorpion systematists (Peters, 1861); see Lowe & Fet (2000) for taxonomic history details. Position of Bothriuridae as related to other families of current parvorder Iurida was ambiguous. Most of the recent authors placed it in Scorpionoidea, and Prendini (2000) demonstrated its basal position within this superfamily. The African genus *Lisposoma* was described under Scorpionidae (subfamily Lisposominae) but later trans-

ferred to Bothriuridae by Francke (1982b). The recognized number and content of subfamilies in Bothriuridae varied: Maury (1973) listed Bothriurinae, Brachistosterninae, and Vachonianinae; Stockwell (1989) listed Bothriurinae and Lisposominae; Lowe & Fet (2000) listed Bothriurinae and Brachistosterninae. Prendini (2000), as a result of the detailed phylogenetic analysis, decided not to recognize any subfamilies. At the same time, Lourenço (2000a) reestablished the monotypic subfamily Lisposominae Lawrence, 1928 based on genus *Lisposoma*, and even elevated it to the family rank. Following Prendini (2000, 2003a, 2003b), we do not accept a separate family Lisposomidae (or subfamily Lisposominae).

Biogeographic history. Bothriurids are a predominantly non-tropical South American group, also present in Australia (several species of *Cercophonius*), India (one species of *Cercophonius*) and South Africa (*Brandbergia* and *Lisposoma*). This vicariant distribution could be a result of Gondwanaland breakup (see a detailed discussion in Prendini, 2003b). It is possible that this family originated in Gondwanaland and was never present in Laurasia, as was first stated by Lamoral (1980: 443). Two South African genera (*Brandbergia* and *Lisposoma*) appear to be the most basal (Prendini, 2003b). The genus *Cercophonius* exhibits a disjunct range between Australia (Koch, 1977; Acosta, 1990) and India (Lourenço, 1996c), which could also reflect a Gondwanaland disjunction (Prendini, 2003b).

Diagnosis. See Prendini (2000) for details on the diagnosis of this family.

Family Liochelidae Fet & Bechly, 2001 (1879)

Type Genus. *Liocheles* Sundevall, 1833.

Synonyms.

Hemiscorpiidae Pocock, 1893, **new synonymy** (valid as subfamily name).

Hadogenidae Lourenço, 1999; type genus *Hadogenes* Kraepelin, 1894.

Non-available name.

Ischnuridae Simon, 1879; type genus *Ischnurus* C.L. Koch, 1837 (= *Liocheles* Sundevall, 1833); see Fet & Bechly (2000, 2001) and ICZN (2003).

Composition. Family Liochelidae includes two subfamilies (Hemiscorpiinae and Liochelinae) and 11 genera, predominantly from the Old World. The content of Liochelidae is changed here compared to that of Ischnuridae in Fet (2000c) and Prendini (2000), since we transfer here the subfamily Hemiscorpiinae (downgraded from family rank). We also reestablish the nominotypic subfamily Liochelinae (a substitute name for Ischnurinae).

Distribution. Asia, Africa, Australia, Oceania, Caribbean, Central and South America.

Taxonomic history. Under the name Ischnuridae, this taxon was introduced by Simon (1879), and later for

a long time considered a subfamily of Scorpionidae. It was reestablished by Lourenço (1985, 1989) as a family. Fet & Bechly (2001) introduced Liochelidae as a new substitute name due to the homonymy with damselfly subfamily Ischnurinae, and this name was adopted by the International Commission for Zoological Nomenclature (ICZN, 2003). See Fet (2000c) for a detailed taxonomic history and Prendini (2000) for phylogenetic analysis. Prendini (2000) provided a detailed phylogenetic analysis of Ischnuridae.

A separate monotypic subfamily Hadogenidae, based on the ischnurid genus *Hadogenes*, was established by Lourenço (1999c) and placed under family Scorpionidae. Later, this subfamily was elevated by Lourenço (2000a) to family rank. We follow Prendini (2000), and do not accept either Hadogenidae or Hadogeninae on cladistic grounds.

Biogeographic history. The liochelids appear to be a typical Gondwanaland element, found in Africa, South America and India (Sissom, 1990; Fet, 2000c), while subfamily Hemiscorpiinae could represent a further migrant to Middle East from Arabia. The genus *Liocheles* could later disperse to Australia from Asia (Koch, 1977, Lourenço, 1985). Origin of the genus *Opisthacanthus* (a predominantly African taxon) in South America has been a subject of discussion (Newlands, 1973; Francke, 1974; Lamoral, 1980; Lourenço, 1985, 1989; Nenilin & Fet, 1992).

Biogeographic history of Hemiscorpiinae could reflect a relict East African-Arabian isolation.

Diagnosis. (This diagnosis is based on derived characters for clade (Liochelidae + Hemiscorpiidae) as presented in Prendini (2000: Fig. 7)). **Synapomorphies.** Median ocular tubercle of carapace shallow, not raised above carapace surface; nongranular surfaces of prosoma, mesosoma, metasoma, and legs punctate; distal denticles of cheliceral movable finger subequal in length; median denticle (MD) rows of chelal finger doubled, sometimes fused at base; distance between chelal ventral trichobothria V_2 and V_3 great, V_3 much closer to V_4 than to V_2 ; telson vesicle of adult male laterally flattened; venom glands simple.

Subfamily Hemiscorpiinae Pocock, 1893

Type Genus. *Hemiscorpius* Peters, 1861.

Composition. This taxon is downgraded here from family to subfamily rank under Liochelidae. The family includes two genera (*Habibiella* and *Hemiscorpius*).

Distribution. Asia (Middle East), Africa (Eritrea, Somalia).

Taxonomic history. This subfamily was traditionally listed under Scorpionidae (Fet, 2000c). Its transfer to Ischnuridae (now Liochelidae) was first suggested in the unpublished classification of Stockwell (1989). It was elevated to the family level simultaneously by Lourenço (2000a) who did not provide any justification,

and by Prendini (2000) who provided a detailed phylogenetic analysis; both papers were published in March 2000. Prendini (2000) demonstrated that Hemiscorpiidae is a sister group of Ischnuridae.

Diagnosis. See Prendini (2000) for details on the diagnosis of this subfamily (as family Hemiscorpiidae).

Discussion. Highly derived features of this subfamily include unusually toxic hemolytic venom of *Hemiscorpius*.

Subfamily Liochelinae Fet & Bechly, 2001 (1879)

Type Genus. *Liocheles* Sundevall, 1833; type genus *Ischnurus* C.L. Koch, 1837 (= *Liocheles* Sundevall, 1833); see Fet & Bechly (2001).

Synonyms.

Hormurini Laurie, 1896; type genus *Hormurus* Thorell, 1876 (= *Liocheles* Sundevall, 1833).

Opisthacanthinae Kraepelin, 1905; type genus *Opisthacanthus* Peters, 1861

Hadogeninae Lourenço, 1999; type genus *Hadogenes* Kraepelin, 1894.

Non-available name.

Ischnurinae Simon, 1879 (ICZN, 2003).

Composition. This subfamily includes nine genera, predominantly from the Old World (only some species of *Opisthacanthus* are found in the New World) (Fet, 2000c; Lourenço, 2001b).

Distribution. Asia, Africa, Australia, Oceania, North America, Central and South America.

Taxonomic history. Prendini (2000) provided a detailed phylogenetic analysis of the liochelinae taxa (as Ischnuridae).

Diagnosis. See Prendini (2000) for details on the diagnosis of this subfamily (as family Ischnuridae).

Family Scorpionidae Latreille, 1802

Type Genus. *Scorpio* Linnaeus, 1758.

Synonyms.

Centrurides C.L. Koch, 1837 (part); type genus *Centrurus* Ehrenberg, 1829 (= *Heterometrus* Ehrenberg, 1828).

Pandinoidae Thorell, 1876 (incorrect original spelling; should be Pandinidae); type genus *Pandinus* Peters, 1861.

Heterometridae Simon, 1879; type genus *Heterometrus* Ehrenberg, 1828 (part) (= *Scorpio* Linnaeus, 1758).

Diplocentridae Karsch, 1880, **new synonymy** (valid as subfamily name).

Composition. The family includes two subfamilies, Diplocentrinae and Scorpioninae, and 12 genera. The content of Scorpionidae is changed here compared to that in Fet (2000g) and in the latest revisions (Prendini, 2000; Prendini et al., 2003), as we add here the former Diplocentridae, which is downgraded to subfamily rank. We also reestablish the monotypic subfamily Scorpi-

oninae, which has the same content as the family Scorpionidae of Prendini (2000) and Prendini et al. (2003).

Distribution. Asia, Africa, North America, South America.

Taxonomic history. Scorpionidae is the earliest scorpion family name, introduced as “famille des Scorpionides” (Latreille, 1802) at the time where order-group and family-group taxa were not yet defined. Originally, it included all known scorpions; other families were introduced first by C.L. Koch (1837). The taxonomic history of Scorpioninae is traced by Fet (2000g; as subfamily Scorpioninae) and of Diplocentrinae, by Sissom & Fet (2000b; as family Diplocentridae). We also provisionally include here the fossil genus *Mioscorpio* Kjellesvig-Waering, 1986 (Miocene of Europe). Fet et al. (2000) and Lourenço (2000a) listed this monotypic genus under family Scorpionidae, as placed by Kjellesvig-Waering (1986) who analyzed the type specimens of this fossil described as *Scorpio zeumeri* by Hadži (1931). Judging from the original description of Hadži, some of the features (chela, carapace, and sternum) of this species closely resemble an extant member of Scorpionidae (subfamily Scorpioninae). Other Tertiary fossils are known for the New World Diplocentrinae (see below).

Biogeographic history. While four genera of Scorpioninae are exclusively Old World taxa (Prendini et al., 2003), our inclusion of Diplocentrinae, with their bizarre disjunct range, gives this family almost a worldwide distribution (except Australia); Tertiary *Mioscorpio* is known from Europe. It is therefore possible that the common ancestor of Scorpionidae was present in Pangean times.

Diagnosis. (This diagnosis is based on derived characters for clade (Scorpionidae + Diplocentridae) as presented in Prendini (2000: Fig. 7)). **Synapomorphies.** Pedipalp patella dorsoexternal carina obsolete; leg tarsus laterodistal lobes rounded, notches at base of median dorsal lobe.

Subfamily Diplocentrinae Karsch, 1880

Type Genus. *Diplocentrus* Peters, 1861.

Synonyms.

Nebinae Kraepelin, 1905, **new synonymy** (valid as tribe name).

Composition. This taxon is downgraded here from family to subfamily rank. The subfamily includes two tribes, Diplocentrini and Nebini, and eight genera.

Distribution. Asia (Middle East), North America, Caribbean, Central and South America.

Taxonomic history. Interestingly, this taxon was originally established as a subfamily of Scorpionidae. Kraepelin (1905) elevated it to the family rank, and it was treated for almost 100 years as a family Diplocentridae (Sissom & Fet, 2000b). Prendini (2000) in a detailed phylogenetic analysis demonstrated its position as

a sister group to Scorpionidae (our subfamily Scorpioninae).

Biogeographic history. The disjunct range of Diplocentrinae includes Middle East and New World. Lamoral (1980: 443) suggested that its origin could be Mesozoic (after fragmentation of Laurasia). It is hardly possible to explain this range by Gondwanaland fragmentation. The subsequent radiation of Diplocentrinae could be Cenozoic, both in tropics and, especially, in the arid zones of North America and the Middle East (burrrowing forms of *Nebo*, *Diplocentrus*, and *Bioculus*).

Diagnosis. See Prendini (2000) for details on the diagnosis of this subfamily (as family Diplocentridae).

Tribe Diplocentrini Karsch, 1880, new rank

Type Genus. *Diplocentrus* Peters, 1861.

Composition. This tribe is established here, and corresponds to the former subfamily Diplocentrinae. It includes seven genera, with most species found in the New World.

Distribution. Asia (Middle East), North America, Caribbean, Central and South America.

Biogeographic history. The most diverse genus, *Diplocentrus*, includes numerous species in the deserts of North America, exhibiting an extensive arid radiation (analogous to that of Vaejovidae in North America, or Scorpioninae and Buthidae in Asia and Africa). Disjunct range of the genus *Heteronebo* between the Caribbean and Middle East is not yet clearly explained (Nenilin & Fet, 1992; Lourenço & Sissom, 2000; Sissom & Fet, 2000b). Santiago-Blay & Craig (1998) reported an Oligocene *Heteronebo* sp. from the amber of Dominican Republic.

Diagnosis. See Prendini (2000) for details on the diagnosis of this tribe (as subfamily Diplocentrinae).

Tribe Nebini Kraepelin, 1905, new rank

Type Genus. *Nebo* Simon, 1878.

Composition. This monotypic tribe is established here, and corresponds to the former subfamily Nebinae; it includes a single genus, *Nebo*.

Distribution. Asia (Middle East).

Biogeographic history. Species of the genus *Nebo* are found mainly in the Arabian Peninsula. Santiago-Blay & Craig (1998) reported an undescribed Oligocene fossil from Mexico (Chiapas amber) belonging to “subfamily Nebinae”, i.e. our tribe Nebini, which currently has only Middle East distribution.

Diagnosis. See Prendini (2000) for details on the diagnosis of this tribe (as subfamily Nebinae).

Subfamily Scorpioninae Latreille, 1802

Type Genus. *Scorpio* Linnaeus, 1758.

Composition. This taxon corresponds to the subfamily Scorpioninae as listed by Fet (2000g) and to family Scorpionidae as listed by Prendini (2000) and

Prendini et al. (2003). It includes four Old World genera: *Heterometrus*, *Opisththalmus*, *Pandinus*, and *Scorpio*. We also provisionally include here the fossil genus *Mioscorpio* Kjellesvig-Waering, 1986 (Miocene of Europe).

Distribution. Asia, Africa.

Taxonomic history. Prendini et al. (2003) provided a detailed phylogenetic analysis of the scorpionine taxa (treated as family Scorpionidae).

Biogeographic history. Scorpioninae are likely an eastern Gondwanaland group by origin (Sissom, 1990; Prendini et al., 2003). Four scorpionine genera exhibit vigorous radiation in the deserts of South Africa (*Opisththalmus*), deserts of North Africa and Middle East (*Scorpio*), tropics of Africa (*Pandinus*), and tropics of Asia (*Heterometrus*; see Couzijn, 1978, 1981; Sissom, 1990). Prendini et al. (2003) discussed in detail the biogeographic history of this group. They treated distribution of *Pandinus* and *Heterometrus* as the result of vicariance induced by the Cretaceous separation of the Indian plate from Africa. Phylogenetic positions of *Opisththalmus* and *Scorpio* was found to be basal to the (*Heterometrus* + *Pandinus*) group. Prendini et al. (2003) also suggested that the initial divergence of the common ancestor of (*Opisththalmus* + *Scorpio*) from the common ancestor of the (*Heterometrus* + *Pandinus*) group must have occurred in eastern Gondwanaland, presumably under semi-arid conditions that already existed before its breakup, i.e., the “Gondwana Desert” and surrounding semi-arid areas. Scorpioninae are notably absent from Madagascar (Lourenço, 1996a).

Diagnosis. See Prendini (2000) for details on the diagnosis of this subfamily (as family Scorpionidae).

Family Urodacidae Pocock, 1893

Type Genus. *Urodacus* Peters, 1861.

Synonyms.

Heteroscorpionidae Kraepelin, 1905, **new synonymy** (valid as subfamily name).

Composition. The content of Urodacidae is changed here compared to that of Prendini (2000), as we include the subfamily Heteroscorpioninae, downgraded from family rank. We also reestablish the nominotypic subfamily Urodacinae. Thus, the family includes two subfamilies—one from Australia, another from Madagascar—with one genus each.

Distribution. Australia and Madagascar.

Taxonomic history. This taxon, long treated as a subfamily of Scorpionidae, was first elevated to the family level by Lourenço (1996a) who followed the unpublished classification of Stockwell (1989). Fet (2000g) still listed it as a subfamily of Scorpionidae, noting that the change in rank requires further justification. Such justification was provided by Prendini (2000) who up-

held Urodacidae as a family and a sister group to family Heteroscorpionidae.

Biogeographic history. Subfamilies Urodacinae and Heteroscorpioninae can be interpreted as remnants of Gondwanaland scorpionoid fauna—two relict genera, one surviving in Madagascar, another in Australia. Koch (1977) discussed biogeographic distribution and desert adaptations of the diverse Australian genus *Urodacus*. Lourenço (1996a, 1996d) discussed *Heteroscorpion* in the context of endemic fauna of Madagascar, which generally is related to the African fauna, diverging with the split of Gondwanaland.

Diagnosis. (This diagnosis is based on derived characters for clade (Heteroscorpionidae + Urodacidae) as presented in Prendini (2000: Fig. 7)). **Synapomorphies.** Chelal fingers with multiple (>2) median denticle (MD) rows; ventral surface of pedipalp patella with single row of 4–20 trichobothria; external surface of pedipalp patellae with 14 or more trichobothria; ventral surface of pedipalp chela with six or more trichobothria; metasomal segments I–IV with single ventral median carina.

Discussion. Based on the many important characters, which genus *Heteroscorpion* uniquely shares with the family Liochelidae, and likewise, does not share with the genus *Urodacus*, we decided to investigate Prendini’s (2000) original cladistic analysis which combined these two genera as sister elements. This questioning of the clade “*Urodacus* + *Heteroscorpion*” was precipitated, in part, by the somewhat “high-level” approach to neobothriotaxy taken by Prendini (2000), which was discussed in detail in Soleglad & Sissom (2001: 71–73). They pointed out that Prendini considered almost all neobothriotaxic conditions found within the superfamily as single derivations within the pedipalp segment surfaces. This approach, in the opinion of Soleglad & Sissom (2001), predictively created severe homoplasy (i.e., the simplistic model did not convey true evolutionary lines for this complicated set of derivations). As stated in the discussion of Soleglad & Sissom (2001), three of these characters, those involving the chelal ventral surface (Prendini’s character 49), and patellar ventral and external surfaces (characters 43 and 45), exhibited the lowest overall character support in his entire analysis. Notwithstanding Prendini’s recent retort (2003b: 155) concerning the existence of “unambiguous homoplasious synapomorphies” —a fact Soleglad & Sissom (2001) *never questioned*—Soleglad & Sissom’s comment was aimed directly at Prendini’s superficial modeling of neobothriotaxy, and in particular, questioned the clade “*Urodacus* + *Heteroscorpion*” which was based on five synapomorphies, *three of which* involved his neobothriotaxy model. By doing a cursory study of the neobothriotaxy exhibited in *Heteroscorpion* and *Urodacus*, it is clear that the two events are separate

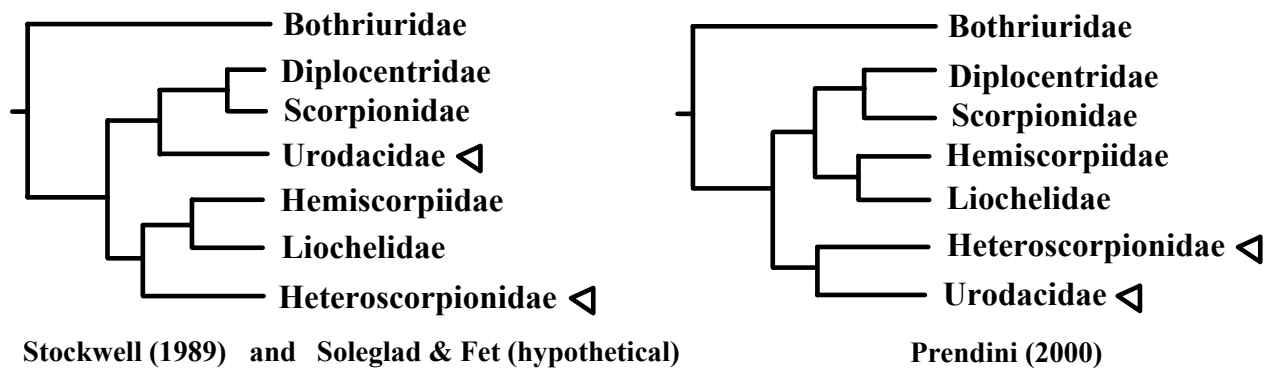


Figure 126: Phylogeny of Recent scorpion superfamily Scorpionoidea showing alternative topologies of Prendini (2000), Stockwell (1989), and Soleglad & Fet (hypothetical topology, as described in this paper). Note the differences in the arrangements involving families Urodacidae and Heteroscorpionidae (indicated by an arrow). Note, for easy readability and comparison we use Prendini's previous result as to family determinations for all taxa (i.e., in this study as well in Stockwell, some of these are or were downgraded to subfamily rank).

derivations: in the patella external surface, none of the series match either in number of accessory trichobothria or in gross positions. In particular, the *eb* series is orthobothriotax in *Heteroscorpion* (as well as in the hemiscorpiine genus *Habibiella*), and contains two accessory trichobothria in *Urodacus* (note: this distinction is obscured in two species exhibiting massive neobothriotaxy, *Heteroscorpion magnus* Lourenço and *Urodacus yaschenkoi* (Birula)). We can conclude that the three characters assigned to the same state by Prendini for these two genera are incorrect (they were assigned to other scorpionoid taxa as well). Consequently we digitized Prendini's (2000: Table 3) original data matrix and made the following alterations: 1) assigned separate states to his neobothriotaxy characters 43, 45, and 49 for the two genera in question (but retained the mappings for the other genera with neobothriotaxy); 2) changed *Heteroscorpion*'s state for character 11 to indicate subequal distal denticles on dorsal/ventral edges of cheliceral movable finger. This state change is indicated by viewing Figs. 11, 12, and 14 of three species of *Heteroscorpion* illustrated by Lourenço (2002b), two of which clearly show the denticles are subequal. Although the distal denticles are not subequal in Fig. 11 (*H. opisthacanthoides*), they do not exhibit the significant difference commonly seen in other scorpionoids as illustrated in our Fig. 45 (*Scorpio*) and Fig. 46 (*Brachistosternus*); 3) character 9, "shape" and dimensions of the sternum, was modified to indicate the posterior tapering as exhibited in *Heteroscorpion* (as indicated in a specimen observed by us). In addition, we augmented this character to reflect the two sternum types recently defined by Soleglad & Fet (2003); 4) character 33, Prendini's modeling of the chelal finger median denticle (MD) rows, was changed to two rows for *Heteroscorpion* since two rows are visible on the distal third of the finger, although fused into "many rows" basally. We also question this somewhat simplistic modeling of this complex structure, considering "one-row", "two-rows", and "multiple rows

(>2)", where we believe *Heteroscorpion* is intermediate. However, this character requires some serious reanalysis involving many species in several genera, something not possible with the token species set used in the "exemplar method"; 5) as with neobothriotaxy, we question Prendini's character 95, where he assigns three disparate genera groups that exhibit a single ventral median carina on metasomal segments I–IV to the same state, *Heteroscorpion*, *Urodacus*, and *Hemiscorpius* + *Habibella*. We assign each group its own state thus removing this assumption of homologous derivation (which also uncouples *Heterometrus* from Hemiscorpiinae as well).

Figure 126 shows the result of these changes to Prendini's data matrix. Interestingly, our result is the same as that originally proposed by Stockwell (1989: Figs. 251, 259), *Heteroscorpion* binding with the liochelins and hemiscorpiines, and *Urodacus* grouping with the scorpionines and diplocentrines. This grouping has an intuitive appeal because, if for no other reason, the very unique and unprecedented character of the rounded lateral distal lobes of the leg tarsus is now cleanly distributed within the superfamily (i.e., nonhomoplasious).

Since our analysis is cursory at best, especially in issues involving the chelal finger dentition, we have not made changes to Prendini's result. Additional study is required in several areas, in particular of chelal finger dentition across the superfamily Scorpionoidea, and a serious analysis of neobothriotaxy within closely related groups involving statistical analysis of many specimens across the species set. In summary, here is a list of characters (some of which were discussed above) that *Heteroscorpion* uniquely shares with subfamilies Liochelinae and Hemiscorpiinae: leg tarsus not exhibiting rounded lateral distal lobes (a key character); simple venom glands (a key character?); dorsal and ventral distal denticles of the cheliceral movable finger approximately same length; sternum tapers posteriorly; sternum is longer than wide; patella internal surface highly

vaulted into a “projection” (a key character); and the chelal palm is somewhat flat, not exhibiting the highly vaulted palm commonly found in Scorpioninae and Diplocentrinae.

Subfamily Urodacinae Pocock, 1893

Type Genus. *Urodacus* Peters, 1861.

Composition. This monotypic subfamily includes a single genus, *Urodacus*.

Distribution. The subfamily is endemic to Australia.

Diagnosis. See Prendini (2000) for details on the diagnosis of this subfamily (as family Urodacidae).

Discussion. See discussion under family Urodacidae.

Subfamily Heteroscorpioninae Kraepelin, 1905

Type Genus. *Heteroscorpion* Birula, 1903.

Composition. This taxon is here downgraded to subfamily rank, and placed in the family Urodacidae. This monotypic subfamily includes a single genus, *Heteroscorpion*.

Distribution. The subfamily is endemic to Madagascar.

Taxonomic history. This monotypic taxon was traditionally listed as a subfamily of Scorpionidae. Lourenço (1985, 1989) suggested that its only genus *Heteroscorpion* belongs to Ischnuridae (now Liochelidae). In an unpublished classification of Stockwell (1989) Heteroscorpioninae was transferred to Ischnuridae as a subfamily. Sissom (1990) listed *Heteroscorpion* under Ischnuridae without subfamilial division. The subfamily Heteroscorpioninae was elevated to the family level by Lourenço (1996a), and subsequently was treated as a family (Fet, 2000b; Prendini, 2000).

Diagnosis. See Prendini (2000) for details on the diagnosis of this subfamily (as family Heteroscorpionidae).

Discussion. See discussion under family Urodacidae.

Family Protoischnuridae Carvalho & Lourenço, 2001 – Extinct.

Type Genus. *Protoischnurus* Carvalho & Lourenço, 2001. – Extinct.

Composition. The family includes two genera: *Protoischnurus* Carvalho & Lourenço, 2001 and *Araripescorpius* Campos, 1986 (the latter assigned here provisionally by Carvalho & Lourenço (2001)).

GEOLOGICAL OCCURRENCE. Lower Cretaceous of Brazil (Crato member, Santana Formation; ca. 110 Mya).

Taxonomic history. *Araripescorpius* was earlier listed under “Scorpionoidea *sensu lato*” (Campos, 1986; Selden, 1993), and under “Orthosternina Incertae Sedis” by Fet et al. (2000). Carvalho & Lourenço (2001) placed this family in the superfamily Scorpionoidea (*sensu*

Lourenço, 2000a) commenting that *Protoischnurus* shows some affinities with the modern families Scorpionidae and Ischnuridae (now Liochelidae).

Biogeographic history. The South American Cretaceous record of Protoischnuridae has a particular biogeographic importance for interpreting scorpion evolution. We interpret Scorpionoidea as the Pangean superfamily based on its modern biogeographic distribution, and typical scorpionoid features of Protoischnuridae confirm that by the time when the Gondwanaland breakup was complete, scorpionoids indeed existed in South America.

Diagnosis. See Carvalho & Lourenço (2001) for details on the diagnosis of this family.

Discussion. We agree with placement of Protoischnuridae in Scorpionoidea. However, more work (currently ongoing) on rich Santana fossils needs to be done to clarify position of *Araripescorpius*, which shares some features with Chactoidea.

Superfamily Incertae Sedis

The fossil (Cretaceous) family Palaeoescorpiidae is placed here in the parvorder Iurida but cannot be currently assigned to any of the extant superfamilies.

Family Palaeoescorpiidae Lourenço, 2003 – Extinct.

Type Genus. *Palaeoescorpius* Lourenço, 2003. – Extinct.

Composition. The family is monotypic, with a single monotypic genus *Palaeoescorpius*.

Geological occurrence. Cretaceous of Europe (France) (amber).

Taxonomic history. The name given by Lourenço (2003) implies some relationship with modern Euscorpidae, and the family was originally placed in the superfamily Chactoidea (*sensu* Lourenço, 2000).

Diagnosis. See Lourenço (2003) for details on the diagnosis of this family.

Discussion. This family indeed has features shared with parvorder Iurida, in particular the important neobothriotaxy on the ventral aspect of patella. However, we do not find any specific features which would allow including Palaeoescorpiidae unequivocally in Chactoidea, as did Lourenço (2003). The reported trichobothrial pattern could as well belong to a member of Scorpionoidea. In Lourenço’s (2003) Figs. 5–9, a partial trichobothrial pattern is shown for the dorsal-external and ventral aspects of the chela (12 trichobothria), and the dorsal and ventral aspects of the patella (29 trichobothria (11 accessory)); trichobothrial pattern of the femur is unknown. In this pattern, major neobothriotaxy is well illustrated on the patellar ventral surface, with 14 trichobothria in view. This is an important observation, since we now know that neobothriotaxy in this species occurred at least 100 Ma ago, derived from the orthobothriotaxy which is presumably Type C (we known from

the five “palaeo-buthids” described by Lourenço & Weitschat, 1996, 2000, 2001, that Type A existed at least 65–55 Ma.). On the chela (from the left pedipalp) we see three ventral trichobothria, presumably V_1 – V_3 and Et_1 with the ventroexternal carina curving inward, toward the internal condyle. The apparent absence of trichobothrium V_4 on the ventral surface is an indication of the euscorpids, endorsing the conclusion made by Lourenço (i.e., it is located on the external surface). On the dorsal-external aspect we see eight trichobothria, six on the palm and two on the fixed finger. The two trichobothria located on the fixed finger probably belong to the db – dt series, and may include as well the most dorsal distal trichobothrium seen on the palm. The three more proximal trichobothria presumably are Db , Dt , and Eb_3 , although, as drawn in the figure, the Db and Dt are dorsal of the well-defined digital carina. The other two trichobothria found on the palm exterior are probably in the Et_1 – Et_5 and/or Est series. Unlike in the chela, there is considerable confusion as to the designations of trichobothria found on the patella, the text of Lourenço and the figures are not consistent. We can see a definite internal trichobothrium (i), d_1 , and a second basal dorsal trichobothrium which more likely belongs to the external series. Fig. 7, which shows the dorsal aspect of the patella, and Fig. 8, which shows a somewhat skewed external view, angled internally, are, in part, composite figures. As it turns out (Lourenço, 2003, pers. comm.) only the dorsal and ventral views were visible on the fossil, the external view shown in Lourenço’s Fig. 8 is a composite of these two views. The external view shows six trichobothria on the ventral side of the externomedian carina and six on the dorsal side, a total of 12 trichobothria. However, if we add in the somewhat displaced basal “dorsal” trichobothrium mentioned above, we have 13 trichobothria, the number found in Type C patterns. Of course, the positions of these trichobothria do not comply with conventional Type C patterns. This would imply, if all these interpretations are correct (which is unlikely), that neobothriotaxy occurred only on the patella ventral surface. In summary, it is clear that this fossil scorpion is probably Type C even though many trichobothria are unaccounted for, including the entire femur, 18 in all (14 alone for the chela).

Parvorder Incertae Sedis (fossil taxa)

The fossil orthostern taxa (families and/or genera) listed below (Carboniferous to Miocene) cannot be currently assigned to any of the parvorders established for Recent superfamilies. We choose also not to assign these taxa to any superfamilies.

Family Archaeobuthidae Lourenço, 2001 – Extinct.

Type Genus. *Archaeobuthus* Lourenço, 2001. – Extinct.

Composition. This monotypic family includes a single monotypic genus, *Archaeobuthus*.

Geological occurrence. Lower Cretaceous of Lebanon (amber), ca. 125Ma.

Taxonomic history. Lourenço (2001c, 2002b) placed Archaeobuthidae in superfamily Buthoidea. In our opinion, there is no current data which confirms placement of Archaeobuthidae either in Buthoidea, or in parvorder Buthida, as defined here.

Diagnosis. See Lourenço (2001c) for details on the diagnosis of this family.

Discussion. *Archaeobuthus* is an important fossil since it is the oldest known orthostern taxon since Carboniferous. Soleglad & Fet (2001) indicated that the reported trichobothrial data places Archaeobuthidae as a sister group to all Recent scorpions. Lourenço (2002b: 38) objected that the observed trichobothrial pattern of *Archaeobuthus* could be incomplete. However, this pattern was originally reported by Lourenço (2001c: 643) as “neobothriotaxy minorante”, i.e. a completely observed set with some “fundamental trichobothria” missing. This implies that the entire set of trichobothria was visible, as assumed by Soleglad & Fet (2001: 4). Another fossil genus, *Palaeoburmesebuthus*, could also belong to this family (see below).

Family Palaeopisthacanthidae Kjellesvig-Waering, 1986 – Extinct.

Type Genus. *Palaeopisthacanthus* Petrunkevitch, 1913. – Extinct.

Composition. The family includes three genera (Jeram, 1994a, 1994b, 1998; Fet, 2000e): *Composcorpis*, *Cryptoscorpis*, and *Palaeopisthacanthus*.

Geological occurrence. Upper Carboniferous of Europe and North America.

Taxonomic history. This family was assigned by Kjellesvig-Waering (1986) to his superfamily “Scorpionoidea” in a very broad sense, equivalent to the current infraorder Orthosterni. We emphatically do not include it either in our Scorpionoidea, or in any other extant superfamily or parvorder.

Biogeographic history. Palaeopisthacanthids, the first known orthostern scorpions, inhabited a wet, humid, tropical flood-basin forest (Jeram, 2001). The European and North American Carboniferous record of Palaeopisthacanthidae has no particular biogeographic importance for further evolution of orthostern scorpions. The age of these fossils corresponds to the beginning of Pangea formation, and it was in Pangea for the next 100 Ma in Permian/Triassic that orthostern lineages evolved and dispersed, surviving as four extant parvorders.

Diagnosis. See Kjellesvig-Waering (1986: 232) and Jeram (1994a: 523) for details on the diagnosis of this family.

Discussion. Absence of Carboniferous orthostern fossils from southern continents is due to a much better

representation and knowledge of coal deposits in the northern continents. The exclusively preserved, rich Carboniferous fossils of Europe and North America (Jeram, 2001) include Orthosterni as well as many other scorpion lineages, which did not survive to our time. Palaeopisthacanthids are the sister group to all extant scorpions (Jeram, 1994a; Soleglad & Fet, 2001), and therefore the key taxon for rooting extant groups.

Family Incertae Sedis (fossil taxa).

Genus *Corniops* Jeram, 1994. – Extinct.

Geological occurrence. Carboniferous of North America.

Taxonomic history. This monotypic genus has not been placed in any family. It was listed by Fet et al. (2000) under “Orthosternina Incertae Sedis”.

Diagnosis. See Jeram (1994a) for details on the diagnosis of this genus.

Genus *Palaeoburmesebuthus* Lourenço, 2002. – Extinct.

Geological occurrence. Cretaceous of Burma (Myanmar) (Burmite amber, 112–98 Ma).

Taxonomic history. This monotypic genus was described (Lourenço, 2002a) as a fragment of metasoma without a family placement; however, Lourenço (2002a: 100) stated that it “is unquestionably a member of the Buthoidea”. This statement, however, was based on shape and sculpture of metasomal segments only. Santiago-Blay et al. (in press) analyzed another fragmentary specimen of *Palaeoburmesebuthus*, with important but partial trichobothrial set on pedipalp chela. Judging from trichobothrial pattern and circular stigmata, this genus could belong to Archaeobuthidae, but the diagnostic characters are not sufficient to make a definite family placement (Santiago-Blay et al., in press). There is no current data which confirms placement of *Palaeoburmesebuthus* either in Buthoidea, or in parvorder Buthida, as defined here.

Diagnosis. See Lourenço (2002a) and Santiago-Blay et al. (in press) for details on the diagnosis of this genus.

Genus *Sinoscorpis* Hong, 1983. – Extinct.

Geological occurrence. Miocene of China.

Taxonomic history. Fet et al. (2000) listed this monotypic genus under family Scorpionidae, as placed by the original author. From the brief original description, is impossible to establish a definite family placement.

Diagnosis. Hong (1983, available in Chinese only) can be consulted for details on the diagnosis of this genus.

Genus *Uintascorpio* Perry, 1985. – Extinct.

Geological occurrence. Eocene of USA (Colorado).

Taxonomic history. Fet et al. (2000) listed this monotypic genus under “Orthosternina Incertae Sedis”. From the original description, it is impossible to establish a definite family placement.

Diagnosis. See Perry (1985) for details on the diagnosis of this genus.

Discussion. *Uintascorpio* shares some features with the parvorder Buthida; Kovařík (1998) even suggested its synonymy with the extant buthid genus *Rhopalurus*. It is the oldest North American scorpion fossil since Carboniferous.

Scorpion Evolution and Historical Biogeography

Lamoral (1980) briefly outlined biogeographic hypotheses for family-level scorpion taxa, following his proposed phylogeny. The only recent comprehensive treatment of scorpion biogeography has been published by Nenilin & Fet (1992) in Russian. This work was based on scorpion systematics of the mid-1980s, and many important changes and interpretations have taken place since that time. Lourenço (1996b, 1998a, 2000a) and Lourenço & Sissom (2000) further commented on general historical and ecological issues, which contributed to the modern distributional patterns of the order, including disjunction and endemism. Table 11 lists present day distribution of families, subfamilies and tribes of Recent scorpions.

Although extinct scorpions are a rather diverse group (Kjellesvig-Waering, 1986), the fossils belonging to the infraorder Orthosterni are not common. The first orthostern scorpions, Palaeopisthacanthidae, are known from the Upper Carboniferous (Pennsylvanian) of the USA and England, ca. 300 Ma old (Jeram, 1994a, 1994b). Unfortunately, no orthostern fossils are known from the following 175 Ma. Several described genera of Permian, Triassic, and Jurassic fossil scorpions (Kjellesvig-Waering, 1986) do not belong to the Orthosterni. The next earliest orthostern fossil is known only from the Cretaceous (Barremian–Aptian, ca. 125 Mya), the genus *Archaeobuthus* from the Lebanese amber, not assigned to any of the existing parvorders. From later in the Cretaceous (ca. 110–100 Mya), fossils exist of the genera *Palaeoburmesebuthus* and *Araripescorpius* (not assigned to any of the existing parvorders), *Palaeoescorpius* (assigned to parvorder Iurida but not to any of the existing superfamilies), and *Protoischnurus* (parvorder Iurida, superfamily Scorpionoidea). It is clear therefore even from this meager handful of fossils that the extant parvorders and superfamilies were already well established by the Cretaceous. Indeed, all major nodes in our phylogeny (Fig. 114) at parvorder and superfamily

	Europe	Asia	Africa	Madagascar	Australia	North America	Central America	South America
Pseudochactidae		X						
Buthidae	X	X	X	X	X	X	X	X
Microcharmidae				X				
Chaerilidae		X						
Iuridae	X	X						
Caraboctonidae						X		X
Caraboctoninae								X
Hadrurinae						X		
Bothriuridae		X	X		X			X
Scorpionidae		X	X			X	X	X
Scorpioninae		X	X					
Diplocentrinae		X	X			X	X	X
Nebini		X	X					
Diplocentrini						X	X	X
Liochelidae		X	X	X	X		X	X
Liochelinae		X	X	X	X		X	X
Hemiscorpiinae		X	X					
Urodacidae				X	X			
Urodacinae					X			
Heteroscorpioninae				X				
Euscorpiidae	X	X	X			X	X	X
Euscorpiinae	X		X					
Megacorminae						X	X	X
Megacormini						X	X	
Chactopsini								X
Scorpiopinae		X				X		
Scorpiopini		X						
Troglocormini						X		
Chactidae	X					X	X	X
Chactinae						X	X	X
Chactini							X	X
Nullibrotheini						X		
Brotheinae	X							X
Brotheini								X
Belisariini	X							
Uroctoninae						X		
Superstitioniidae						X		X
Vaejovidae						X		

Table 11: Geographic distribution of Recent scorpions. Each of the six superfamilies are grouped in alternating shaded areas.

level have to precede, well in advance, the Cretaceous family Protoischnuridae.

An additional “upper bracket” might come from the distribution of modern-day families, some of which bear

a clear trace of Gondwanaland breakup at the level below family. There is first of all family Bothriuridae (Scorpionoidea), with its modern genera in South Africa, Australia, Asia and, especially, South America (Pren-

dini, 2000, 2003a, 2003b). The Gondwanaland breakup happened roughly in Jurassic–Cretaceous (170 to 130 Mya); by the beginning of Cretaceous (145 Mya) most continents were already separated. If we interpret Bothriuridae as a family which originated in Gondwanaland and was never present in Laurasia, then the common ancestor of this family should have existed before Cretaceous. At the same time, Bothriuridae is a sister group of Liochelidae and Scorpionidae, but the latter families also have Gondwanaland signature taxa, first of all isolated subfamilies Heteroscorpioninae on Madagascar, and Urodacinae in Australia; possibly the disjunct subfamily Diplocentrinae; and maybe even the genus *Opisthacanthus* (Liochelidae), distributed in Africa and South America. It is then conceivable that all the families of Scorpionoidea were established by the end of Jurassic (146 Mya). Presence of Protoischnuridae fossils at 110 Mya does not contradict this assumption.

The superfamilies Buthoidea, Iuroidea, and Chactoidea, on the other hand, had to be established before the supercontinent Pangea started breaking apart in early Jurassic (Sinemurian), i.e. about 200 Mya (Brown & Lomolino, 1998; Scotese, 2002). This follows from their modern distribution, which is worldwide in Buthoidea (for which Pangean origin was first recognized by Birula (1917a, 1917b)), and worldwide but patchy in Iuroidea and Chactoidea (notably excluding Australia). None of the latter two superfamilies or any of their included families exhibits specifically “Gondwanaland” patterns: among Iuroidea, Caraboctonidae are found in the Americas, and Iuridae, in the Mediterranean; Chactidae is predominantly South American but with an important relict, *Belisarius*, in the Mediterranean; Euscorpiidae are disjunct among South America, Mexico, Southeast Asia, and the Mediterranean. Superstitioniidae are found in both South and North America, and Vaejovidae are endemic to North America. If any traces of Gondwanaland isolation could be found in non-scorpionoid superfamilies, these are expressed at the level of genera and groups of genera (such as *Ananteris* in Buthidae; see also Fet et al., 2003). Therefore, early history of modern superfamilies has to be Pangean. Lourenço (1996b: 441) stated that “the main event responsible for determining the biogeographic patterns of scorpions on a palaeogeographic scale, has been the fragmentation of Pangea and subsequent continental drift”. We would caution, however, that not all vicariant ranges in modern scorpions (at the level of family and below) are interpretable by continental drift, and can be also explained by differential extinction and survival of relict taxa (Eskov, 1984, 1992, 2002; Nenilin & Fet, 1992).

The supercontinent Pangea was already forming at the Upper Carboniferous, from where we have the “lower bracket” fossils of Orthosterni. Therefore, the following 100 Ma of scorpion evolution took place within Pangea, before it started breaking apart. These

100 Ma embrace roughly the Permian period (290 to 251 Mya) and the Triassic period (251 to 206 Mya). Jeram (2001) indicated that the diversification of orthostern scorpions which followed in Permian/Triassic “can be attributed to their adoption of nocturnal habits, smaller adult body sizes, and burrowing behavior” as well as to ever-growing predation pressure from terrestrial tetrapods. It is reasonable therefore to place origin of four extant orthostern parvorders to Pangean times as well, provided that Palaeopisthacanthidae are the outgroup to all extant parvorders. The fate of these four extant parvorders was different. Two of them (Buthida and Iurida) still enjoy the world domination, albeit in Iurida with significant disjunctions possibly due to extinctions (Iuroidea, Chactoidea). Conversely, two other parvorders (Pseudochactida and Chaerilida) currently survive only in Asia as relict monotypic genera, *Pseudochactas* and *Chaerilus*. We cannot speculate where exactly the four orthostern parvorders originated within Pangea, but it is reasonable to assume that they should have been established during the Permian to Triassic time. It is important to note that this was also the time of evolutionary diversification of “reptiles” (Futuyma, 1998), who likely were (and still are) the competitors and, especially, predators of the terrestrial orthostern scorpions (Jeram, 2001). Further through Cretaceous, many animal taxa persisted as relicts while other perished during the global restructuring of ecosystems (Zherikhin, 1978). It is possible that the primitive orthostern groups survived in such a relict condition. While Pseudochactida and Chaerilida remain only as relicts, Iurida and especially Buthida experienced a tertiary boost of radiation, notably due to the aridization in the Old World deserts (Nenilin & Fet, 1992).

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Appendix A

Characters and Character States

This Appendix describes each character and assigned states used in the cladistic analysis presented in this paper. Many of the character descriptions and homologies hypothesized in this Appendix are discussed in detail elsewhere in this paper, in particular, in sections involving character and cladistic analyses. For those characters not specifically discussed in those sections, we provide here brief rationale for their state assignments. Tables 3 and 4 denote the exact character states assigned to the 60 taxa evaluated in this analysis. All characters are described in this Appendix, including three uninformative characters (autapomorphic). The 62 characters defining orthobothriotaxy are not described in this Appendix; see Soleglad & Fet (2001) for a description of these characters and Table 4 in this paper for specific character state assignments. Ordered *character 1* described below replaces these 62 existence characters.

All characters are assigned a weight of one and are unordered except the following:

- Character 1: orthobothriotaxy (full ordering)
- Character 19: trichobothria *Db–Dt* positions (partial ordering)
- Character 27: patellar trichobothrium v_3 vertical position (full ordering)
- Character 41: cheliceral movable finger, subdistal denticles (partial ordering)
- Character 42: cheliceral movable finger, ventral edge (partial ordering)
- Character 60: leg pedal spurs (partial ordering)
- Character 82: female genital operculum (partial ordering)
- Character 102: number of lateral eyes (partial ordering)

The use of *primary/secondary* characters force an “additive binary” ordering to derivations. Where this is used, the secondary character always follows the primary character and they are labeled as such.

Characters described below are grouped by their structural type. If a character is fundamental, it is flagged with “[FUND]”, if uninformative, “[UNINFORM]”, and if ordered, “[ORD]” or “[PART-ORD]”. If a character is not discussed in the character or cladistics analyses sections of this paper, a brief statement specifying the assumptions as to the assignment per state is included. The state “-” specifies “uninformative data” and “?” specifies “unknown data”.

Trichobothria

Trichobothria characters are divided into orthobothriotaxy (i.e., existence of individual trichobothria or patterns), positions of orthobothriotaxic trichobothria by pedipalp segment, and neobothriotaxy by pedipalp segment.

Orthobothriotaxy - existence

Characters 1–26: Chela: Existence analysis (weighting based on Sankoff character)

Characters 1–23: Patella: Existence analysis (weighting based on Sankoff character)

Characters 1–13: Femur: Existence analysis (weighting based on Sankoff character)

See **Appendix E** for the Sankoff character definition and derivation maps and Table 4 for the data matrix for these 62 existence characters.

Character 1: Orthobothriotaxy [FUND, ORD]

- (0): Type P, Palaeopisthacanthidae
- (1): Type F1, Archaeobuthidae
- (2): Type D, Pseudochactida
- (3): Type A, Buthida
- (4): Type B, Chaerilida
- (5): Type C, Iurida

This ordered character replaces the 62 existence characters presented above.

Orthobothriotaxy - positional

Femur: Types P, F1, A, B & D

Breakdown of Vachon's (1975) femoral *alpha-beta* pattern: based on genera *Archaeobuthus*, *Pseudochactas* and *Chaerilus*, we break down the *alpha-beta* pattern into three characters: orientation of trichobothria $d_1–d_3$ and $d_3–d_4$ as they relate to the dorsoexternal carina, and the surface location of trichobothrium d_2 .

Character 2: Femoral sub-pattern: $d_1 \rightarrow d_3$ [FUND]

- (0): *parallel* to dorsoexternal carina (rarely *beta*)
- (1): points *toward* dorsoexternal carina (typically *beta*)
- (2): points *away* from dorsoexternal carina (*alpha*)
- (-): Type C pattern

Character 3: Femoral sub-pattern: $d_3 \rightarrow d_4$ [FUND]

- (0): *parallel* to dorsoexternal carina (rarely *beta*)
- (1): points *away* from dorsoexternal carina (typically *beta*)
- (2): points *toward* dorsoexternal carina (*alpha*)
- (-): Type C pattern

Character 4: Placement of d_2 [FUND]

- (0): on *dorsal* surface (usually *beta*)
- (1): on *internal* surface (usually *alpha*)
- (-): Type C pattern

Femur: Type C**Character 5:** Femur: d and i alignment

- (0): d is proximal to i
- (1): d is equal or definitely distal to i
- (-): Type D, A, and B patterns

This character is discussed in detail in Soleglad & Sissom (2001: 46–47, Figs. 73–87).

Character 6: Femur: d position

- (0): mid- to semi-mid segment (Euscorpiidae)
- (1): next to *dorsoexternal* carina
- (-): Type D, A, and B patterns, Vaejovidae

This character, in part, is discussed in detail in Soleglad & Sissom (2001: 46–47, Figs. 73–87).

Chela: Type C**Character 7:** Chela palm: V_4 position

- (0): ventral surface
- (1): external surface (Euscorpiinae, Megacorminae)
- (-): Type D, A, and B patterns

This character is discussed in detail in Soleglad & Sissom (2001: 51–54, Figs. 88–99).

Character 8: Chela palm: Eb_1 position

- (0): external surface
- (1): ventral surface or on ventroexternal (VI) carina
- (-): Type D, A, and B patterns

Character 9: Chela palm: Et_2 position [FUND]

- (0): external surface
- (1): ventral surface
- (-): Type D, A, and B patterns

The ventral location of trichobothrium Et_2 is considered a synapomorphy for the scorpionoid family Bothriuridae.

Character 10: Chela palm: ib position [FUND]

- (0): on fixed finger, midfinger to finger base

- (1): at extreme base of fixed finger or on palm (Chactoidae)
- (2): at extreme base of fixed finger or on palm (Scorpionoidea)
- (-): Type D, A, and B patterns

Character 11: Chela palm: it position

- (0): on fixed finger, midfinger to finger base (Vaejovidae)
- (1): at extreme base of fixed finger (Superstitioniidae)
- (2): on palm, next to articular membrane (Euscorpiidae, Chactidae)
- (3): at extreme base of fixed finger or on palm (Scorpionoidea)
- (4): on distal aspect of finger (Iuridae)
- (5): on distal aspect of finger (*Chactopsis*)
- (6): on distal aspect of finger (*Alacran*)
- (-): Type D, A, and B patterns

Similar character derivations in disparate groups are given their own states (a general hypothesis).

Character 12: Chela palm: V_1-V_4 orientation [FUND]

- (0): in straight line, extending across entire palm
- (1): angled internally (V_2) or in straight line, not extending across entire palm (Chactoidae(-V))
- (2): angled towards internal aspect (Scorpionoidea)
- (-): Type D, A, and B patterns

Similar character derivations in different superfamilies are given their own states (a general hypothesis).

Character 13: Chela fixed finger: $db-dt$ and $eb-et$ position [FUND]

- (0): evenly spread out on finger
- (1): on distal half of finger (Iuroidea)
- (2): on proximal half of finger (Scorpionoidea)
- (3): on distal half of finger (Chactoidae)
- (-): Type D and A patterns

Similar character derivations in different superfamilies are given their own states (a general hypothesis).

Character 14: Chela fixed finger: ib/it relative orientation

- (0): together
- (1): separated (Iuridae)
- (2): separated (Euscorpiidae)
- (3): separated (Superstitioniidae)
- (-): Type D, A, and B patterns

Similar character derivations in disparate groups are given their own states (a general hypothesis).

Character 15: Chela palm: Et_5 position

- (0): on palm
- (1): well on fixed finger (Caraboctonidae)
- (-): Type D, A, and B patterns

This models the unique chelal trichobothrium positions as seen in iuroid family Caraboctonidae. This character is realized, in part, due to the adoption of Stockwell's (1989) alternative interpretation of chelal trichobothrial homologies for this scorpion group (see detailed discussion in **Character Analysis** section). The issue of Et_1 - Et_5 positions as seen in chactoid genus *Brotheas* is addressed in *character 22* below.

Character 16: Chela palm: Et_1 position

- (0): external surface (Iuridae)
- (1): ventral surface
- (-): Type D, A, and B patterns

This unique position of Et_1 as seen in the Old World iuroids is considered primitive; it is found on ventral surface in all other Type C scorpions.

Character 17: Additional chelal petite trichobothria, esb , Est , and V_2 [FUND]

- (0): present (Iuridae)
- (1): not present
- (-): Type D, A, and B patterns

Three additional petite trichobothria are found in the Old World iuroids (family Iuridae), unprecedented in other Type C scorpions.

Character 18: Chela palm: V_2 and V_3

- (0): evenly spaced
- (1): greatly separated, distance between V_2 and V_3 much greater than distances between V_1 and V_2 and V_3 and V_4
- (-): Type D, A, and B patterns

This spacing between trichobothria V_2 and V_3 is quite conspicuous in many scorpionid and liochelid genera.

Character 19: Position of chelal trichobothria Db/Dt [PART-ORD]

- (0): Db/Dt basal, proximal of palm midpoint (Vaejovidae, Euscorpidae, and Uroctoninae)
- (1): Db basal, Dt base of fixed finger (Superstitioniidae)
- (2): Db basal, Dt palm midpoint (Chactinae)
- (3): Db/Dt very basal (*Belisarius*)
- (4): Db proximal to distal of base, Dt past midpoint-finger base (*Neochactas*)
- (5): Db distal to base, Dt well past midpoint (*Brotheas*)

- (-): non-chactoids

Character 20: Chelal trichobothria positions: et - eb series of finger (**primary**)

- (0): esb closest to finger edge with respect to eb (Vaejovidae, Superstitioniidae)
- (1): eb closest to finger edge with respect to esb (next to membrane) (Chactidae, Euscorpidae)
- (-): non-chactoids

Character 21: Chelal finger eb - et series (**secondary**)

- (0): no change, eb closest to finger edge (see above)
- (1): esb and eb in straight line, eb most proximal (Brotheina)
- (2): esb and eb in straight line, eb most proximal (Scorpiopinae)
- (3): esb and eb in straight line, eb most proximal (*Chactopsis*)
- (-): non-chactids and non-euscorpids

Similar character derivations in disparate groups are given their own states (a general hypothesis).

Character 22: Chelal Et_1 - Et_5 series, position of Et_3 - Et_5

- (0): Et_5 on midpalm (all Chactidae other than Brotheina)
- (1): Et_5 on fixed finger (Brotheina)
- (-): non-chactids

Patella: Type B/C**Character 23:** Patella ventral, V_3 position [FUND]

- (0): on ventral surface
- (1): on external surface
- (-): Type D and A patterns

Character 24: Patella ventral, V_2 position [FUND]

- (0): on ventral surface
- (1): on external surface (Iuridae)
- (2): on external surface (Typhlochactini)
- (-): Type D and A patterns

Similar character derivations in disparate groups are given their own states (a hypothesis).

Character 25: Additional patellar petite trichobothria, et_2 and eb_2 [FUND]

- (0): present (Iuridae)
- (1): no, other Type C
- (-): non-Type C

Two additional petite trichobothria are found in the Old World iuroids (family Iuridae), unprecedented in other Type C scorpions.

Character 26: Alignment of patellar external trichobothria series esb_1-esb_2

- (0): esb_1-esb_2 slant downwards
- (1): esb_1-esb_2 either parallel to the patella width, or slant upwards (Superstitioniidae)
- (-): non-chactoids

The unusual “upward” slant of the esb_1-esb_2 trichobothrial series is exclusively found in the chactoid family Superstitioniidae, only the unique genus *Alacran* is an exception.

Character 27: Vertical position of patellar v_3 trichobothrium [ORD]

- (0): proximal or equal to midpoint, proximal of est and et_3 ; distance between v_3 and $v_2 <$ distance between v_2 and v_1 (Chactidae, Euscorpiidae)
- (1): distal of midpoint, distal or equal to est and et_3 ; distance between v_3 and $v_2 \geq$ distance between v_2 and v_1 (Vaejovidae, Superstitioniidae)
- (-): non-chactoids

This character addresses the somewhat lower position of patellar trichobothrium v_3 in the families Euscorpiidae and Chactidae than that found in families Vaejovidae and Superstitioniidae, where v_3 is found adjacent to or distal of trichobothrium est .

Character 28: Patella: em_1-em_2 and esb_1 vertical alignment

- (0): em_1-em_2 and esb_1 near midsegment (Vaejovidae, Brotheinae, Uroctoninae, Superstitioniidae)
- (1): em_1-em_2 and esb_1 proximal (1/3 distance from proximal edge) (Chactinae)
- (2): em_1-em_2 and esb_1 proximal (1/3 distance from proximal edge) (Scorpiopinae)
- (-): non-chactoids

We consider the similar trichobothrial positions as exhibited in chactid subfamily Chactinae and the euscorpiid subfamily Scorpiopinae as independent derivations (a hypothesis).

Character 29: Patella: comparative distance em_1-em_2 and esb_1-esb_2

- (0): distance between esb_1 and $esb_2 \leq$ distance between em_1 and em_2 (Chactinae, Euscorpiidae)
- (1): distance between esb_1 and $esb_2 \gg$ distance between em_1 and em_2 (Brotheinae, Uroctoninae)
- (-): non-chactoids, Vaejovidae

Trichobothria – Neobothriotaxy (Additive)

We implement a high-level modeling scheme in our approach to neobothriotaxy, based primarily on putative family designations. We divide this modeling into two

types, Type A (the buthoids) and Type C (the iuroids, scorpionoids, and chactoids). We suspect that subtractive neobothriotaxy found in some buthid genera may imply a primitive state of these genera. On the other hand, additive neobothriotaxy in the buthids is clearly derived and therefore is considered autapomorphic to the genera involved. For the substantial additive neobothriotaxy found in Type C scorpions we make no inter-familial assumptions as to common derivations of neobothriotaxy. We believe that neobothriotaxic conditions must be studied in great detail in closely related groups in order to establish potential connections across major familial groups.

Type A

Character 30: Neobothriotaxy found on patella

- (0): absent
- (1): present (*Liobuthus*)
- (-): non Type A pattern

Character 31: Neobothriotaxy found on femur

- (0): absent
- (1): present (*Liobuthus*)
- (-): non Type A pattern

Type C

Character 32: Neobothriotaxy found on chelal ventral surface

- (0): absent
- (1): present (Iuroidea)
- (2): present (Bothriuridae)
- (3): present (Urodacidae)
- (4): present (Liochelidae)
- (5): present (Scorpionidae)
- (6): present (Hemiscorpiinae)
- (7): present type *Ch1* (Chactinae)
- (8): present type *Ch2* (Brotheinae)
- (9): present type *Ch3* (Uroctoninae)
- (a): present type *Eu1* (Euscorpiinae, Megacorminae)
- (b): present type *Eu2* (Scorpiopinae)
- (c): present (Vaejovidae)
- (d): present type *Su1* (Superstitioniidae)
- (-): Type D, A, and B patterns

Character 33: Neobothriotaxy found on chelal external surface

- (0): absent
- (1): present (Iuroidea)
- (2): present (Bothriuridae)
- (3): present (Urodacidae)
- (4): present (Liochelidae)
- (5): present (Scorpionidae)
- (6): present (Hemiscorpiinae)
- (7): present type *Ch1* (Chactinae)

- (8): present type *Ch2* (Brotheinae)
- (9): present type *Ch3* (Uroctoninae)
- (a): present type *Eu1* (Euscorpiinae, Megacorminae)
- (b): present type *Eu2* (Scorpiopinae)
- (c): present (Vaejovidae)
- (d): present type *Su1* (Superstitioniidae)
- (-): type D, A, and B patterns

Character 34: Neobothriotaxy found on chelal internal surface

- (0): absent
- (1): present (Iuroidea)
- (2): present (Bothriuridae)
- (3): present (Urodacidae)
- (4): present (Liochelidae)
- (5): present (Scorpionidae)
- (6): present (Hemiscorpiinae)
- (7): present type *Ch1* (Chactinae)
- (8): present type *Ch2* (Brotheinae)
- (9): present type *Ch3* (Uroctoninae)
- (a): present type *Eu1* (Euscorpiinae, Megacorminae)
- (b): present type *Eu2* (Scorpiopinae)
- (c): present (Vaejovidae)
- (d): present type *Su1* (Superstitioniidae)
- (-): type D, A, and B patterns

Character 35: Neobothriotaxy found on patella ventral surface

- (0): absent
- (1): present (Iuroidea)
- (2): present (Bothriuridae)
- (3): present (Urodacidae)
- (4): present (Liochelidae)
- (5): present (Scorpionidae)
- (6): present (Hemiscorpiinae)
- (7): present type *Ch1* (Chactinae)
- (8): present type *Ch2* (Brotheinae)
- (9): present type *Ch3* (Uroctoninae)
- (a): present type *Eu1* (Euscorpiinae, Megacorminae)
- (b): present type *Eu2* (Scorpiopinae)
- (c): present (Vaejovidae)
- (d): present type *Su1* (Superstitioniidae)
- (-): type D, A, and B patterns

Character 36: Neobothriotaxy found on patellar external surface

- (0): absent
- (1): present (Iuroidea)
- (2): present (Bothriuridae)
- (3): present (Urodacidae)
- (4): present (Liochelidae)
- (5): present (Scorpionidae)
- (6): present (Hemiscorpiinae)
- (7): present type *Ch1* (Chactinae)
- (8): present type *Ch2* (Brotheinae)
- (9): present type *Ch3* (Uroctoninae)

- (a): present type *Eu1* (Euscorpiinae, Megacorminae)
- (b): present type *Eu2* (Scorpiopinae)
- (c): present (Vaejovidae)
- (d): present type *Su1* (Superstitioniidae)
- (-): type D, A, and B patterns

Character 37: Number of accessory trichobothria in *est* series (*Ch1* neobothriotaxy)

- (0): 2 accessory (Chactini)
- (1): 3 accessory (Nullibrotheini)
- (-): non-Chactinae

Character 38: Number of accessory trichobothria in patellar ventral series (*Ch1* neobothriotaxy)

- (0): 3 accessory (Chactini)
- (1): 4 accessory (Nullibrotheini)
- (-): non-Chactinae

Chelicerae

Character 39: Movable finger, distal denticle alignment

- (0): ventral extends considerably beyond dorsal
- (1): ventral dorsal approximately equal
- (2): ventral > dorsal (Euscorpiidae)
- (3): ventral == dorsal (Euscorpiidae)
- (4): ventral >> dorsal (Scorpionoidea)
- (5): ventral == dorsal (Scorpionoidea: Liochelinae and Hemiscorpiinae)

These character distinctions have family and sub-family level relevance in the euscorpiids and the scorpionoids.

Character 40: Movable finger, dorsal edge: basal denticle [FUND]

- (0): 1 basal denticle
- (1): 2 basal denticles (Buthidae)
- (2): absent (Pseudochactidae)

Character 41: Movable finger, dorsal edge: subdistal denticles [FUND, PART-ORD]

- (0): 1 subdistal denticle
- (1): 2 subdistal denticles (Caraboctonidae)
- (2): 2 subdistal denticles (Bothriuridae, reversal)
- (3): 2 subdistal denticles (Chactoidea)
- (4): 1–2 subdistal denticles, variable in genus (Superstitioniidae)

Movable finger, ventral edge: basic high level evolution based on palaeopisthacanthids. We hypothesize the crenulated edge is primitive: from this primitive state, we assume three independent basic transformations: 2 denticles, 1 large basal denticle, and smooth. We assume all other crenulations and dentitions (other than *Chaerilus* or *Pseudochactas*) found throughout the chactoids is derived from a “smooth” edge.

Character 42: Movable finger, ventral edge (**primary**) [FUND, PART-ORD]

- (0): crenulated to small denticles (Palaeopisthacanthidae, Pseudochactidae, Chaerilidae)
- (1): two large denticles (Buthoidea)
- (2): one very LARGE rounded denticle (Iuroidea)
- (3): smooth (other)

Character 43: Movable finger, ventral edge (**secondary**) (only state = 3 of *character 42* is applicable)

- (0): smooth (from state-3 in *character 42*)
- (1): crenulate (Megacorminae)
- (2): crenulate (Scorpiopinae)
- (3): crenulate (Uroctoninae)
- (4): crenulate (Nullibrotheini)
- (5): crenulate (*Paruroctonus* and related genera)
- (6): crenulate (*Pseudouroctonus* and related genera)
- (-): non-chactoids

We consider the numerous occurrences of crenulations found on the ventral edge of the cheliceral movable finger in the chactoids to be quite localized.

Character 44: Fixed finger, median and basal denticles

- (0): median and basal denticles on a “trunk”
- (1): median and basal denticles separate, not on a “trunk” (Chaerilidae)
- (2): median and basal denticles separate, not on a “trunk” (Superstitioniidae)
- (3): median and basal denticles fused as a single denticle (*Archaebuthus*)

Character 45: Fixed finger, denticles on ventral surface (**primary**) [FUND]

- (0): 4–5, major protuberances (Palaeopisthacanthidae, Pseudochactidae, Chaerilidae)
- (1): 0–2 (2), major protuberances (Buthoidea)
- (2): absent

Character 46: Fixed finger, denticles on ventral surface (**secondary**)

- (0): none (state-2 of *character 45*)
- (1): present, Euscorpiidae (*Troglocormus*)
- (2): present, Vaejovidae (*Paruroctonus*, related genera and some *Pseudouroctonus*)
- (-): non-Iurida

As with crenulations on the ventral edge of the cheliceral movable finger, the occurrences of dentition on the ventral surface of the fixed finger found in many chactoids are considered localized to the genera involved.

Pedipalp Chelal Finger Dentition

Character 47: Fundamental chelal finger median denticle (MD) row alignment (**primary**) [FUND]

- (0): oblique, primitive
- (1): non-oblique

The oblique alignment, a primitive condition, is exhibited in the palaeopisthacanthids, archaebuthids and all primitive Recent scorpions. In addition, it is also found in the iuroids.

Character 48: Fundamental chelal finger median denticle (MD) row alignment (**secondary**) [FUND]

- (0): non-oblique (state-1 from *character 47*)
- (1): oblique (Superstitioniidae)
- (-): primitive oblique

We consider the oblique condition of the MD row exhibited in the superstitioniids to be a secondary derivation from a non-oblique condition.

Character 49: Inner accessory denticles (IAD) [FUND]

- (0): Absent
- (1): Present (Euscorpiidae)
- (-): type D, A, and B patterns

This was discussed in detail in revision of family Euscorpiidae by Soleglad & Sissom (2001: 33–40).

Character 50: Outer denticle (OD) removed from MD row

- (0): no
- (1): yes, conspicuous (Euscorpiidae)
- (2): yes (Chactini)
- (3): yes (Scorpionoidea)
- (-): type D, A, and B patterns

In the subfamily Chactinae we see a tendency, at least basely, of the dislocation of the OD to the external aspect of the finger. It is the most exaggerated on Chactinae tribe Chactini, extending to most of the finger, where we see also the enlargement of the basal OD, highly exaggerated in genus *Teuthraustes*.

Character 51: Outer accessory denticles (OAD)

- (0): absent (Euscorpiinae)
- (1): present, irregular (Megacorminae)
- (2): present, alternating (Scorpioninae)
- (-): Type D, A, and B patterns

This was discussed in detail in revision of family Euscorpiidae by Soleglad & Sissom (2001: 33–40).

Character 52: Accessory denticles, miscellaneous

- (0): no
- (1): accessory, outside median groups (*Centruroides*)
- (-): type C pattern

Character 53: “multiple rows”

- (0): no
- (1): yes
- (2): minimal (*Diplocentrus*)
- (-): non-scorpionoids

This characterization (adopted, in part, from Prendini (2000)) is somewhat superficial. Clearly, a detailed analysis of all scorpionoid genera needs to be conducted, where multiple species per genus are considered. Issues involving two rows, more than two rows, multiple rows only present basally, etc., need to be carefully quantified. This analysis proved to be quite difficult in the family Euscorpidae (Soleglad & Sissom, 2001), which was not resolved to any satisfaction until several species with simple patterns were investigated. This, in turn, allowed the determination of homologies in species with more complex patterns.

Character 54: Chelal finger internal denticle (ID) development

- (0): normal, larger than median row denticles
- (1): significantly larger than median denticles (Superstitioniinae)
- (-): Type D, A, and B patterns

Character 55: Chelal movable finger, number of denticle groups in median denticle (MD) row

- (0): 5–6 (*Anuroctonus*, Brotheinae)
- (1): 7–9 (Chactini)
- (2): 7–8 (*Uroctonus*)
- (-): non-chactid

Character 56: Chelal fixed finger, basal outer denticle (OD)

- (0): normal size
- (1): highly enlarged (*Teuthraustes*)
- (-): non-chactoid

Leg Spination**Character 57:** Leg tarsal armature (**primary**) [FUND]

- (0): primitive state, unknown (Palaeopisthacanthidae)
- (1): dual median spinule rows (Pseudochactida)
- (2): numerous irregularly positioned setae (Buthida, Chaerilida)
- (3): ventrally positioned spinule clusters (Iuroidea)
- (4): large paired laterally positioned socketed spinoid setae (Scorpionoidea)
- (5): small laterally positioned socketed setae and/or ventrally positioned spinules (Chactoidea)

Character 58: Leg tarsal armature (**secondary**)

- (0): spinules, no modification (Uroctoninae, Chactinae, Vaejovidae)

- (1): stout setae (usually as two ventral lateral rows) (Brotheinae)
- (2): elongated clusters of spinules (*Superstitionia*)
- (3): setal pairs flanking ventral surface, ventral spinules absent or minimal (Typhlochactinae)
- (4): thin seta-like spines (Scorpionoidea: some Liochelidae)
- (5): elongated clusters of setae/spinules (*Troglotayosicus*)
- (-): non-chactoids and non-scorpionoids

Character 59: Tibial spurs, legs III–IV

- (0): present, legs III–IV
- (1): present, leg IV (*Microcharmus*)
- (2): absent

We assume both tibial spurs are present in the palaeopisthacanthids, based on their presence in Carboniferous genus *Pulmonoscorpis* (Jeram, 1994b).

Character 60: Pedal spurs [FUND, PART_ORD]

- (0): two, both retrolateral and prolateral present
- (1): one, prolateral present (Scorpionoidea)
- (2): two spurs (secondary development, most Bothriuridae)
- (3): 0–2, variable in genus (Typhlochactinae)

The primitive state is two pedal spurs. The loss of the retrolateral spur is constant in the superfamily Scorpionoidea, and the fact that two pedal spurs are found in many bothriurids is considered a secondary development from a single spur condition (i.e., a “reversal”). We see variability in the number of pedal spurs in genera *Sotanochactas* and *Typhlochactas*, from no spurs to both present. Due to *Alacran*’s apparent close taxonomic position to *Typhlochactas*, we assign the same state to this genus (only the prolateral pedal spur is present in *Alacran*).

Character 61: Leg tarsus distal termination

- (0): “squared off”, epitarus (= tarsomere III) exposed (most scorpions)
- (1): “rounded”, surrounding epitarus (Scorpionidae)

Note that this is a combination of Prendini’s (2000) character 65, states 1 and 2. We do not see the distinction reported between *Diplocentrus* and *Scorpio*. *D. ochoterenai*, a large species, is in our ingroup. Stockwell (1989) stated that in some large species of *Diplocentrus* the rounded tarsal terminus was present, implying that this reduced condition of the rounded terminus of the tarsus is variable in this subfamily. Also, the rounded tarsus terminus is reported for the Old World diplocetrine genus *Nebo*, suggesting, maybe, that this unique condition is becoming less exaggerated in some New World diplocetrine species.

Character 62: Leg tarsus ventral distal spinule (*VDS*) pairs

- (0): 1 pair (or one spinule) (Vaejovidae, Euscorpidae, Chactidae)
- (1): 2+ pairs (Euscorpidae)
- (2): 2+ pairs (Vaejovidae)
- (-): non-chactoids

We consider the differences in *VDS* pair numbers exhibited in the chactoid families Vaejovidae and Euscorpidae to be independently derived, thus they are assigned different states. We consider the condition of a single *VDS* pair to be primitive within superfamily Chactioidea, since this is the condition for both basal groups in Vaejovidae (*Vaejovis nitidulus*, *Serradigitus*, and *Paruroctonus* and related genera) and Euscorpidae (*Euscorpium*). Multiple *VDS* pairs is derived in vaejovid genera *Pseudouroctonus* and the “eusthenura” and “punctipalpi” groups of *Vaejovis*. In Euscorpidae, subfamily Megacorminae exhibits derived multiple *VDS* pairs.

Sternum/Maxillary Lobes/Coxae

The characters depicting sternum, maxillary lobe, and leg coxae attributes are described in detail in Soleglad & Fet (2003).

Character 63: Sternum basic type [FUND]

- (0): type 1 – posterior depression, outer ridge, single internal process (primitive)
- (1): type 2 – posterior emargination, lateral lobes; two internal processes (parvorder Iurida)

Character 64: Sternum type 1 [FUND]

- (0): no horizontal compression or concave region, minimal outer ridge (Palaeopisthacanthidae, Pseudochactidae)
- (1): minor compression, minimal outer ridge, concave region marginal (Chaerilidae)
- (2): horizontal compression, outer ridge and concave region well-developed (Buthoidea)
- (-): sternum type 2

Character 65: Sternum type 1, with horizontal compression

- (0): small-medium depression, short concave area, outer ridge proximal
- (1): maximum depression, well developed concave area and outer ridge
- (-): type 1 sternum scorpions without compression and type 2 sternum

This character grossly quantifies horizontal compression within the buthoids.

Character 66: Sternum type 2 [FUND]

- (0): no vertical compression
- (1): vertical compression (Bothriuridae)
- (-): type 1 sterna scorpions

Character 67: Sternum, length/posterior width

- (0): length \leq width (Euscorpidae)
- (1): length $>$ width (Euscorpidae: Scorpioninae)
- (2): length \leq width (Scorpionoidea: non-bothriurids)
- (3): length $>$ width (Hemiscorpiinae)
- (4): length \geq width (Typhlochactinae)
- (5): length $<$ width (Superstitioniinae)
- (-): other groups

The relative length/width proportions of the scorpion sternum are important locally within certain closely related groups. This character models significant proportional differences within the euscorpids, the superstitioniids, and the scorpionoids.

Character 68: Sternum, posterior width and anterior width proportions

- (0): definitely anterior width wider than posterior (Liochelidae)
- (1): equal or posterior wider

The unusual condition of a anterior to posterior tapering of a sternum is exclusively found in the scorpionoid family Liochelidae, exaggerated in genera such as *Liocheles*. Although *Heteroscorpium* is not specifically involved in our cladistic analysis, its sternum, which is slightly longer than wide, also exhibits this tapering of the sternum.

Character 69: Sternum apex/lateral lobes

- (0): apex pointed, depressed; lateral lobes convexed
- (1): apex rounded, minimal depression; lateral lobes flat (Typhlochactinae)
- (-): sternum type 1

This character models the unusual shaped sternum apex and flat lateral lobes exhibited in the superstitioniid subfamily Typhlochactinae. It remains to be determined if this simplification in the sternum surface is due to cave adaptation.

Character 70: Maxillary lobes I [UNIFORM]

- (0): non-spatulate
- (1): spatulate (Chaerilidae)

This character is autapomorphic for the parvorder Chaerilida. It was also reported for the fossil scorpion *Palaeopisthacanthus schucherti* by Kjellesvig-Waering (1986) but Jeram (1994a) disagreed with this interpretation.

Character 71: Maxillary lobes I

- (0): rounded, terminating flush with lobes II
- (1): evenly narrowed, terminating beyond lobes II (Iochelinae)

Character 72: Leg coxae II & IV proportions: IV/II (anterior lengths)

- (0): $IV_L/II_L = 1.3 - 2.0$
- (1): $IV_L/II_L = 2.2 - 2.9$ (Buthoidea)
- (2): $IV_L/II_L = 2.3 - 2.6$ (Caraboctonidae)

This character addresses the elongation of leg coxae IV exhibited in most buthoid scorpions and New World iuroids as described by Soleglad & Fet (2003).

Hemispermatothore/Genital Operculum**Character 73:** Hemispermatothore general shape [FUND]

- (0): primitive form (UNKNOWN)
- (1): fusiform (Chaerilidae)
- (2): flagelliform (Buthoidea)
- (3): lamelliform (Scorpionoidea and Chactoidea)

The primitive form of the hemispermatothore is unknown. We assign a “null state” as primitive. We follow Stockwell (1989) in assuming that the *fusiform* hemispermatothore is relatively primitive (i.e., primitive within Recent scorpions, since the hemispermatothore of the relict *Pseudochactas* is unknown at this time).

Character 74: Lamina terminus [FUND]

- (0): without “crest”
- (1): with “crest” (Bothriuridae)
- (-): non-lamelliform

Character 75: Paraxial organ with internobasal reflection of sperm duct [FUND]

- (0): absent
- (1): present and complex (Scorpionoidea)

This character is adopted directly from Stockwell (1989) and Prendini (2000).

Character 76: Hemispermatothore capsule

- (0): capsule absent (Iuroidea)
- (1): capsule present, at least weakly
- (2): capsule present, significant development (Scorpionoidea)
- (-): non-lamelliform

Character 77: Hemispermatothore ental channel

- (0): absent
- (1): present (*Euscorpis* and *Megacormus*)

The unique ental channel found in some euscorpoid subfamilies (Euscorpinae and Megacorminae) has been described and illustrated by Sissom (1994), Soleglad & Sissom (2001), Fet & Soleglad (2002), and Gantenbein et al. (2002).

Character 78: Hemispermatothore truncal flexure

- (0): present
- (1): not present (Scorpiopinae, Brotheinae, Chactinae)
- (-): non-chactoids

The presence of a truncal flexure is considered primitive in the chactoids, where it is found in family Vaejovidae, and subfamilies Uroctoninae, Euscorpinae, and Megacorminae. It is lost in subfamilies Scorpiopsinae, Brotheinae, and Chactinae.

Character 79: Hemispermatothore lamina terminus

- (0): thin to medium blade-like, modest to medium tapering (Euscorpinae, Megacorminae, Uroctoninae, Superstitioniidae, Vaejovidae)
- (1): tenuous, thin, highly tapered (Scorpiopinae, Brotheinae, Chactinae)
- (2): spatulate, wider than base (Typhlochactinae)
- (-): non-chactoids

The hemispermatothore lamina terminus is flat and blade-like with modest to medium tapering in family Vaejovidae, and subfamilies Euscorpinae, Megacorminae, Uroctoninae, and Superstitioniinae. It becomes quite thin, tenuous and highly tapered in subfamilies Scorpiopinae, Brotheinae, and Chactinae. In the typhlochactines, it is spatulate, wider than its base. The lamina terminus and the presence or absence of the truncal flexure (the previous character) may be dependent characters since we see the same scorpion group differentiation.

Character 80: Hemispermatothore laminar “hook” on lamina base

- (0): absent (Euscorpidae, Chactidae, Superstitioniidae)
- (1): present (Vaejovidae)
- (-): non-chactoids

Character 81: Genital papillae of male

- (0): visible entire length of genital operculum (Pseudochactidae, Chaerilidae, *Calchas*)
- (1): conspicuously visible at posterior edge of genital operculum (Chactoidea)
- (2): under genital operculum, do not extend posteriorly or modestly visible
- (3): absent (*Hadrurus*)

Character 82: Sclerites of the genital operculum of female [PART-ORD]

- (0): separated for most of length (Pseudochactidae, Buthoidea, Chaerilidae, Iuroidea)
- (1): generally fused (Scorpionoidea, and some Vaejovidae)
- (2): loosely connected (Bothriuridae, *Hadogenes*)
- (3): separated at the posterior 20–25% of their length (*Vaejovis nitidulus*, *Paruroctonus* and *Pseudouroctonus*)
- (4): loosely connected (Superstitioniidae, Euscorpidae)
- (5): separated for most of length (Chactidae)

This character is partially ordered as (0, (1, (2, 3, (4, (5))))). The sclerites of the genital operculum are separated for most of its length in the primitive Recent scorpions. We see an essentially fused genital operculum in most scorpionoids and some vaejovids; a loosely connected set of plates in most bothriurids as well as in the superstitioniids and euscorpids, all derived from a fused genital operculum. We see secondary development in the complete separation of genital operculum as exhibited in the family Chactidae.

Metasoma/Telson

Character 83: Dorsal lateral carinae, segment V [UNIFORM]

- (0): present (Palaeopisthacanthidae)
- (1): absent (Recent scorpions)

Character 84: Ventral median carina, segment V [FUND]

- (0): distinctly paired (Palaeopisthacanthidae and Pseudochactidae)
- (1): single

The paired ventral median carinae of metasomal segment V is a primitive condition exhibited in genus *Pseudochactas*, unprecedented in Recent scorpions.

Character 85: Ventral median carinae, segments I–IV

- (0): paired
- (1): single (Hemiscorpiinae)
- (2): single (Urodacidae)
- (3): single (Euscorpidae)
- (4): single (Vaejovidae, *Syntropis*)
- (5): single (Vaejovidae, *Vaejovoidus*)

We considered the condition of a single ventral median carina on metasomal segments I–IV to be localized to individual scorpion groups. Therefore, we assign a separate state to each scorpion group where it occurs.

Character 86: Lateral carinae, metasomal segment V

- (0): present and complete (Palaeopisthacanthidae)
- (1): partially present (most Recent scorpions)
- (2): absent (most Buthoidea)
- (3): absent (Scorpionoidea)
- (4): absent (Euscorpidae)
- (5): absent (Superstitioniidae)
- (6): absent (Vaejovidae)

The lateral carinae of metasomal segment V are present in the palaeopisthacanthids and is present, in part, in most Recent scorpions. It is absent in most buthoids however, and a few scattered genera throughout the scorpionoids and chactoids. Consequently, we assign separate states to these losses, not considering them homologous to that of the major loss seen in the buthoids.

Character 87: Lateral carinae, metasomal segment IV

- (0): present, complete (Palaeopisthacanthidae)
- (1): absent (most Recent scorpions)
- (2): present, partial (Iuroidea: *Hadrurus* and *Hadruroides*)
- (3): present, partial (Chactidae)
- (4): present, partial (Vaejovidae)

The lateral carinae of metasomal segment IV is present in the palaeopisthacanthids but essentially obsolete in Recent scorpions. There are scattered occurrences of its presence however, to which we assign separate states.

Character 88: Metasomal segment IV, dorsal-lateral carina termination

- (0): not conspicuous, angles downward to articulation condyle
- (1): conspicuously flared, straight (most Vaejovidae)
- (-): non-chactoids

Character 89: Transverse anterior carinae [UNIFORM]

- (0): well developed on all five segments (Palaeopisthacanthidae)
- (1): developed on at least basal segments I–III
- (2): absent, or slight remnants

Jeram (1994a) considered the presence of a transverse anterior carina to be a primitive character, which he reported for all segments of the palaeopisthacanthids. This subtle carina was detected on the basal segments of *Pseudochactas*, and also, exhibiting various degrees of development, on some other scorpions.

Character 90: Telson, subaculear tooth/tubercle

- (0): none
- (1): tooth (Buthoidea)
- (2): tubercle (Diplocentrinae)

We distinguish a “tooth”, typically found in the buthoids, from a “tubercle”, found in the diplocentrines. They are not homologous derivations and certainly exhibit considerably different formations: the “tubercle” is a rounded, well developed, blunt projection from the aculeus base, and does not exhibit much variability in its size across the subfamily; in contrast, the “tooth” is more pointed, less massive, but exhibiting considerable variability in its size and overall length. It can also be serrated, exhibiting multiple points along its outer surface.

Pedipalpal Ornamentation

Chela

Character 91: Chela: fundamental configuration [FUND]

- (0): “Eight (8) carinae” configuration (*D2*, *V2* absent, *I* present)
- (1): “Ten (10) carinae” configuration (9–10 present, usually *D2* vestigial and *I* missing)

Pseudochactas has a flat chelal palm, similar in structure to that seen in the chactoid family Euscorpidae. Only five carinae are visible: the digital (*D1*), and ventroexternal (*V1*) are very strong and distinct, *V1* formed in a straight line, meeting the external condyle; the ventrointernal (*V3*) carina, which meets the internal condyle is also well developed, though showing a rounded form; the dorsomarginal (*D4*) carina is also present, but in a very rounded form; and the dorsointernal (*D5*) carina is weakly developed. Carinae subdigital (*D2*), dorsosecondary (*D3*), ventromedian (*V2*), external (*E*), and internal (*I*) are missing. We assign *Pseudochactas* to the “8-carinae” configuration due to the definite absence of *D2* and *V2*. The absence of *D3* is common in many scorpion groups whose chelal palm is flat (i.e., the euscorpids). Due to the rounded external and internal surfaces we could not determine whether *E* and *I* are present. Possibly this reduced configuration could prove to be a primitive form of the “8-carinae” configuration and *E* and *I* carina are derived in later groups.

Character 92: Chela, *V1* carina distal termination

- (0): terminates at external condyle completely, or in part, split distally
- (1): curves inward, trichobothrium *Et1* external to carina
- (2): entire carina “torqued” inward, trichobothrium *Et2* follows to ventral aspect (some Bothriuridae)

In many bothriurids, we find the *V1* carina positioned between the external and internal condyles. This shift of the entire carina could be the cause of the shift of

trichobothrium *Et2* to the internal surface of the palm, a diagnostic character for this family.

Character 93: Chela, overall orientation

- (0): rounded (Scorpionidae, Bothriuridae)
- (1): flat (Liochelidae)
- (2): rounded (Chactidae, Superstitioniidae)
- (3): flat, “hexagon-shaped” (Euscorpidae)
- (4): rounded (most Vaejovidae)
- (5): flat (Vaejovidae, *Pseudouroctonus* and *Uroctonites*)
- (-): “8-carinae” configuration

We consider the round/flat dichotomy seen in many scorpion groups to have derived separately and therefore their occurrences are assigned separate states.

Patella

Character 94: Patella, fundamental configuration [FUND]

- (0): 7 carinae (Palaeopisthacanthidae, Pseudochactida, Buthida)
- (1): 6 carinae (Chaerilida)
- (2): 5 (Iurida)

Character 95: Patella, dorsomedian (*DMc*) carina [FUND]

- (0): absent (non-buthoids)
- (1): present (Buthoidea and *Archaeobuthus* (?))

Character 96: Patella, dorsal patellar spur (DPS) carina development, 5-carinae configuration [FUND]

- (0): absent (Iuroidea, Euscorpidae, Chactidae, Superstitioniidae, Scorpionoidea)
- (1): present (Vaejovidae)
- (-): non-Iurida

Character 97: Patella, internal surface with a vaulted “projection”

- (0): weak to obsolete
- (1): strong to medium (Liochelidae)
- (-): non-Iurida

The unique vaulted condition of the internal aspect of the pedipalp patella is found exclusively in the liochelids. It is also found in the genus *Heteroscorpion*. This vaulted projection should not be confused with the well developed patellar spurs found in some scorpion groups (i.e., euscorpids).

Character 98: Dorsal patellar spur (DPS) and Ventral patellar spur (VPS), overall development

- (0): weak to obsolete
- (1): well-developed (Euscorpidae)
- (2): developed (Uroctoninae)
- (-): non-chactoids

Miscellaneous characters

Character 99: Venom gland epithelium walls overall construction

- (0): simple (Pseudochactidae, Liochelidae, *Calchas*)
- (1): folded

We follow Stockwell's (1989) analysis for this character, in part, by considering the venom glands in the scorpionoid family Liochelidae as "simple". We also consider the glands found in *Calchas* and *Pseudochactas* (as reported in this paper) as "simple".

Character 100: Number of "cells" in ovariterus [FUND]

- (0): reticulate mesh of 6 cells
- (1): reticulate mesh of 8 cells (Buthidae)

This character is based on Pavlovsky's (1924a, 1925) work, where dozens of scorpion genera were analyzed. We follow Stockwell (1989) here by hypothesizing that the "eight cell" condition is derived in the buthoids.

Character 101: Stigma shape: partitioned by superfamilial and/or upper clades

- (0): circular, small (Palaeopisthacanthidae, Archaeobuthidae, Chaerilidae)
- (1): oval, small (Pseudochactidae and *Microcharmum*)
- (2): slit-like, small to long (most Buthoidea)
- (3): oval (Iuroidea)
- (4): slit-like (Iuroidea)
- (5): oval (Scorpionoidea)
- (6): slit-like (Scorpionoidea)
- (7): circular, small (*Troglotayosicus*, Chactinae, most Brotheinae)
- (8): oval, small (most Superstitioniidae, Euscorpiidae)
- (9): oval, medium to long (Uroctoninae and *Paravaejovis*)
- (a): slit-like, medium to long (Vaejovidae and *Brotheas*)

All major Recent scorpion groups exhibit small circular to oval stigmata as well as more elongated slit-like stigmata. Within these groups we see numerous derivations spanning these shapes: the fossil groups and the chaerilids exhibit small circular stigmata; the primitive genus *Pseudochactas* and the buthoid *Microcharmum* have small oval stigmata; most buthoid genera exhibit elongated, slit-like stigmata. Superfamilies Iuroidea and Scorpionoidea have both small oval shaped stigmata (e.g., *Calchas*, *Hadruioides*, *Bothriurus*, *Liocheles*, *Urodacus*, etc.) as well as slit-like stigmata (e.g., *Iurus*, *Hadrurus*, *Brachistosternus*, *Scorpio*, *Diplocentrus*,

etc.). The chactoids exhibit small circular, small oval, and elongated slit-like stigmata: the family Vaejovidae in general has slit-like stigmata, and most Chactidae have small circular stigmata. It is clear from the diversity exhibited in the shape of the stigma across all major groups that these derivations happened independently and therefore are assigned separate states.

Character 102: Number of lateral eyes on carapace [PART-ORD]

- (0): 2 (relatively primitive) (Chaerilidae)
- (1): 3 (Iuroidea, Scorpionoidea, Vaejovidae)
- (2): 0–2 (Euscorpiidae, Chactidae, Superstitioniidae)
- (3): 2 (Urodacidae)
- (4): 3–4 (Uroctoninae)
- (5): 3 (Scorpiopini)
- (-): Pseudochactidae and Buthoidea

Although the number of lateral eyes found in Recent scorpions has been considerably overemphasized in the past, especially in the differentiation of the vaejovids and chactids, they do provide some consistency within certain groups. This character is partially ordered as (0, (1, ((2, (4, 5)), 3))). This ordering suggests the following derivations: we consider the two eyes found in the chaerilids as "relatively primitive"; from this state we have three eyes as found in the iuroids, scorpionoids, and vaejovids (note, *Calchas* has two lateral eyes, reflecting the primitive state as seen in *Chaerilus*). Family Urodacidae loses an eye, a derivation from the three-eye state; similarly, none to two lateral eyes exhibited in families Euscorpiidae, Chactidae, and Superstitioniidae are also derived from a three-eye state. Finally, the three to four eyes found in the chactid subfamily Uroctoninae is a derivation from a two-eye state. For completeness here, we see primitive genus *Pseudochactas* with one lateral eye, and the buthoids usually with three to five eyes, clearly a derivation for this superfamily.

Character 103: Relative pectines development (number of teeth)

- (0): reduced development (Euscorpiidae, Chactidae, Superstitioniidae)
- (1): well-developed (Vaejovidae)
- (-): non-chactoids

Character 104: Pectinal fulcra development

- (0): present (Vaejovidae, most Chactidae)
- (1): absent (most Superstitioniidae)
- (2): absent (*Belisarius*)
- (3): absent (Euscorpiidae)
- (4): variable within the genus (Euscorpiidae)
- (-): non-chactoids

The presence or absence of pectinal fulcra has been considered an important character in Recent scorpion

systematics. We consider it important only within certain groups and any loss of these structures across groups are clearly independent derivations and therefore are assigned separate states in this analysis. Consequently, we consider the loss of fulcra as exhibited in most Superstitioniidae (all cave adapted), in chactid genus *Belisarius* (also cave adapted), and the loss found in many euscorpoid genera in subfamilies Megacorminae and Scorpiopinae to be separate derivations within these taxonomic assemblages. In addition, although not included in our ingroup, species previously assigned to the synonymized chactid genus *Taurepania* (subfamily Brotheinae) have lost the fulcra (five species, including one subterranean).

Character 105: Pectinal lamellae development

(0): middle lamellae bead-like, all plates well delineated; fulcra, if present, well-formed

(1): single plate, or two, semi-fused with anterior lamellae; fulcra, if present, quite reduced in size

(2): single plate, or two, semi-fused with anterior lamellae

(?): entire genus lacks fulcra

(-): non-chactoids

This character is ignored in genera lacking fulcra, since in all cases, scorpions without fulcra also have a reduced middle lamellae development. On the other hand, if at least one species in the genus has well-developed middle lamellae, then we conclude that reduced lamellae in other species are due to smaller pectines. *Megacormus granosus* and *M. gertschi* are good examples, the latter with well delineated bead-like middle lamellae as compared to the former, with a reduced number of teeth (3) and thus with plate-like middle lamellae.

Appendix B

DNA Phylogeny: Pilot Data for High-Level Scorpion Systematics

This Appendix describes results of a pilot project to assess high-level scorpion phylogeny and systematics through comparative analysis of DNA sequences available mainly from, and published by, our research group (V. Fet, B. Gantenbein, M. E. Soleglad, et al.). While more fragmentary than our all-inclusive morphological treatment presented in the main body of this paper, this analysis sheds some light not only at the relationships among scorpion parvorders but also at the applicability of certain genes to the phylogenetic analysis in scorpions at different taxonomic levels.

Introduction

With the advent of polymerase chain reaction (PCR) in the late 1980s, comparative DNA sequence analysis became a choice approach to infer animal phylogenies based on molecular data (Simon et al., 1994; Swofford et al., 1996). A limited number of genes (both mitochondrial and nuclear) have been utilized routinely during the last decade for numerous animal groups. Nuclear 18S rRNA gene sequence analysis is usually used at higher taxonomic levels (Chalwatzis et al., 1996; Giribet et al., 1999, 2002). For example, Wiegmann et al. (2000) used 18S gene to resolve Mesozoic-aged divergences in Lepidoptera (Insecta). Among nuclear genes, variable domain sequences of the ribosomal 28S rRNA gene have been utilized as well as 18S genes for recovering phylogenies at the high levels, e.g. by Giribet et al. (1999) for suborders of Opiliones (Arachnida). Mitochondrial genes, both protein-coding (cytochrome b, cytochrome oxidase I and II) and ribosomal (12S and 16S rDNA) are commonly utilized for low-level (genus/species) molecular systematic studies (Simon et al., 1994). At the same time, mitochondrial ribosomal genes are also used at higher taxonomic levels; for instance, complete 16S and 12S rRNA gene sequences have been recently used to infer phylogeny of mammals (Hudelot et al., 2003), with the finding that the mitochondrial rRNA genes are “extremely informative at many levels of the tree”. Prendini et al. (2003) recently combined nuclear (28S rRNA) and mitochondrial (12S and 16S rRNA, cytochrome oxidase I) gene sequence data to investigate phylogeny between four genera of Scorpionidae.

A portion of 16S rRNA gene has been used by our research group and its collaborators for several years to study species-level phylogenetic relationships within scorpion genera *Euscorpius* (Euscorpiidae), *Hadrurus* (Caraboctonidae), *Mesobuthus* (Buthidae) and *Centruroides* (Buthidae) (Fet, 2003; Fet et al., 2002, 2003;

Gantenbein et al., 1999, 2000, 2001a, 2001b, 2002, 2003; Huber et al., 2001; Scherabon et al., 2000; Towler et al., 2001). Recently, we (Fet et al., 2003) applied sequence comparison analysis of the same portion of 16S rRNA gene to investigate relationships within 17 genera of family Buthidae. The recovered phylogeny had variable support in different branches; however, we could make certain decisions on monophyly and relationships of groups of genera.

In the current investigation, we used the existing (both published and unpublished) data accumulated by our research group during genus-level phylogenetic studies which covered a variety of genera across the family Buthidae (parvorder Buthida) and families Caraboctonidae, Chactidae, Euscorpiidae, and Vaejovidae (parvorder Iurida), along with the new data on Chaerilidae (parvorder Chaerilida, genus *Chaerilus*) and Pseudochactidae (parvorder Pseudochactida, genus *Pseudochactas*). We sought to demonstrate whether the high-level phylogenetic resolution in scorpions (superfamily level and higher) could be obtained using a portion of 16S gene (ca. 400 bp). The total selection of taxa included 55 species belonging to 29 genera, seven families, five superfamilies, and four parvorders.

In addition, we compared the partial nuclear 18S rRNA gene sequence (856 bp, including a large variable region V4) in a selection of seven species belonging to seven genera, six families, five superfamilies, and four parvorders. The 18S sequences of the representatives (one species each) of the genera *Androctonus*, *Smeringurus*, and *Hadrurus* were taken from GenBank, while we obtained new 18S sequences for the genera *Centruroides*, *Chaerilus*, *Euscorpius*, and *Pseudochactas*.

Methods

We used standard DNA extraction and amplification protocols as described in Gantenbein et al. (1999, 2000a). Genomic DNA was extracted from fresh or preserved (in 95–98% ethanol) muscle tissue (usually a leg) by using a standard Qiagen™ DNeasy extraction kit. Extracted DNA was amplified by the polymerase chain reaction (PCR) in the Perkin Elmer 2400 PCR Thermocycler by using conditions and primers as described in Gantenbein et al. (1999). The mitochondrial LSU (large ribosomal subunit) 16S rRNA gene PCR primers as published by Gantenbein et al. (1999) corresponded to the positions 12,867–12,884 and 13,328–13,308 in the *Drosophila yakuba* mitochondrial genome, or to the positions 11,173–11,190 and 11,625–11,606 in the *Limulus*

polyphemus mitochondrial genome (Lavrov et al., 2000). The forward primer was a scorpion-specific version of the “universal” primer 16Sbr, or LR-J-12887, while the reverse primer had a scorpion-specific sequence designed by one of the authors (V.F.). The nuclear SSU (small ribosomal subunit) 18S rRNA gene PCR primers, also designed by V.F., were based on conserved areas of partial scorpion 18S sequences (GenBank; Wheeler & Hayashi, 1998), and were: 5' AAA CGG CTA CCA CAT CCA AG 3' (forward) and 5' CAA CTA AGA ACG GCC ATG CA 3' (reverse). These primers corresponded to the positions 405–423 and 1,280–1,299 in the full 18S rRNA gene sequence of *Androctonus australis* (Buthidae) (GenBank X77908; unpublished), or to the positions 7–25 and 880–899 in the partial 18S rRNA gene sequence of *Smeringurus mesaensis* (Vaejovidae) (GenBank AF062950; Wheeler & Hayashi, 1998). The resulting PCR product was verified on 1% agarose electrophoretic gel and purified by Ultrafree MC 30000 cellulose filters (Millipore, Inc.). Automated Sanger dideoxy sequencing of the double-stranded PCR product was performed at the Integrated Biotechnology Laboratories, Riverbend Research Lab, University of Georgia, Athens, Georgia, USA (<http://www.ors.uga.edu/ibl>), on the ABI 9600 Sequencer. DNA sequences were aligned using Clustal X 1.81 (Thompson et al., 1997). The 16S rDNA fragment corresponded after alignment to 396 bp; and 18S rDNA fragment corresponded after alignment to 854 bp. The software package PAUP* Version 4.0b10 (Swofford, 1998) was used to perform all cladistic phylogenetic analyses of aligned DNA sequences via Maximum Parsimony (MP) algorithm under different weighting assumptions. Bootstrap support values were obtained by 1000 pseudoreplicates, repeated five times, and presented as mean values. Cladograms for the molecular sequences from PAUP* were generated by Tree-View (Win 32) Version 1.5.2 (Page, 1998).

Material

All taxa used for DNA study are listed below (total 62 DNA sequences belonging to seven families, 28 genera and 56 species). Detailed label data is available from the authors. Previously published DNA sequences (total 39) are referenced below; of these, 34 sequences have been published by our research group (Fet et al., 2001, 2002, 2003; Gantenbein et al., 1999, 2001a, 2001b, 2003; Scherabon et al., 2000). New DNA sequences which are published here (total 24) were deposited to GenBank (<http://www.ncbi.nih.gov/Genbank>) under accession numbers AY368238–AY368244, AY368246–AY368258, AY371537–AY371539, and AY450931.

Taxa used for 16S rRNA gene sequences:

Buthidae (17 genera, 23 species): *Androctonus amoreuxi* (Audouin, 1826), Morocco (AY226175; Fet et

al., 2003); *Anomalobuthus rickmersi* Kraepelin, 1900, Kazakhstan (AY226170; Fet et al., 2003); *Apistobuthus pterygocercus* Finnegan, 1932, Oman (AY226178; Fet et al., 2003); *Buthacus yotvatensis* Levi, Amitai & Shulov, 1973, Oman (AY226173; Fet et al., 2003); *Buthus occitanus* (Amoreux, 1789), Morocco (AY226172; Fet et al., 2003); *Centruroides bani* Armas & Marcano Fondeur, 1987, Dominican Republic (AJ288644; Gantenbein et al., 2001b); *Centruroides exilicauda* (Wood, 1863), Cabo San Lucas, Baja California Sur, Mexico (AJ288640; Gantenbein et al., 2001b); *Centruroides infamatus* (C. L. Koch, 1844), Michoacán, Mexico (AF439753; Towler et al., 2001); *Centruroides limpidus* (Karsch, 1879), Queretaro, Mexico (AF439764; Towler et al., 2001); *Centruroides vittatus* (Say, 1821), Arkansas, USA (AJ288643; Gantenbein et al., 2001b); *Compsobuthus arabicus* Levy, Amitai & Shulov, 1973, United Arab Emirates (AY226177; Fet et al., 2003); *Grosphus madagascariensis* (Gervais, 1843), Madagascar (AY226168; Fet et al., 2003); *Hottentotta jayakari* (Pocock, 1895), United Arab Emirates (AY226176; Fet et al., 2003); *Kraepelinia palpator* (Birula, 1903), Badghyz, Turkmenistan (AY226181; Fet et al., 2003); *Leiurus quinquestriatus* (Ehrenberg, 1828), Oman (AY226174; Fet et al., 2003); *Liobuthus kessleri* Birula, 1898, Turkmenistan (AY226180; Fet et al., 2003); *Lychas mucronatus* (Fabricius, 1798), Southeast Asia (AF370855; Giribet et al., 2001); *Mesobuthus caucasicus* (Nordmann, 1840), Kapchagai, Kazakhstan (AJ550674; Gantenbein et al., in press); *Mesobuthus eupeus* (C. L. Koch, 1839), Kazakhstan (AY228141; Fet et al., 2003); *Mesobuthus gibbosus* (Brullé, 1832), Litchoro, Greece (AY368239); *Orthochirus innesi* Simon, 1910, Morocco (AY226171; Fet et al., 2003); *Rhopalurus abudi* Armas & Marcano Fondeur, 1987, Dominican Republic (AY226169; Fet et al., 2003); *Vachoniolus globimanus* Levy, Amitai & Shulov, 1973, Oman (AY226179; Fet et al., 2003).

Caraboctonidae (2 genera, 4 species): *Hadrurus arizonensis* Ewing, 1928, Yuma Co., Arizona, USA (AF32551; Fet et al., 2001); *Hadrurus obscurus* Williams, 1970, ABDSP, California, USA (AF318508; Fet et al., 2001); *Hadrurus pinteri* Stahnke, 1969, Isla Danzante, Baja California Sur, Mexico (AF312267; Fet et al., 2001); *Hadrurides charcasus* (Karsch, 1879), Ecuador (AY450931).

Chaetidae (1 genus, 2 species): *Anuroctonus phaiodactylus* (Wood, 1863), Utah, USA (AY368240); *Anuroctonus* sp., San Diego Co., California, USA (AY368241).

Chaerilidae (1 genus, 1 species): *Chaerilus* sp., Mapur Island, Indonesia (AY368238).

Euscorpidae (1 genus, 8 species): *Euscorpis balearicus* Caporiacco, 1950, Mallorca, Balears, Spain (AJ309208; Gantenbein et al., 2001a); *Euscorpis carpathicus* (Linnaeus, 1767), Romania, Baile Herculane

(AY172337; Fet et al., 2002); *Euscorpium flavicaudis* (DeGeer, 1778), Vaucluse, France (AJ389381; Gantenbein et al., 1999); *Euscorpium gamma* Caporiacco, 1950, Carinthia, Austria (AJ249555; Scherabon et al., 2000), *Euscorpium germanus* (C. L. Koch, 1837), Carinthia, Austria (AJ249553; Scherabon et al., 2000); *Euscorpium hadzii* Caporiacco, 1950, Dubrovnik, Croatia (AY172339; Fet et al., 2002); *Euscorpium italicus* (Herbst, 1800), Brissago, Switzerland (AJ389378; Gantenbein et al., 1999); *Euscorpium tergestinus* (C. L. Koch, 1837), Mathis, France (AJ389376; Gantenbein et al., 2001a).

Pseudochactidae (1 genus, 1 species): *Pseudochactas ovchinnikovi* Gromov, 1998, Babatag, Uzbekistan (AY226167; Fet et al., 2003).

Vaejovidae (4 genera, 16 species): *Paruroctonus boreus* (Girard, 1854), Washington, USA (AY368242); *Paruroctonus luteolus* (Gertsch & Soleglad, 1966), ABDSP, California, USA (AY368243); *Paruroctonus silvestrii* (Borelli, 1909), California, USA (AY368244); *Serradigitus gertschi* (Williams, 1968), San Diego Co., California, USA (AY368246); *Serradigitus minutus* (Williams, 1970), Cabo San Lucas, Baja California Sur, Mexico (AY368247); *Serradigitus subtilimanus* (Soleglad, 1972), ABDSP, California, USA (AY368248); *Serradigitus torridus* Williams & Berke, 1986, California, USA (AY368249); *Smeringurus aridus* (Soleglad, 1972), ABDSP, California, USA (AY368252); *Smeringurus mesaensis* (Stahnke, 1957), ABDSP, California, USA (AY368250); *Smeringurus vachoni* (Stahnke, 1957), Yuma, Arizona, USA (AY368251); *Vaejovis eusthenura* (Wood, 1863), Cabo San Lucas, Baja California Sur, Mexico (AY368253); *Vaejovis hirsuticauda* Banks, 1910, ABDSP, California, USA (AY368254); *Vaejovis punctipalpi* (Wood, 1863), Cabo San Lucas, Baja California Sur, Mexico (AY368255); *Vaejovis puritanus* Gertsch, 1958, ABDSP, California, USA (AY368256); *Vaejovis spinigerus* (Wood, 1863), Yuma, Arizona, USA (AJ389383; Gantenbein et al., 1999); *Vaejovis waeringi* Williams, 1970, ABDSP, California, USA (AY368257).

Taxa used for 18S rRNA gene sequences (6 families, 7 genera, 7 species):

Buthidae: *Androctonus australis* (L., 1578) (X77908, unpublished; submitted by Chalwatzis et al. 1994); *Centruroides exilicauda* (Wood, 1863), Yuma, Arizona, USA (AY371539).

Caraboctonidae: *Hadrurus arizonensis* Ewing, 1928, USA (AF062949; Wheeler & Hayashi, 1998).

Chaerilidae: *Chaerilus* sp., Mapur Island, Indonesia (AY371538).

Euscorpiidae: *Euscorpium italicus* (Herbst, 1800), Metsovo, Greece (AY371537).

Pseudochactidae: *Pseudochactas ovchinnikovi* Gromov, 1998, Babatag, Uzbekistan (AY368258).

Vaejovidae: *Smeringurus mesaensis* (Stahnke, 1957), USA (AF062950; Wheeler & Hayashi, 1998).

Results

The phylogenetic trees resulting from Maximum Parsimony analysis are presented in Figs. B-1 and B-2 for 16S rRNA gene data, and in Fig. B-3 for 18S rRNA gene data. The genus *Pseudochactas* was selected as an outgroup in both 16S and 18S analyses.

The 16S rRNA analysis included 55 taxa from seven families: Buthidae, Caraboctonidae, Chaerilidae, Chaerilidae, Euscorpiidae, Pseudochactidae, Vaejovidae. Of 396 total characters, 105 characters were constant and 44 (1:1:0 weighting) or 41 (3:1:0 weighting) variable characters were parsimony-uninformative, resulting in 247 (1:1:0 weighting) or 250 (3:1:0 weighting) parsimony-informative characters. Heuristic Search without weighting transitions versus transversions (i.e. 1:1:0 transversions: transitions: indels weighting) yielded 18 MP trees, length 1,801 steps, CI (excluding uninformative characters) = 0.3051, RI (excluding uninformative characters) = 0.6430. The strict consensus of these 18 trees is presented in Fig. B-1. Heuristic Search with weighting 3:1:0 transversions: transitions: indels yielded 3 MP trees, length 3,446 steps, CI (excluding uninformative characters) = 0.2844, RI (excluding uninformative characters) = 0.6818. The strict consensus of these 3 trees is presented in Fig. B-2.

The 18S rRNA analysis included seven taxa from six families: Buthidae, Caraboctonidae, Chaerilidae, Euscorpiidae, Pseudochactidae, Vaejovidae. Of 854 total characters, 703 characters were constant, 94 variable characters were parsimony-uninformative, and 57 were parsimony-informative. Heuristic Search without weighting transitions versus transversions (i.e. 1:1:0 transversions: transitions: indels weighting) yielded a single MP tree, length 182 steps, CI (excluding uninformative characters) = 0.7857, RI (excluding uninformative characters) = 0.7931. Heuristic Search with weighting 3:1:0 transversions: transitions: indels yielded a single MP tree, length 370 steps, CI (excluding uninformative characters) = 0.7821, RI (excluding uninformative characters) = 0.7964. These trees are presented in Fig. B-3.

Discussion

The major conclusion which follows from these analyses is that all four scorpion parvorders (Pseudochactida, Buthida, Chaerilida, and Iurida) are indeed well-supported as expected from morphology analysis, and three "primitive" parvorders (Pseudochactida, Buthida, Chaerilida) were contrasted with Iurida. In all analyses, parvorder Iurida was monophyletic with a very

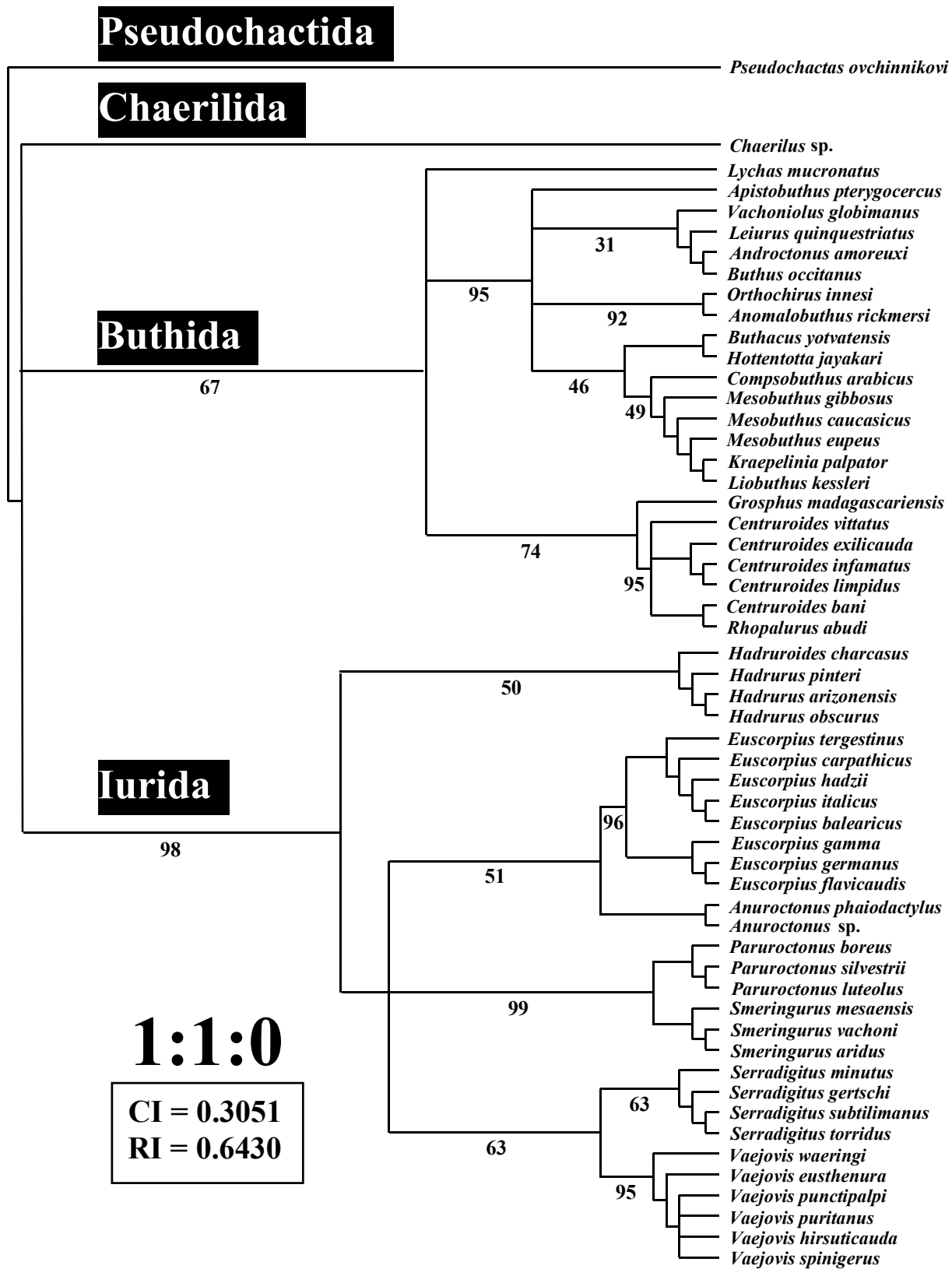


Figure B-1: Cladogram (Maximum Parsimony) showing phylogeny of 55 taxa based on 16S mtDNA sequences (transversion, transition and indel weighting = 1:1:0). Strict consensus of 18 MPTs. Bootstrap support depicted below selected branches (based on the mean of five separate sequences, 1000 replicates each). *CI* = consistency index, *RI* = retention index.

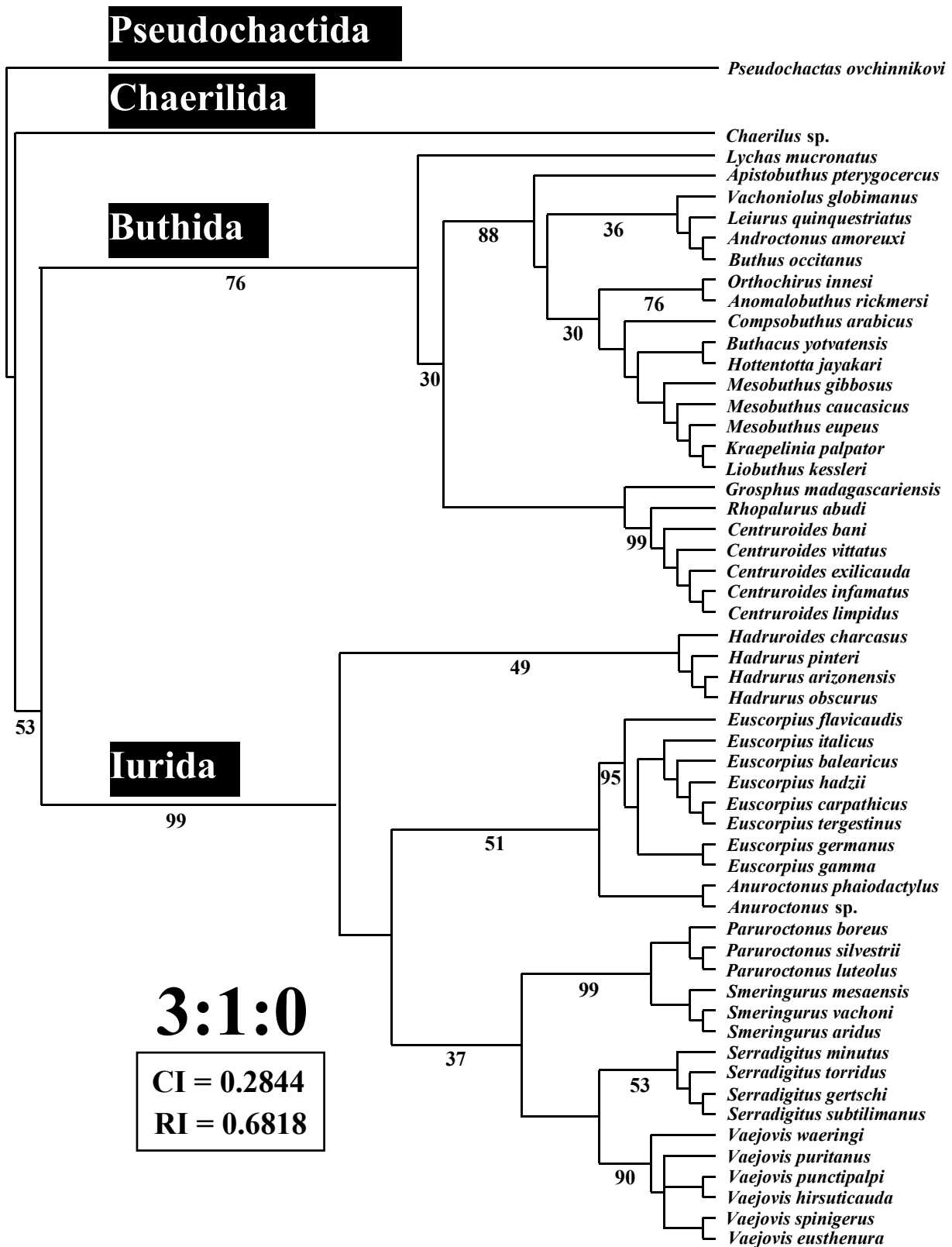


Figure B-2: Cladogram (Maximum Parsimony) showing phylogeny of 55 taxa based on 16S mtDNA sequences (transversion, transition and indel weighting = 3:1:0). Strict consensus of 3 MPTs. Bootstrap support depicted below selected branches (based on the mean of five separate sequences, 1000 replicates each). *CI* = consistency index, *RI* = retention index.

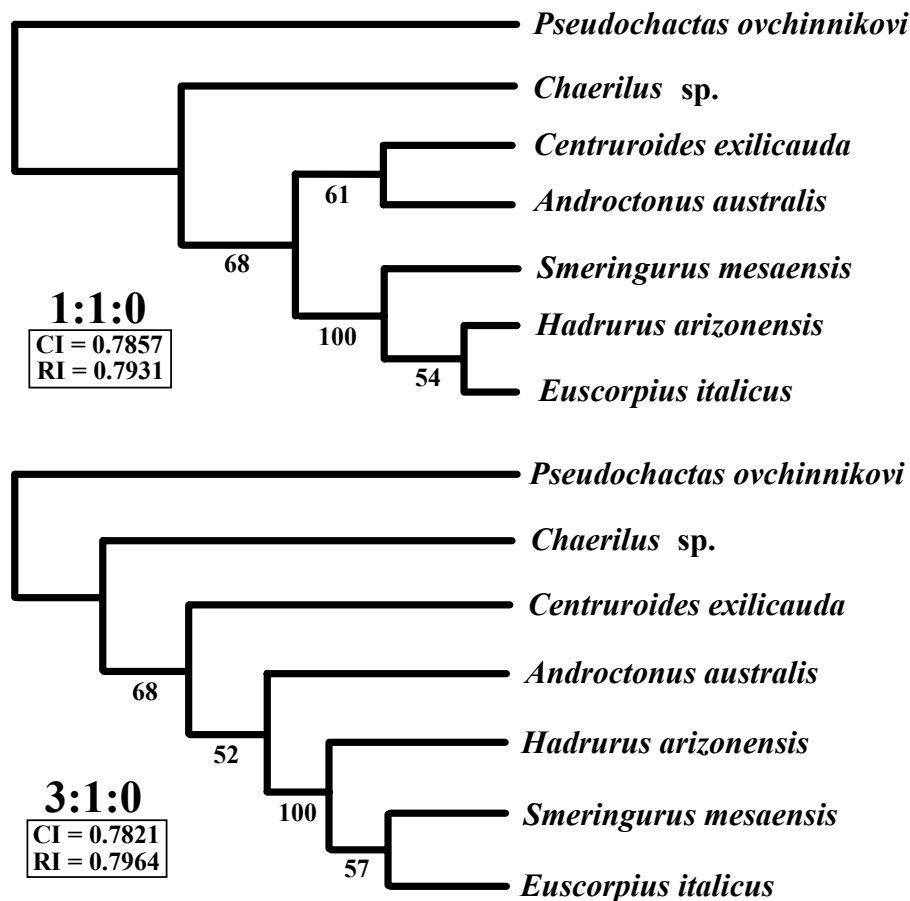


Figure B-3: Cladogram (Maximum Parsimony) showing phylogeny of 7 taxa based on 18S mtDNA sequences (transversion, transition and indel weighting = 1:1:0 and 3:1:0). Bootstrap support depicted below selected branches (based on the mean of five separate sequences, 1000 replicates each). *CI* = consistency index, *RI* = retention index.

high support (98–99% bootstrap in both 1:1:0 and 3:1:0 weighing in 16S analysis, and 100% in both 18S analyses). Expected monophyly of Buthida was well-supported in 16S analysis with 67% bootstrap in 1:1:0, and 76% in 3:1:0 weighing assumptions. (Two buthid taxa used in 18S analysis showed monophyly with 61% support only under 1:1:0 weighing; under 3:1:0 weighing they were not monophyletic, configured in a ladderized form.

In all topologies, parvorder Pseudochactida was clearly a sister group to other three parvorders (clade Chaerilida+Buthida+Iurida), a result firmly supported by morphological analysis as well (see Fig. 114). Placement of the parvorder Chaerilida varied in DNA analyses. In 16S analysis under 1:1:0 option, the clade (Chaerilida+Buthida+Iurida) formed a polytomy. However, under 3:1:0 weighing in 16S analysis Chaerilida formed a sister group to (Buthida+Iurida) clade, albeit weakly supported (53%). Support for Chaerilida as the sister group to (Buthida+Iurida) clade was even more pronounced in 18S topologies (68% in both 1:1:0 and 3:1:0 weighing); 18S data are expected to yield better results at higher taxonomic levels. These results conflict with the phylogeny based on the analysis of all morphological characters (Fig. 114), which supported Chaerilida as a sister group of Iurida. Possible reasons for the conflict of

these phylogenies could be an insufficient resolution given by DNA genes used in this pilot study; additional problems could include the primitive and relict nature of Chaerilida, which are represented in extant fauna only by a single monotypic family, and/or the highly derived, though primitive, parvorder Buthida. Phylogenetic placement of Chaerilida remains one of the major issues of high-level extant scorpion systematics to be further investigated.

Within parvorder Iurida, the superfamily Iuroidea was solidly expected from morphological analysis to form the sister group to superfamily Chactoidea. For 16S data this topology was recovered but was not heavily supported by bootstrap, exhibiting only 49–50%. 18S analysis also weakly (57%) supported Iuroidea as a sister group to Chactoidea, but only under 3:1:0 weighing scheme; more stringent weighing to 1:1:0 splits Chactoidea monophyly with *Hadrurus*. In the same fashion, within superfamily Chactoidea, the solidly expected monophyly of Vaejoidea was not recovered by 16S data, and clade (Euscorpidae+Chactidae) had a very weak support (51%).

Some 16S rRNA topologies were well-supported below the family level, and are worth pursuing further with more DNA and morphological analysis. For example, monophyly of the clade including vaejoivid genera

Paruroctonus and *Smeringurus* was supported with 99% bootstrap for both weighing schemes. A number of topologies recovered in our 16S tree confirmed the phylogeny as published before at family- or genus-level, e.g. phylogeny of the genus *Hadrurus* (Caraboctonidae) (Fet et al., 2001), or close relationship between such Old World genera of Buthidae as *Orthochirus* and *Anomalobuthus* (Fet et al., 2003). Presence of at least two (or more) monophyletic clades in Buthidae (potentially of subfamily rank), recovered first by Fet et al. (2003) in 16S data analysis, is again supported here. One clade of Buthidae includes predominantly Palearctic arid genera (13 genera in our selection; bootstrap support 88 % under 3:1:0 weighing and 95% under 1:1:0 weighing). Another possible clade brings together *Grosphus* (Madagascar) and New World genera *Centruroides* and *Rhopalurus* (supported only under 1:1:0 weighing at 74 %). Interestingly, the tropical buthid genus *Lychas* from Asia formed a separate clade under both weighing schemes. Some other supported clades in 16S data analysis challenged accepted taxonomy: e.g. monophyly of *Centruroides* (Buthidae) was not supported under 1:1:0 weighting, but the 95 to 99% support was observed for the clade including *Centruroides* (Buthidae) and a related genus *Rhopalurus*. Such discrepancies further confirm that more investigation is needed into phylog-

eny of polytypic scorpion genera, and such studies are ongoing (for *Centruroides*, see Gantenbein et al., 2001b; Towler et al., 2001).

In general, as with any other animal group, DNA sequence analysis can reveal more insights into scorpion phylogeny at various taxonomic levels, provided that resolution (“phylogenetic signal”) is recovered from specific variable gene region(s), and taxa representation is sufficient. In practice, it will take a considerable effort to test phylogenetic hypotheses, which often are clearly presented by morphological analysis. A scorpion molecular systematist is further challenged by the obvious relict character of many scorpion groups at various levels and its long-term effect on DNA homoplasy levels. Scorpions present a challenge to a phylogenetic researcher with their monotypic taxa (such as *Belisariini* or *Chaerilidae*) and their long, relict history of isolation and extinction (e.g. in many *Iuroidea* and *Chactoidea*). Further advances in scorpion phylogeny will bring together effort in both molecular and morphological analyses. We also should not forget that many corners of the world have not yet been seriously “blacklighted”, and could yield new and possibly very important pieces of the relict scorpion puzzle, as it happened during the last 100 years with such remarkable “missing link” taxa as *Calchas* or *Pseudochactas*.

Appendix C Metasomal Carinae Configuration Charts

In this Appendix we present the development of individual metasomal carinae for a representative set of Recent scorpions (92 species). For details on the phylogeny, terminology and overall orientation of these carinae see detailed discussion elsewhere in this paper. In this **Appendix** we are interested in the *presence* or *absence* of a carina, is it paired or singular, and if present to what degree. A carina's ornamentation, i.e., smooth, granulated, serrulate, etc., is not distinguished, which in general is a species level distinction. For the *lateral carina* (= L) which, in general, exhibits a reduction in development from the basal to terminal segments, we state a percentage of development with respect to the segments overall length: from a posterior to anterior direction for

segments I–IV, and anterior to posterior on V (e.g., if 50% for segment III, the carina begins posteriorly extending to the midpoint of the segment). For the *ventral median secondary* (= VMS) carinae (primarily relevant to the buthoids), the percentage is based on an anterior to posterior perspective. I – V = metasomal segments; carinae: D = dorsal, DL = dorsal lateral, L = lateral, VL = ventral lateral, VM = ventral median, VMS = ventral median secondary; P = paired, S = singular, ‘-’ = inapplicable; Y = carinae terminates posteriorly in ‘Y-shape’ pattern (relevant to genus *Chaerilus*), C = crescent-shaped transverse carina (relevant to buthoids and diplocentrines); *obso* = obsolete, *wk* = weak, ? = indeterminable.

	I	II	III	IV	V
D	P	P	P	P	-
DL	P	P	P	P	P
L	P	P, 67%	P, 33%	obso	P, 50%
VL	P	P	P	P	P
VM	P	P	P	P	P
VMS	-	-	-	-	-

Pseudochactas ovchinnikovi

	I	II	III	IV	V
D	P	P	P	P	-
DL	P	P	P	P	P
L	P	P, 50%	P, 40%	obso	P, 70%
VL	P	P	P	P	P
VM	P	P	P	P	S (Y)
VMS	-	-	-	-	-

Chaerilus variegatus

	I	II	III	IV	V
D	P	P	P	P	-
DL	P	P	P	P	P
L	P	P, ?%	P, ?%	?	P, 80%
VL	P	P	P	P	P
VM	P	P	P	P	S (Y)
VMS	-	-	-	-	-

Chaerilus petzelkai

	I	II	III	IV	V
D	P	P	P	P	-
DL	P	P	P	P	P
L	P	P, 30%	P, 30%	obso	P, 70%
VL	P	P	P	P	P
VM	P	P	P	P	S (Y)
VMS	-	-	-	-	-

Chaerilus celebensis

	I	II	III	IV	V
D	P	P	P	P	-
DL	P	P	P	P	P
L	P	P, 50%	P, 30%	obso	obso
VL	P	P	P	P	P
VM	P	P	P	P	S
VMS	-	-	-	-	P, 80%

Leiurus quinquestriatus

	I	II	III	IV	V
D	P	P	P	P	-
DL	P	P	P	P	P
L	P	P, 70%	P, 50%	obso	obso
VL	P	P	P	P	P
VM	P	P	P	P	S (C,wk)
VMS	-	-	-	-	P, 65%

Mesobuthus caucasicus

	I	II	III	IV	V
D	P	P	P	P	-
DL	P	P	P	P	P
L	P	obso?	obso?	obso	obso
VL	P	P	P	P	P
VM	P	P	P	P	S
VMS	-	-	-	-	-

Parabuthus sp.

	I	II	III	IV	V
D	P	P	P	P	-
DL	P	P	P	P	P
L	P	P, 80%	P, 50%	obso	obso
VL	P	P	P	P	P
VM	P	P	P	P	S
VMS	-	-	-	-	P, 25%

Rhopalurus junceus

	I	II	III	IV	V
D	P	P	P	P	-
DL	P	P	P	P	P
L	P	P, 80%	P, 60%	obso	P, 80%
VL	P	P	P	P	P
VM	P	P	P	P	S
VMS	-	-	-	-	P, 90%

Alayotityus nanus

	I	II	III	IV	V
D	P	P	P	P	-
DL	P	P	P	P	P
L	P	P, 80%	obso	obso	obso
VL	P	P	P	P	P
VM	P	P	P	P	S
VMS	-	-	-	-	-

Liobuthus kessleri

	I	II	III	IV	V
D	P	P	P	P	-
DL	P	P	P	P	P
L	P	P	P	P, 60%	obso
VL	P	P	P	P	P
VM	P	P	P	P	S
VMS	-	-	-	-	P, 70%

Hottentotta minax

	I	II	III	IV	V
D	P	P	P	P	-
DL	P	P	P	P	P
L	P	P, 30%	obso	obso	obso
VL	P	P	P	P	P
VM	P	P	P	P	S
VMS	-	-	-	-	P, 40%

Anomalobuthus rickmersi

	I	II	III	IV	V
D	P	P	P	P	-
DL	P	P	P	P	P
L	P	P	P, 50%	obso	obso
VL	P	P	P	P	P
VM	P	P	P	P	S
VMS	-	-	-	-	-

Compobuthus matthiesseni

	I	II	III	IV	V
D	P	P	P	P	-
DL	P	P	P	P	P
L	P	P	P, 50%	obso	obso
VL	P	P	P	P	P
VM	P	P	P	P	S
VMS	-	-	-	-	P, 75%

Microtityus jaumei

	I	II	III	IV	V
D	P	P	P	P	-
DL	P	P	P	P	P
L	P	P, 50%	P, 30%	obso	obso
VL	P	P	P	P	P
VM	P	P	P	P	S
VMS	-	-	-	-	(pigment)

Uroplectes vittatus

	I	II	III	IV	V
D	P	P	P	P	-
DL	P	P	P	P	P
L	P	P, 90%	P, 50%	obso	obso
VL	P	P	P	P	P
VM	P	P	P	P	S
VMS	-	-	-	-	P, 40%

Grosphus sp.

	I	II	III	IV	V
D	P	P	P	P	-
DL	P	P	P	P	P
L	P	P, 80%	P, 70%	obso	obso
VL	P	P	P	P	P
VM	P	P	P	P	S
VMS	-	-	-	-	-

Androctonus bicolor

	I	II	III	IV	V
D	P	P	P	P	-
DL	P	P	P	P	P
L	P	P, 10%	obso	obso	obso
VL	P	P	P	P	P
VM	P	P	P	P	S
VMS	-	-	-	-	-

Isometrus maculatus

	I	II	III	IV	V
D	P	P	P	P	-
DL	P	P	P	P	P
L	P	P	P, 25%	obso	obso
VL	P	P	P	P	P
VM	P	P	P	P	S
VMS	-	-	-	-	-

Lychas sp.

	I	II	III	IV	V
D	P	P	P	P	-
DL	P	P	P	P	P
L	P	P, 30%	P, 25%	obso	obso
VL	P	P	P	P	P
VM	P	P	P	P	S (C)
VMS	-	-	-	-	P, 75%

Buthacus yotvatensis

	I	II	III	IV	V
D	P	P	P	P	-
DL	P	P	P	P	P
L	P	P, 15%	obso	obso	obso
VL	P	P	P	P	P
VM	P	P	P	P	S
VMS	-	-	-	-	-

Centruroides exilicauda

	I	II	III	IV	V
D	P	P	P	P	-
DL	P	P	P	P	P
L	P	P, 65%	P, 50%	obso	obso
VL	P	P	P	P	P
VM	P	P	P	P	S
VMS	-	-	-	-	P, 40%

Razianus zarudnyi

	I	II	III	IV	V
D	P	P	P	P	-
DL	P	P	P	P	P
L	P	obso	obso	obso	obso
VL	P	P	P	P	P
VM	P	P	P	P	S
VMS	-	-	-	-	P, 30%

Tityus nematochirus

	I	II	III	IV	V
D	P	P	P	P	-
DL	P	P	P	P	P
L	P	P, 30%	P, 20%	obso	obso
VL	P	P	P	P	P
VM	P	P	P	P	S
VMS	-	-	-	-	-

Orthochirus scrobiculosus

	I	II	III	IV	V
D	P	P	P	P	-
DL	?	?	?	?	P
L	?	?	?	?	?
VL	P	P	P	P	P
VM	?	?	?	?	?
VMS	-	-	-	-	-

Karasbergia methueni

	I	II	III	IV	V
D	P	P	P	P	-
DL	P	P	P	obso	P
L	P	P	obso	obso	obso
VL	P	P	obso	obso	obso
VM	P	P	obso	obso	obso
VMS	-	-	-	-	-

Microbuthus sp.

	I	II	III	IV	V
D	P	P	P	P	-
DL	P	P	P	P	P
L	P	P, 70%	P, 60%	obso	obso
VL	P	P	P	P	P
VM	P	P	P	P	S
VMS	-	-	-	-	-

Buthus occitanus

	I	II	III	IV	V
D	P	P	P	P	-
DL	P	P	P	P	P
L	P	P	?	?	P, 70%
VL	P	P	P	P	P
VM	P	P	P	P	S
VMS	-	-	-	-	-

Microcharmus hauseri

	I	II	III	IV	V
D	P	P	P	P	-
DL	P	P	P	P	P
L	P, 70%	P, 50%	P, 30%	obso	P, 65%
VL	P	P	P	P	P
VM	P	P	P	P	S
VMS	-	-	-	-	-

Calchas nordmanni

	I	II	III	IV	V
D	P	P	P	P	-
DL	P	P	P	P	P
L	P, 70%	P, 40%	P, 10%	obso	P, 60%
VL	P	P	P	P	P
VM	P	P	P	P	S
VMS	-	-	-	-	-

Iurus dufourei

	I	II	III	IV	V
D	P	P	P	P	-
DL	P	P	P	P	P
L	P, 70%	P, 40%	P, 10%	obso	P, 5%
VL	P	P	P	P	P
VM	P	P	P	P	S
VMS	-	-	-	-	-

Caraboctonus keyserlingi

	I	II	III	IV	V
D	P	P	P	P	-
DL	P	P	P	P	P
L	P, 80%	P, 60%	P, 50%	P, 40%	P, 40%
VL	P	P	P	P	P
VM	P	P	P	P	S
VMS	-	-	-	-	-

Hadruidoidea maculatus

	I	II	III	IV	V
D	P	P	P	P	-
DL	P	P	P	P	P
L	P,90%	P,70%	P,60%	P,40%	P,40%
VL	P	P	P	P	P
VM	P	P	P	P	S
VMS	-	-	-	-	-

Hadrurus obscurus

	I	II	III	IV	V
D	P	P	P	P	-
DL	P	P	P	P	P
L	P,90%	P,80%	P,70%	P,60%	P,40%
VL	P	P	P	P	P
VM	P	P	P	P	S
VMS	-	-	-	-	-

Hadrurus aztecus

	I	II	III	IV	V
D	P	P	P	P	-
DL	P	P	P	P	P
L	obso	obso	obso	obso	P, 30%
VL	P	P	P	P	P
VM	P	P	P	P	S
VMS	-	-	-	-	-

Scorpio maurus

	I	II	III	IV	V
D	P	P	P	P	-
DL	P	P	P	P	P
L	obso	obso	obso	obso	P, 40%
VL	P	P	P	P	P
VM	P	P	P	P	S
VMS	-	-	-	-	-

Opisththalmus sp.

	I	II	III	IV	V
D	P	P	P	P	-
DL	P	P	P	P	P
L	P, 40%	P, 10%	obso	obso	P, 60%
VL	P	P	P	P	P
VM	P	P	P	P	S
VMS	-	-	-	-	-

Heterometrus longimanus

	I	II	III	IV	V
D	P	P	P	P	-
DL	P	P	P	P	P
L	P, 60%	P, 50%	P, 40%	obso	P, 50%
VL	P	P	P	P	P
VM	P	P	P	P	S
VMS	-	-	-	-	-

Pandinus imperator

	I	II	III	IV	V
D	P	P	P	P	-
DL	obso	obso	obso	obso	P
L	obso	obso	obso	obso	obso
VL	P	P	P	P	P
VM	P	P	P	P	S
VMS	-	-	-	-	-

Hadogenes troglodytes

	I	II	III	IV	V
D	P	P	P	P	-
DL	P	P	P	P	P
L	P, wk	?	?	?	P, 40%
VL	P	P	P	P	P
VM	P	P	P	P	S
VMS	-	-	-	-	-

Cheloctonus sp.

	I	II	III	IV	V
D	P	P	P	P	-
DL	P	P	P	P	P
L	obso	obso	obso	obso	obso
VL	P	P	P	P	P
VM	P	P	P	P	S
VMS	-	-	-	-	-

Liocheles sp. (Guadalcanal – Solomon Islands)

	I	II	III	IV	V
D	P	P	P	P	-
DL	P	P	P	P	P
L	?	obso	obso	obso	obso
VL	P	P	P	P	P
VM	P	P	P	P	S
VMS	-	-	-	-	-

Opisthacanthus lepturus

	I	II	III	IV	V
D	P	P	P	P	-
DL	P	P	P	P	P
L	obso	obso	obso	obso	P, 15%
VL	P	P	P	P	P
VM	S	S	S	S	S
VMS	-	-	-	-	-

Hemiscorpius maindroni

	I	II	III	IV	V
D	P	P	P	P	-
DL	P	P	P	P	P
L	P	P, 20%	P, 15%	obso	P, 50%
VL	P	P	P	P	P
VM	S	S	S	S	S
VMS	-	-	-	-	-

Urodacus manicatus

	I	II	III	IV	V
D	P	P	P	P	-
DL	P	P	P	P	P
L	P	P	P, wk	P, wk	P, 40% wk
VL	P	P	P	P	P
VM	P	P	P	P	S (C)
VMS	-	-	-	-	-

Diplocentrus ochoterenai

	I	II	III	IV	V
D	P	P	P	P	-
DL	P	P	P	P	P
L	P	P, 50%	obso	obso	P, 40%
VL	P	P	P	P	P
VM	P	P	P	P	S (C)
VMS	-	-	-	-	-

Bioculus comondae

	I	II	III	IV	V
D	P	P	P	P	-
DL	P	P	P	P	P
L	P, 50%	P, 30%	P, 20%	obso	P, 90%
VL	P	P	P	P	P
VM	obso	obso	obso	obso	S
VMS	-	-	-	-	-

Brachistosternus ehrenberghii

	I	II	III	IV	V
D	P	P	P	P	-
DL	P	P	P	P	P
L	P, 80%	P, 30%	P, 20%	obso	P, 70%
VL	P	P	P	P	P
VM	obso	P	P	P	S
VMS	-	-	-	-	-

Cercophonius squama

	I	II	III	IV	V
D	P	P	P	P	-
DL	P	P	P	P	P
L	obso	obso	obso	obso	obso
VL	P	P	P	P	P
VM	?	?	S	S	S
VMS	-	-	-	-	-

Euscorpis italicus

	I	II	III	IV	V
D	P	P	P	P	-
DL	P	P	P	P	P
L	P, 80%	P, 30%	obso	obso	P, 40%
VL	P	P	P	P	P
VM	S	S	S	S	S
VMS	-	-	-	-	-

Megacormus gertschi

	I	II	III	IV	V
D	P	P	P	P	-
DL	P	P	P	P	P
L	P, 80%	P, 60%	P, 50%	obso	P, 60%
VL	P	P	P	P	P
VM	P	P	P	P	S
VMS	-	-	-	-	-

Chactopsis insignis

	I	II	III	IV	V
D	P	P	P	P	-
DL	P	P	P	P	P
L	P, 90%	obso	obso	obso	P, 90%
VL	P	P	P	P	P
VM	P	P	P	P	S
VMS	-	-	-	-	-

Euscorpiops binghamii

	I	II	III	IV	V
D	P	P	P	P	-
DL	P	P	P	P	P
L	P, 90%	P, 30%	P, 15%	obso	P, 50%
VL	P	P	P	P	P
VM	P	P	P	P	S
VMS	-	-	-	-	-

Neoscorpions tenuicauda

	I	II	III	IV	V
D	P	P	P	P	-
DL	P	P	P	P	P
L	P, 90%	P, 70%	P, 40%	obso	P, 65%
VL	P	P	P	P	P
VM	P	P	P	P	S
VMS	-	-	-	-	-

Alloscorpions lindstroemii

	I	II	III	IV	V
D	P	P	P	P	-
DL	P	P	P	P	P
L	P, 70%	obso	obso	obso	P, 65%
VL	P	P	P	P	P
VM	P	P	P	P	S
VMS	-	-	-	-	-

Troglocormus willis

	I	II	III	IV	V
D	P	P	P	P	-
DL	P	P	P	P	P
L	P, 80%	P, 30%	P, 20%	obso	P, 50%
VL	P	P	P	P	P
VM	P	P	P	P	S
VMS	-	-	-	-	-

Brotheas granulatus

	I	II	III	IV	V
D	P	P	P	P	-
DL	P	P	P	P	P
L	P,40%	P,25%	P,10%	obso	P,40%
VL	P	P	P	P	P
VM	?	?	P	P	S
VMS	-	-	-	-	-

Neochactas delicatus

	I	II	III	IV	V
D	P	P	P	P	-
DL	P	P	P	P	P
L	obso	obso	obso	obso	P,65%
VL	P	P	P	P	P
VM	?	?	?	P	S
VMS	-	-	-	-	-

Belisarius xambeui

	I	II	III	IV	V
D	P	P	P	P	-
DL	P	P	P	P	P
L	P,50%	P,40%	P,20%	obso	obso
VL	P	P	P	P	P
VM	?	?	?	?	S
VMS	-	-	-	-	-

Hadrurochactas schaumii

	I	II	III	IV	V
D	P	P	P	P	-
DL	P	P	P	P	P
L	P,90%	P,40%	P,40%	P,30%	P,90%
VL	P	P	P	P	P
VM	P	P	P	P	S
VMS	-	-	-	-	-

Nullibrotheas allenii

	I	II	III	IV	V
D	P	P	P	P	-
DL	P	P	P	P	P
L	P,70%	P,40%	P,30%	obso	P,65%
VL	P	P	P	P	P
VM	P	P	P	P	S
VMS	-	-	-	-	-

Teuthraustes oculatus

	I	II	III	IV	V
D	P	P	P	P	-
DL	P	P	P	P	P
L	obso	obso	obso	obso	P,50%
VL	P	P	P	P	P
VM	?	?	?	?	S
VMS	-	-	-	-	-

Chactas sp.

	I	II	III	IV	V
D	P	P	P	P	-
DL	P	P	P	P	P
L	P,40%	P,20%	obso	obso	P,20%
VL	P	P	P	P	P
VM	P	P	P	?	S
VMS	-	-	-	-	-

Anuroctonus phaiodactylus

	I	II	III	IV	V
D	P	P	P	P	-
DL	P	P	P	P	P
L	P	P,40%	P,25%	obso	P,50%
VL	P	P	P	P	P
VM	P	P	P	P	S
VMS	-	-	-	-	-

Uroctonus mordax

	I	II	III	IV	V
D	P	P	P	P	-
DL	P	P	P	P	P
L	P	P,75%	P,60%	obso	P,65%
VL	P	P	P	P	P
VM	P	P	P	P	S
VMS	-	-	-	-	-

Vaejovis nitidulus

	I	II	III	IV	V
D	P	P	P	P	-
DL	P	P	P	P	P
L	P	P,60%	P,35%	obso	P,75%
VL	P	P	P	P	P
VM	?	?	P	P	S
VMS	-	-	-	-	-

Vaejovis solegladi

	I	II	III	IV	V
D	P	P	P	P	-
DL	P	P	P	P	P
L	P	P,35%	P,20%	obso	P,50%
VL	P	P	P	P	P
VM	P	P	P	P	S
VMS	-	-	-	-	-

Vaejovis carolinianus

	I	II	III	IV	V
D	P	P	P	P	-
DL	P	P	P	P	P
L	P	P,80%	P,70%	obso	P,60%
VL	P	P	P	P	P
VM	P	P	P	P	S
VMS	-	-	-	-	-

Vaejovis vorhiesi

	I	II	III	IV	V
D	P	P	P	P	-
DL	P	P	P	P	P
L	P,90%	P,30%	P,5%	obso	P,40%
VL	P	P	P	P	P
VM	P	P	P	P	S
VMS	-	-	-	-	-

Vaejovis eusthenura

	I	II	III	IV	V
D	P	P	P	P	-
DL	P	P	P	P	P
L	P	P,40%	P,30%	obso	P,30%
VL	P	P	P	P	P
VM	P	P	P	P	S
VMS	-	-	-	-	-

Vaejovis vittatus

	I	II	III	IV	V
D	P	P	P	P	-
DL	P	P	P	P	P
L	P,80%	P,30%	P,20%	obso	P,60%
VL	P	P	P	P	P
VM	P	P	P	P	S
VMS	-	-	-	-	-

Vaejovis punctipalpi

	I	II	III	IV	V
D	P	P	P	P	-
DL	P	P	P	P	P
L	P,80%	P,30%	P,20%	obso	P,65%
VL	P	P	P	P	P
VM	P	P	P	P	S
VMS	-	-	-	-	-

Vaejovis intrepidus cristimanus

	I	II	III	IV	V
D	P	P	P	P	-
DL	P	P	P	P	P
L	P,80%	P,40%	P,30%	obso	P,25%
VL	P	P	P	P	P
VM	P	P	P	P	S
VMS	-	-	-	-	-

Vaejovis gravicaudus

	I	II	III	IV	V
D	P	P	P	P	-
DL	P	P	P	P	P
L	P,80%	P,40%	P,30%	obso	P,40% wk
VL	P	P	P	P	P
VM	P	P	P	P	S
VMS	-	-	-	-	-

Vaejovis punctatus

	I	II	III	IV	V
D	P	P	P	P	-
DL	P	P	P	P	P
L	P	P,40%	P,25%	obso	P,35%
VL	P	P	P	P	P
VM	P	P	P	P	S
VMS	-	-	-	-	-

Paruroctonus boreus

	I	II	III	IV	V
D	P	P	P	P	-
DL	P	P	P	P	P
L	P,90%	P,30%	P,20%	obso	P,30%
VL	P	P	P	P	P
VM	P	P	P	P	S
VMS	-	-	-	-	-

Paruroctonus stahnkei

	I	II	III	IV	V
D	P	P	P	P	-
DL	P	P	P	P	P
L	P	P,30%	P,10%	obso	P,45%
VL	P	P	P	P	P
VM	P	P	P	P	S
VMS	-	-	-	-	-

Smeringurus mesaensis

	I	II	III	IV	V
D	P	P	P	P	-
DL	P	P	P	P	P
L	P,95%	P,10%	obso	obso	P,65%
VL	P	P	P	P	P
VM	P	P	P	P	S
VMS	-	-	-	-	-

Smeringurus aridus

	I	II	III	IV	V
D	P	P	P	P	-
DL	P	P	P	P	P
L	P	P,50%	P,40%	P,10%	P,45%
VL	P	P	P	P	P
VM	S	S	S	S	S
VMS	-	-	-	-	-

Vejovoidus longiunguis

	I	II	III	IV	V
D	P	P	P	P	-
DL	P	P	P	P	P
L	P	P,45%	P,40%	obso	P,60%
VL	P	P	P	P	P
VM	P	P	P	P	S
VMS	-	-	-	-	-

Paravaejovis pumilis

	I	II	III	IV	V
D	P	P	P	P	-
DL	P	P	P	P	P
L	P	P,50%	P,30%	obso	P,90%
VL	P	P	P	P	P
VM	P	P	P	P	S
VMS	-	-	-	-	-

Serradigitus subtilimanus

	I	II	III	IV	V
D	P	P	P	P	-
DL	P	P	P	P	P
L	P,80%	P,70%	P,40%	obso	P,65%
VL	P	P	P	P	P
VM	P	P	P	P	S
VMS	-	-	-	-	-

Serradigitus wupatkiensis

	I	II	III	IV	V
D	P	P	P	P	-
DL	P	P	P	P	P
L	P	P,60%	P,45%	obso	P,80%
VL	P	P	P	P	P
VM	P	P	P	P	S
VMS	-	-	-	-	-

Serradigitus calidus

	I	II	III	IV	V
D	P	P	P	P	-
DL	P	P	P	P	P
L	P	P,10%	obso	obso	obso
VL	P	P	P	P	P
VM	obso	S	S	S	S
VMS	-	-	-	-	-

Syntropis macrura

	I	II	III	IV	V
D	P	P	P	P	-
DL	P	P	P	P	P
L	P,90%	P,25%	P,10%	obso	P,45%
VL	P	P	P	P	P
VM	P	P	P	P	S
VMS	-	-	-	-	-

Pseudouroctonus reddelli

	I	II	III	IV	V
D	P	P	P	P	-
DL	P	P	P	P	P
L	P,80%	P,40%	P,30%	obso	P,70%
VL	P	P	P	P	P
VM	P	P	P	P	S
VMS	-	-	-	-	-

Pseudouroctonus andreas

	I	II	III	IV	V
D	P	P	P	P	-
DL	P	P	P	P	P
L	P	P,40%	P,25%	obso	P,70%
VL	P	P	P	P	P
VM	P	P	P	P	S
VMS	-	-	-	-	-

Pseudouroctonus apacheanus

	I	II	III	IV	V
D	P	P	P	P	-
DL	P	P	P	P	P
L	P,80%	P,20%	P,10%	obs	P,40%
VL	P	P	P	P	P
VM	P	P	P	P	S
VMS	-	-	-	-	-

Uroctonites huachuca

	I	II	III	IV	V
D	P	P	P	P	-
DL	P	P	P	P	P
L	obso	obso	obso	obso	obso
VL	obso	obso	obso	obso	P
VM	obso	obso	obso	obso	S
VMS	-	-	-	-	-

Superstitionia donensis

	I	II	III	IV	V
D	P	P	P	P	-
DL	P,20%	P,10%	P,5%	obso	P
L	obso	obso	obso	obso	obso
VL	P	P	P	P	P
VM	obso	obso	obso	obso	obso
VMS	-	-	-	-	-

Alacran tartarus

	I	II	III	IV	V
D	P,wk	P,wk	P,wk	P,wk	-
DL	obso	obso	obso	obso	P,wk
L	obso	obso	obso	obso	obso
VL	obso	obso	obso	obso	obso
VM	obso	obso	obso	obso	obso
VMS	-	-	-	-	-

Typhlochactas granulatus
(after Sissom & Cokendolpher, 1998)

	I	II	III	IV	V
D	P,wk	P,wk	P,wk	P,w	-
DL	obso	obso	obso	obso	P,wk
L	obso	obso	obso	obso	obso
VL	obso	obso	obso	obso	obso
VM	obso	obso	obso	obso	obso
VMS	-	-	-	-	-

Sotanochactas elliotti
(after Mitchell, 1971)

Appendix D

Relative Pectinal Development in the Superfamily Chactoidea

As established elsewhere in this paper, it is clear that the pectines is considerably more developed in the family Vaejovidae than it is in Chactoidea(-V). This Appendix presents detailed data on the distribution of the total lengths and pectinal tooth counts for Chactoidea(-V) and Vaejovidae. Although in this analysis only adult females were considered, the distinct delineation between the family sets revealed in this data for the female gender is also exhibited by the male counterpart. A large majority of this data was extracted from a number of sources, in particular the following publications were key in the compilation of this data (this list is not necessarily complete): **Chactoidea(-V)**: Mello-Leitão (1945), González-Sponga (1978, 1982, 1991, 1996a, 1996b), Soleglad (1976b), Francke (1981, 1982a, 1986), Tikader & Bastawade (1983), Sissom (1988), Fet & Soleglad (2002); **Vaejovidae**: Hoffmann (1931), Gertsch & Soleglad (1966, 1972), Soleglad (1972a, 1972b), Williams (1980), Sissom (1989, 1991), Sissom & Francke (1981, 1985), and Sissom & Stockwell (1991).

The following approach was used in the compilation of this data: the total length was based on the reported maximum size of a given species and the pectinal tooth count (single pecten) was based on a linear mean of the reported number range for the female gender. Clearly, the overall integrity of the data is contingent, in part, on the number of specimens and their geographical distribution involved in the study. For large population studies, as exemplified by most of the studies conducted by Williams (i.e., Williams, 1980) for the vaejovids, the data is more comprehensive than those data that is based, for example, on small samples and/or solitary specimens. Therefore, one must factor this in when evaluating the data. However, integrity issues in some of data notwithstanding, the magnitude of difference separating the families Chactoidea(-V) and Vaejovidae presented herein, based on over 150 samples, is significant and therefore the observation that the “pectines are more developed in the vaejovids than they are in the other chactoid families”, is certainly a valid observation.

As stated elsewhere in this paper, a metric for evaluating a relative pectinal development is more meaningful if it is presented as a ratio. This conclusion is based on the observation (Soleglad, 1973) that in general, the overall pectinal development of scorpions is confined within related species groups and, within a group, the development increases or decreases depending on the anatomical size of the species. I.e., larger species within a group in general have larger pectines than smaller species of the same group. By constructing a ratio based on the species size and “average pectinal

tooth count”, we can, in part, quantify species groups by this ratio. Although the pecten is composed of several types of plates (anterior and middle lamellae, fulcra, teeth), we decided that the number of teeth was a good choice for this analysis; i.e., it is easily observable and is usually reported by almost all authors, even in earlier contributions dating back to the 1800s. Finally, the pectinal development refers to the number of teeth only, not the overall size of the pecten nor its shape and/or number of the other plates.

Following is data which breaks this ratio into several small related groups within the two family sets. Note, a *smaller number* implies a *more developed* pecten relative to the species total length. Scatter charts and bar histograms showing the actual distribution of individual samples follow.

Vaejovidae

Vaejovis, “nitidulus” + “mexicanus” groups

1.59–3.26 (2.319) (±0.404) [020]: {1.92–2.72}→0.174

Pseudouroctonus + Uroctonites

2.44–5.64 (3.589) (±1.088) [012]: {2.50–4.68}→0.303

Syntropis, Vaejovis, “eusthenura” + “punctipalpi” groups

2.24–4.23 (3.241) (±0.504) [021]: {2.74–3.74}→0.155

Paruroctonus + Smeringurus + Vejovoidus + Paravaejovis

2.00–3.88 (2.852) (±0.526) [022]: {2.33–3.38}→0.184

Serradigitus

1.43–2.54 (1.915) (±0.363) [016]: {1.55–2.28}→0.189

Vaejovidae

1.43–5.64 (2.757) (±0.800) [091]: {1.96–3.56}→0.290

Chactoidea(-V)

Uroctoninae

5.27– 7.69 (6.222) (±1.291) [003]: {4.93– 7.51}→0.208

Brotheinae

3.24–10.83 (5.657) (±2.464) [011]: {3.19– 8.12}→0.436

Chactinae

3.29– 9.17 (6.577) (±1.839) [016]: {4.74– 8.42}→0.280

Chactidae

3.24–10.83 (6.204) (±2.037) [030]: {4.17– 8.24}→0.328

Megacorminae

3.44– 9.00 (6.671) (±2.013) [008]: {4.66– 8.68}→0.302

Euscorpinae

4.31– 7.08 (5.395) (±0.773) [011]: {4.62– 6.17}→0.143

Scorpiopinae

5.56– 9.60 (7.176) (±1.287) [011]: {5.89– 8.46}→0.179

Euscorpidae

3.44– 9.60 (6.388) (±1.545) [030]: {4.84– 7.93}→0.242

Superstitioniidae

3.00–13.80 (5.759) (±4.532) [005]: {1.23–10.29}→0.787

Chactoidea(-V)

3.00–13.80 (6.255) (±2.067) [065]: {4.19– 8.32}→0.330

In all the ranges we see that the standard error ranges are considerably smaller than the absolute ranges. This is also indicated by the large coefficients of variability caused by proportionally large standard deviations. The cause of this, in part, is that the pectinal tooth

counts do not reach comparable increases or decreases at the end-points of the total length within a related group. That is, for the largest or smallest species within a related group, the pectinal tooth count does not increase or decrease commensurately. For example, in the chactids, we see that the anatomically small genus *Vachoniochactas* accounts for the lowest ratio values, ratios less than 3.3; for the vaejovoid genus *Smeringurus*, which contains some of the largest species in the superfamily, we see a somewhat high ratio, greater than 3.5. Within the vaejovoids, the combination of genera *Pseudouroctonus* and *Uroctonites* exhibit the most reduced pectines, a mean ratio value of 3.589; in contrast genus *Serradigitus* has the most developed pectines, with a small mean ratio value of 1.915. In Chactoidea(-V) we see consistency

within families Euscorpiidae and Chactidae, only Superstitioniidae showing great variability. In the latter, the unique genus *Alacran* is completely removed from the other species, causing most of this variability. As stated elsewhere in this paper, the mean ratio value for Chactoidea(-V) is more than twice as large as the mean ratio value for the vaejovoids (i.e., 6.255 vs. 2.757). In addition, we see a 39.4% separation gap of the standard error range between the two superfamilies.

Following are plus/minus standard error and scatter charts showing the detailed distribution of the *total length/pectinal tooth count* ratio for 91 samples of Vaejovidae and 65 samples of Chactoidea(-V).

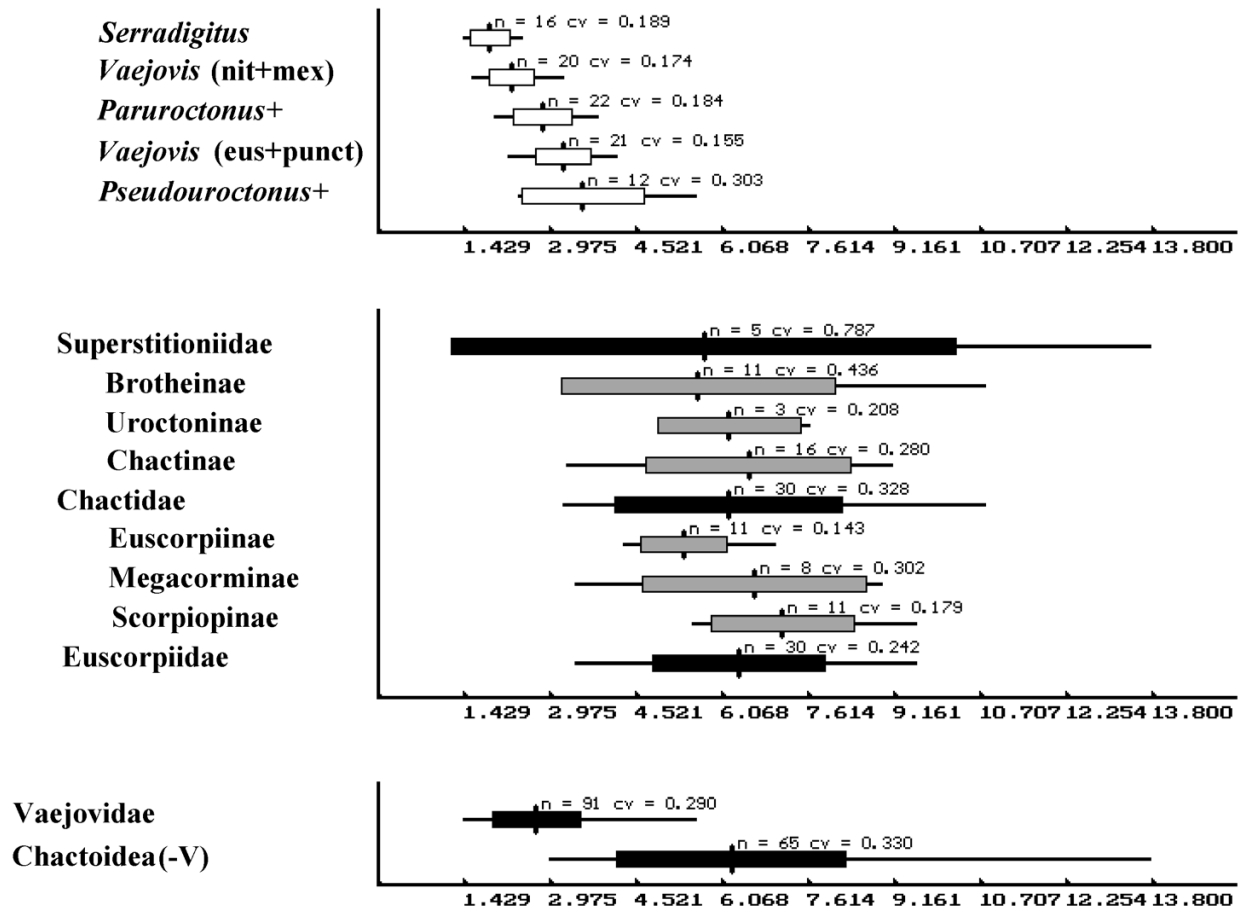


Figure D-1: Total length/pectinal tooth count ratio (female) for families Vaejovidae and Chactoidea(-V). *White* bars depict vaejovoid genera and/or their groups, *gray* bars depict subfamilies, and *black* bars depict families. *nit* = 'nitidulus' group, *mex* = 'mexicanus' group, *eus* = 'eusthenura' group, *punct* = 'punctipalpi' group, *Paruroctonus* + = *Paruroctonus* + *Smeringurus* + *Vaejovoidus* + *Paravaejovis*, *Pseudouroctonus* + = *Pseudouroctonus* + *Uroctonites*. Horizontal bar minimum, maximum, corrected minimum/maximum (mean-SD and mean+SD), and mean; *n* = number of samples, *cv* = coefficient of variability (SD/mean).

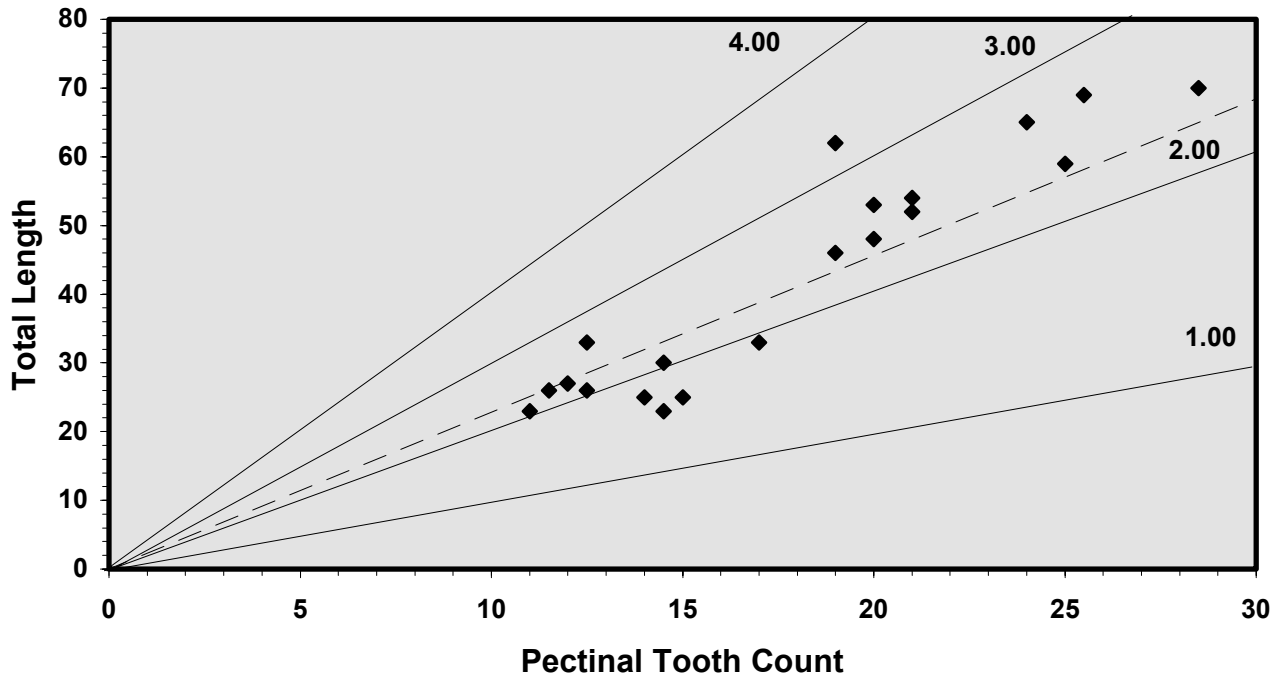


Figure D-2: Scatter chart of *Total Length/Pectinal Tooth Count* ratio (female) for genus *Vaejovis*, “nitidulus” and “mexicanus” groups. Number of samples = 20; solid diagonal axis lines depict integer ratio values; dashed line depicts the mean ratio value.

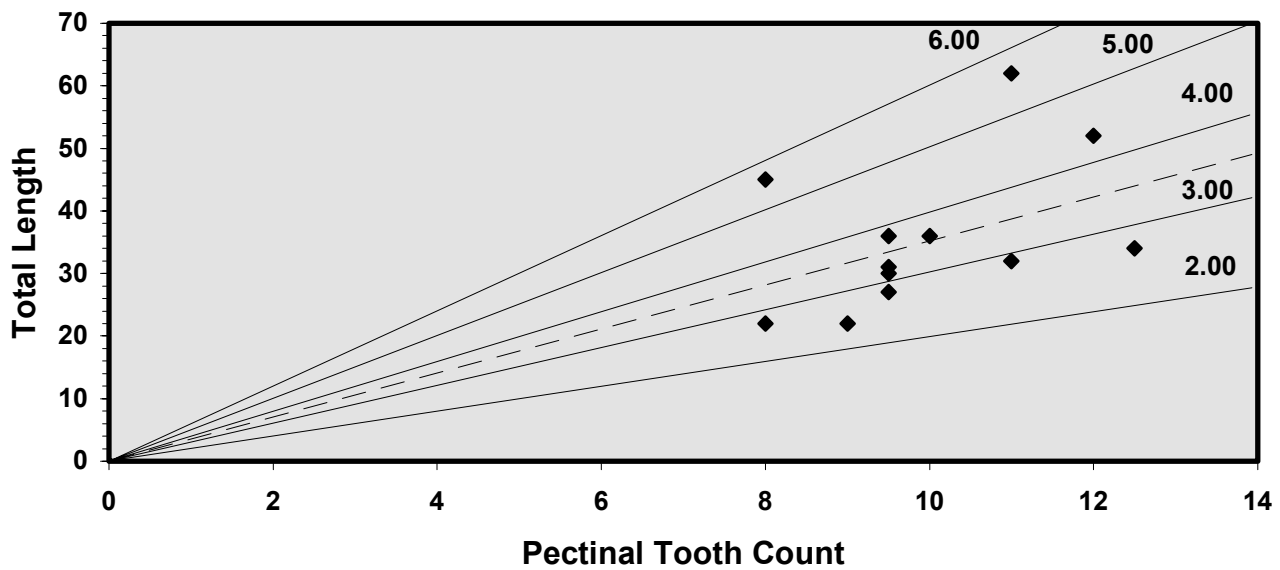


Figure D-3: Scatter chart of *Total Length/Pectinal Tooth Count* ratio (female) for genera *Pseudouroctonus* and *Uroctonites*. Number of samples = 12; see Fig. D-2 for definition of other conventions.

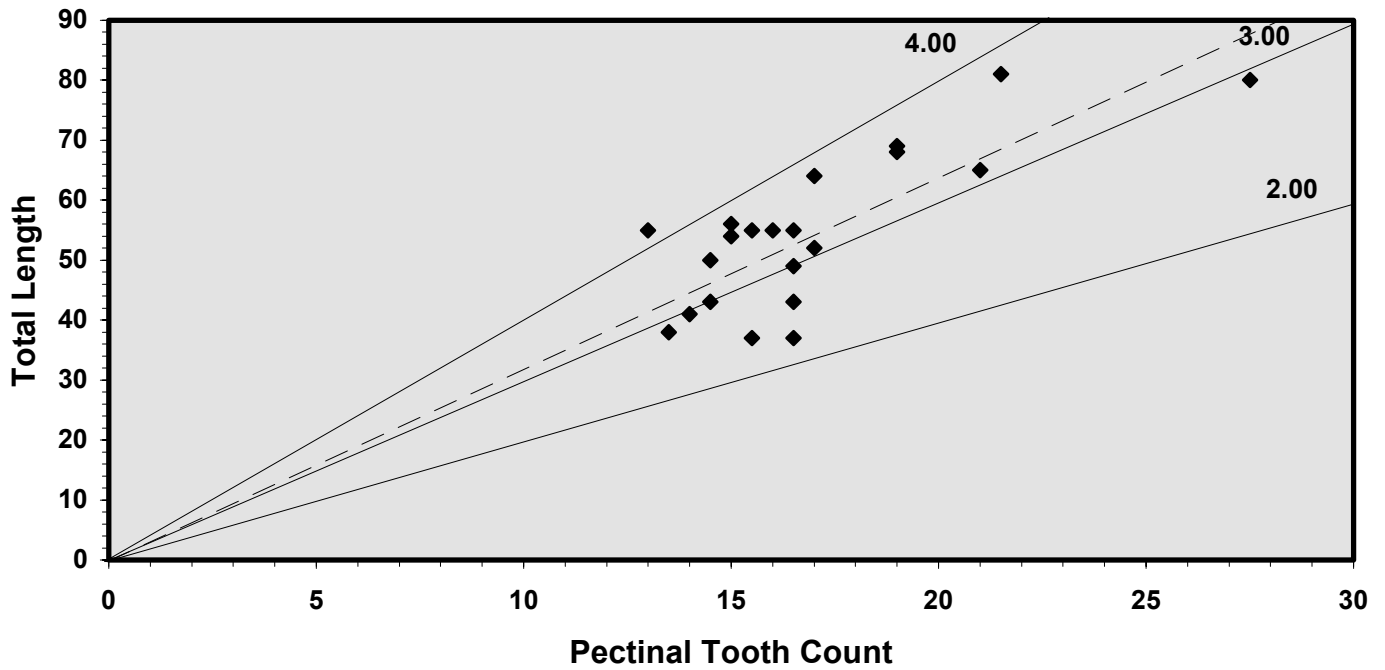


Figure D-4: Scatter chart of *Total Length/Pectinal Tooth Count* ratio (female) for genera *Syntropis* and *Vaejovis*: “eusthenura”, “punctipalpi”, and “intrepidus” groups. Number of samples = 21; see Fig. D-2 for definition of other conventions.

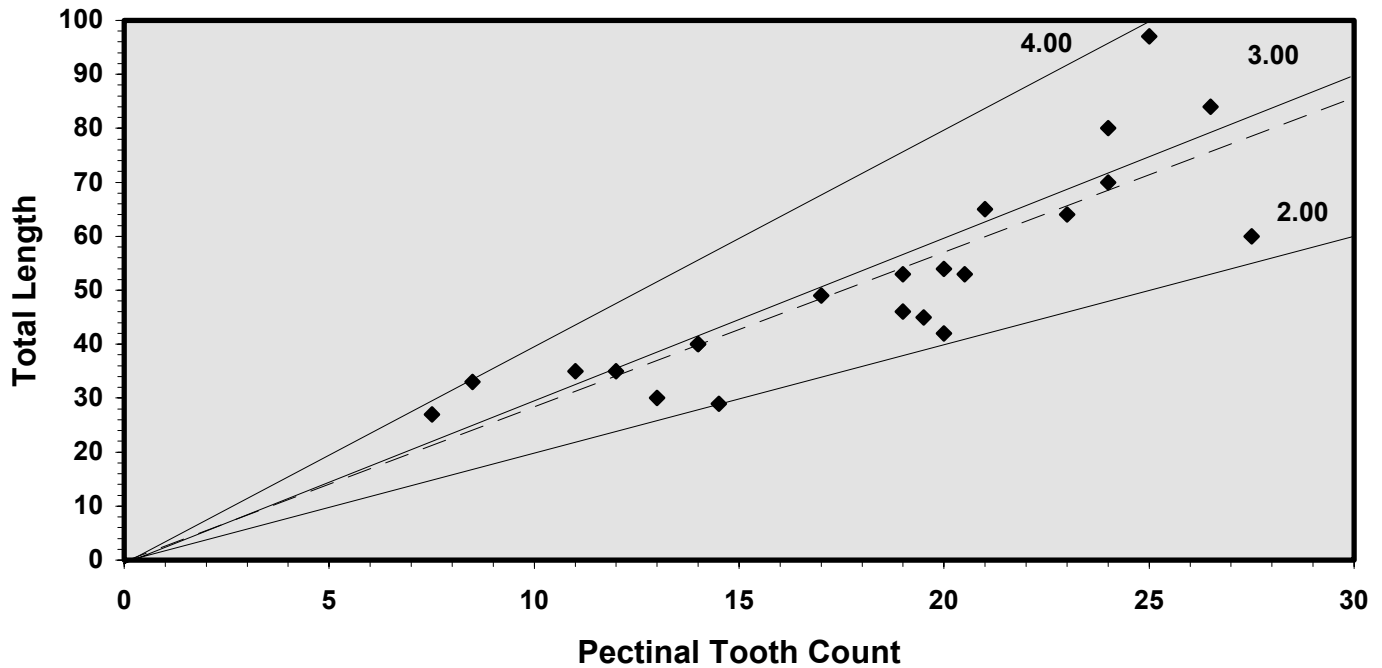


Figure D-5: Scatter chart of *Total Length/Pectinal Tooth Count* ratio (female) for genera *Paruroctonus*, *Smeringurus*, *Vaejovoidus* and *Paravaejovis*, number of samples = 22; see Fig. D-2 for definition of other conventions.

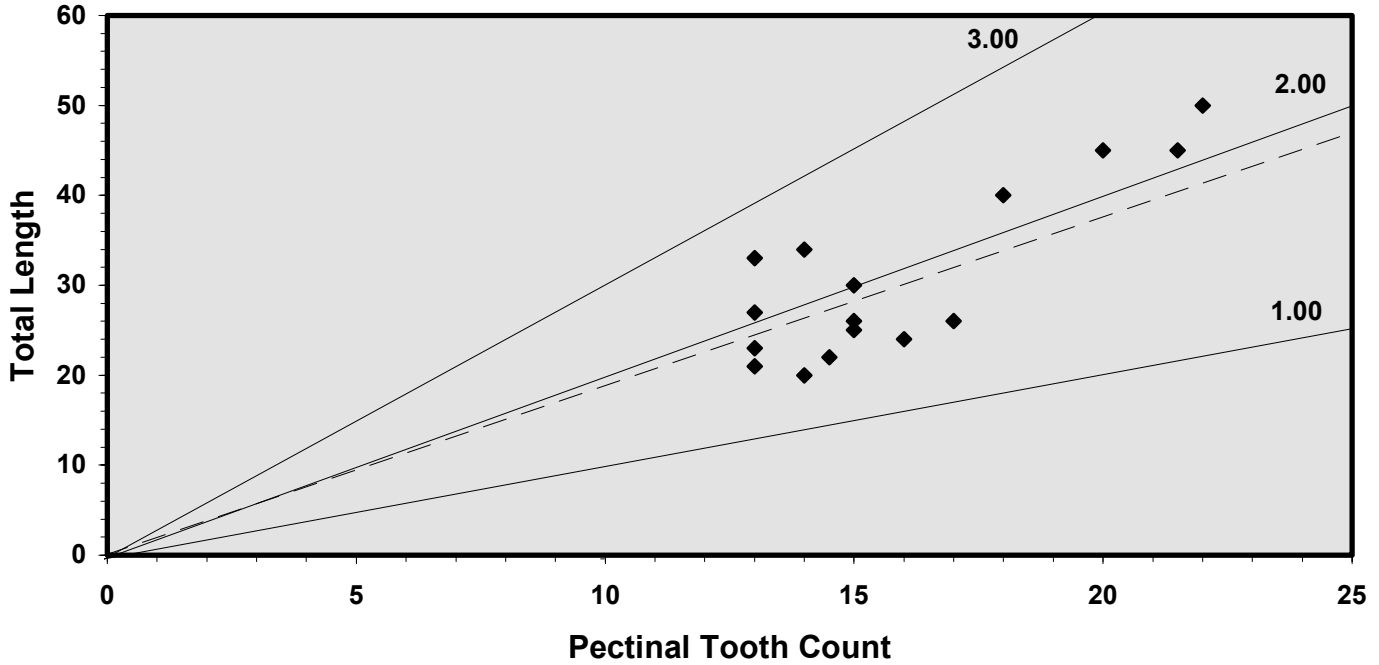


Figure D-6: Scatter chart of *Total Length/Pectinal Tooth Count* ratio (female) for genus *Serradigitus*; number of samples = 16; see Fig. D-2 for definition of other conventions.

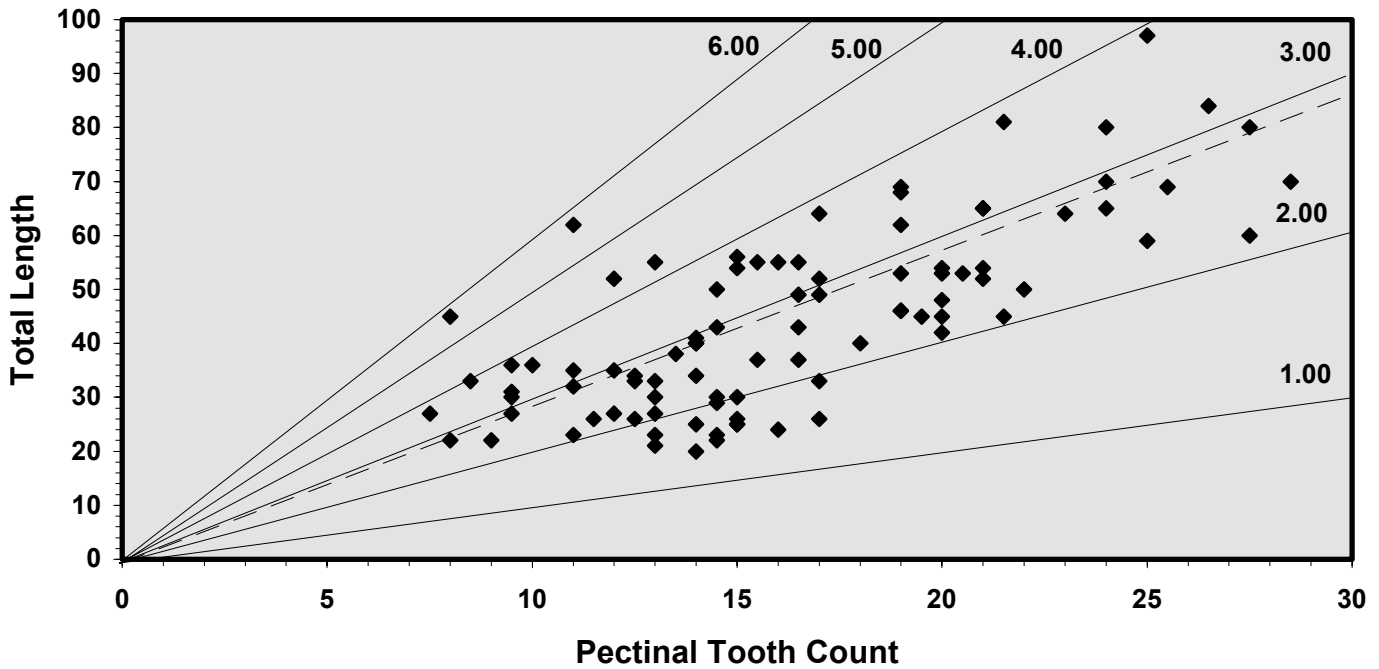


Figure D-7: Scatter chart of *Total Length/Pectinal Tooth Count* ratio (female) for family Vaejovidae; number of samples = 91; see Fig. D-2 for definition of other conventions.

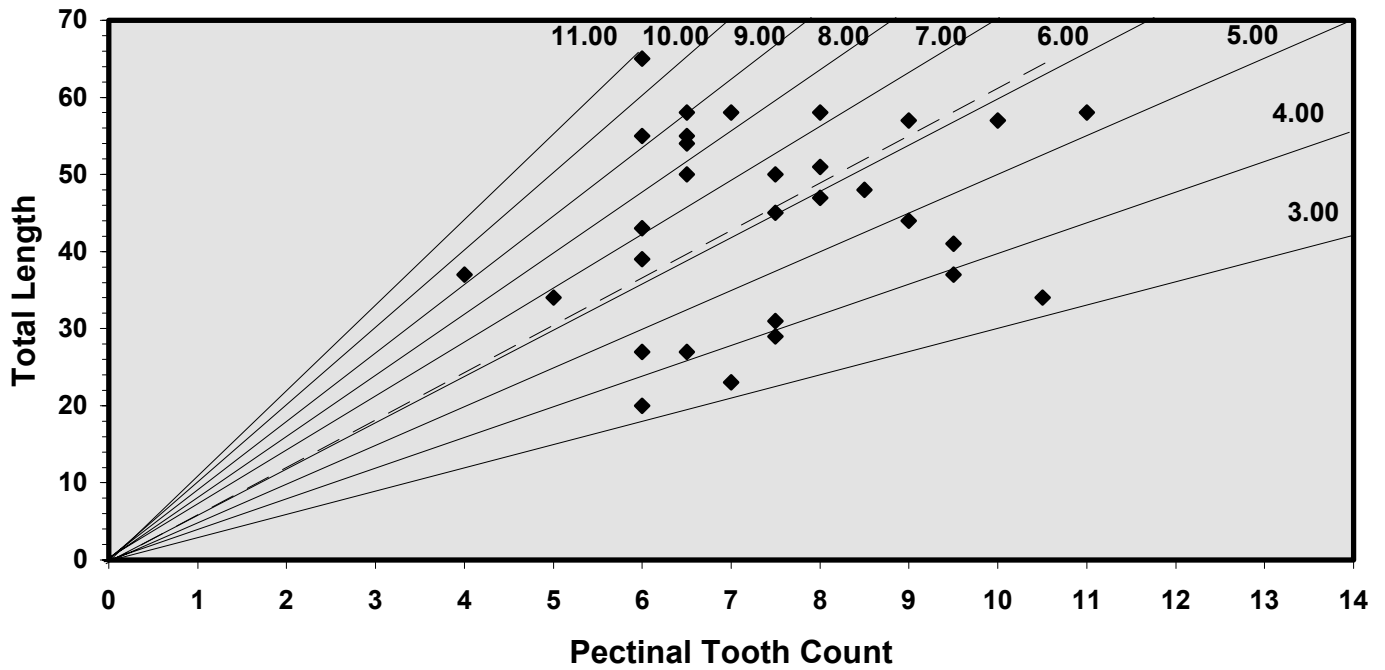


Figure D-8: Scatter chart of *Total Length/Pectinal Tooth Count* ratio (female) for family Chactidae; number of samples = 30; see Fig. D-2 for definition of other conventions.

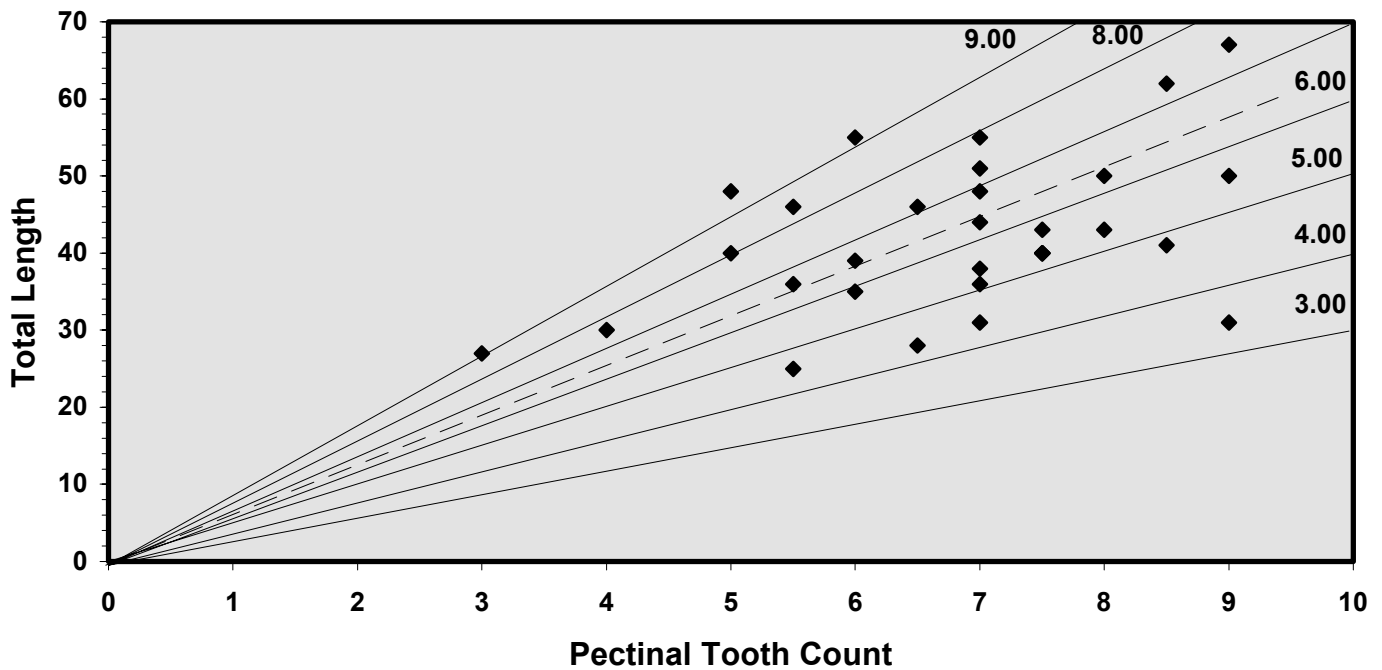


Figure D-9: Scatter chart of *Total Length/Pectinal Tooth Count* ratio (female) for family Euscorpiidae; number of samples = 30; see Fig. D-2 for definition of other conventions.

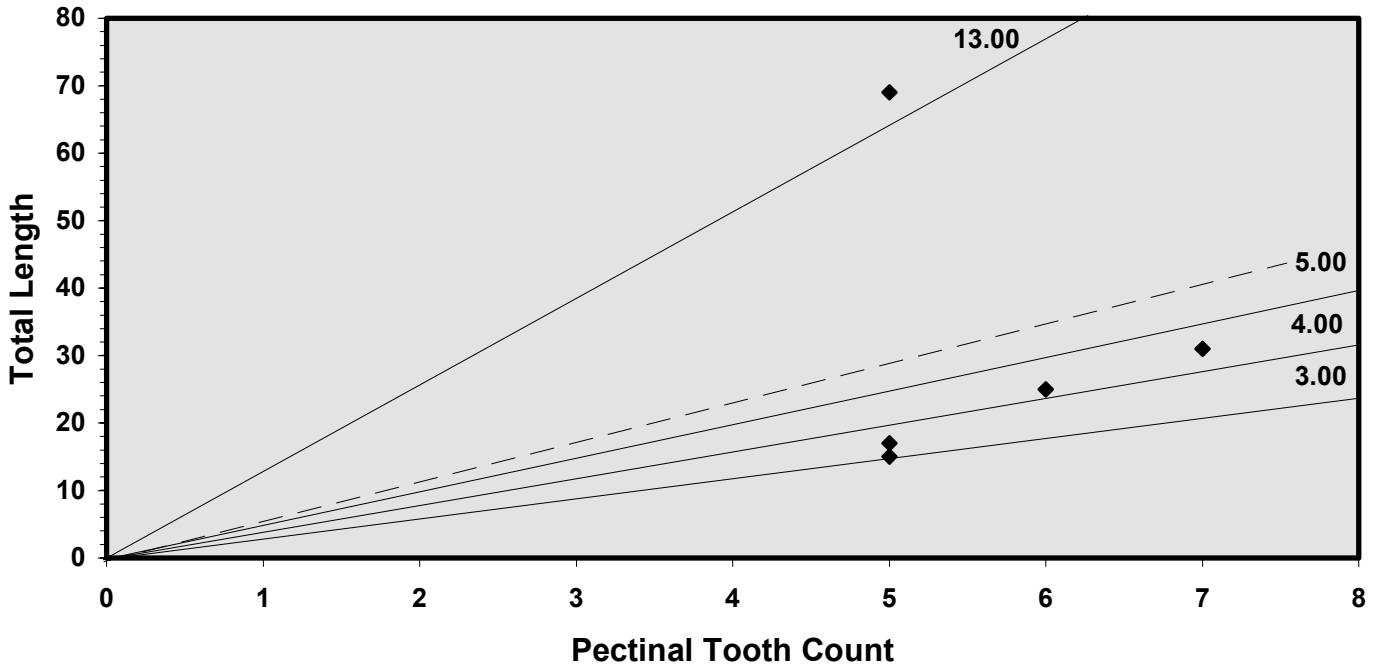


Figure D-10: Scatter chart of *Total Length/Pectinal Tooth Count* ratio (female) for family Superstitioniidae; number of samples = 5; see Fig. D-2 for definition of other conventions.

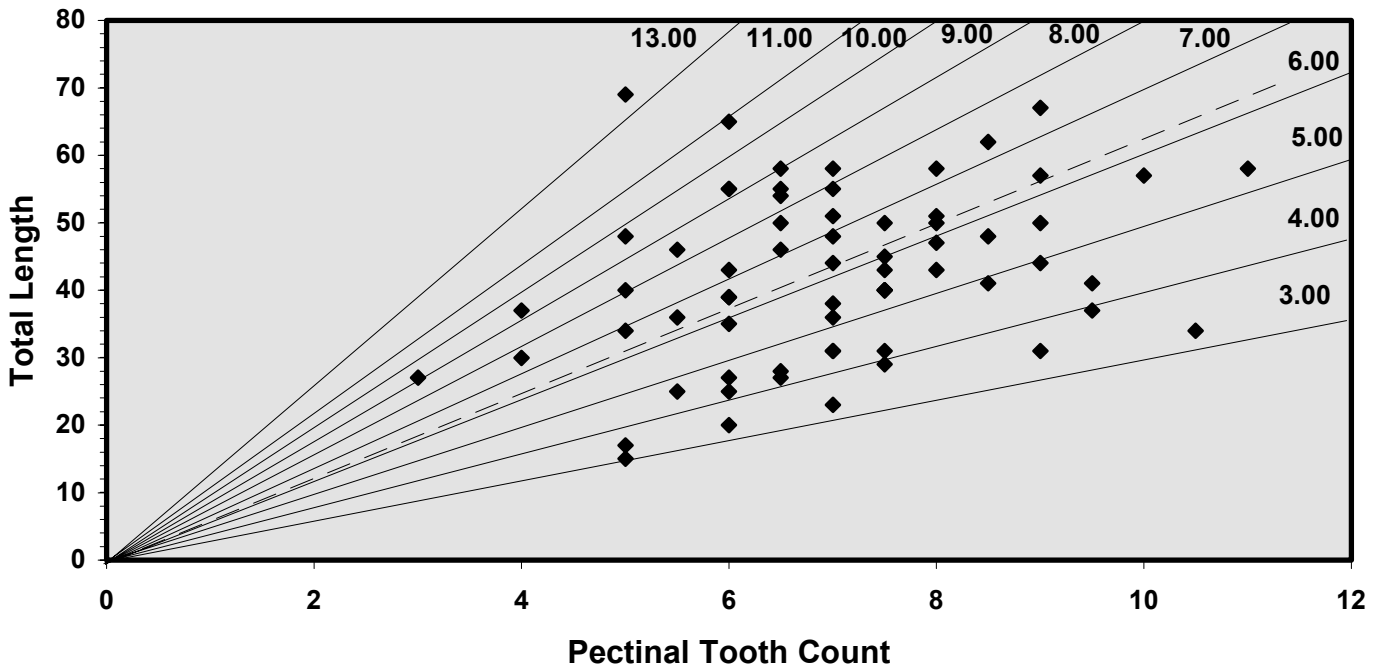


Figure D-11: Scatter chart of *Total Length/Pectinal Tooth Count* ratio (female) for families Chactoidea(-V); number of samples = 65; see Fig. D-2 for definition of other conventions.

Appendix E Trichobothria Derivation Maps

Soleglad & Fet (2001) presented the evolution of orthobothriotaxy by establishing homology of each individual trichobothrium across all orthobothriotaxic types for Recent scorpions and two fossil groups, the Carboniferous palaeopisthacanthids and the Cretaceous genus *Archaeobuthus*. Soleglad & Fet (2001; Appendix B) presented a set of derivation maps which traced the derivation of each trichobothrium across all nodes presented in their final cladogram (the pedipalp, Fig. 8). Due to the slight topological differences from the original cladogram of Soleglad & Fet (2001), (P, (F1, ((D, A), (B, (C))))), and that derived in this current study, (P, (F1, (D, (A, (B, (C)))))), we present in this Appendix a new

set of derivation maps (Figs. E-1 – E-3). We should also note that, in this new topology, the subclade from the original topology, "... (D+A) ...", is replaced with "... A+(B+C) ...".

In Soleglad & Fet's (2001) original study as well as in this current paper, each trichobothrium is assigned to a special Sankoff character defined as follows:

	Absent	Petite	Full
Absent	0	1	2
Petite	1	0	1
Full	2	1	0

Fossil Nodes			Recent Nodes		Terminal Nodes					
Prototypic Palaeopisthacanthids	Prototypic Archaeobuthids	Prototypic Recent	A+(B+C)	B+C	P	F1	D	A	B	C
<i>i</i> ₁	●									
<i>i</i> ₂	●			□						
<i>i</i> ₃		●		□			●			
<i>i</i> ₄		●		□			●			
<i>d</i> ₁	●									
<i>d</i> ₂		●		□		○	○			
<i>d</i> ₃	●									□
<i>d</i> ₄		●								□
<i>d</i> ₅	●									□
<i>e</i> ₁		●								
<i>e</i> ₂		●								□
<i>e</i> ₃	○		□							○
<i>e</i> ₄										●

Figure E-1: Derivation map of femoral orthobothriotaxy. Large filled circle, full trichobothrium; small filled circle, petite trichobothrium; large open circle, full trichobothrium, homoplasious; small open circle, petite trichobothrium, homoplasious; 'L' inside rectangle, trichobothrium loss. P = Type P (palaeopisthacanthids), F1 = Pattern F1 (archaeobuthids), A = Type A (buthoids), B = Type B (chaerilids), C = Type C (iuroids, scorpionoids, and chactoids), D = Type D (pseudochactids). Informative trichobothria are inside *rectangle*.

	Fossil Nodes			Recent Nodes		Terminal Nodes					
	Prototypic Palaeopisthacanthids	Prototypic Archaeobuthids	Prototypic Recent	A+(B+C)	B+C	P	F1	D	A	B	C
<i>eb</i> ₁	●										
<i>eb</i> ₂			●								
<i>eb</i> ₃											●
<i>eb</i> ₄											●
<i>eb</i> ₅											●
<i>esb</i> ₁			●								
<i>esb</i> ₂											●
<i>em</i> ₁		●		⊙			⊙	⊔			
<i>em</i> ₂											●
<i>est</i>		●									
<i>et</i> ₁	●										
<i>et</i> ₂			●								
<i>et</i> ₃											●
<i>d</i> ₁	●										
<i>d</i> ₂		●									
<i>d</i> ₃			●		⊔			⊙	⊙		
<i>d</i> ₄										●	
<i>d</i> ₅							●			●	
<i>v</i> ₁										●	
<i>v</i> ₂										●	
<i>v</i> ₃										●	
<i>i</i> ₁		●									
<i>i</i> ₂											●

Figure E-2: Derivation map of patellar orthobothriotaxy. See Fig. E-1 for definition of figure icons.

	Fossil Nodes			Recent Nodes		Terminal Nodes					
	Prototypic Palaeopisthacanthids	Prototypic Archaeobuthids	Prototypic Recent	A+(B+C)	B+C	P	F1	D	A	B	C
<i>Eb</i> ₁	●										
<i>Eb</i> ₂	●										
<i>Eb</i>₃				●	●						
<i>Esb</i>											●
<i>Est</i>	●										
<i>Et</i> ₁	●										
<i>Et</i> ₂											●
<i>Et</i> ₃											●
<i>Et</i>₄				●							L
<i>Et</i> ₅											●
<i>Db</i>											●
<i>Dt</i>											●
<i>V</i> ₁	●										
<i>V</i>₂				●			⊙		⊙	L	⊙
<i>V</i>₃							⊙				⊙
<i>V</i>₄							⊙				⊙
<i>eb</i>	●										
<i>esb</i>		●					⊙	⊙	L		
<i>est</i>	●										
<i>et</i>	●										
<i>db</i>		●									
<i>dsb</i>											●
<i>dst</i>											●
<i>dt</i>		●									
<i>ib</i>			●				⊙		⊙	L	
<i>it</i>			●								

Figure E-3: Derivation map of chelal orthobothriotaxy. See Fig. E-1 for definition of figure icons.

AN ESSAY ON SCORPION

by Victor Fet

1.

One-twelfth of you were born under this sign.
 A vile tail-biting beast, 'tis also mine
 Subject of study. In the times of yore
 When alchemists were to bypass the ore
 To get the gold—the scorpion, alas,
 Was just too bad to be ignored, and thus
 Hundreds of rare specimens, no doubt,
 Were ground down in bulk by some imposing lout,
 Or burnt alive with lashing metasomas
 Amidst sulphuric mist and vile aromas.
 Be as it may, Linnaeus comes to mind—
 Who, in his System, every type and kind,
 Variety and species, form and race
 Positioned well in God-appointed place.
 Six kinds of scorpion—the whole distinguished lot—
 Were given names in their generic slot,
 Named *Scorpio* by Carolus the Great,
 In year seventeen and fifty-eight.

2.

Should we recite the further flow of gents
 Who, far away from history's events,
 Took time from serving either Mars or Venus
 Describing scorpions, the genus after genus?
 Should we recall how, from the Middle East,
 Hemprich and Ehrenberg took every vicious beast?
 How years were spent by those who learned them well—
 Pocock, Birula, Kraepelin, Thorell?
 How long it took to set the notions right,
 Decade after decade, night after night,
 Eyes on the eyepiece, focused on the claw,
 To formulate the scorpion lore and law?
 'Twas not until a gently flowing breeze
 Showed to someone a character that is
 The most important clue to build a tree,
 Which could reveal their true phylogeny—
 Their ancient history. 'Tis feature fine and fair:
 A trichobothrium; a thin and trembling hair.

3.

Thus followed an impressive overhaul
 By Max Vachon, that most industrious Gaul,
 Of the entire, diverse tail-stinging folk
 From every nook and cranny, every walk
 Of life. Three major Types—A, B, and C—
 Were clearly set for everyone to see.

Type A—for buthids. Mighty is their race,
 Found in all continents, in nearly every place,
 In deserts or in tropics, high and low,
 They everywhere in black light brightly glow.
 With an immensely potent venom, those
 Beasts, as a rule, have thin and weaker claws.
 Type B—for chaerilids, to Asian climes endemic,
 A real prize for every academic,
 Rare animals with rather relict features,
 Observing games of life from distant bleachers.
 Type C—for everybody else. Alas,
 A lot of things were dumped together thus.

4.

Let's now climb the all-inclusive Tree
 Which represents all the taxonomy,
 Based on cladistic tools of modern trade,
 Each group a good, monophyletic clade,
 Accounting for the arguments of late,
 All skill and poignancy brought up-to-date,
 Trying to evade a homoplasious trap
 While gaining good support from the bootstrap.
 Thus goes the Tree: within the extant borders
 Of orthosterns we count four *parvorders*;
 The first is Pseudochactida. Its sole
 Genus and species hails from the shores of ole
 Good Ocean Tethys, God knows how stuck
 In mountain valleys with a relict's luck,
 In far Uzbekistan. Its features rare
 Are now exposed—ancient, weird and bare
 For all to see. Uniquely, to our day,
 These tiny *Pseudochactas* cling to clay.

5.

The second clade are Buthida. Still they
 Fit nicely in the old Vachon's Type A.
 The third clade are Chaerilida. Unclear
 Is their true place: appearing to be near
 The buthids, they are pulled into the shade
 Of the Type C—Iurida, the clade
 Of most complexity, where our attention lies
 (Although it wouldn't bring the Nobel Prize).
 As for the families, Iurida have ten
 ('Tis surely less than mice but more than men);
 And they have superfamilies. Our tree
 Supports three clades of those, and *only* three.
 First clade, the iuroids most strange,
 Are surely witnesses of ancient change,
 Tectonic moves, extinctions run galore,
 And now disjunct from Greece to Ecuador.
 (Among these relics, don't forget to list
 The hairy *Hadrurus*, a giant desert beast).

6.

Scorpionoids are another branch,
 With ancient splits of geographic range:
 Here bothriurids, with the sternum wide,
 Enjoyed a riotous Jurassic ride
 On scattered portions of Gondwanaland.
 See urodacids, coming to the end
 Of such a ride on far Australian sea;
 See scorpionids, liochelids see
 With crablike claws and Guinness-record length
 (Their venom, though, is of a low strength).
 Those animals present a worthy case
 Of ancient branch which bore a giant race.
 Our *true* attention, though, now veers astray
 To superfamily both bright and gray:
 Bright with diversity—and gray with mist
 Of true enigmas. Last but not the least,
 Come the chactoids. Go forth, my line,
 And through the clouds with a true vision shine!

7.

Chactoids stand alone. A lot of tries
 Were made in vain—by number of their eyes,
 Spurs, spines, and trichs—to crack this group, to find
 What brings together the chactoid kind.
 Here's what we see and say: the vaejovids are "in",
 But not *Uroctonus*! This genus now has been
 With *Anuroctonus* allied and, in a bold
 Supported move, brought to the chactid fold.
 So was that Spanish relic, pale and blind
 Old *Belisarius*, the most ancient kind;
 With brotheines, the true rainforest crowd,
 Its stands alone, with its disjunction proud.
 Things fall together, carinae run true,
 And setae don't obscure the spinule view.
 Thus remnants of the history do cling
 To other remnants, and forever sing
 From those branches of the mighty tree
 Where truth of history is now set free.

Huntington, West Virginia
November 16, 2003

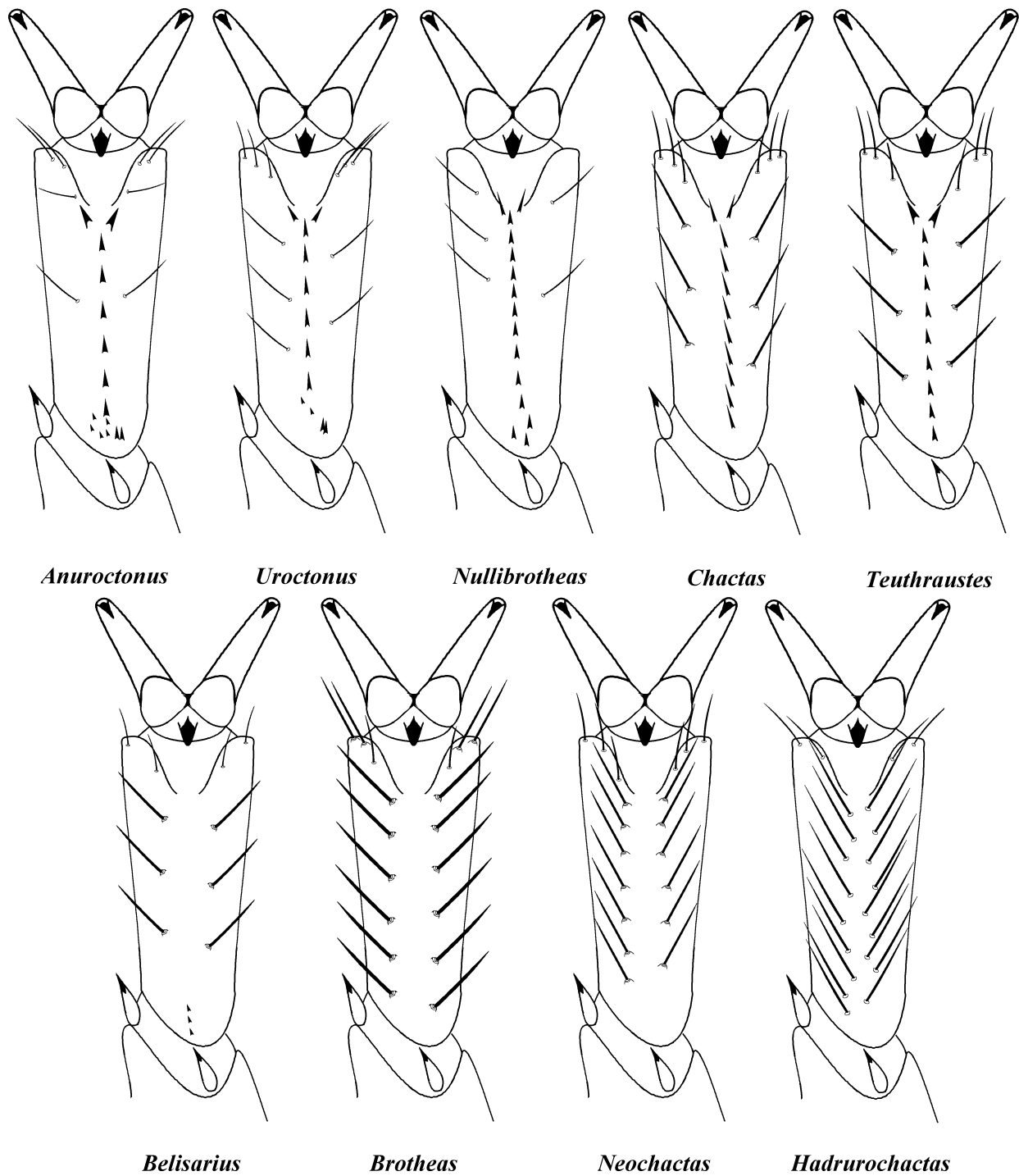


Figure 39: Diagrammatic ventral view of leg tarsus showing the basic arrangement of *setal/spinule* configurations of representative chactid genera.

Chactoidea – This superfamily complies with *setal/spinule configuration 5*: moderate to well-developed lateral pairs of setae and a median row of spinules. The sockets of the setal pairs are of small to moderate development, never as large or significant as those seen in the spinoid setae of the scorpionoids or as

that seen in most buthoids and chaerilids. The ventral median spinule row is present in all vaejooids and in a large majority of the euscorpoids and chactids as well. The dominance of setal pairs versus the median spinule row creates several sub-configurations within these two large assemblages of taxa (Figs. 31–39). The spinule

median row is present in all vaejovids, the lateral setal pairs are of weak to moderate development. Within the vaejovids, the number of *ventral distal spinule pairs* is considered an important taxonomic character, separating some of the vaejovid genera and *Vaejovis* groups. Both one-pair and multiple-pair groups are illustrated in Figs. 35–38: *Vaejovis punctatus* and *Pseudouroctonus reddelli* (Figs. 35–36), and *Serradigitus gertschi* and *Smeringurus grandis* (Figs. 37–38), multiple-pair and one-pair, respectively. This character also proved to be important in the distinction of some euscorpoid genera (Soleglad & Sissom, 2001: 62–64). Williams & Savary (1991) defined the vaejovid genus *Uroctonites* based, in part, on the slightly heavier setal pairs found on the ventral aspect of the tarsus, in contrast to those found in other species of *Pseudouroctonus*. The chactid subfamilies Chactinae and Uroctoninae are similar to the vaejovids, all equipped with a median spinule row terminated by a single pair of distal spinules; the setal pairs are weakly developed in Uroctoninae (represented by *Anuroctonus* in Fig. 34) and well-developed on most Chactinae (represented by *Nullibrotheas* in Fig. 32). Subfamily Brotheinae has essentially lost the median spinule row showing a strong emphasis on the setal pair configuration: *Brotheas* and *Belisarius* (Fig. 33) with strongly developed setal pairs, and the other genera (e.g., *Neochactas*, *Hadrurochactas*) with thinner but more numerous setal pairs (see Fig. 39 for the overall configurations of setal and spinule arrangements for family Chactidae). In the superstitioniids we see three configurations. In subfamily Typhlochactinae (which includes *Alacran*), the median spinule row is essentially absent (minor development is reported in *T. mitchelli* (Sissom, 1988)) and the setal pairs are prevalent, but never as well-developed or numerous as those seen in the brotheines. In subfamily Superstitioniinae, which includes *Superstitionia* and *Troglotayosicus*, we see two patterns. In *Superstitionia*, we see a very unique, dense clustering of elongated spinules, which is similar, under normal magnification, to the spinules clusters seen in young *Calchas* specimens, although more dense and continuous but never forming concentrated clusters of setae as seen in some of the other iuroids (Figs. 10 and 26). The *Troglotayosicus* tarsus has not been examined by us so our observations are based solely on the description and illustration provided by Lourenço (1981: 654, Fig. 43): although the figure shows socketed setae, the text uses the term “spinules (spiniformes)”; whether they are setae, spinules, or a mixture of both, they are in any case quite numerous, elongated, and irregularly positioned. If these “setae” turn out to be spinules, at least for the median area, then we can possibly see a taxonomic connection between this form and that exhibited by *Superstitionia*—both spinule sets would be exceptionally elongated and closely set, which is unprecedented in the chactoids.

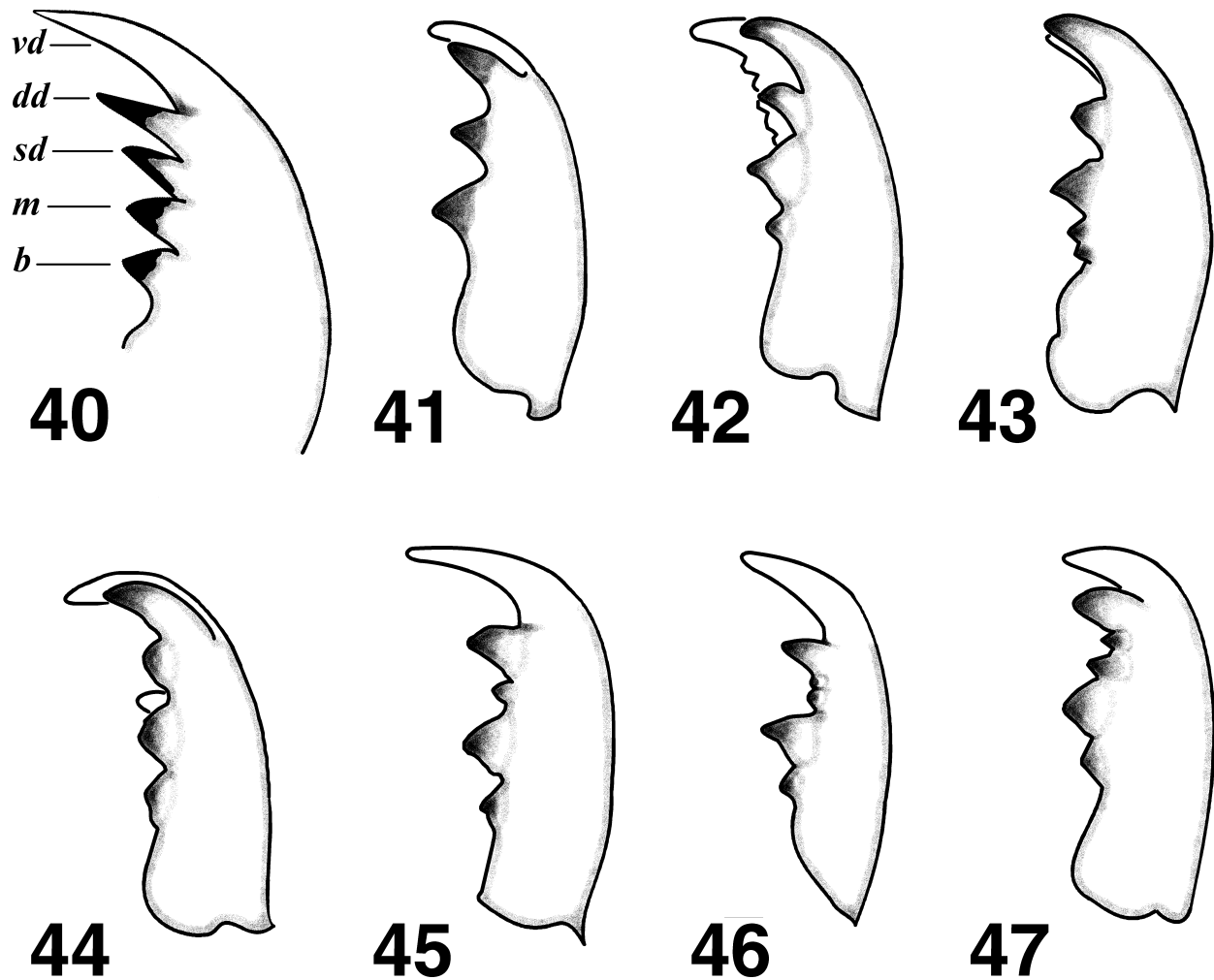
Chelicerae

The chelicerae are an important taxonomic structure in the diagnoses of high-level as well as low-level scorpion taxonomic groups. Vachon (1963) formally defined the basic cheliceral configurations found in Recent scorpions as well as established a nomenclature for identifying various denticles found on this structure. In our analysis, which proposes the palaeopisthacanthids as a primitive form for cladistic purposes, four important aspects of cheliceral dentition are considered: the dorsal and ventral aspects of the movable finger, and the dorsal and ventral aspects of the fixed finger. Of particular importance are: the presence or absence of fundamental denticles on the dorsal edge of the movable finger, the dentition on the ventral edge of the movable finger, the orientation of the denticles of the fixed finger, and the presence or absence of accessory denticles (i.e., “protuberances”) on the ventral surface of the fixed finger. As a character of lesser importance, we also consider the relative alignment of the distal denticles terminating the dorsal and ventral edges of the movable finger.

Kjellesvig-Waering (1986) and Jeram (1994a) described and illustrated the chelicerae of two Carboniferous palaeopisthacanthid scorpions. Kjellesvig-Waering (1986: 233, Text-Fig. 103-E) illustrated the chelicerae for *Palaeopisthacanthus schucherti*, and Jeram (1994a: 534, Text-Fig. 4-E) described and illustrated the chelicerae for *Compsoscorpium elegans*. Of particular importance here is the fact that the chelicerae of these two fossil genera match quite closely in overall structure and dentition. We adopt these descriptions and illustrations as the primitive condition for this important structure, using both genera as a composite when necessary to complete the information.

Movable finger. The cheliceral movable finger has two distinct cutting edges (dorsal and ventral), which enclose the denticulate edge of the fixed finger when a chelicera is closed. These two edges exhibit variability in their overall development as well as in specific dentition configurations.

Dorsal edge. In Fig. 40, we show *Palaeopisthacanthus schucherti* as illustrated by Kjellesvig-Waering (1986). In this diagrammatic drawing we see that the dorsal edge is considerably reduced, the ventral distal denticle extending well beyond the dorsal distal denticle. All four dorsal denticles are well-developed, however, especially a somewhat large subdistal denticle. For fossil scorpion *Compsoscorpium elegans*, Jeram (1994a) writes: “... moveable finger has a superior row of five teeth which increases in size distally ...”. We take exception to Jeram’s count of five denticles for this edge. We suspect that, when viewing the movable finger from the dorsal aspect, that the ventral distal denticle was included in this count. We therefore propose here that *Compsoscorpium* has four denticles on the dorsal edge, as

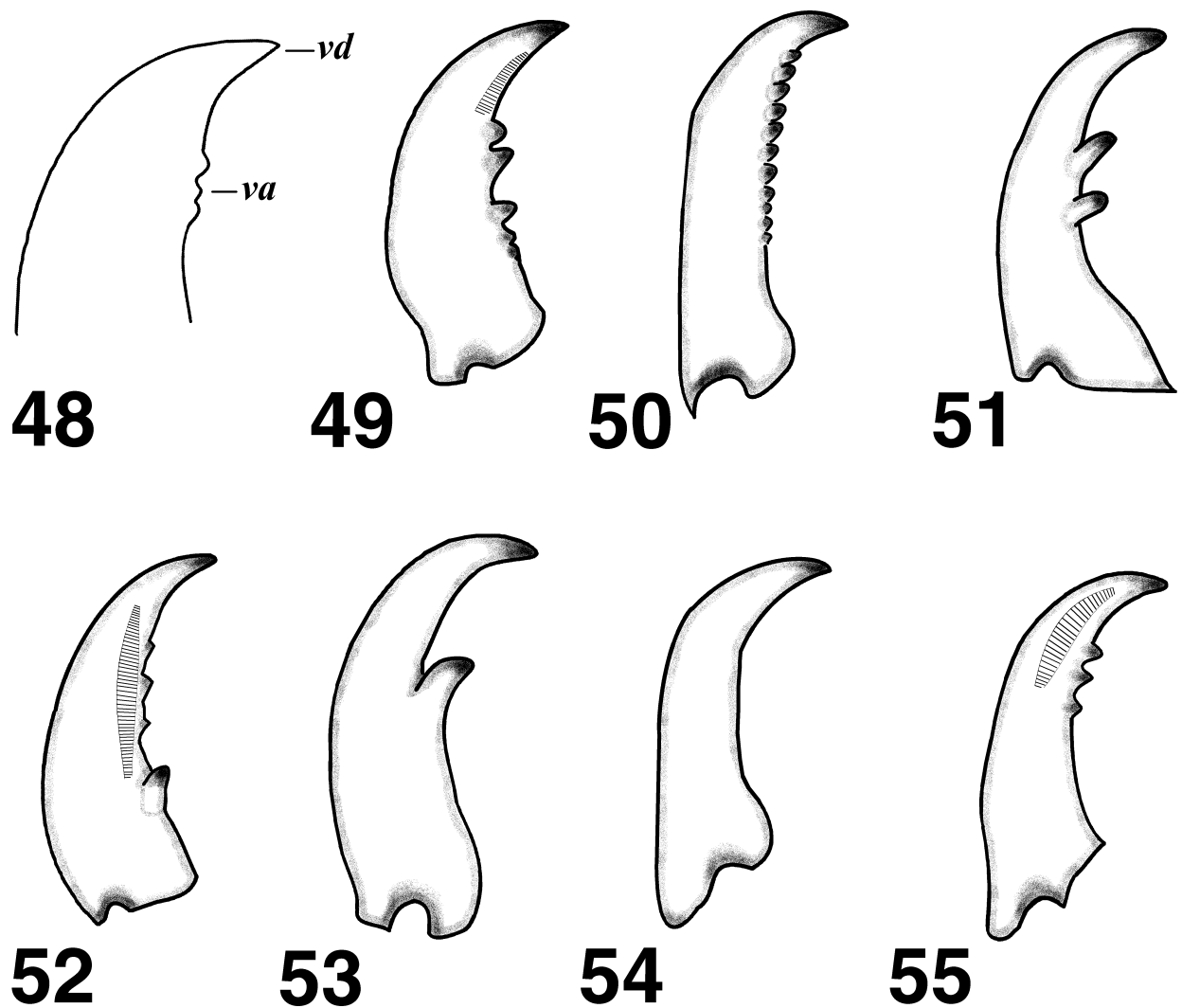


Figures 40–47: Cheliceral movable finger, dorsal aspect. **40.** *Palaeopisthacanthus schucherti* (after Kjellesvig-Waering, 1986: Text-Fig. 103-E, in part). **41.** *Pseudochactas ovchinnikovi*. **42.** *Chaerilus variegatus*. **43.** *Androctonus bicolor*. **44.** *Iurus dufourei*. **45.** *Scorpio maurus*. **46.** *Brachistosternus ehrenbergii*. **47.** *Hadrurus aztecus*. Note that the ventral edge is not shaded in order to contrast it with its dorsal counterpart. *vd* = ventral distal (denticle), *dd* = dorsal distal, *sd* = subdistal, *m* = median, *b* = basal.

that reported and illustrated for *Palaeopisthacanthus*. If one views Kjellesvig-Waering's (1986: Text-Fig. 103-E) original illustration of the chelicerae, which shows all denticles pigmented, the dorsal/ventral edges are not discernable when viewed from the dorsal aspect. Only when viewed internally (a view also shown in this figure) do the two edges become apparent. Jeram's observation that the denticles increase in size distally is consistent with our illustration of *Palaeopisthacanthus* (Fig. 40). Therefore, we see consistency within the two palaeopisthacanthid genera in the dentition of the cheliceral dorsal edge of the movable finger. We consider this configuration of four denticles a primitive condition: dorsal distal (*dd*), a single subdistal (*sd*), median (*m*), and single basal (*b*) denticles.

In Figures 40–47, we illustrate the dorsal edge of the movable finger of several Recent scorpion groups. In Fig. 40 (*Palaeopisthacanthus schucherti*) we illustrate

the hypothesized primitive condition, as discussed above. We see that the primitive condition of four denticles is found in parvorder Chaerilida (Fig. 42), Old World iuroids, and in most scorpionoids. We consider this configuration plesiomorphic for these groups. This primitive condition, which exhibits single subdistal (*sd*) and basal (*b*) denticles, is found in both Old World iuroid genera, *Iurus* (Fig. 44) and *Calchas*, and consistently in scorpionoid families Scorpionidae (represented by *Scorpio* in Fig. 45) and Liochelidae, as well as in some bothriurid genera (i.e., *Bothriurus*, *Timogenes*, and *Vachonia* (Prendini, 2000: 48)). However, Prendini considered the occurrence of a single subdistal denticle in these three bothriurid genera as derived from a two subdistal denticle state (i.e., a reversal, since these genera formed the most internal aspect of his bothriurid clade (see Prendini's Fig. 2)). Two primitive Recent scorpion parvorders, Pseudo-



Figures 48-55: Cheliceral movable finger, ventral aspect. **48.** *Palaeopisthacanthus schucherti* (after Kjellesvig-Waering, 1986: Text-Fig. 103-E, in part). **49.** *Pseudochactas ovchinnikovi*. **50.** *Chaerilus variegatus*. **51.** *Androctonus bicolor*. **52.** *Calchas nordmanni*. **53.** *Iurus dufourei*. **54.** *Liocheles* sp. (Papua New Guinea). **55.** *Nullibrotheas allenii*. The dorsal edge is not shown. *vd* = ventral distal (denticle), *va* = ventral accessory denticle (s).

chactida and Buthida, do not comply entirely with the hypothesized primitive condition. In Pseudochactida (Fig. 41), we see a single subdistal denticle, but the basal denticle is *missing*. We consider the absence of the basal denticle a derivation for this parvorder. In Buthida (represented by *Androctonus* in our Fig. 43), we also see a single subdistal denticle but the basal denticle is *doubled*, clearly a derived condition for this parvorder. For New World iuroid genera (represented by *Hadrurus* in Fig. x), and most bothriurid genera (represented by *Brachistosternus* in Fig. 46), we have two subdistal denticles. With a few exceptions, all chactoids have two subdistal denticles, which we consider a synapomorphy for this superfamily. For superstitioniid subfamily Typhlochactinae we see several species with a single subdistal denticle (i.e., *Sotanochactas elliotti*, *Typhlochactas cavicola*, *T. sylvestris*, and *T. granulosus*); and one minute species, *T. mitchelli*, has three dorsal

denticles, presumably missing the basal denticle. Interestingly, species *T. rhodesi* and *T. reddelli* are equipped with two subdistal denticles (see Sissom & Cokendolpher (1998: Table 1)). Due to the cave adaptation of these highly specialized scorpions, we do not consider the number of subdistal denticles of a particular taxonomic importance. Clearly, this somewhat arbitrary condition exhibited in this scorpion group is derived from a two subdistal denticle configuration. Gertsch & Soleglad (1972: Fig. 36) illustrated a single subdistal denticle for vaejovid *Uroctonites montereus* and also reported it as single in *U. sequoia*.

Ventral edge. As with the dorsal edge, we have good information on the dentition of the ventral edge of the movable finger for the two fossil Carboniferous genera, *Palaeopisthacanthus* and *Compsoscorpium*. In our Figure 48, showing *Palaeopisthacanthus schucherti* (after Kjellesvig-Waering, 1986), we see an edge with

three small crenulations or denticles. For *Compsoscorprius elegans*, Jeram (1994a) writes: "... inferior dentition consists of the large distal tooth and an inferior row of approximately twelve small accessory teeth ...". Again this is consistent with *Palaeopisthacanthus*, both fossil genera exhibiting a crenulated ventral edge and an enlarged distal denticle. We consider this condition primitive.

Figure 48 illustrates the primitive ventral edge for fossil *Palaeopisthacanthus schucherti*. Figures 49–55 illustrate the ventral edge of the cheliceral movable finger for several Recent scorpion groups. We see the primitive condition of several accessory denticles exhibited in parvorders Pseudochactida (Fig. 49) and Chaerilida (Fig. 50). We considered this crenulation to be plesiomorphic for these two parvorders. In parvorder Buthida (represented by *Androctonus* in our Fig. 51), we see two well-developed denticles, which is clearly a derivation for this parvorder. The presence of these distinct denticles is essentially conserved in Buthida, representing well over 75 genera. In parvorder Iurida, we have two fundamental configurations for the ventral edge of the movable finger: 1) a large single basal denticle, and, 2) a smooth edge. Superfamily Iuroidea is equipped with a large single denticle on the ventral edge (Figs. 52–53). The denticle is the most developed in the genus *Iurus* (Fig. 53) where it is situated midfinger and flares outward almost forming a tripod when the finger edge is viewed internally (i.e., the tripod is formed by the dorsal and ventral distal denticles and this large ventral denticle). In the genus *Calchas* (Fig. 52), the denticle is smaller and more basal. In addition, in some specimens of *Calchas*, we see irregular crenulation similar to that exhibited in the primitive condition (this is illustrated in Fig. 52). One could hypothesize that this relict genus retained the primitive state. In New World iuroids, genera *Hadrurus* and *Hadruidoidea* have a well-developed basal denticle situated on the proximal half of the segment, and in genus *Caraboctonus*, the denticle is smaller and more basally situated. Superfamilies Scorpionoidea (represented by *Liocheles* in Fig. 54) and Chactoidea have a smooth ventral edge of the movable finger. In Chactoidea there are several examples of ventral crenulations in various forms. These are all considered secondary development, having been derived from a smooth edge. This same hypothesis was proposed by Soleglad & Sissom (2001: 73–74). In family Euscorpidae, Soleglad & Sissom (2001: Fig. 207) proposed two separate derivations of a crenulated ventral edge, for subfamilies Megacorminae and Scorpipinae, respectively. In this paper, we also propose two separate crenulated ventral edge derivations for the family Chactidae, subfamily Uroctoninae and tribe Nullibrotheini (subfamily Chactinae) (Fig. 55). In the family Vaejoidea, several genera exhibit ventral crenulations to one degree or another: *Paruroctonus* and related

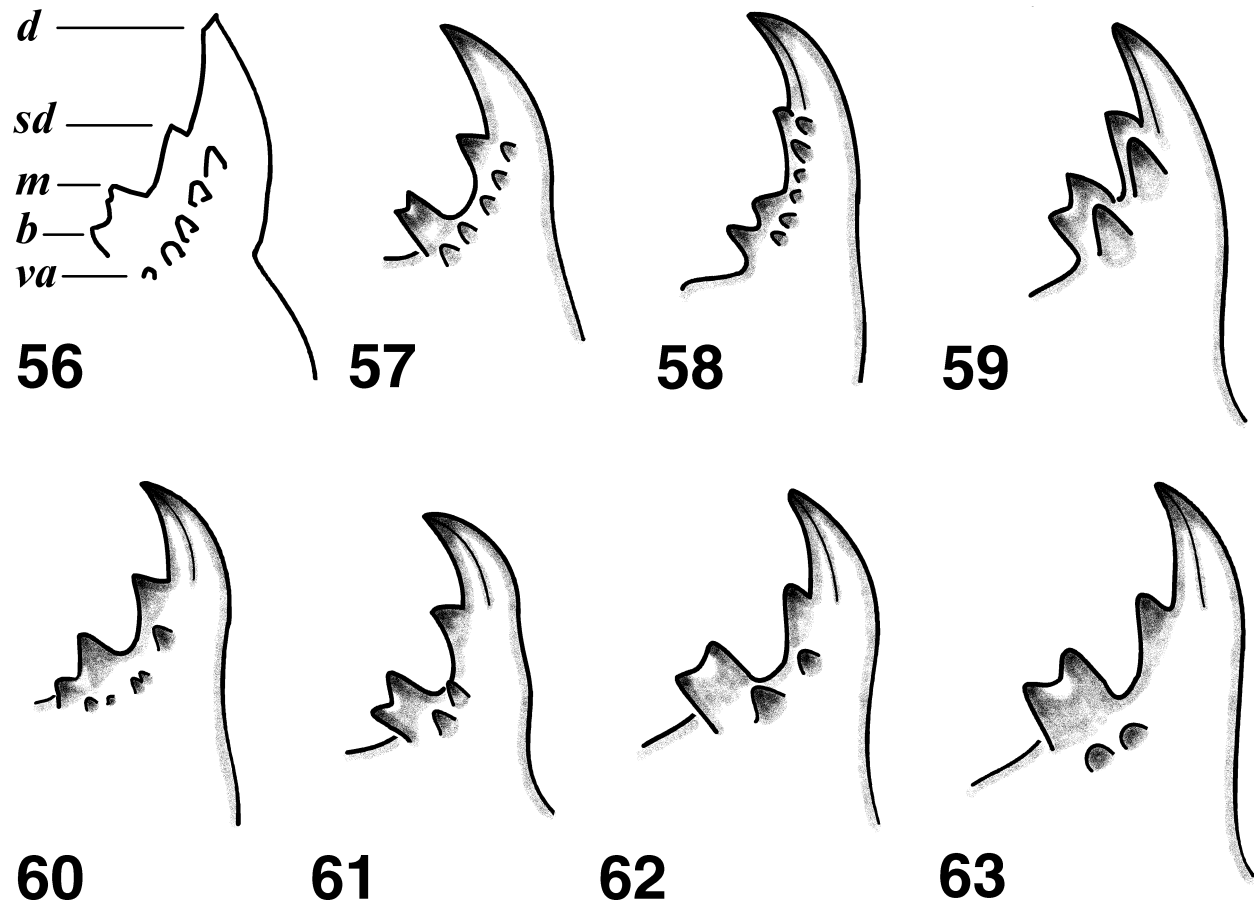
genera (*Smeringurus* and *Vejovoides*), and *Pseudo-uroctonus* (in part) and *Uroctonites*.

Dorsal/ventral distal denticle alignment. For fossil genera *Palaeopisthacanthus* and *Compsoscorprius*, Kjellesvig-Waering (1986) and Jeram (1994a) reported an enlarged ventral distal denticle, contrasted to a smaller, more offset dorsal distal denticle (Fig. 40). This feature, again, illustrates consistency in the chelicerae of these two palaeopisthacanthid genera.

In Recent scorpions, the relative proportional development of the dorsal and ventral distal denticles has diagnostic value in some scorpion groups. For the three primitive parvorders, Pseudochactida (Fig. 41), Chaerilida (Fig. 42), and Buthida (represented by *Androctonus* in Fig. 43), we see a well-developed dorsal distal denticle, slightly offset from its ventral counterpart. In particular, in Buthida, the dorsal distal denticle often extends beyond the ventral denticle, which is, in general, a characteristic of this large scorpion group. Interestingly, none of these three primitive parvorders exhibit the primitive state as seen in the palaeopisthacanthids, the significantly offset dorsal edge. In superfamily Iuroidea we see a well-developed dorsal distal denticle in genus *Iurus* (Fig. 44), with lesser development in other genera. In the scorpionoids we see that family Liochelidae and subfamily Heteroscorpioninae have a well-developed dorsal distal denticle, approximately the same length as its ventral counterpart. In contrast, other scorpionoids have a very reduced dorsal distal denticle (represented by *Scorpio* and *Brachistosternus* in Figs. 45–46). The relative proportions of these two distal denticles were used as a diagnostic character by Soleglad & Sissom in Euscorpidae (2001: 57–59) for distinguishing the very developed dorsal distal denticle exhibited in the subfamily Scorpipinae. At a more localized scale, several species of the vaejooid genus *Paruroctonus* have a very reduced dorsal edge of the movable finger (e.g., *P. gracilior*, *P. stahnkei*, *P. becki* (see Gertsch & Soleglad, 1966: Figs. 34, 37, 40), *P. williamsi*, and *P. pecos* (see Sissom & Francke, 1981: Figs. 28, 32)). This may possibly provide some diagnostic rationale for grouping two or more of these species.

Fixed finger. The cheliceral fixed finger has only one denticulate cutting edge, which we refer to in this paper as the dorsal edge. The dentition of the fixed finger, in general, is quite static in scorpions, only exhibiting subtle variations in their configuration, thus providing some diagnostic value. The ventral surface of this finger does not form a cutting edge; it may be smooth or be equipped with one or more denticles of variable development (sometimes referred to as "protuberances").

Dorsal edge. The dorsal edge of the fixed finger has been illustrated for both fossil genera discussed above, both exhibiting four fundamental denticles: distal (*d*),



Figures 56-63: Cheliceral fixed finger, ventral aspect. **56.** *Compsoscorpilus elegans* (after Jeram, 1994a: Text-Fig. 4-E, in part). **57.** *Pseudochactas ovchinnikovi*. **58.** *Chaerilus variegatus*. **59.** *Androctonus bicolor*. **60.** *Troglocormus willis*. **61.** *Pseudo-uroctonus reddelli*. **62.** *Smeringurus grandis*. **63.** *Vejovoidus longiunguis*. *d* = distal (denticle), *sd* = subdistal, *m* = median, *b* = basal, *va* = ventral accessory.

single subdistal (*sd*), median (*m*), and basal (*b*) denticles. In our Figure 56 of *Compsoscorpilus elegans* (after Jeram, 1994a), we see that the median and basal denticles are conjoined on a common trunk, a configuration usually found in Recent scorpions. Kjellesvig-Waering (1986) illustrates the fixed finger for *P. schucherti* with the median and basal denticles somewhat flush with the finger edge. Kjellesvig-Waering (1986: 233) reports: "... the fixed ramus seems to correspond closely to the arrangement in the genus *Chaerilus* ...". He was referring to the flush orientation of the median and basal denticles of the dorsal edge of the fixed finger, a diagnostic character for the genus *Chaerilus* (Fig. 58).

All Recent scorpions exhibit the fundamental four denticles of the dorsal edge of the cheliceral fixed finger (Figs 57-63) (one exception, see below). Parvorder Chaerilida has a separate, non-conjoined median and basal denticle configuration (Fig. 58). This is considered a derivation for this parvorder since it is consistently found in all known species (even though this same configuration was described by Kjellesvig-Waering for

genus *Palaeopisthacanthus*). The non-conjoined denticle pair is also seen, in part, in the euscorpoid genus *Troglocormus* (Fig. 60) as well as in many superstitioniids such as *Troglotayosicus* (Lourenço, 1981: Fig. 44), *Alacran* (Francke, 1982a: Fig. 4), *Sotanochactas elliotti* (Mitchell, 1971: Figs. 6-7), *Typhlochactas cavicola* (Francke, 1986: Fig. 4) and *T. rhodesi* (Mitchell, 1968: Figs. 4-5). Again, the minute scorpion *T. mitchelli* exhibits the most radical departure, only equipped with three denticles (Sissom, 1988: Fig. 2), the basal denticle presumably is lost.

Ventral surface. Jeram (1994a) reports for *C. elegans*: "... fixed finger ... Inferior dentition consists of a row of five subequal teeth ..." In our Figure 56 (after Jeram, 1994a), we see that the ventral surface of the fixed finger is equipped with somewhat low-profile denticles adjacent to the subdistal, median, and basal dorsal denticles. Kjellesvig-Waering (1989) illustrates the fixed finger for *Palaeopisthacanthus schucherti* but does not show ventral dentition. However, it is not clear which view is being shown, and therefore, we do not know exactly whether these ventral accessory denticles

are present in this species. Consequently, we consider the condition illustrated and described by Jeram (1994a) for *C. elegans* as primitive.

The ventral surface of the cheliceral fixed finger is illustrated for all major Recent scorpion groups in Figures 57–63. In the primitive condition, based on Jeram's (1994a) description of *Compsoscorpheus elegans* (our Fig. 56), we see five small denticles on the ventral surface. In primitive Recent scorpion parvorders we also see denticles on this surface. For Pseudochactida (Fig. 57), four to five small denticles are present (variable within the same species, *Pseudochactas ovchinnikovi*), remarkably in the same configuration as that seen in the primitive condition. In Chaerilida (Fig. 58), we see a series of substantial denticles, six in our example of *Chaerilus variegatus* (Stockwell (1989: Fig. 53) illustrated eight small denticles for *C. granulatus*). In some *Chaerilus* species these denticles are less developed: in *C. tryznai*, we see six pigmented denticles of medium development; in species *C. chapmani* (a troglobitic species) and *C. tichyi*, five weakly developed and faintly pigmented denticles are present. We consider the ventral denticles present in these two parvorders plesiomorphic. In parvorder Buthida (represented by *Androctonus* in Fig. 59), we see two well-developed denticles, indicative, in general, of this large scorpion group. We consider this specialized variant of the ventral dentition of the fixed finger a derivation for the parvorder Buthida. However, there are some exceptions in the Buthida for this configuration. The following genera lack these denticles: *Karasbergia* (Lamoral, 1979: 555) and *Uroplectes* (Sissom, 1990: 94). Sissom (1990: 97) and Fet et al. (2001a: 184–185) also report that genera *Anomalobuthus*, *Hemibuthus*, *Isometroides*, *Liobuthus*, *Lychas*, *Pectinibuthus*, and *Psammobuthus* are equipped with only one ventral denticle. A single ventral denticle is also found in some species of New World genera *Alayotityus*, *Centruroides*, *Microtityus*, *Rhopalurus*, *Tityus*, and *Zabius* (R. Teruel, pers. comm., 2003). In parvorder Iurida, ventral dentition is essentially absent; where it does occur it is considered a localized derivation for that group. In family Euscorpidae we see as many as five small ventral denticles in genus *Troglocormus* (Fig. 60). For the related vaejovid genera *Paruroctonus*, *Smeringurus* (Fig. 62), and *Vejovoidus* (Fig. 63), we see two to three small ventral denticles. Gertsch & Soleglad (1966: Fig. 42) illustrated three denticles for *Smeringurus mesaensis*. These ventral denticles are also found in some species of *Pseudouroctonus* (represented by *P. reddelli* in Fig. 61). Gertsch & Soleglad (1972: Fig. 31) illustrated three such denticles for species *P. cazieri*. These occurrences of ventral denticles are only of localized importance, maybe providing diagnostic characters at the genus level.

Trichobothria

Trichobothria, their fundamental orthobothriotaxic patterns, basic positional orientation within these patterns, and neobothriotaxy, all play an important role in this study. Fundamental orthobothriotaxic patterns provide major synapomorphies at the parvorder levels defined herein; basic trichobothria positional patterns are important at the superfamily level as well as lower levels such as families, subfamilies and tribes, discussed and/or defined in this study; neobothriotaxy is critical, in part, in differentiating the subfamilies within the family Chactidae. In this section we discuss relevant trichobothria characterizations involving all of these subjects.

Soleglad & Fet (2001) presented a formal cladistic procedure for evaluating the evolution of orthobothriotaxic patterns in Recent scorpions. In their analysis individual trichobothrium homologies were hypothesized spanning all defined orthobothriotaxic types including two fossil groups, the palaeopisthacanthids and the genus *Archaeobuthus*. Crucial to this approach was that each trichobothrium was treated as a separate cladistic character. This same technique currently is being applied to the complicated neobothriotaxy found in the euscorpoid genus *Euscorpheus* (Fet & Soleglad, in progress), thus establishing homology in key accessory trichobothria. Many of the observations presented in this paper concerning the trichobothrial positions and/or patterns of orthobothriotaxy found in the Vaejoidea and Chactidae(-V) families are based on preliminary results of an ongoing cladistic study of the Type C pattern (Soleglad, in progress). In this study all 48 trichobothria comprising the Type C pattern are mapped onto "positional grids", thus allowing the cladistic characterization of individual trichobothria positions.

Orthobothriotaxic patterns: In this current study the same set of existence criteria and corresponding homologies as established in Soleglad & Fet (2001), involving 62 existence characters, were incorporated with the other structural characterizations established in this paper. The resulting phylogeny deviated slightly from that derived in the other study which was based solely on orthobothriotaxy. The phylogeny in this study is formally contrasted in detail with that of Soleglad & Fet (2001) elsewhere in this paper, where differences in support and trichobothria derivations are presented.

In this study, the totality of all characterizations provides a basic topology outlining the parvorders established herein. As it turns out each Recent scorpion parvorder established in this study corresponds directly to a basic orthobothriotaxic pattern type, as formally defined by Vachon (1974), types A, B and C, and Soleglad & Fet (2001), types P, F1, and D:

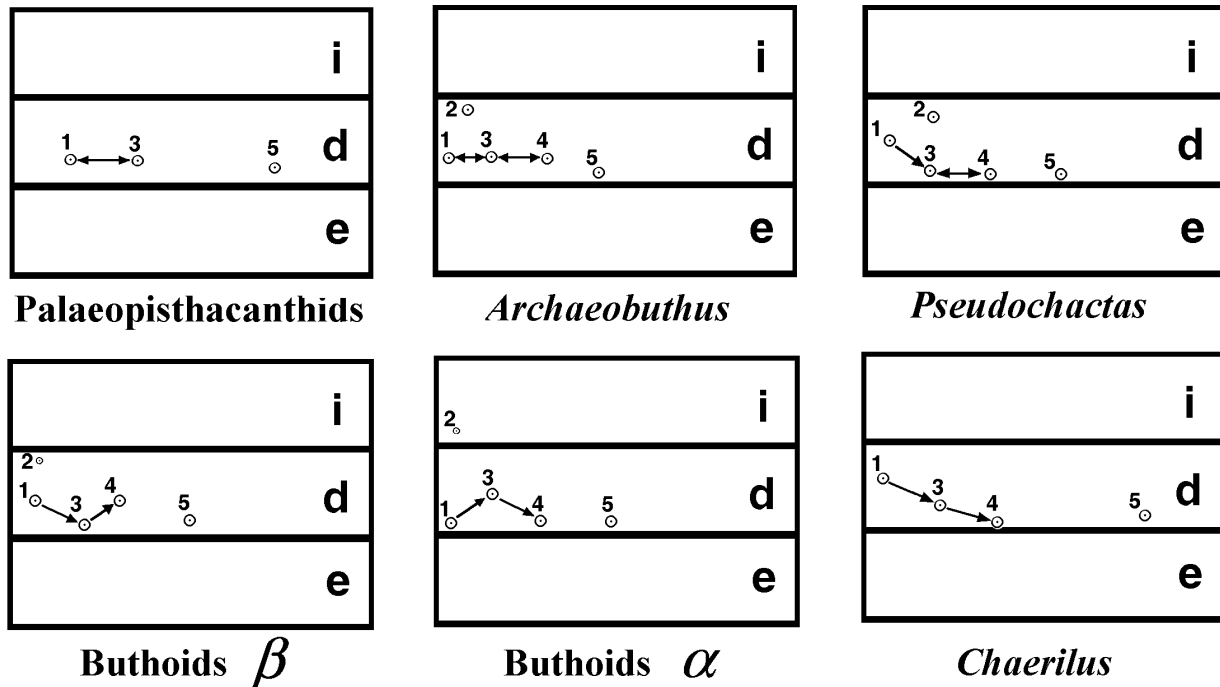


Figure 64: Femur *alpha/beta* trichobothria pattern of fossil and primitive Recent scorpions (after Soleglad & Fet (2001: Fig. 4), in part). Designations reflect three sub-patterns: trichobothria d_1 – d_3 alignment with respect to dorsoexternal carina, trichobothria d_3 – d_4 alignment with respect to dorsoexternal carina, and d_2 surface position (dorsal or internal). Arrowheads depict direction of alignment, double arrowheads depict parallel alignment. i = internal surface, d = dorsal surface, e = external surface.

Type P, family Palaeopisthacanthidae
 Type F1, family Archaeobuthidae
 Type D, parvorder Pseudochactida
 Type A, parvorder Buthida
 Type B, parvorder Chaerilida
 Type C, parvorder Iurida

Although we model orthobothriotaxy as a six-state ordered character, we also present the actual derivations on an individual trichobothrium basis for the four Recent scorpion parvorders (see **Appendix E**). These can be considered synapomorphies for each parvorder.

Trichobothria positions – femur: The *alpha/beta* pattern established by Vachon (1975) for the Type A configuration is an important character in the taxonomy of buthoid scorpions. Sissom (1990: 93) used it as his primary couplet in his extensive key to buthoid genera. Vachon (1975) identified the positional orientation of femoral dorsal trichobothria d_1 , d_3 and d_4 as well as the dorsal/internal position of d_2 . Soleglad & Fet (2001) discussed this basic pattern as it related to the fossil scorpion *Archaeobuthus* and Recent scorpion *Pseudochactas*. These two species did not comply specifically with either *alpha* or *beta* patterns as originally defined by Vachon. Soleglad & Fet (2001) hypothesized homology of all, or part, of the trichobothria involved in the *alpha/beta* pattern across all primitive Recent scorpions. In particular, *Arch-*

aeobuthus, *Pseudochactas* and the buthoids exhibit all four trichobothria and *Chaerilus* has three, lacking d_2 . Consequently, in this study, we have divided the original pattern as defined by Vachon into three separate characters. This further breakdown of the *alpha/beta* pattern is necessary in order to adequately place *Archaeobuthus*, *Pseudochactas* and *Chaerilus* within this scheme originally designed for the buthoids. Following is a breakdown of the *alpha/beta* pattern into three sub-patterns (Fig. 64):

- *Alpha/beta* sub-pattern: alignment of d_1 – d_3
 - parallel to dorsoexternal carina (primitive)
 - points toward dorsoexternal carina (β)
 - points away from dorsoexternal carina (α)
- *Alpha/beta* sub-pattern: alignment of d_3 – d_4
 - parallel to dorsoexternal carina (primitive)
 - points away from dorsoexternal carina (β)
 - points toward dorsoexternal carina (α)
- *Alpha/beta* sub-pattern: placement of d_2
 - on dorsal surface (primitive and β)
 - on internal surface (α)

In Vachon's (1975: Figs. α , β) original definition for the *alpha* pattern, d_1 – d_3 point away and d_3 – d_4 point

toward the dorsoexternal carina, and d_2 is located on the internal surface. In contrast, these conditions are reversed in the *beta* pattern. In *Archaeobuthus*, $d1-d3-d4$ trichobothria are in a straight line, thus both sub-pattern alignments are parallel to the dorsoexternal carina, and $d2$ is located on the dorsal surface, which we hypothesize here as primitive states. *Pseudochactas* exhibits the same pattern as *Archaeobuthus* except $d1-d3$ point toward the dorsoexternal carina, a *beta* pattern characteristic. Soleglad & Fet (2001: 24, 28) considered the pattern exhibited by *Pseudochactas* as intermediate between *Archaeobuthus* and *beta* pattern buthoids, thus exhibiting the most primitive femoral pattern found in Recent scorpions. As discussed in detail in the section concerning cladistics, this breakdown of the *alpha/beta* pattern provides more resolution in the topology of these primitive genera as well as possibly providing additional insight into the phylogeny of the buthoids. The effects of this modified *alpha/beta* model is discussed further in the section dealing with cladistic analysis.

Homologies – Caraboctoninae: For the iuroid subfamily Caraboctoninae, Stockwell (1989: 114, Figs. 175–176) proposed an important change to the trichobothria homology scheme as originally suggested by Vachon for genus *Caraboctonus* (Vachon, 1974: Figs. 154–156) and followed by Francke & Soleglad for two species of *Hadruroides* (1980: Figs. 9–12, 27–30). We accept these alternative homologies for several reasons. As stated by Stockwell, this interpretation is more parsimonious since it is less disruptive to trichobothria positions normally encountered within the Type C pattern. In particular, Vachon suggested that palm trichobothria *Db* and *Dt* occurred on the middle of the fixed finger, an essentially unprecedented position for these trichobothria (albeit, Vachon, 1974: Figs. 190–192, also made similar homologies for euscorpoid genus *Chactopsis*). In Stockwell's interpretation, these trichobothria are designated on the distal aspect of the palm. Although distally situated, their relative distance and positions are comparable to other configurations normally found on the proximal aspect of the palm; in addition, *Db* and *Dt* straddle the digital carina, also typical of Type C pattern scorpions, therefore, this new interpretation is a more intuitive designation. Finally, under this new interpretation, the pattern of the *db-dsb-dst-dt* series is now consistent with other Type C pattern scorpions, another reason to accept this new interpretation.

This new interpretation also establishes common patterns found within the superfamily Iuroidea as well as within the family Caraboctonidae. Stockwell's new scheme (see our Fig. 65) involves the following six changes to homology:

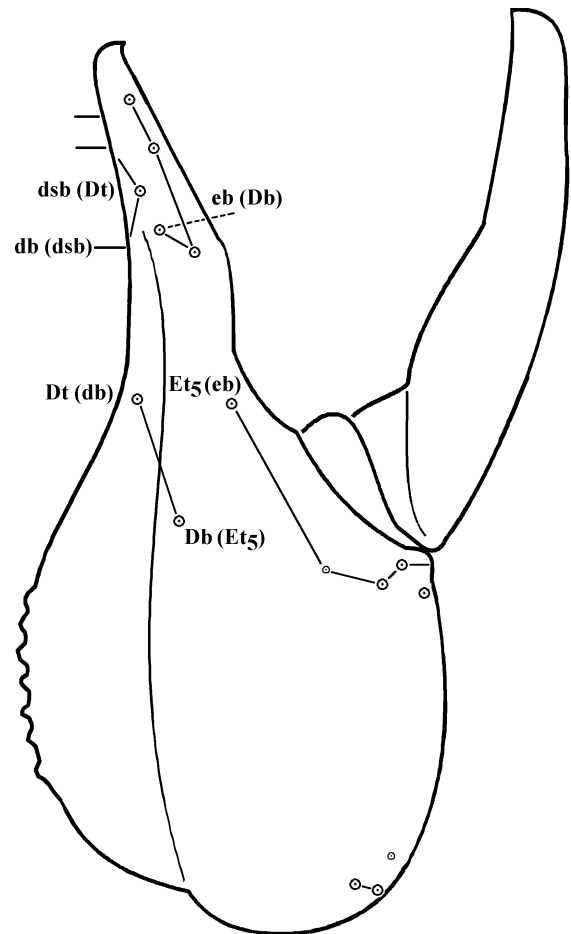


Figure 65: Diagrammatic pattern (external view) of *Hadruroides charcasus* showing alternative chelal trichobothria designations for subfamily Caraboctoninae based on Stockwell's (1989: Figs. 175–176) interpretation. Connected trichobothrial series depict new interpretations; trichobothria designations in parentheses depict Vachon's (1974: Figs. 154–156) original designations.

Db replaces *Et5*
Dt replaces *db*
Et5 replaces *eb*
db replaces *dsb*
eb replaces *Db*
dsb replaces *Dt*

Stockwell's interpretation of trichobothria *esb* and *eb* could also be reversed, but we accept these designations for overall completeness with his change. Based on these changes in homology we see that 1) the superfamily Iuroidea show chelal fixed finger trichobothria series *db-dt* and *eb-et* on the distal half to two-thirds of the finger (*Calchas*, due to its short fingers, exhibits *db* on the base, but otherwise complies with this position for the other seven trichobothria); 2) in family Caraboctonidae, palm trichobothrium *Et5* is found on the chelal fixed finger (as exhibited in genus *Hadrurus*

(Soleglad, 1976a)). These characters are reflected in the cladistic analysis presented elsewhere in this paper.

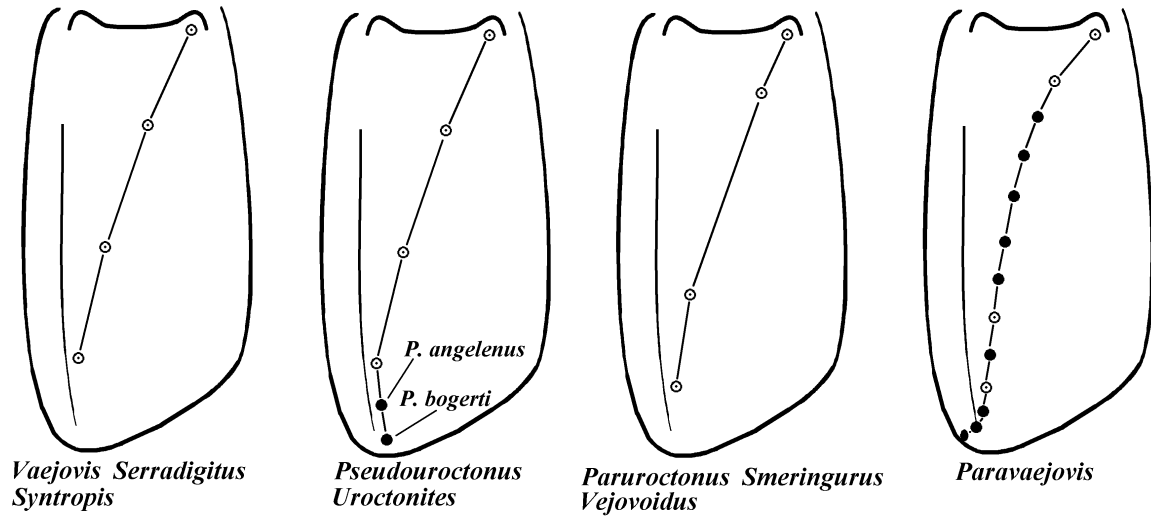
Chactoidae – orthobothriotaxy: There are a number of subtle but significant differences in the positions and overall patterns of orthobothriotaxy separating families Vaejoidea and Chactoidae(-V). These are found on both the pedipalp chela and patella.

Chela – V_1 – V_4 series: In the Vaejoidea the ventral trichobothrial series V_1 – V_4 is in general aligned in a straight line, V_1 positioned distally close to the internal articulation condyle of the movable finger and V_4 situated proximal on the palm, quite close to the ventroexternal carinae. The individual trichobothria are roughly evenly spaced. This pattern is quite consistent across all genera of Vaejoidea (Fig. 66). For *Paruroctonus* and related genera (*Smeringurus*, *Vejoividus*, and *Paravaejovis*) we see a small positional difference between trichobothria V_1 , V_2 and V_3 : distance between V_2 and V_3 is noticeably larger than that seen in other typical vaejoidea, due in part, to the slightly closer proximity of trichobothria V_1 and V_2 , and likewise more proximal positioning of V_3 . Since *Paravaejovis* is neobothriotaxic in this series, we have hypothesized the designation of orthobothriotaxic trichobothria based on this presumed relationship, thus the feature just described is also illustrated for this genus. For the Chactoidae(-V), we see that the V_1 – V_2 – V_3 juncture conspicuously angles toward the internal aspect of the palm. There is only one exception to this, which is exhibited by euscorpoid subfamilies Euscorpinae and Megacorminae. In this pattern, we see an exceptional short series, with V_4 being positioned on the external aspect of the palm. Soleglad & Sissom (2001) considered this a synapomorphy for the family Euscorpidae which reversed itself in the tribe Scorpipini, subfamily Scorpipinae. In addition, there is a general tendency in Chactoidae(-V) for the ventral trichobothria series to be shorter in length, V_4 not positioned as far proximally. Presumably this is caused, in part, by the internal angling of the V_1 – V_2 – V_3 juncture. The shortest ventral series is found in the Brotheinae subtribe Brotheina (Figs. 66, 89–90). ***ib*–*it* series:** For the vaejoidea, the internal trichobothrial series *ib*–*it* is positioned on the chelal fixed finger, never on the palm (Figs. 67–78), although *ib* in some species of the genera *Pseudouroctonus* and *Uroctonites* is situated quite close to the palm, located next to the extreme finger edge of the articular membrane (Fig. 73–74). In the vaejoidea, the *ib*–*it* series is situated more proximally in the “mexicanus” and “nitidulus” groups of *Vaejovis* (Figs. 71–72), the more distal positions exhibited on the genus *Serradigitus* and to some degree, *Vaejovis* groups “punctipalpi” and “eusthenura”. In *Paruroctonus* and related genera, the *ib*–*it* series is somewhat basal, especially species *P. stahnkei* and *P. gracilior* (Fig. 75), but never as basal as that seen in some *Pseudouroctonus* or *Uroctonites* species. In the Chactoidae(-V), the *ib*–*it*

series is essentially found on the chelal palm, next to the movable finger articular membrane (see Figs. 81–90). In the family Superstitioniidae, we see the basal positioning of this series limited to trichobothrium *ib*, although *it* is usually quite close to the membrane. In genus *Alacran*, trichobothrium *it* is situated midfinger, quite distant from *ib*, which is located basally. For the other families making up Chactoidae(-V), the *ib*–*it* series is located well on the chelal palm, adjacent to the fixed finger articulation membrane (Figs. 81–90). ***eb*–*et* series:** In Vaejoidea, the fixed finger trichobothrial series *eb*–*et* is arranged in an essentially straight line with basal trichobothrium *eb* angling towards the dorsal edge of the finger (Fig. 79). This basic pattern is constant throughout the family. Within the vaejoidea, the angle formed by trichobothria *esb* and *eb* is more exaggerated in the genera *Pseudouroctonus* and *Uroctonites*, and, to a degree, in genus *Paravaejovis* (Fig. 79). In Chactoidae(-V) the pattern exhibited by this series is variable, but, in general, not conforming to the pattern found in the vaejoidea (*Superstitionia* is the only exception). In the family Chactidae we see a radical angling of the trichobothria *est*–*esb*–*eb* juncture towards the dorsal edge of the fixed finger, *eb* situated quite close to the articular membrane, *esb* position more dorsally in the finger (Fig. 79). This same configuration is also found on the euscorpoid subfamilies Euscorpinae and Megacorminae. For the euscorpoid subfamily Scorpipinae, the superstitioniids, and chactid subtribe Brotheina, the *eb*–*et* series is arranged in a straight line, no angling whatsoever at the *est*–*esb*–*eb* trichobothria juncture. For the scorpipines and Brotheina, we consider this a derivation from the unique angling of the *est*–*esb*–*eb* juncture as seen in the other chactids. In the superstitioniids, we consider the variations exhibited derived from that seen in the vaejoidea.

Patella: In family Vaejoidea we see that ventral trichobothrium v_3 is situated on the external aspect of the patella, positioned somewhat distally on the segment, at least above trichobothrium *est* and sometimes *et*₃—this pattern is constant in the entire family (Fig. 80). Within the vaejoidea we see subtle positional differences in some of the genera. For example, in genera *Serradigitus* and *Syntropis*, v_3 is found above the *et*₃ trichobothrium and in contrast, we see v_3 situated below *et*₃ in *Paruroctonus* and related genera (Fig. 80). In Chactoidae(-V) we see the external placement of v_3 only in the superstitioniid genera *Superstitionia* and *Troglotayosicus*, subfamily Superstitioniinae (Fig. 80). In all other superstitioniids (subfamily Typhlochactinae), v_3 is situated on the ventral aspect. Interestingly, in genera *Typhlochactas* and *Sotanochactas*, we see that ventral trichobothrium v_2 is found on the external aspect of the patella, a condition only matched in the Old World iuroids. What is interesting about the external positioning of v_3 in genera *Superstitionia* and *Trog-*

Vaejoidea



Superstitioniidae + Euscorpidae + Chactidae

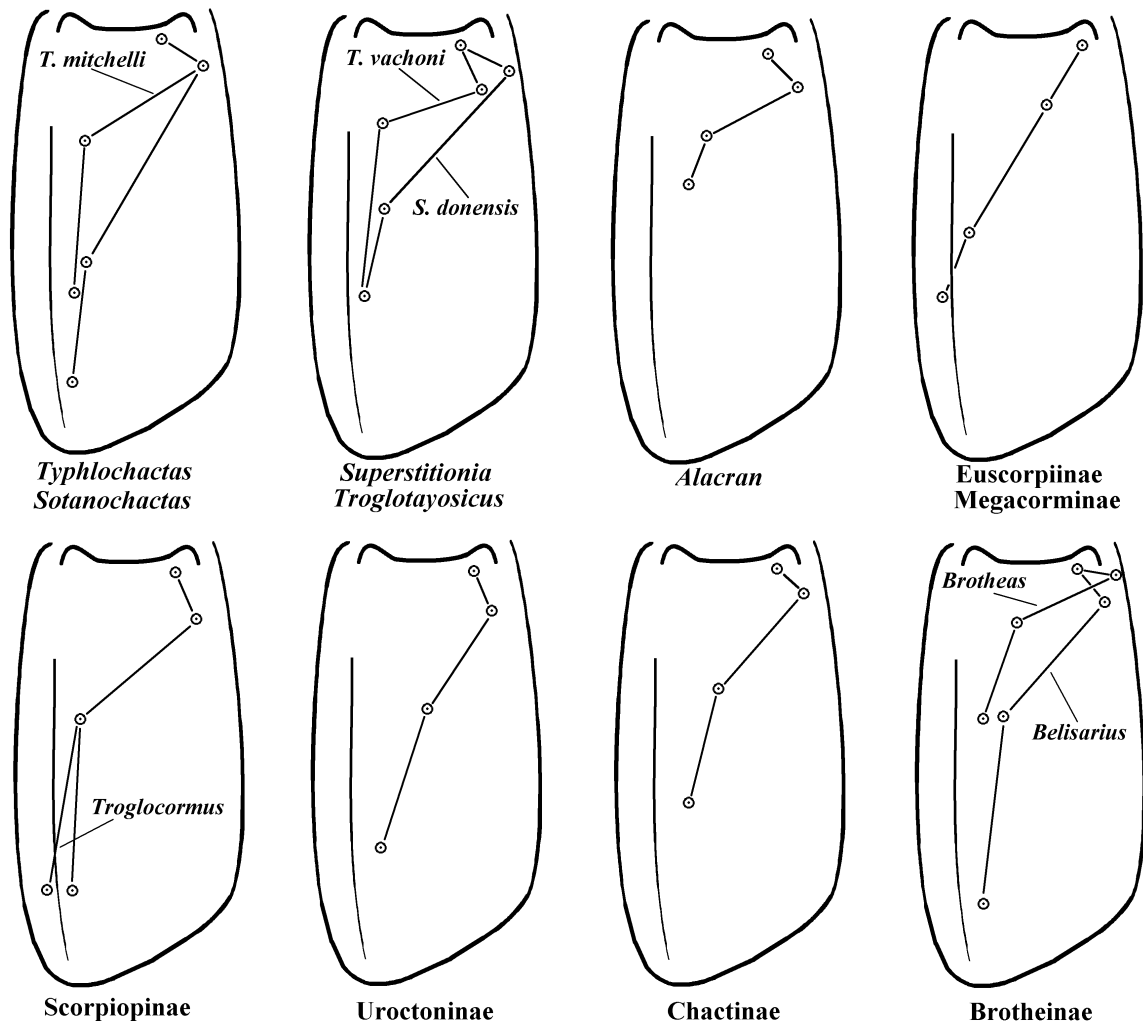
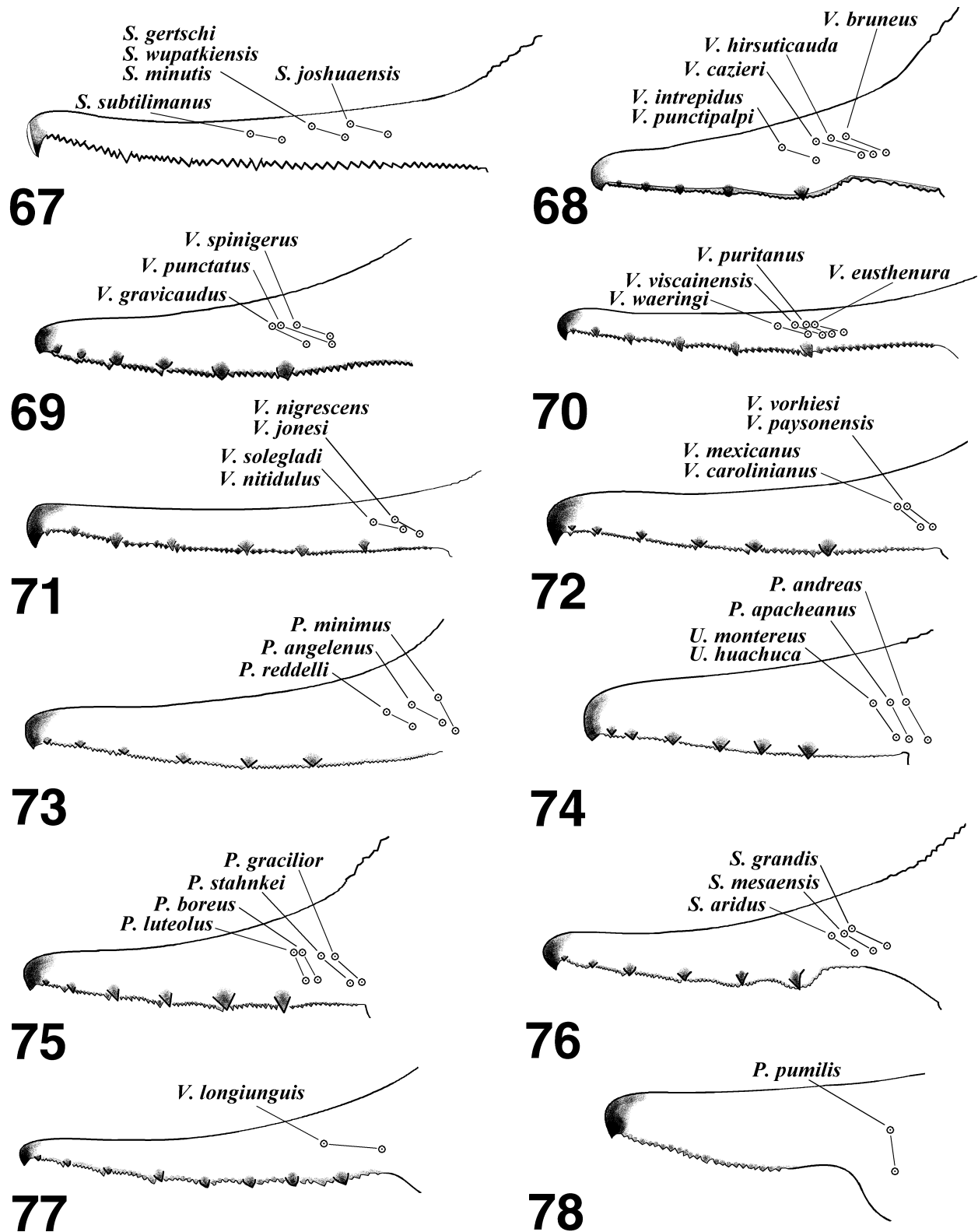
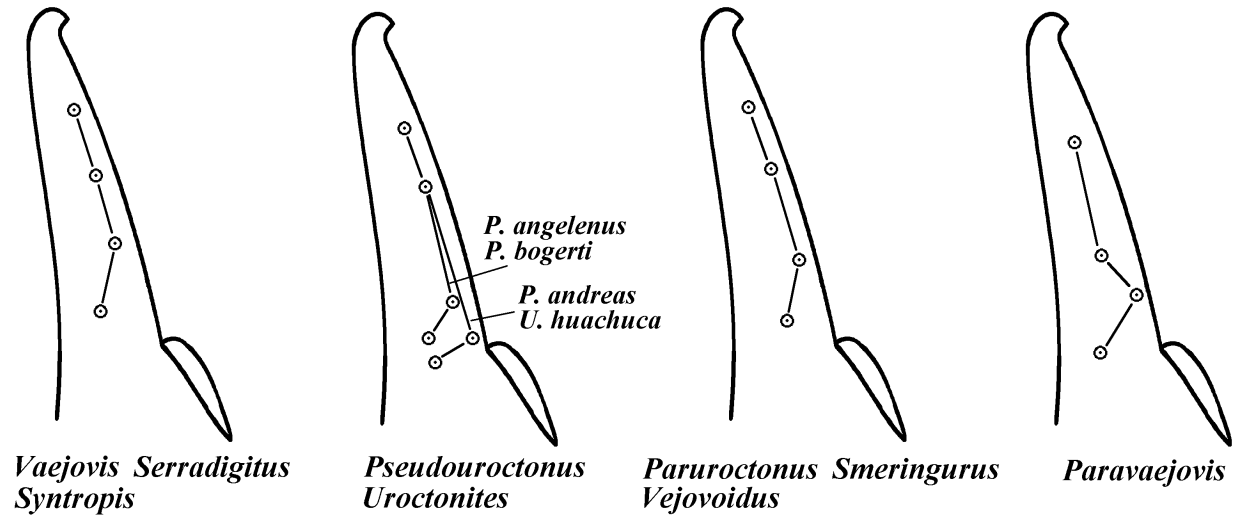


Figure 66: Diagrammatic trichobothrial patterns of ventral aspect of chela (partial) for superfamily Chactoidea. Distinctions within a pattern are identified by representative genera and/or species. Open circles depict the orthobothriotaxic series V_1-V_4 ; closed circles depict hypothesized accessory trichobothria.



Figures 67-78: Relative positions of chelal trichobothria series *ib-it* for major vaejovoid genera showing representative species. 67. *Serradigitus*. 68. *Vaejovis*, 'punctipalpi' and 'intrepidus' (*V. intrepidus cristimanus*) groups. 69. *Vaejovis*, 'eusthenura' group. 70. *Vaejovis*, 'eusthenura' group. 71. *Vaejovis*, 'nitidulus' group. 72. *Vaejovis*, 'mexicanus' group. 73. *Pseudouroctonus* (*P. minimus castaneus*). 74. *Pseudouroctonus* and *Uroctonites*. 75. *Paruroctonus*. 76. *Smeringurus*. 77. *Vejevovoides*. 78. *Paravaejovis*.

Vaejoidea



Superstitioniidae + Euscorpiidae + Chactidae

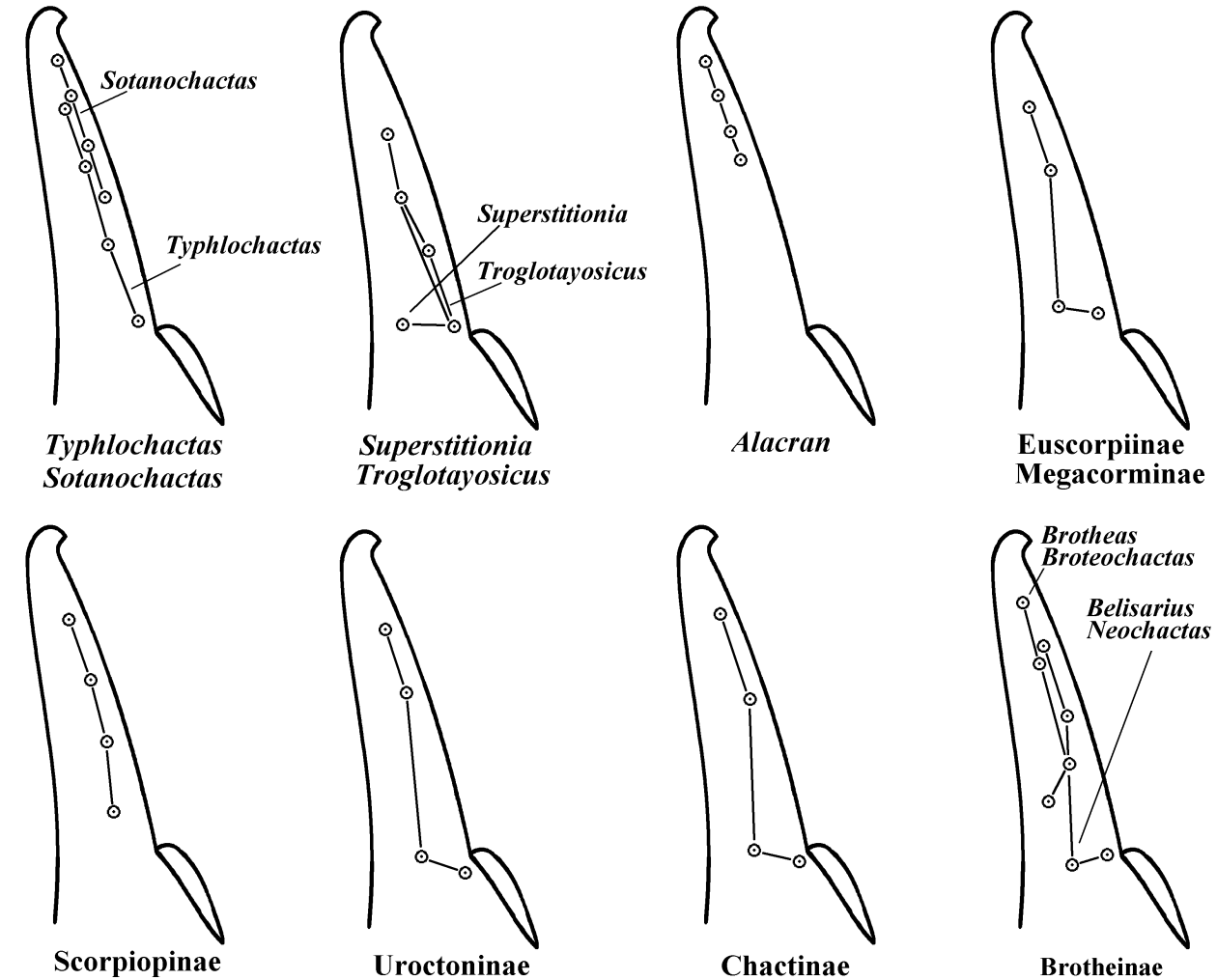
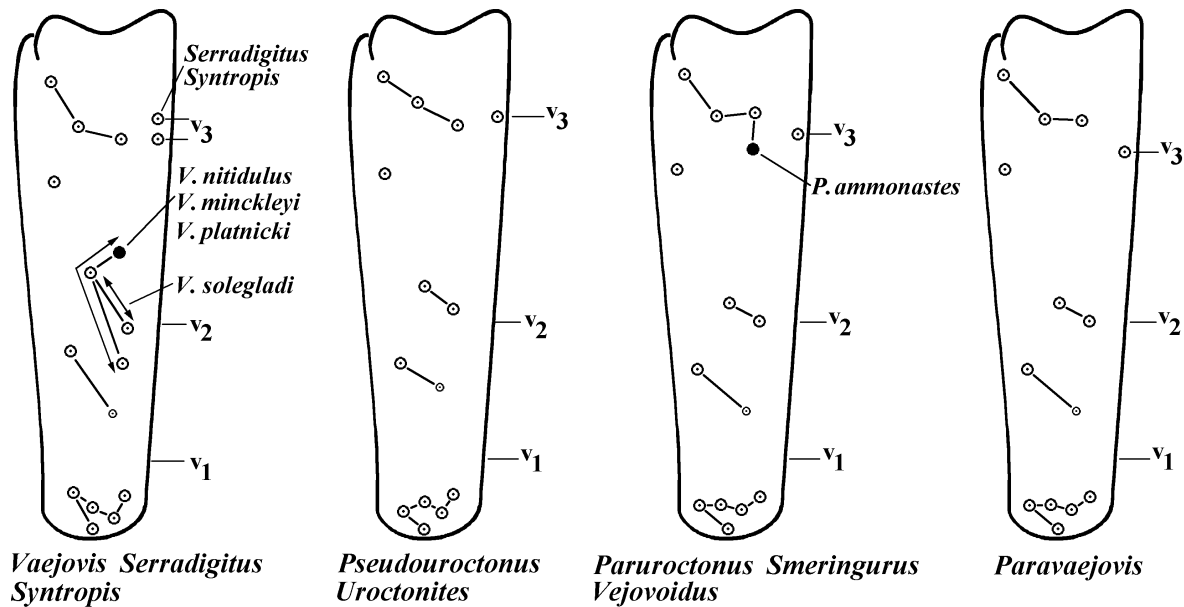


Figure 79: Diagrammatic trichobothrial patterns of chelal fixed finger (partial) showing *eb-et* series for superfamily Chactoidea. Distinctions within a pattern are identified by representative genera and/or species.

Vaejoidea



Superstitioniidae

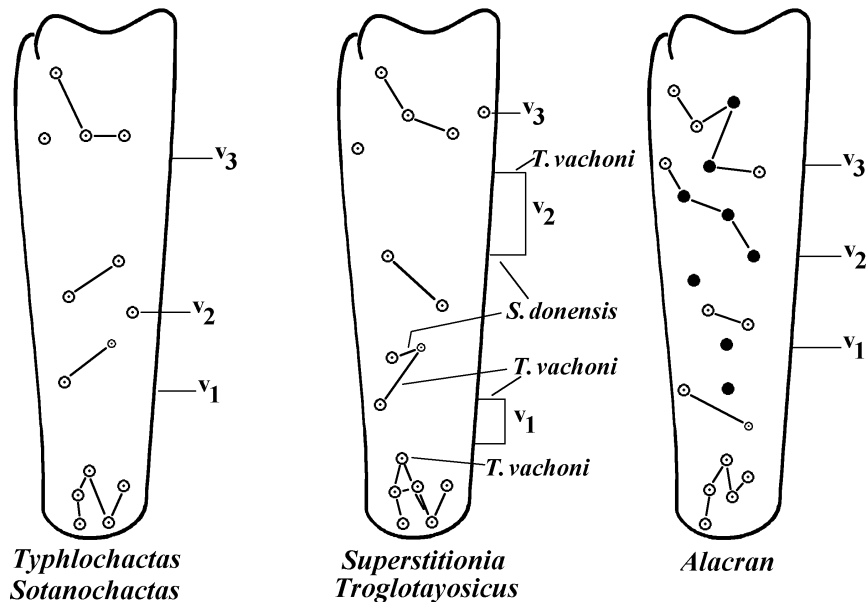


Figure 80: Diagrammatic trichobothrial patterns of external aspect of patella for chactoid families Vaejoidea and Superstitioniidae. Distinctions within a pattern are identified by representative species. Open circles depict orthobothriotaxic trichobothria; closed circles depict hypothesized *accessory* trichobothria.

lotayosicus is that it is found above et_3 —a condition very similar to that found in many of the vaejooids. With the other chactoid families, Chactidae and Euscorpidae, which in general are highly neobothriotaxic on the patellar ventral surface, we find trichobothrium v_3 located on the ventral surface. Fortunately, within this

large assemblage of taxa we have two orthobothriotaxic genera (family Chactidae), *Uroctonus* and *Belisarius*, which we can use to hypothesize orthobothriotaxic trichobothria within this series in other genera (see below). In both *Belisarius* and *Uroctonus*, we see that v_3 is roughly midsegment to proximal on this surface,

definitely below trichobothria *est* and *et*₃, and the distance between trichobothria *v*₃ and *v*₂ is equal to or less than that between *v*₂ and *v*₁.

Vaejovidae – neobothriotaxy: Unlike Chactoidea(-V), the vaejovids are essentially void of any major neobothriotaxy (terms *major* and *minor* in this paper refer to the extent of additive neobothriotaxy). Only one species, *Paravaejovis pumilis*, exhibits major neobothriotaxy, this found on the ventral aspect of the chelal palm (Fig. 66). This neobothriotaxy is variable, providing a range (mean) of 11–14 (12.256), based on 117 samples (Soleglad & Sissom, 2001: Table 3). Except for *Paravaejovis*, we only find minor neobothriotaxy in a few scattered genera and/or species in the Vaejovidae: Soleglad & Gertsch (1972: Fig. 70) reported for species *Pseudouroctonus bogerti* two additional ventral trichobothria in the chelal ventral series. In this study we report one accessory trichobothrium in this same series for species *P. angelenus*. Based on very limited material it is not known to what extent variability is found with these additional accessory trichobothria in these two closely related species. Haradon (1984: Figs. 25–26) reported an additional trichobothrium in the patellar external *et* series for species *Paruroctonus ammonastes* Haradon (see our Fig. 80). Haradon (1984: 325, Table 2) states "... high incidence of 15 external trichobothria on brachium ...". Note, this count includes the externally placed *v*₃ trichobothrium. Since Haradon provided a range for this count (14–15), we must assume there is minor variability in the absence-presence of this accessory trichobothrium. Probably the most important occurrence of neobothriotaxy found in the vaejovids is that found in several species of the *Vaejovis* "nitidulus" group. This neobothriotaxy is represented by a single accessory trichobothrium found midsegment on the external aspect of the patella. Sissom & Francke (1985) reported this condition for species *V. nitidulus* and *V. minckleyi* Williams, and Sissom (1991) reported it for species *V. kochi* Sissom, *V. platnicki* Sissom, and *V. rubrimanus* Sissom. Sissom & Francke (1985) hypothesized that the accessory trichobothrium belonged to the *esb* series. However, based on the comparative alignment of the *em* series on species of this group which lack the accessory trichobothrium, *em*₁–*em*₂ slanting *downward*, we hypothesize here that the accessory trichobothrium belongs to the *em* series (Fig. 80). In order to realize Sissom & Francke's original interpretation, the *em*₁–*em*₂ series must slant upwards. Accompanying our interpretation is the longer distance between trichobothria *em*₁ and *em*₂. Since this condition is found in multiple species in the "nitidulus" group, spanning a somewhat large geographical area in Mexico (Coahuila, Nuevo León, San Luis Potosí, Querétaro, and Distrito Federal), it suggests a significant phylogenetic relationship between these species within this group.

Chactidae – neobothriotaxy: Within the family Chactidae, we hypothesize three independent instances of major neobothriotaxy: *Anuroctonus* in subfamily Uroctoninae; all genera in subfamily Chactinae, including tribes Nullibrotheini and Chactini; and all genera in tribe Brotheini in subfamily Brotheinae. It is interesting to point out here that only two genera in Chactidae exhibit orthobothriotaxy, *Belisarius* (Fig. 87), tribe Belisariini, subfamily Brotheinae, and *Uroctonus* (Fig. 81), subfamily Uroctoninae. These two genera are very important in the definition of Chactidae since they provide crucial information in the determination of orthobothriotaxic trichobothria in the other chactid genera where extensive neobothriotaxy exists. This, in turn, provides key characters in distinguishing Chactidae from the other Chactoidea(-V) families. By comparing the trichobothrial patterns of the chela and patella of these two genera, *Belisarius* and *Uroctonus*, we see that key trichobothrial series are very similar in position. **Chela:** *Db* and *Dt* located basally on the chela; *Eb*₁ is situated close to the ventroexternal carina or on the internal aspect of the palm; the *V*₁–*V*₂–*V*₃ juncture angles toward the internal aspect of the palm; *ib* and *it* are situated on the palm, adjacent to the articular membrane of the movable finger; *eb* is situated quite close to the movable finger articular membrane; *esb* found more mid-finger, so that *est*–*esb*–*eb* juncture angles outward towards the dorsal edge of the fixed finger. **Patella:** *v*₁–*v*₃ are situated on the ventral aspect of the patella; *v*₃ is located proximal to external trichobothria *est* and *et*₃ so that the distance between trichobothria *v*₃ and *v*₂ is less than or equal to the distance between *v*₂ and *v*₁; *esb*₁ is located midsegment; *esb*₂ is situated quite close to *eb* series.

Uroctoninae: *Anuroctonus* exhibits major variable neobothriotaxy. This neobothriotaxy is found on the ventral aspect of the chela as well as on the ventral and external surfaces of the patella (Fig. 82). Great variability in the number of accessory trichobothria are found in most of the series of these two pedipalp segments: chelal ventral series numbers range from as low as 12 to many as 26; patella ventral aspect, 10–19; and patella external aspect (which includes ventral accessory trichobothria extending from the ventral aspect), 23–34 (ranges based on over 800 samples for the chela and 150 for the patella). Of course, the external aspect of the patella exhibits several series, some of which do not reflect variability either because they are orthobothriotaxic, or have a fixed number of accessory trichobothria (see discussion below). It is important to note that we are currently revising the genus *Anuroctonus* (Soleglad & Fet, in progress) and can state here that the variability just stated in these series is due, in part, to speciation, therefore the stated ranges involve more than one species. We use the pattern found in *Uroctonus* to determine important orthobothriotaxic

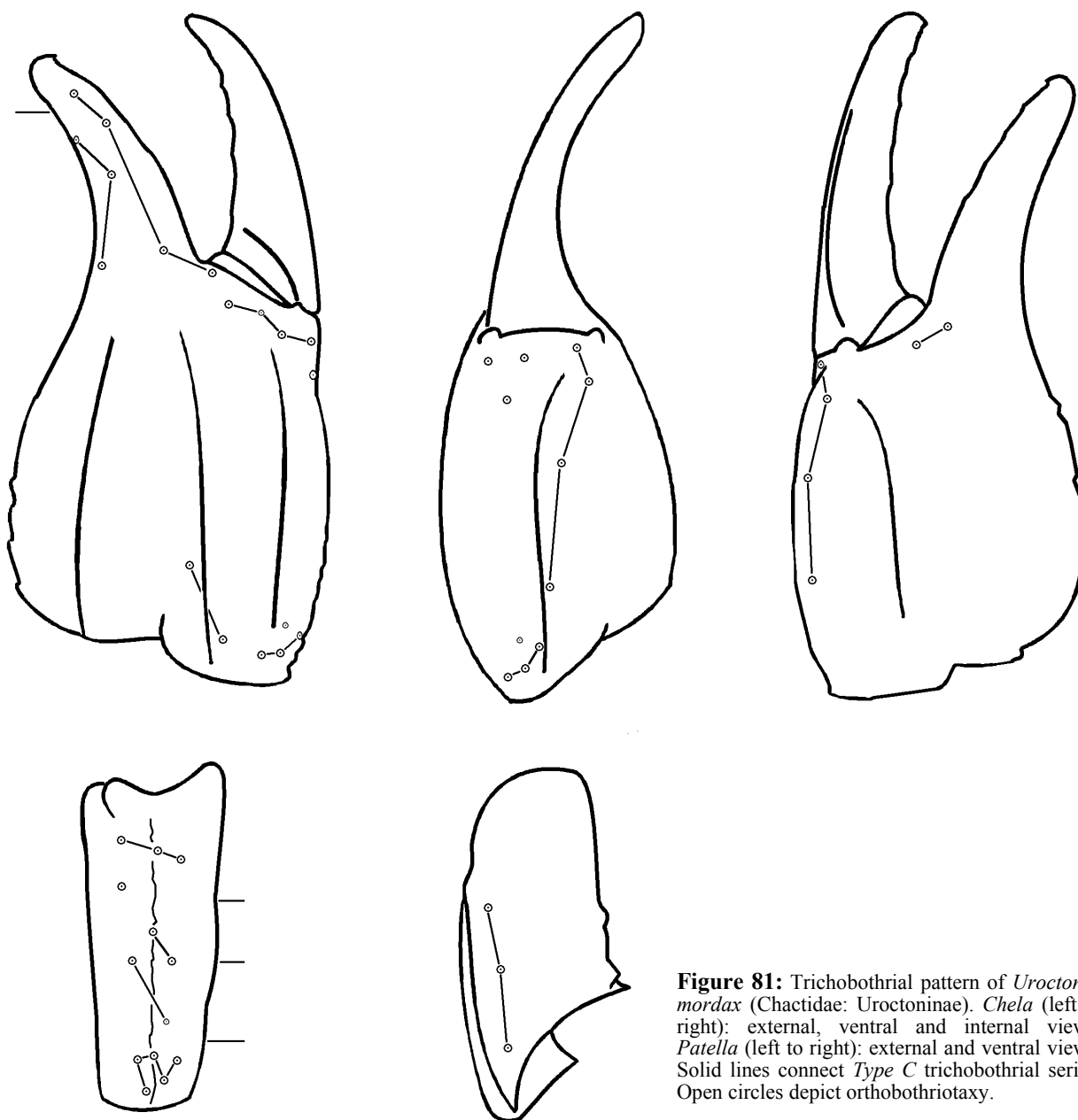


Figure 81: Trichobothrial pattern of *Uroctonus mordax* (Chactidae: Uroctoninae). *Chela* (left to right): external, ventral and internal views. *Patella* (left to right): external and ventral views. Solid lines connect Type C trichobothrial series. Open circles depict orthobothriosity.

trichobothria in the complicated pattern found in *Anuroctonus*. **Chela:** the ventral series in *Anuroctonus* continues onto the external surface extending into the Eb_1 – Eb_3 palm series. Using *Uroctonus* as a point of reference we see that the ventral accessory trichobothria split the Eb series, Eb_1 being situated on the ventroexternal carina. The designation of V_1 and V_2 reflects the Chactoid(-V) characteristic of the V_1 – V_2 – V_3 juncture angling towards the internal aspect of the palm, the designations of V_3 and V_4 are more arbitrary, but do reflect the somewhat short length of the series as a whole as it extends down the palm. **Patella:** v_1 – v_3 are based on comparable positions of these trichobothria found in *Uroctonus*, also, the most proximal trichobothrium in *Anuroctonus* is clearly accessory as

indicated by its petite form; ventral accessory trichobothria extend onto the external aspect of this segment, mixing somewhat with the et series; we hypothesize that the eb series, which contains seven trichobothria (two accessory) and series est , which contains three accessory trichobothria, are static; the et , em and esb series show variability in numbers of accessory trichobothria. Similarities in trichobothrial series positions between *Uroctonus* and *Anuroctonus* are as follows: **Chela:** Db and Dt are situated basally on the chelal palm; ib and it are situated on the palm, adjacent to the articular membrane of the movable finger; est – esb – eb juncture angles toward the dorsal aspect of the fixed finger, eb is situated quite close to the articulation membrane of the movable finger. Based on established

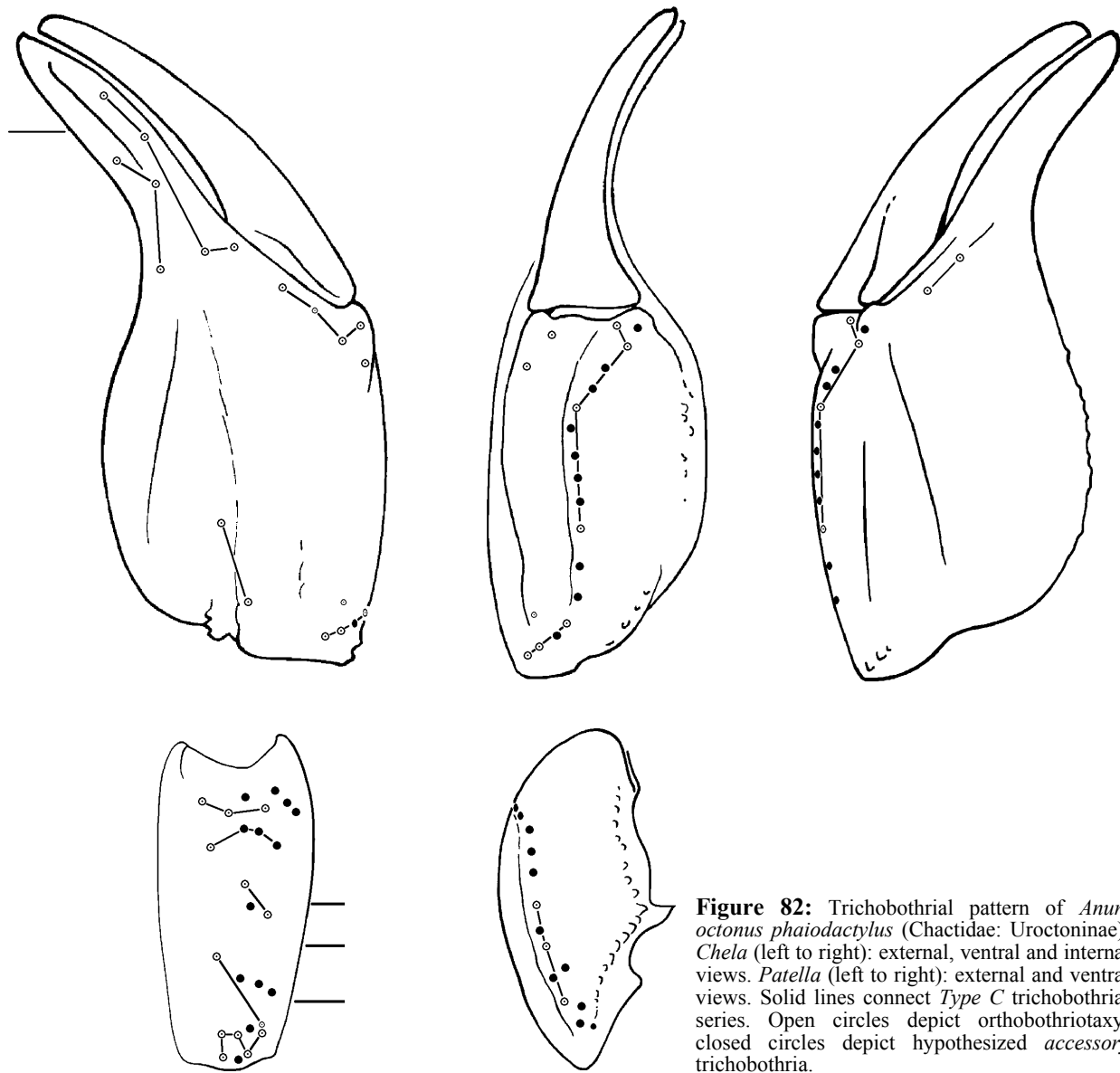


Figure 82: Trichobothrial pattern of *Anuroctonus phaiodactylus* (Chactidae: Uroctoninae). *Chela* (left to right): external, ventral and internal views. *Patella* (left to right): external and ventral views. Solid lines connect Type C trichobothrial series. Open circles depict orthobothriotaxy; closed circles depict hypothesized accessory trichobothria.

homologies using *Uroctonus*, Eb_1 is close to or on the internal aspect of the palm, $V_1-V_2-V_3$ juncture angles toward the internal face of the palm. **Patella:** distance between trichobothria esb_1 and esb_2 is extensive, esb_1 is positioned midsegment and esb_2 is situated close to the eb series; v_3 is found on the ventral surface proximal to external trichobothria est and et_3 . The neobothriotaxic pattern described and illustrated in this paper for *Anuroctonus* is consistent with that suggested by Vachon (1974: Fig. 143).

Chactinae: All genera in subfamily Chactinae exhibit major fixed neobothriotaxy. This complicated pattern shows little or no variability within tribes Chactini (genera *Chactas* (Fig. 83), *Teuthraustes* (Fig. 84), and *Vachoniochactas* (Fig. 85)) and Nullibrotheini (genus *Nullibrotheas* (Fig. 86)). Neobothriotaxy is restricted to the patella only, and exhibited both on the

ventral and external surfaces. This neobothriotaxy is represented by two distinct, yet very similar, patterns, representing Chactini and Nullibrotheini, respectively. **Chactini** (Figs. 83–85): the ventral aspect of the patella contains five trichobothria (two accessory); the external series eb , esb and em are orthobothriotaxic, accessory trichobothria being found in series est with three trichobothria (two accessory) and et with five trichobothria (two accessory). In this pattern we see that the em series is proximal of midsegment and the esb_1 is located proximally, consequently distance between trichobothria esb_1 and esb_2 is quite small. We consider these conditions to be diagnostic of this subfamily. The designation of orthobothriotaxic trichobothria v_1-v_3 is determined using *Belisarius* and *Uroctonus* as a basis as well as noting the petite size of the most proximal trichobothrium which we hypothesize is accessory.

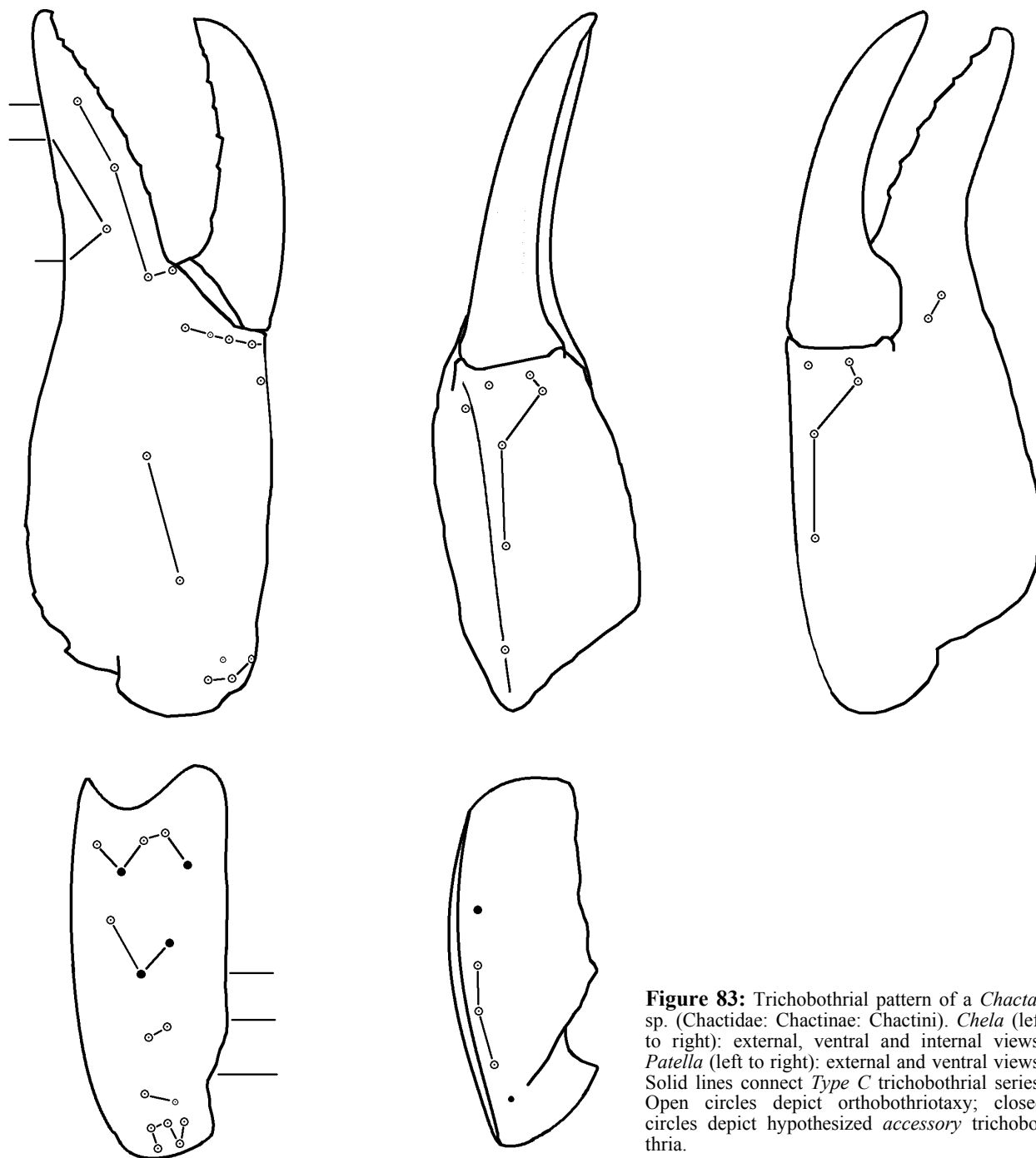


Figure 83: Trichobothrial pattern of a *Chactas* sp. (Chactidae: Chactinae: Chactini). *Chela* (left to right): external, ventral and internal views. *Patella* (left to right): external and ventral views. Solid lines connect *Type C* trichobothrial series. Open circles depict orthobothriotaxy; closed circles depict hypothesized *accessory* trichobothria.

Nullibrotheini (Fig. 86): the ventral aspect of the patella contains six trichobothria (three accessory); external series *eb*, *esb* and *em* are orthobothriotaxic, accessory trichobothria being found in series *est* with four trichobothria (two accessory) and *et* with five trichobothria (two accessory). Comparing the patterns in these two tribes we see that they only differ in the number of ventral and *est* series trichobothria (each by one trichobothrium). In addition, we see that the individual series are situated in similar positions, both with the *esb* series situated quite proximal on the

segment. On the chela, the two tribes also are quite similar, reflecting typical chactid characters: *ib* and *it* are situated on the palm, adjacent to the articular membrane; V_1 – V_2 – V_3 juncture angles towards the internal face; V_1 – V_4 series is situated on distal half of palm; Eb_1 is situated close to ventroexternal carina or found on internal aspect; *est*–*esb*–*eb* juncture angles toward the dorsal aspect of fixed finger, *eb* situated quite close to articular membrane; *Db*–*Dt* series is found on the proximal half of the palm, but never basally. The neobothriotaxic pattern described above and illustrated in this paper is

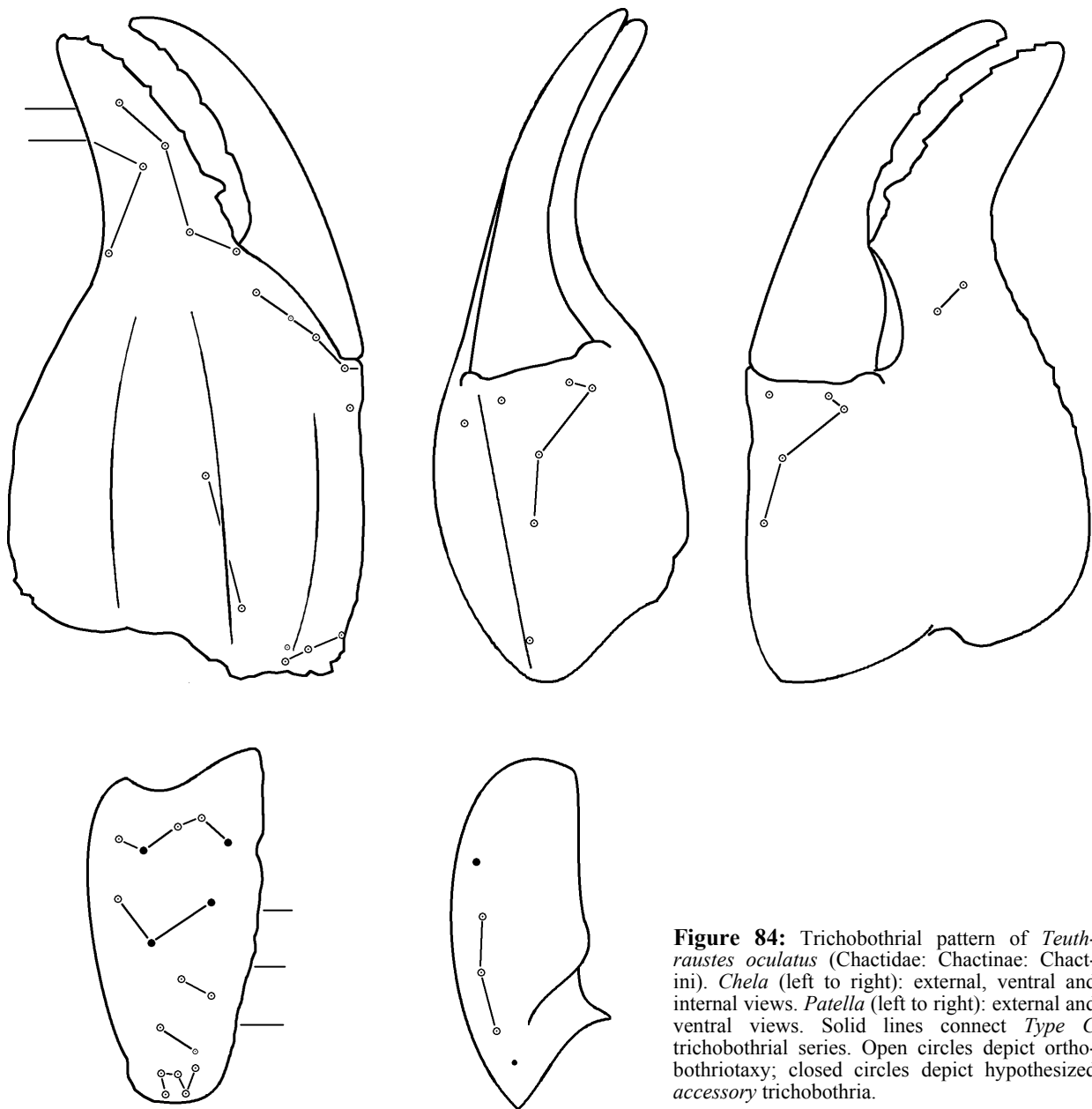


Figure 84: Trichobothrial pattern of *Teuthraustes oculatus* (Chactidae: Chactinae: Chactini). *Chela* (left to right): external, ventral and internal views. *Patella* (left to right): external and ventral views. Solid lines connect Type C trichobothrial series. Open circles depict orthobothriotaxy; closed circles depict hypothesized accessory trichobothria.

consistent with Vachon's (1974: Figs. 174–175) designations. Noted exceptions (these exceptions are based on existing literature and therefore are not necessarily complete or accurate) to this fixed neobothriotaxic pattern, which are as follows: Patella, ventral aspect: four (not five) trichobothria (one (not two) accessory), *Chactas barravierai* (Lourenço, 1997: Fig. 56); Patella, external aspect: series *et* with four (not five) trichobothria (one (not two) accessory), *Vachoniochactas ashleeae* (Lourenço, 1994: Fig. 8).

Brotheinae: The two tribes in subfamily Brotheinae are separated, in part, by the neobothriotaxy found in Brotheini but lacking in monotypic tribe Belisariini (genus *Belisarius* (Fig. 87)) which is orthobothriotaxic. As with subfamily Chactinae, this complicated neobothriotaxic pattern is in general fixed *within* and

between its genera, *Brotheas* (Fig. 89), *Broteochactas*, *Hadrurochactas* (Fig. 90), and *Neochactas* (Fig. 88). This neobothriotaxic pattern is present on the patella only, exhibiting accessory trichobothria on both the ventral and external segment surfaces: seven trichobothria (four accessory) are found on the ventral aspect of the patella; the designation of orthobothriotaxic trichobothria v_1 – v_3 are based on the comparison with sister tribe Belisariini (genus *Belisarius*), and the petite form of the most proximal trichobothrium which is clearly accessory. External series *eb* and *em* are orthobothriotaxic, series *esb* with six trichobothria (four accessory), *est* with five trichobothria (four accessory) and *et* with six trichobothria (three accessory). The two tribes in subfamily Brotheinae share many similarities in chelal trichobothria positions: *ib* and *it* are situated on

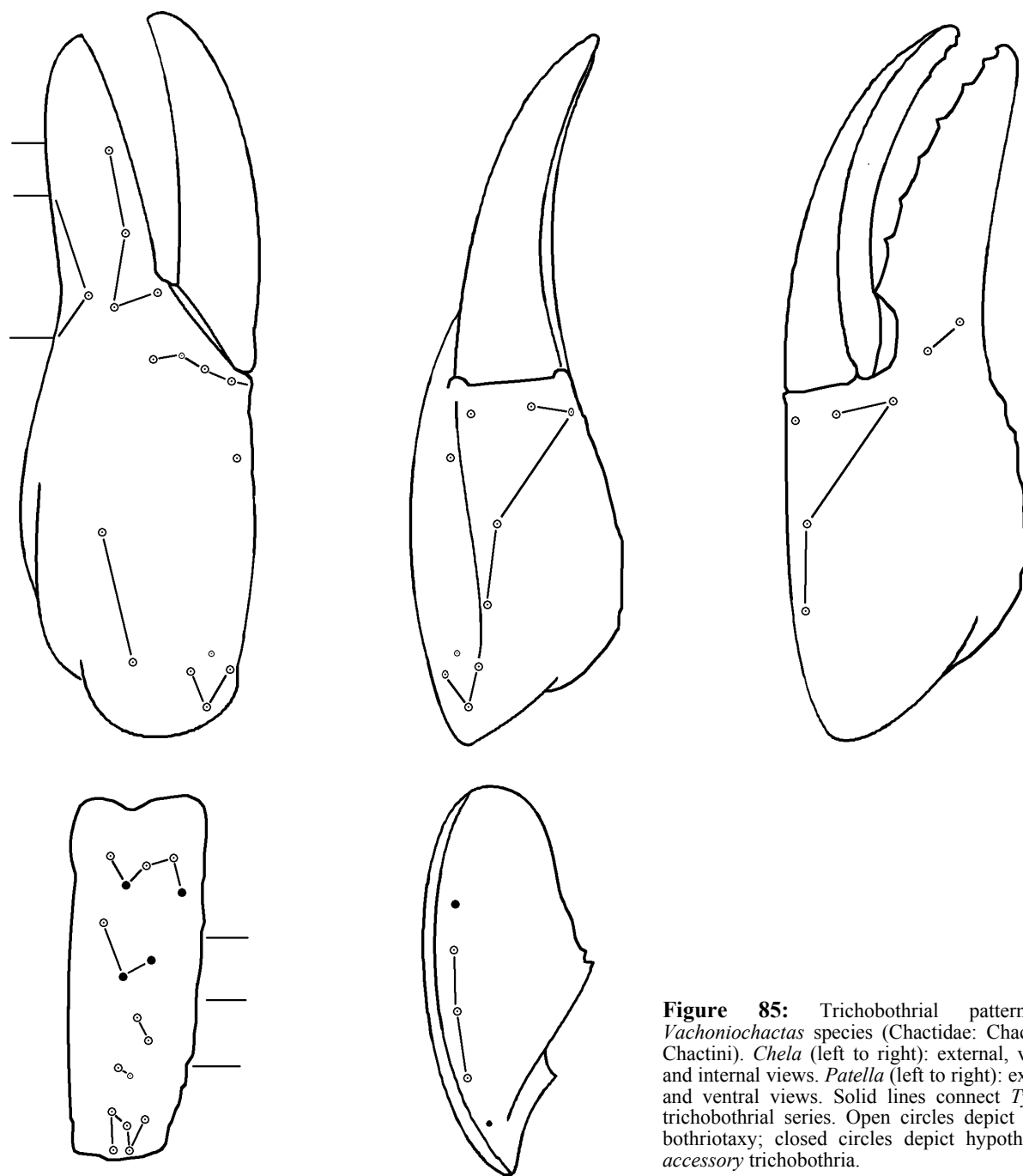


Figure 85: Trichobothrial pattern of *Vachoniochactas* species (Chactidae: Chactinae: Chactini). *Chela* (left to right): external, ventral and internal views. *Patella* (left to right): external and ventral views. Solid lines connect *Type C* trichobothrial series. Open circles depict orthobothriotaxy; closed circles depict hypothesized accessory trichobothria.

the palm, adjacent to the articular membrane; $V_1-V_2-V_3$ juncture angle towards the internal aspect of the palm, extremely exaggerated in Brotheini; Eb_1 is either situated on the ventroexternal carina or on the internal aspect of the palm. Other chelal trichobothria series positions are discussed below in section on subtribes. The neobothriotaxic pattern described and illustrated here deviates from Vachon's (1974: Fig. 176) original designations as follows: est_2 is changed to esb_1 , and esb_1 is designated as accessory. This change is more consistent with *Belisarius*, based on its position of esb_1 .

Exceptions to this fixed neobothriotaxic pattern are as follows (these exceptions are based on illustrations from existing literature and therefore it is not necessarily complete or accurate): Patella, ventral aspect: eight (not seven) trichobothria (five (not four) accessory), *Cayooca venezuelensis* (González-Sponga, 1996a: 4) (note, this increase in one trichobothrium is diagnostic, in part, for this monotypic genus); Patella, external aspect: series esb with five (not six) trichobothria (three (not four) accessory), *Neochactas neblinensis* (González-Sponga, 1991: Fig. 10).

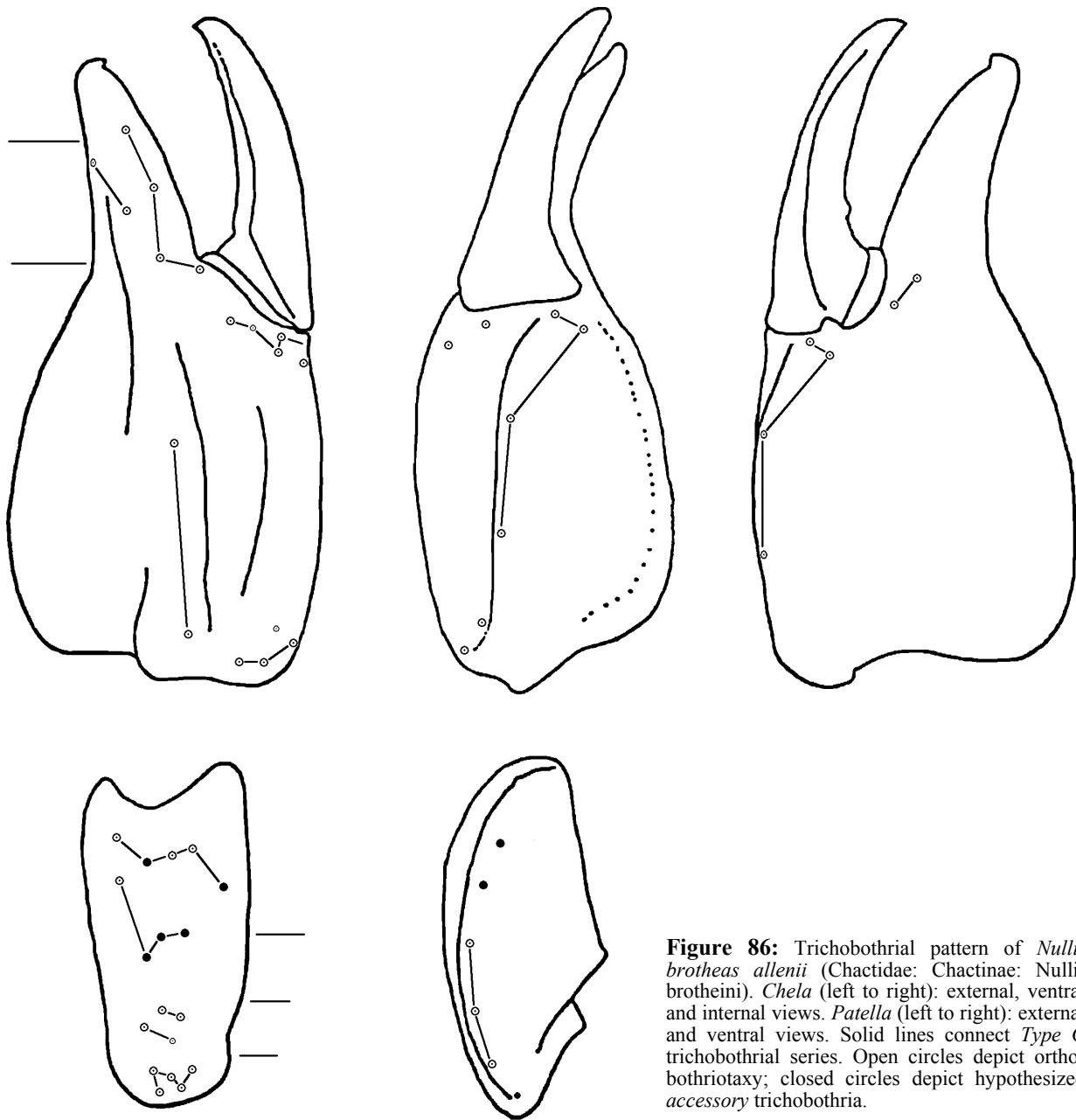


Figure 86: Trichobothrial pattern of *Nullibrotheas allenii* (Chactidae: Chactinae: Nullibrotheini). *Chela* (left to right): external, ventral and internal views. *Patella* (left to right): external and ventral views. Solid lines connect Type C trichobothrial series. Open circles depict orthobothriotaxy; closed circles depict hypothesized accessory trichobothria.

Brotheini – subtribes: Within the tribe Brotheini we isolate two subtribes, **Neochactina** and **Brotheina**. These two subtribes are delineated by unique trichobothria positional differences in three key chelal series. Subtribe Neochactina contains genus *Neochactas* (Fig. 88) and Brotheina contains three genera: *Brotheas* (Fig. 89), *Broteochactas*, and *Hadrurochactas* (Fig. 90). These subtribes are distinguished as follows: **subtribe Neochactina:** series *eb-et* is situated on the proximal two-thirds of the fixed finger, *est-esb-eb* juncture angles toward the dorsal aspect of the finger, *eb* situated quite close to the articular membrane; series *Et₃-Et₅* is situated on the distal aspect of the palm, never extending to the fixed finger; *Db* and *Dt* are located on the middle of the palm, *Dt* proximal of trichobothrium *Est*. **subtribe**

Brotheina: series *eb-et* is situated on the distal two-thirds of the fixed finger, *est-esb-eb* juncture angles toward the cutting edge of the finger, *eb* found on the finger midpoint, not close to the articular membrane; series *Et₃-Et₅* is located distally on the palm, *Et₅*, and sometimes *Et₄*, found on the fixed finger; *Db* and *Dt* are located on distal half of the palm, *Dt* usually distal of trichobothrium *Est*. It is important to note here that subtribe Neochactina complies with the other two chactid subfamilies as to the positional distinctions of these three trichobothria, and therefore it is clear that these positional differences defining subtribe Brotheina are *derived*. This distinction, in part, was illustrated by Vachon (1974: Figs. 224–225) for genera *Broteochactas* (= our *Neochactas*) and *Brotheas*. See the classification

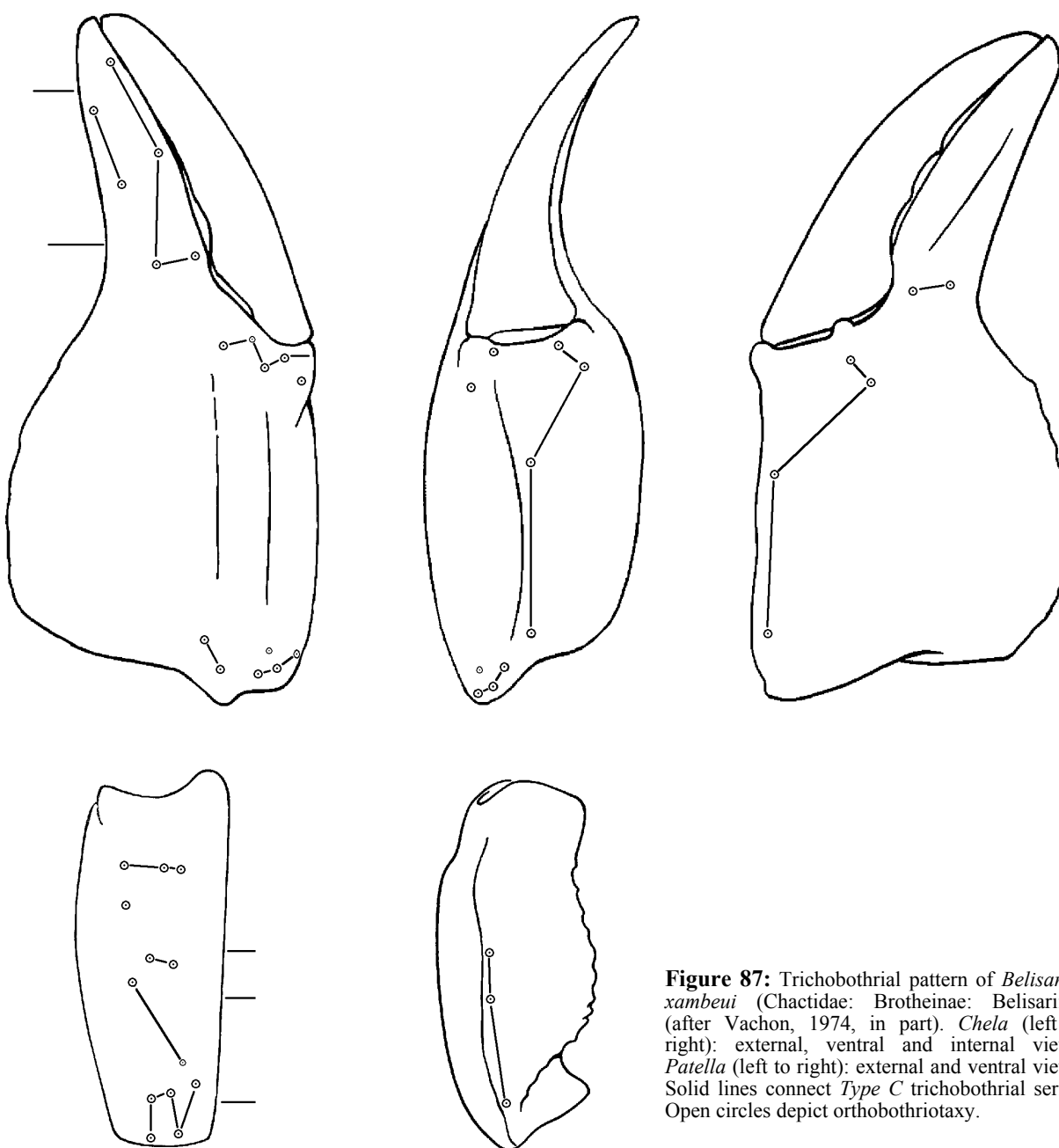


Figure 87: Trichobothrial pattern of *Belisarius xambeui* (Chactidae: Brotheinae: Belisariini) (after Vachon, 1974, in part). *Chela* (left to right): external, ventral and internal views. *Patella* (left to right): external and ventral views. Solid lines connect *Type C* trichobothrial series. Open circles depict orthobothriotaxy.

section below for more discussion and further refinement of these two subtribes.

Chactoid neobothriotaxy – formal definition of types: Above we described the three instances of neobothriotaxy found in the family Chactidae. Here, we formally state their definitions and type assignment for future reference. In addition, for completeness and reference in later sections, we also define the single neobothriotaxy pattern type found in family Superstitioniidae (i.e., *Alacran*) and the two neobothriotaxic pattern types for the family Euscorpidae (discussed in detail in Soleglad & Sissom, 2001: 45–55). The definition of these formal types implies that they

evolved separately within the families in which they occurred, a hypothesis of this paper.

It is important to mention here, that except for *Paravaejovis* (Vaejovidae) and *Hadrurus* (Caraboctonidae), the only other extant major neobothriotaxic patterns occur in superfamily Scorpionoidea. In the only two major cladistic analyses which considered the scorpionoids, Stockwell (1989) and Prendini (2000), neobothriotaxy was completely ignored by the former and the latter, in general, considered all individual instances of neobothriotaxy within the superfamily to have occurred in the *same evolutionary lineage*. We discuss the affects of this somewhat “conservative”

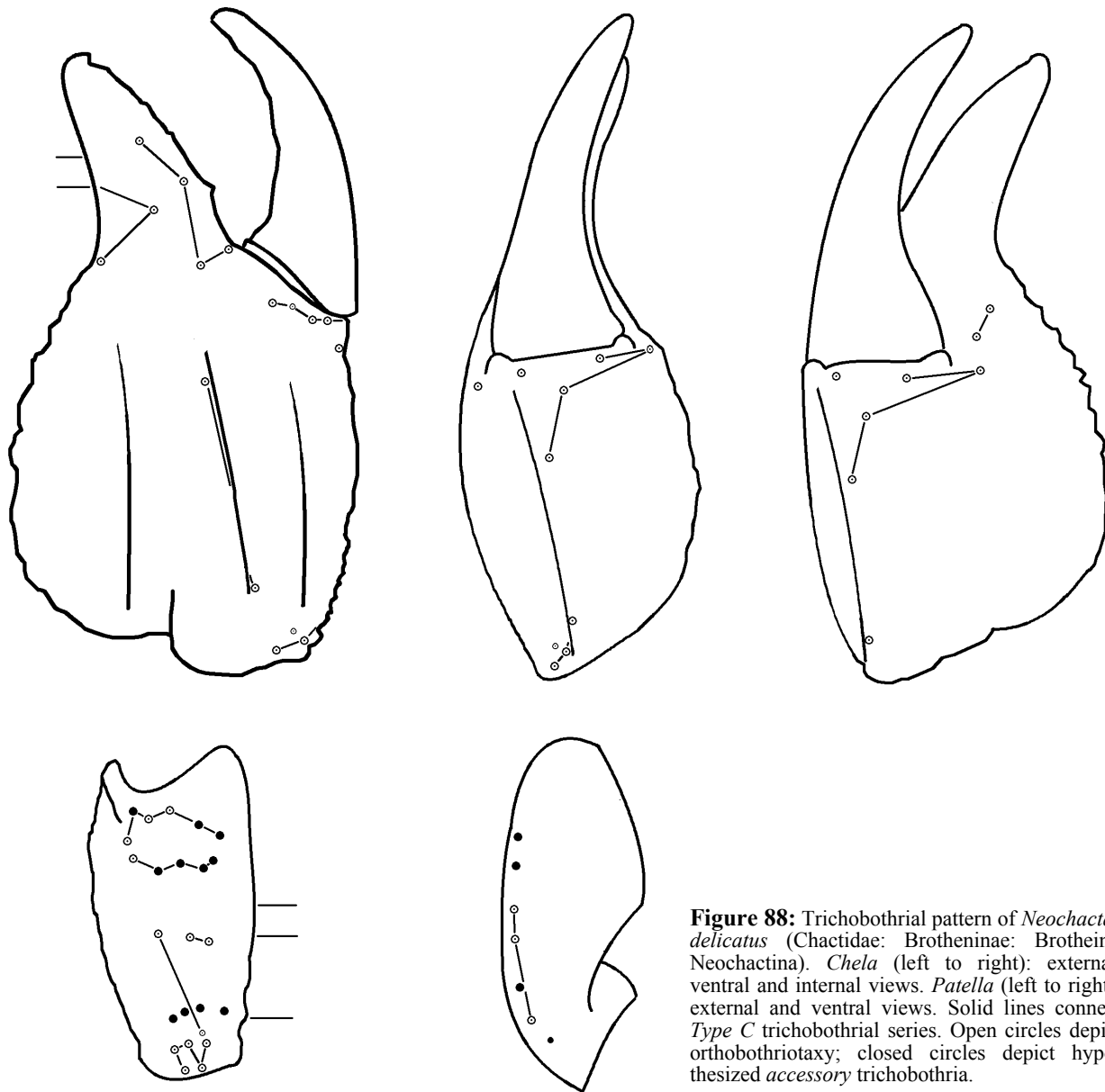


Figure 88: Trichobothrial pattern of *Neochactas delicatus* (Chactidae: Brotheninae: Brotheini: Neochactina). *Chela* (left to right): external, ventral and internal views. *Patella* (left to right): external and ventral views. Solid lines connect Type C trichobothrial series. Open circles depict orthobothriotaxy; closed circles depict hypothesized accessory trichobothria.

approach to the modeling of neobothriotaxy offered by Prendini in the sections dealing with cladistics and classification.

Chactid neobothriotaxic type Ch1: Neobothriotaxy is limited to the ventral and external aspects of the patella, and is fixed in general pattern and in number of accessory trichobothria. **Patella ventral surface:** 4–6 (5) trichobothria (1–3 (2) accessory), positioned in a linear line; most proximal trichobothrium (accessory) is petite in size. **Patella external surface:** 17–18 (17) trichobothria (4–5 (4) accessory) distributed by series as follows: $eb = 5$ (no accessory); $esb = 2$ (no accessory), located proximally, distance between esb_1 and esb_2 is minimal, approximating distance between em_1 and em_2 ; $em = 2$ (no accessory), located proximal of segment midpoint; $est = 3-4$ (3) (2–3 (2) accessory), $est_1-est_2-est_3$

form a V-like pattern; $et = 4-5$ (5) (1–2 (2) accessory). This neobothriotaxic type is found exclusively in subfamily Chactinae (Figs. 83–86).

Chactid neobothriotaxic type Ch2: Neobothriotaxy is limited to the ventral and external aspects of the patella, and is fixed in general pattern and in number of accessory trichobothria. **Patella ventral surface:** 7–8 (7) (4–5 (4) accessory), positioned in linear line; most proximal trichobothrium (accessory) is petite in size. **Patella external surface:** 23–24 (24) trichobothria (10–11 (11) accessory) distributed by series as follows: $eb = 5$ (no accessory); $esb = 5-6$ (6) (3–4 (4) accessory), esb_1 located midsegment, distance between esb_1 and esb_2 is considerably greater than distance between em_1 and em_2 ; $em = 2$ (no accessory), located midsegment; $est = 5$ (4 accessory), pattern irregular; $et = 6$ (3 accessory), pattern

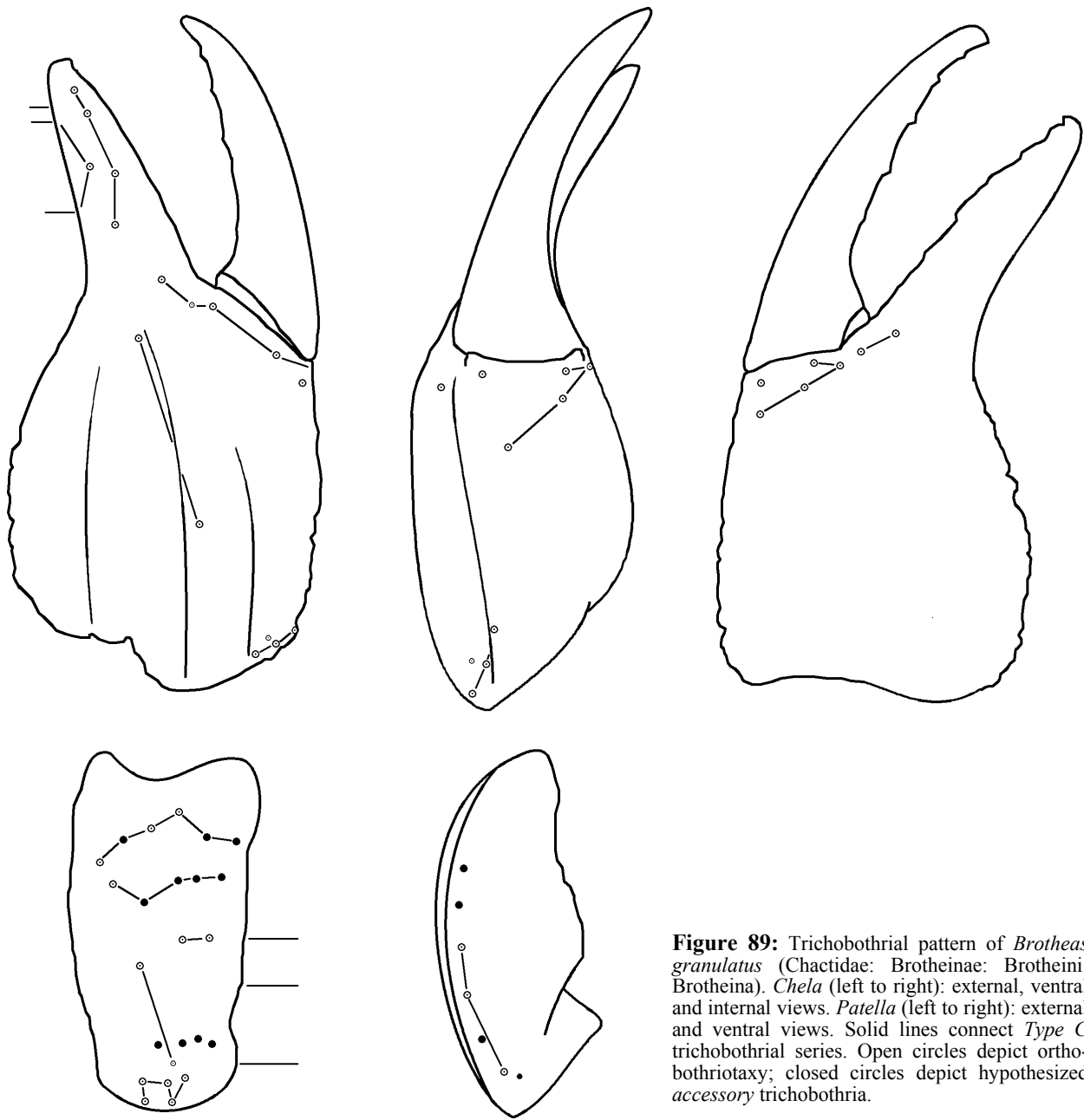


Figure 89: Trichobothrial pattern of *Brotheas granulatus* (Chactidae: Brotheinae: Brotheini: Brotheina). *Chela* (left to right): external, ventral and internal views. *Patella* (left to right): external and ventral views. Solid lines connect Type C trichobothrial series. Open circles depict orthobothriotaxy; closed circles depict hypothesized accessory trichobothria.

irregular. This neobothriotaxic type is found exclusively in subfamily Brotheinae, tribe Brotheini (Figs. 88–90).

Chactid neobothriotaxic type Ch3: Neobothriotaxy is found on the ventral aspect of the chela and the ventral and external aspects of the patella, and is variable, in part, in general pattern and in number of accessory trichobothria. **Chela ventral surface:** 12–26 (mean is species dependent) (8–22 accessory), extends to extreme proximal aspect of palm where it extends onto the external surface. **Patella ventral surface:** 10–19 (mean is species dependent) (7–16 accessory), extends to distal one-quarter and continues onto the external surface; these “wrap around” accessory trichobothria number 2–5 (mean is species dependent); total number of trichobothria attributed to ventral series, including both

ventral and external surfaces, is 12–24; trichobothria are sometimes doubled proximally into two rows, the most distal trichobothrium (accessory) is petite in size. **Patella external surface:** 18–25 (mean is species dependent) distributed by series as follows: $eb = 7$ (2 accessory); $esb = 2$, esb_1 located midsegment, distance between esb_1 and esb_2 is considerably greater than distance between em_1 and em_2 ; $em = 2-7$ (0–5 accessory); $est = 4$ (3 accessory); $et = 3-5$ (0–2 accessory). [Note, in this pattern the designation of accessory trichobothria for the em series is arbitrary, although they occur in regions occupying both the em and esb series.] This neobothriotaxic type is found exclusively in subfamily Uroctoninae, genus *Anuroctonus* (Fig. 82).

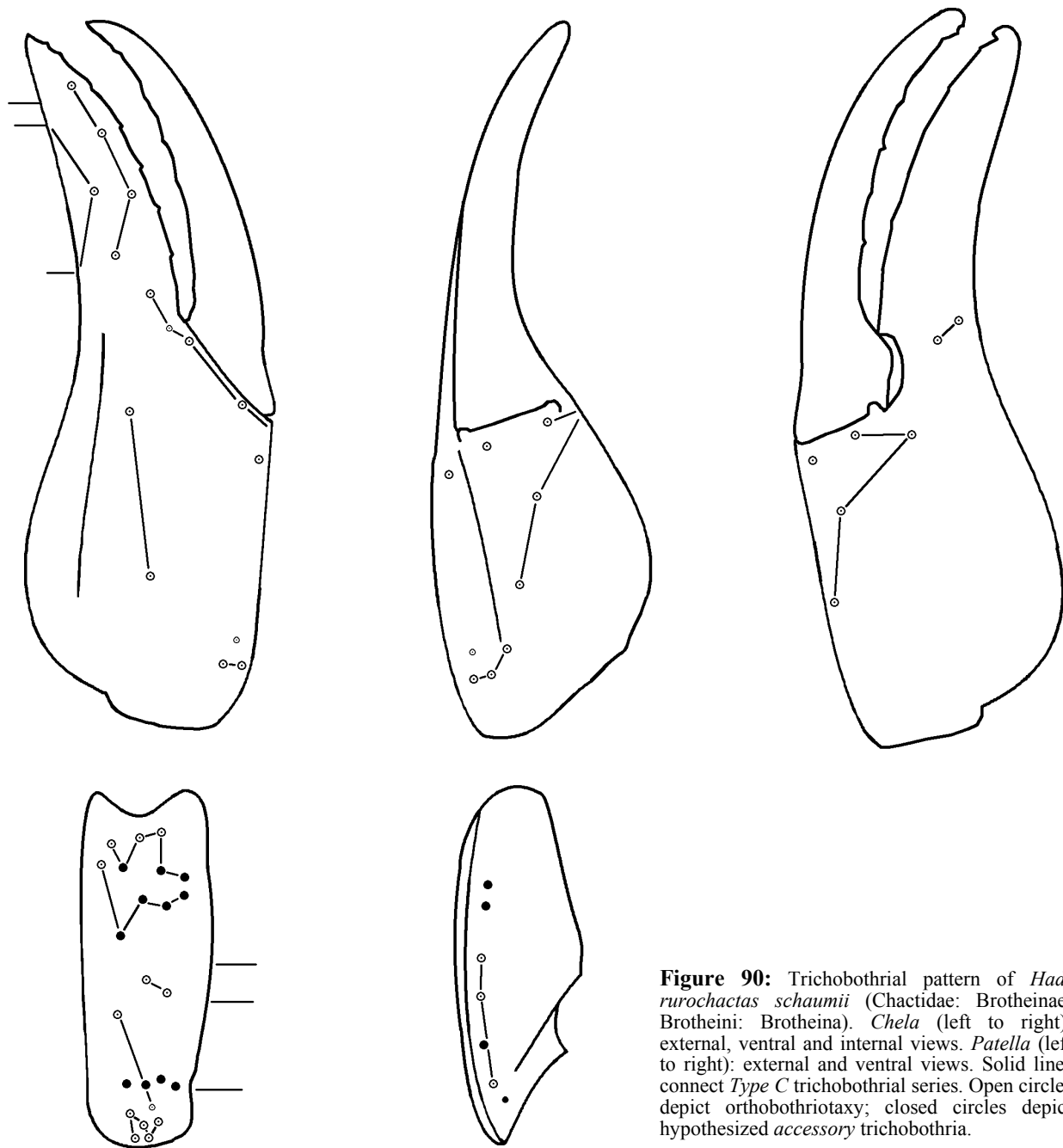


Figure 90: Trichobothrial pattern of *Hadrurochactas schaumii* (Chactidae: Brotheinae: Brotheini: Brotheina). *Chela* (left to right): external, ventral and internal views. *Patella* (left to right): external and ventral views. Solid lines connect Type C trichobothrial series. Open circles depict orthobothriotaxy; closed circles depict hypothesized accessory trichobothria.

Superstitioniid neobothriotaxic type Su1: Neobothriotaxy is found on the external aspects of the chela and the patella. Due to the lack of material, variability in pattern and number of accessory trichobothria is not well defined. **Chela external surface:** For the unique scorpion *Alacran*, we find minor neobothriotaxy on the chela, three external accessory trichobothria, two on the proximal half of the palm close to the ventroexternal carina and one on the inner base of the fixed finger. **Patella external surface:** 20–21 trichobothria distributed by series as follows: $eb = 5$ (no accessory), $esb = 2$ (no accessory), $em = 5$ (3 accessory), $est = 4$ (3 access-

ory), and $et = 5$ (2 accessory). The assignment of accessory trichobothria to a particular series is arbitrary. Francke (1982a: 52, Figs. 5–11) states "... tibia with 26–27 trichobothria ..." but did not specify where the variability occurred. We suspect that it is found presumably on the external aspect but exactly where on the surface is not known. This neobothriotaxic type is found exclusively in subfamily Typhlochactinae, genus *Alacran* (Fig. 80).

EuscorpIID neobothriotaxic type Eu1: Neobothriotaxy is found on the ventral aspect of the chela, in part, and the ventral and external aspects of the patella, and is

variable, in part, in general pattern and in number of accessory trichobothria. **Chela ventral surface:** Neobothriotaxy on this surface is only found on three species in the genus *Euscorpium*: *E. flavicaudis*, *E. italicus*, and *E. naupliensis*. In the first species (subgenus *Tetra-trichobothrius*) the number of accessory trichobothria (two, is fixed); for the other two species (subgenus *Polytrichobothrius*) the number is variable, 8–13 trichobothria (4–9 accessory). **Patella ventral surface:** 5–14 trichobothria (2–11 accessory), positioned in linear line (in genus *Chactopsis*, this series angles at trichobothria v_5 or v_6); most proximal trichobothrium (accessory) is petite in size. **Patella external surface:** 19–40+ trichobothria distributed by series as follows: $eb = 7$ –13 (2–8 accessory), $esb = 2$ –3 (0–1 accessory), esb_a (specific to subgenus *Polytrichobothrius*) = 0–11 (0–11 accessory), $em = 2$ –6 (0–4 accessory), positioned midsegment, $est = 4$ –5 (3–4 accessory), and $et = 3$ –10 (0–7 accessory). This neobothriotaxic type is found in subfamilies Euscorpiinae and Megacorminae (see Soleglad & Sissom (2001: Figs. 88–92, 106–111).

Euscorpiid neobothriotaxic type Eu2: Neobothriotaxy is found on the ventral aspect of the chela, in part, and the ventral and external aspects of the patella, and is variable, in part, in general pattern and in number of accessory trichobothria. **Chela ventral surface:** Neobothriotaxy on this surface is only found on genus *Alloscorpions* where it numbers 9–15 (5–11 accessory). **Patella ventral surface:** 6–19 trichobothria (3–16 accessory), positioned in linear line; most proximal trichobothrium (accessory) is petite in size. **Patella external surface:** 17–26 trichobothria, distributed by series as follows: $eb = 5$ (0 accessory), $esb = 2$ (0 accessory), $em = 2$ (0 accessory), positioned proximally, $est = 4$ –10 (3–9 accessory), and $et = 4$ –7 (1–4 accessory). This neobothriotaxic type is found in subfamily Scorpiopinae. Note, the numbers above exclude genus *Dasyscorpions* which exhibits massive neobothriotaxy on the pedipalp patella, 23 ventral trichobothria (20 accessory) and well over fifty on the external surface. The topology resulting in Soleglad & Sissom's (2001) analysis implies that this derivation occurred after the major neobothriotaxy found throughout the subfamily Scorpiopinae, thus is autapomorphic for *Dasyscorpions*. See Soleglad & Sissom (2001: Figs. 93–99, 100–105) for illustrations of this neobothriotaxic pattern type.

Pedipalp ornamentation – patella

The patella carinal configurations have been analyzed for all taxa in our cladistic ingroup as well as several other species outside our study. The development of the patellar spurs, the number of carinae, their relationship to the patellar spurs, are all considered important diagnostic characters.

Nomenclature: Vachon (1952: 60–61, Figs. 66–68) illustrated the eight major carinae found on the pedipalp patella. Interestingly, these figures were based on a buthid, the major representative of his monumental study in scorpions. The terminology used by Vachon was also recommended by Stahnke (1970: 310: Table 1, Part 2). We follow this nomenclature as well, with a couple of exceptions involving the carinae that extend from the patellar spurs found on the internal surface of the patella. Figure 91, which illustrates a diagrammatic cross-section of the patella, depicts the nomenclature used in this paper for all eight carinae found on this pedipalp segment. The Dorsal Patellar Spur (DPS) and Ventral Patellar Spur (VPS) (terminology first introduced by Soleglad & Sissom (2001: 59–62)) may be optionally part of internal carinae, the spurs providing the proximal beginning of the individual carinae. We identify these carinae as the DPS_c and VPS_c carinae, replacing Vachon and Stahnke's terminology of *internal dorsal* and *internal ventral*, respectively. Alternatively, the spurs can be solitary, without an interconnecting carina. The identification of these spurs is dependent on the scorpion group in concern. Some groups, the euscorpiids for example, have very well developed spurs, the euscorpiines and megacormines with a strong DPS and the scorpiopines with both spurs showing medium to strong development. As reported by Soleglad & Sissom (2001), each patellar spur is accompanied by a somewhat stout seta at its base which makes for easy identification even if the spur is small or near obsolete. The internal surface of the patella, where the patellar spurs are situated, sometimes can be vaulted, providing a very pronounced projection from the segment. This projection is even more exaggerated if accompanied by well-developed patellar spurs.

Fossil development – the palaeopisthacanthids: Jeram (1994a: 535) provided detailed information on the patella carinal development for the Carboniferous scorpion *Compsoscorpium elegans*: "... The precise number of carinae cannot be established in the flattened fossil material, but at least seven were present. Two internal carinae bear particularly large tubercles, each carrying a single setal follicle ..." Clearly, Jeram was referring to both patellar spurs, each with a single seta. This fact implies that these spurs are not a recent development in the extant scorpions. Based on this partial data, we are hypothesizing this as the primitive state for the number of carinae (seven) for the pedipalp patella since it is the best information available to date. We also know that the DPS_c and VPS_c are present as well, thus establishing the primitiveness of these two internal carinae. In addition we are assuming here (as a hypothesis) that of the eight carinae identified in our Figure 91, DM_c is the only carina absent in the palaeopisthacanthids.

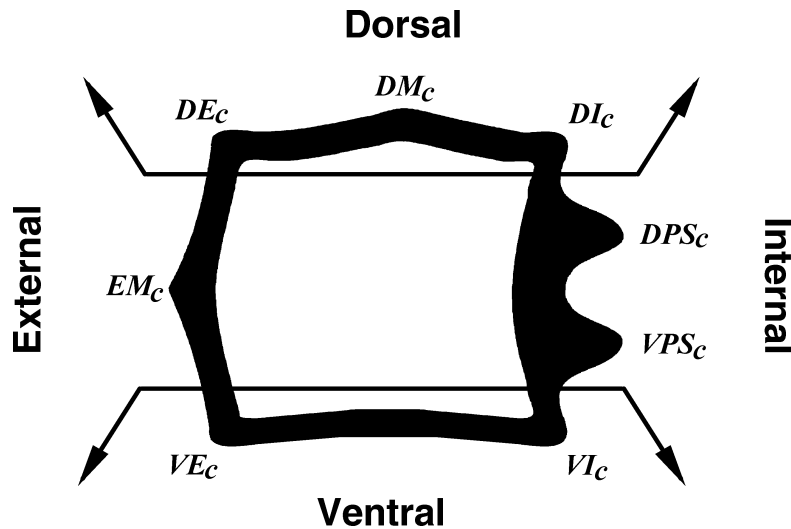


Figure 91: Diagrammatic cross-section of a pedipalp patella depicting carinal terminology. Dorsal carinae: DE_c = dorsoexternal carina, DM_c = dorsomedian carina, DI_c = dorsointernal carina. Ventral carinae: VE_c = ventroexternal carina, VI_c = ventrointernal carina; External carina: EM_c = exteromedian carina; Internal carinae: DPS_c = Dorsal Patellar Spur carina, VPS_c = Ventral Patellar Spur carina.

Lourenço (2001: 645, Fig. 13) writes for the Cretaceous scorpion *Archaeobuthus estephani* "... tibia with three dorsal carinae observable ..." This comment is interesting since it may imply that this species has DM_c , exclusively a buthoid carina (see below), although it is not clear exactly which carinae are actually present. Lourenço's figure may also imply this as well, since we see a weak line of granules situated between what are presumably DI_c and DE_c . Of course, we cannot definitely determine how many and/or which carinae occur in this species even though one could assume the granulated internal aspect shown in the figure is carina DPS_c .

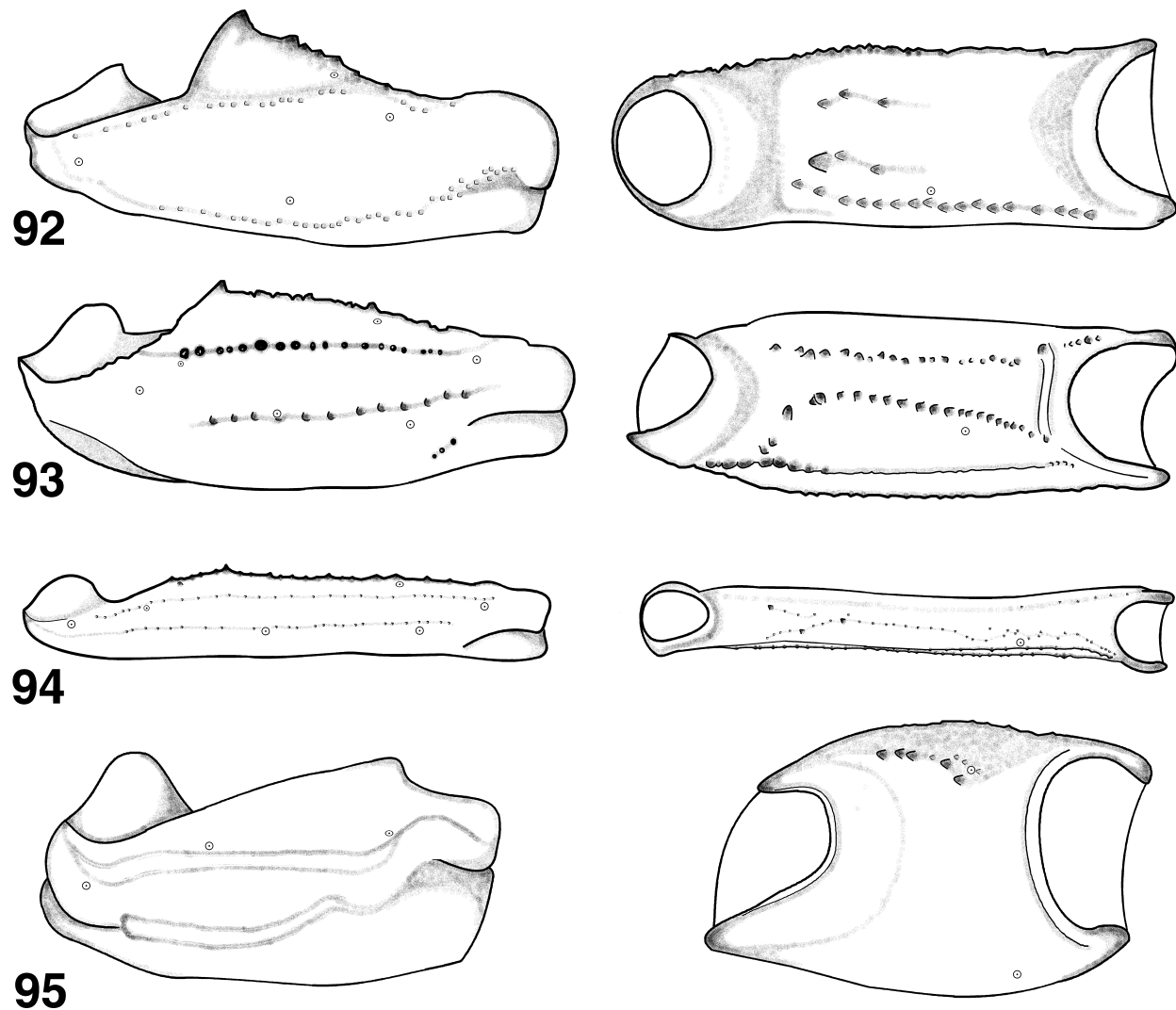
For the five "palaeo-buthid" genera (Baltic amber, 65–55 Ma), described by Lourenço and Weitschat (1996, 2000, 2001), we have sparse information on the patellar carina development, as follows: For genus *Palaeotityobuthus*, patella is unknown; for genera *Palaeoprotobuthus* and *Palaeolychas*, patella "... feebly carinate ..."; genus *Palaeoakentrobuthus*, "... with 5 keels: one internal, 3 dorsal and 1 external, other faces not visible ...", presumably DM_c is present on this genus based on the report of three dorsal carinae; and genus *Palaeoananteris*, "... tibia with 7 keels ...", Fig. 2-c shows the absence of DM_c , consistent with the number of carinae reported. Assuming this report is accurate, we have a buthoid without the DM_c carina (see below).

Recent scorpions: In Recent scorpions we see definitive patterns of patellar carinal configurations within its basic clades. Of particular diagnostic importance is the presence/absence of carinae DM_c , DPS_c , and VPS_c , these, in part, provide important distinctions within Recent scorpions. Also of importance is the development of the patellar spurs and, in general, to what degree the internal surface of the patella is vaulted. In general all Recent scorpions exhibit the fundamental minimal set of five carinae, two dorsal, DE_c

and DI_c , two ventral, VE_c and VI_c , and one external, EM_c , but there are many important exceptions. Below we characterize the patellar carinal configuration for each parvorder.

Pseudochactida: *Pseudochactas* exhibits seven carinae, including the patellar spur carinae DPS_c and VPS_c (Fig. 92). We consider this configuration plesiomorphic for this parvorder, since we have hypothesized the same configuration for the Carboniferous palaeopisthacanthids. In this unique scorpion species we see a well-developed vaulted internal projection from which the two patellar spurs are visible, DPS more developed than VPS . Carinae DPS_c and VPS_c are well-developed, but only extend to midsegment.

Buthida: In this analysis we find eight carinae (as illustrated in Fig. 91) present on all buthoid genera evaluated. This parvorder differs from the primitive state as exhibited in the palaeopisthacanthids and Pseudochactida with the presence of the DM_c carina. We consider this carina derived for the parvorder Buthida, thus a synapomorphy — it is not found in any other Recent scorpion. In Figures 93–94 we illustrate the patellar carinae for two buthoid genera, representing both the Old and New Worlds (*Mesobuthus* and *Tityus*). In both figures we can see a somewhat well-developed DM_c carina, extending most of the length of the segment. In Buthida, the patellar spur carinae, DPS_c and VPS_c , are also well-developed, again, extending most of the segments length, especially DPS_c . In *Tityus* (Fig. 94), in contrast to *Mesobuthus* (Fig. 93), we see a somewhat weak VPS_c , essentially merging into DPS_c . This weak VPS_c is also exhibited in genera *Isometrus*, *Lychas* and *Uroplectes* (based on limited number of species sampled). The patellar spurs themselves, DPS and VPS , are not particularly well developed in this parvorder as, for example, seen in some groups in parvorder Iurida. Stockwell (1989: 93–94) also mentioned the DPS_c carina

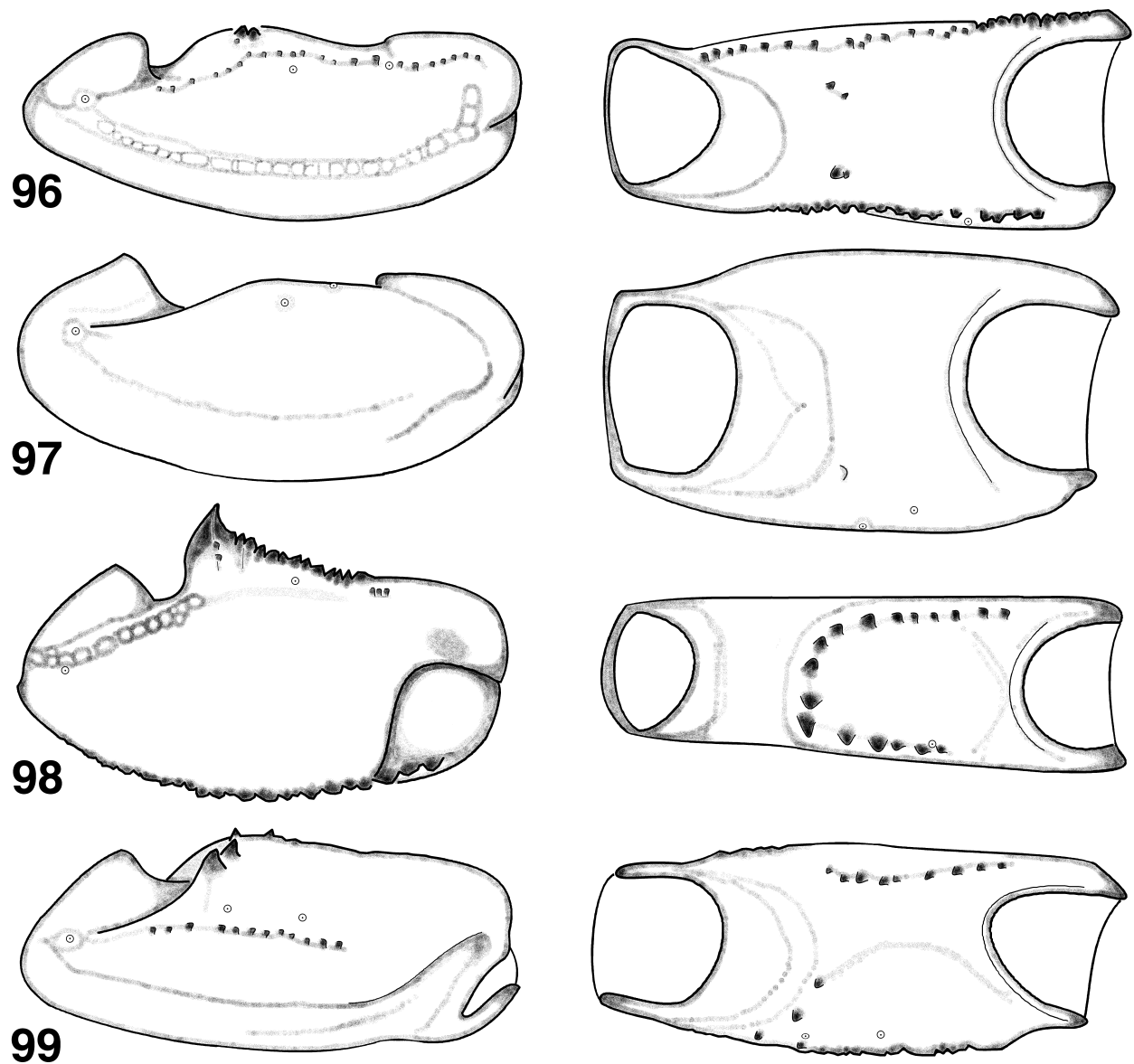


Figures 92-95: Pedipalp patella showing dorsal and internal carinae. Dorsal (left) and internal (right) views (note, in internal view, dorsal surface of patella is situated on bottom aspect of figure). **92.** *Pseudochactas ovchinnikovi*. **93.** *Mesobuthus caucasicus*. **94.** *Tityus nematochirus*. **95.** *Chaerilus variegatus*. Note presence of dorsomedian carinae, DM_c , in the two buthoid genera (Figs. 93-94).

considering it a separate derivation than that seen in the vaejovids (see below). He, however, did not mention the DM_c or VPS_c carinae.

Chaerilida: As noticed by Stockwell (1989), the patella of the chaerilids is quite exceptional, the dorsointernal aspect is somewhat concaved, providing a vaulted appearance to the ventrointernal edge. The DPS is not present, but the VPS is present along with an accompanying VPS_c carina. Thus, *Chaerilus* has six carinae on this segment, missing DPS_c and DM_c . As a possible connection to the unusual patellar shape, the trichobothrial patterns are also interesting on the chaerilid patella (Fig. 95). It is the only Recent scorpion that is equipped with two internal trichobothria, the unique trichobothrium i_2 (as identified in Soleglad & Fet (2001: Fig. 3)) being positioned quite close to the VI_c carina. In line with this additional trichobothrium, we

see that *Chaerilus* also is equipped with three ventral trichobothria, hypothesized by Soleglad & Fet (2001: 10) to be homologous to those found in Type C orthobothriotaxy. However, considering positional analysis, we see that trichobothria v_2 and v_3 are positioned quite close to the VI_c carina (as is i_2). One, therefore, could hypothesize that these trichobothria are connected to the i_2 trichobothrium based on their close proximity, thus these are totally new trichobothria (Stockwell (1989: 100), in part, also considered this as a possibility). If this is the case, then we only have one ventral trichobothrium homologous with Type C orthobothriotaxy, v_1 (their positions are essentially identical in both parvorders). Soleglad & Fet (2001), in general, did not incorporate positional considerations, instead maximizing the minimal number of trichobothria in all homology analyses. This alternative hypothesis

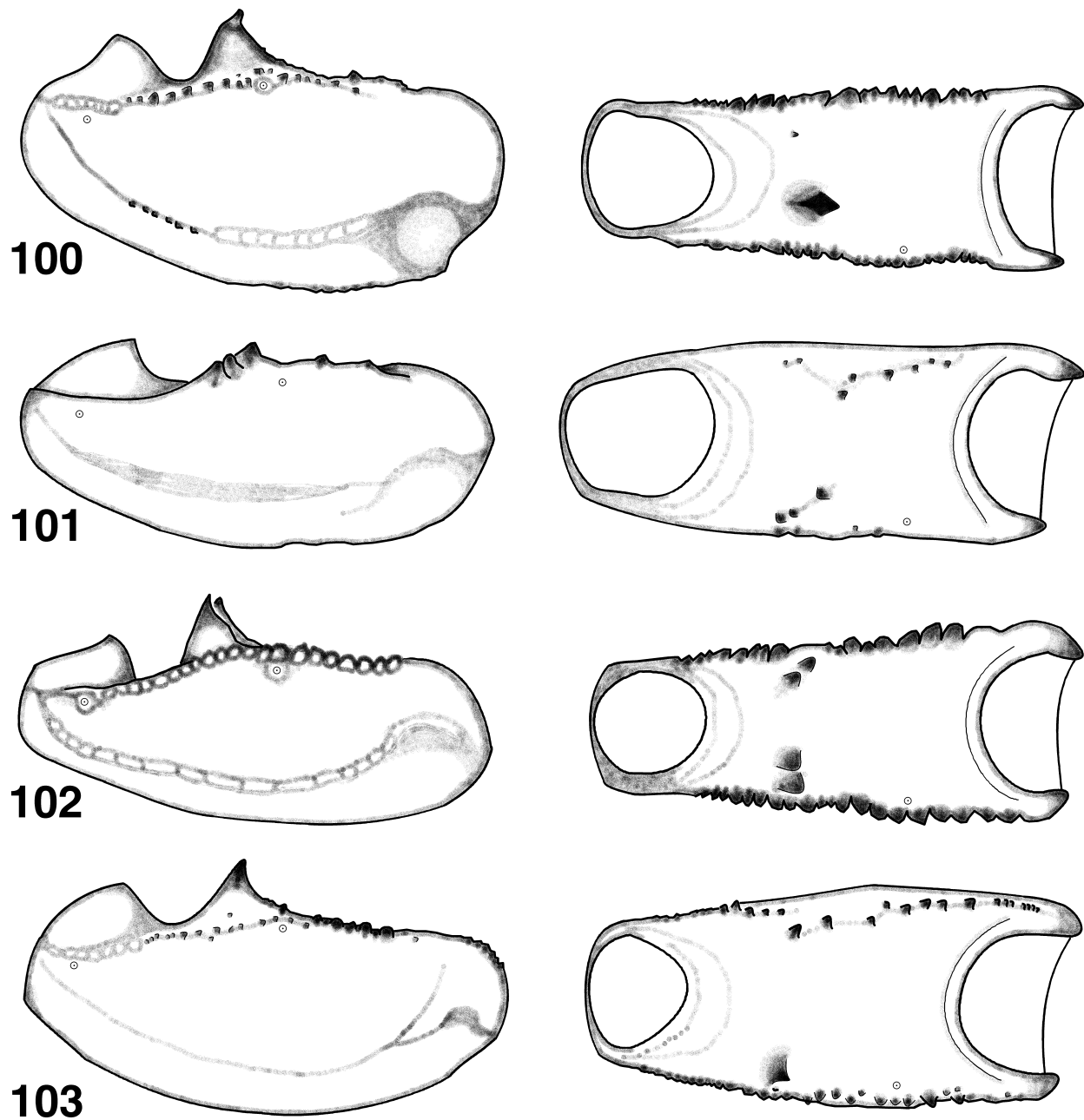


Figures 96-99: Pedipalp patella showing dorsal and internal carinae. Dorsal (left) and internal (right) views (note, in internal view, dorsal surface of patella is situated on bottom aspect of figure). **96.** *Calchas nordmanni*. **97.** *Bothriurus araguayae*. **98.** *Liocheles* sp. (Papua New Guinea) **99.** *Bioculus comondae*.

would weaken the taxonomic connection between the two parvorders, Chaerilida and Iurida, by establishing only one common ventral patellar trichobothrium (note that only these two parvorders exhibit any ventral trichobothria on the patella in Recent scorpions).

Iurida: Great diversity is present in the patellar carinal development in parvorder Iurida. In general, only the basic five carinae are present, but some superfamilies and families, exhibit an additional carinae. The DM_c carina is absent, being found exclusively in Buthida. The patellar spur development can be exceptional in this parvorder; the families Liochelidae, Euscorpidae, and chactid subfamily Uroctoninae exhibit significant development of at least one of the spurs.

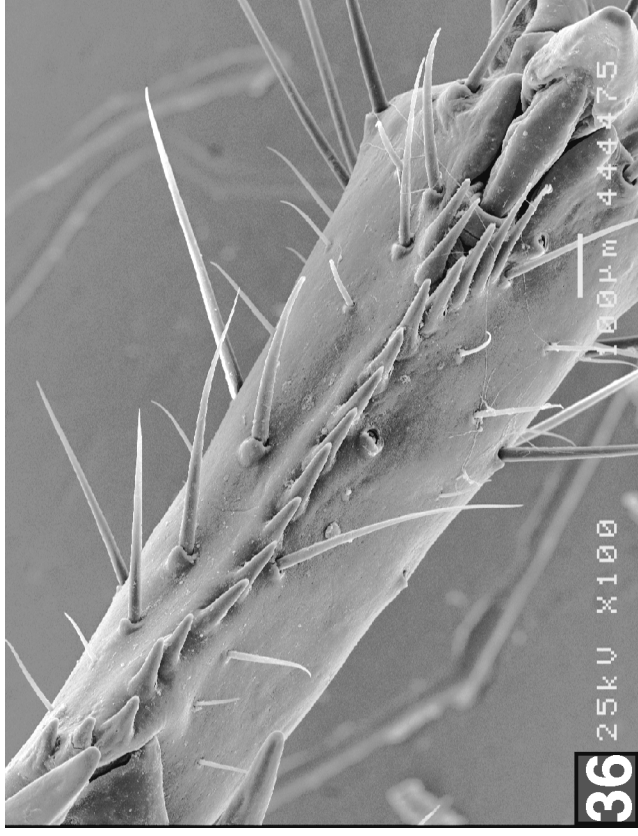
Iuroidea: In this small superfamily we see the basic configuration of the five patellar carinae. For the Old World family Iuridae, the internal aspect of the patella, which is slightly vaulted, is armed with small doubled patellar spurs (represented by *Calchas* in Fig. 96). In *Hadruioides* (Caraboctonidae), the internal aspect is more vaulted, also with small doubled patellar spurs. The North American genus *Hadrurus* has an exceptionally flat internal surface on this segment, exhibiting absolutely no vaulting. Both patellar spurs are absent and the internal surface is densely covered with long, stout setae, making the identification of patellar spur setae impossible.



Figures 100-103: Pedipalp patella showing dorsal and internal carinae. Dorsal (left) and internal (right) views (note, in internal view, dorsal surface of patella is situated on bottom aspect of figure). **100.** *Euscorpius naupliensis*. **101.** *Chactas* sp. **102.** *Uroctonus mordax mordax*. **103.** *Anuroctonus* sp.

Scorpionoidea: In the scorpionoids, we see that family Bothriuridae is essentially equipped with five basic carinae, missing both patellar spur carinae as well as exhibiting underdeveloped DPS and VPS (represented by *Bothriurus* in Fig. 97). The same is true for subfamily Scorpioninae (family Scorpionidae), which exhibits a very flat internal surface, showing little or no vaulting. In the diplocentrines, we see that dorsal carinae DI_c and DE_c are positioned in close proximity, caused, in part, by the lowering of the DI_c carina (represented by *Bioculus*

in Fig. 99). This interpretation is supported by the unusual position of dorsal trichobothrium d_2 which is found above carina DI_c , on the internal aspect of the patella. In the family Liochelidae, the internal surface of the patella is considerably vaulted, with a well-developed DPS (represented by *Liocheles* in Fig. 98) (*Cheloctonus* does not have the vaulted condition, which is presumably a reversal of this unusual character as suggested by Prendini (2000: 49)). The DI_c and VI_c carinae are disrupted from a proximal to anterior



Figures 35-38: Leg tarsus, lateral-ventral view of vaejoivid genera showing setal and spinule configurations. **35.** *Vaejoivis punctatus*. **36.** *Pseudouroctonus reddelli*. **37.** *Serradigitus g. gertschi*. **38.** *Smeringurus grandis*.