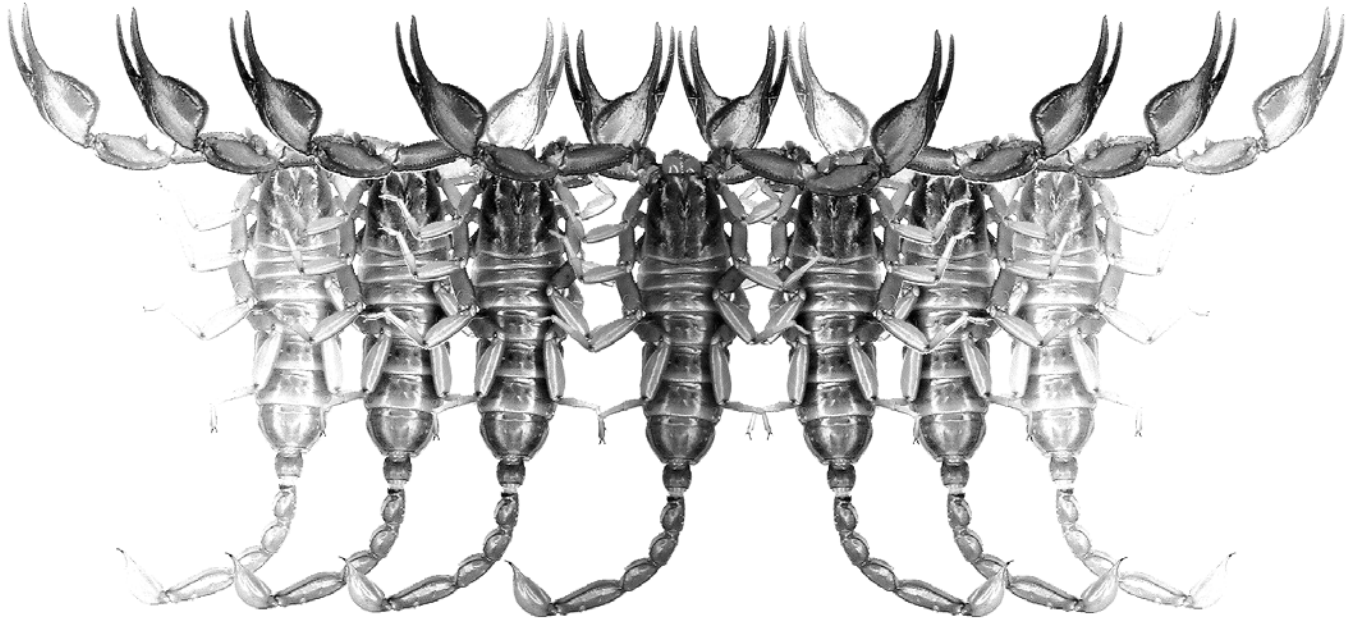


Euscorpilus

Occasional Publications in Scorpiology



**The Systematic Position of the Scorpion Genera
Heteroscorpion Birula, 1903 and *Urodacus* Peters, 1861
(Scorpiones: Scorpionoidea)**

Michael E. Soleglad, Victor Fet, and František Kovařík

April 2005 — No. 20

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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

Publication date: 8 April 2005

The systematic position of the scorpion genera *Heteroscorpion* Birula, 1903 and *Urodacus* Peters, 1861 (Scorpiones: Scorpionoidea)

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Summary

Stockwell (1989), in an unpublished revision, suggested the elevation of subfamily Urodacinae to the family rank, and considered Heteroscorpioninae a subfamily of Ischnuridae. Heteroscorpioninae was formally elevated to the family rank by Lourenço (1996a), and Urodacinae, by Prendini (2000). As a result of a detailed cladistic analysis, Prendini (2000, 2003b) considered families Heteroscorpionidae and Urodacidae to be sister groups, although an alternative topology was available. Soleglad & Fet (2003b) questioned the results of Prendini (2000) but nevertheless retained the monophyly of *Heteroscorpion* and *Urodacus* pending more detailed analysis; they recognized two valid monotypic subfamilies, Heteroscorpioninae and Urodacinae, under Urodacidae. Our present detailed cladistic re-analysis of *Heteroscorpion* and *Urodacus* confirms the phylogeny proposed by Stockwell (1989), which also is the “suboptimal” topology of Prendini (2000, 2003b). The family Urodacidae is abolished; the subfamily Urodacinae is transferred to Scorpionidae. Hemiscorpiidae Pocock, 1893 is accepted as a senior synonym of Liochelidae, and Hormurinae Laurie, 1896, as a senior synonym of Liochelinae. The subfamily Heteroscorpioninae is transferred to Hemiscorpiidae. As a result, the superfamily Scorpionoidea currently includes three families: Bothriuridae (with two subfamilies, Bothriurinae and Lisposominae), Hemiscorpiidae (with three subfamilies, Hemiscorpiinae, Heteroscorpioninae, and Hormurinae), and Scorpionidae (with three subfamilies, Diplocentrinae, Scorpioninae, and Urodacinae).

Introduction

Kraepelin (1905) placed two peculiar genera, *Urodacus* Peters, 1861 from Australia and *Heteroscorpion* Birula, 1903 from Madagascar, in two separate monotypic subfamilies of Scorpionidae Latreille, 1802: Urodacinae Kraepelin, 1905 and Heteroscorpioninae Kraepelin, 1905. Lourenço (1985, 1989) suggested that the genus *Heteroscorpion* belongs to Ischnuridae Simon, 1879 (most recently treated as Liochelidae Fet & Bechly, 2001 (1879)). Stockwell (1989), in an unpublished monograph, suggested the elevation of Urodacinae Pocock, 1893 to family rank, and considered Heteroscorpioninae Kraepelin, 1905 a subfamily of Ischnuridae Simon, 1879. Both taxa were formally elevated to the family rank: Heteroscorpionidae by Lourenço (1996a), and Urodacidae, by Prendini (2000). Lourenço (1996a) agreed with the phylogeny of Stockwell (1989) in his placement of Heteroscorpionidae. As a result of a de-

tailed cladistic analysis, Prendini (2000) considered families Heteroscorpionidae and Urodacidae to be sister groups.

Soleglad & Fet (2003b) questioned the results of Prendini (2000) but retained the monophyly of *Heteroscorpion* and *Urodacus* pending more detailed analysis; they, however, recognized two monotypic subfamilies, Heteroscorpioninae and Urodacinae, under the family Urodacidae. Soleglad & Fet (2003b) listed several characters that *Heteroscorpion* uniquely shares with subfamilies Liochelinae and Hemiscorpiinae, which Soleglad & Fet (2003b) included in family Liochelidae. They stated that additional study is warranted in several areas, in particular, the chelal finger dentition and the analysis of neobothriotaxy within closely related groups, across the superfamily Scorpionoidea.

The goal of this study was to perform further phylogenetic analysis of *Heteroscorpion* and *Urodacus* as outlined in the suggestions of Soleglad & Fet (2003b).

Background: a short history

Phylogeny of Stockwell (1989). The topology of superfamily Scorpionoidea resulting from Stockwell's (1989: Table 11, Figs. 251, 259) detailed cladistic analysis is essentially the same as the topology presented further in this paper. Differences in the two topologies involve family-group name levels and slight differences in the intra-topologies of families Scorpionidae and Ischnuridae. Whereas in our analysis we recognize three scorpionoid families (Bothriuridae, Scorpionidae, and Hemiscorpiidae), Stockwell recognized five families (Bothriuridae, Scorpionidae, Ischnuridae, Diplocentridae, and Urodacidae). Stockwell's (1989) clade Urodacidae + Diplocentridae + Scorpionidae is equivalent to our family Scorpionidae = Urodacinae + Diplocentrinae + Scorpioninae. For families Bothriuridae and Hemiscorpiidae (formerly Ischnuridae), Stockwell's (1989) and our topologies agree: Bothriuridae = Bothriurinae + Lisposominae and Hemiscorpiidae = Hemiscorpiinae + Heteroscorpioninae + Hormurinae (formerly Ischnurinae).

Stockwell's (1989) formally unpublished analysis of superfamily Scorpionoidea was quite comprehensive with the single exception of neobothriotaxy. Curiously, neobothriotaxy was completely ignored by Stockwell (1989) for the superfamily Scorpionoidea whereas, in strong contrast, in the same work he constructed complex models of neobothriotaxy for Chactoidea (Soleglad & Sissom, 2001: 71).

Phylogeny of Prendini (2000). Prendini (2000) considered families Heteroscorpionidae and Urodacidae as sister groups. This topology was selected out of several alternative hypotheses obtained in Prendini's original analysis: one supporting Heteroscorpionidae + Urodacidae, and another, among others, supporting Heteroscorpionidae + (Hemiscorpiidae + Ischnuridae) topology (Prendini, 2000, Fig. 3). The topology selected by Prendini (2000: Fig. 2, Fig. 3a) was based on equal weighting and the ordering of 13 characters. Other interesting alternative topologies were the byproduct of implied weight analysis involving six concavity constant settings (1–6). Implied weighting assigns fractional weights to homoplasious characters (i.e., non-homoplasious characters are not affected and therefore retain a weight of 1), the amount of weight reduction being based on the degree of homoplasy. The effect of implied weighting is a function of the concavity constant value, the smaller the value the more impact on the result.

In Prendini's (2000) analysis, four implied weighting results (concavity constant values = 6 (Fig. 3c), 4–5 (Fig. 3d), 3 (Fig. 3e), and 1–2 (Fig. 3f)) resulted in Heteroscorpionidae ladderizing with the clade Hemiscorpiinae + Ischnuridae; such a relationship is endorsed both, in part, by our analysis and that of Stockwell (1989). For

concavity constant = 6 (the least intrusive setting), a ladderized topology of Urodacidae + (Heteroscorpionidae + (Hemiscorpiidae + Ischnuridae)) was obtained. For concavity constant = 4–5, Urodacidae formed a polytomy with the clade Heteroscorpionidae + (Hemiscorpiidae + Ischnuridae), thus further reducing the relationship of Urodacidae and Heteroscorpionidae. For concavity constant = 3 (medium impact, the default value in PAUP (= 2 in this system for the GOLOBOFF mode)), we get the family level topology endorsed in this paper and by Stockwell (1989). For concavity constants of 1–2 (the most intrusive settings), one sees a highly unlikely topology where all clades are ladderized, with family Diplocentridae on the outside, and Ischnuridae + Hemiscorpiidae on the inside.

Considering both the effect of implied weighting on the topology discussed above and the fact that implied weighting lessens the impact of homoplasious characters, the concern stated by Soleglad & Sissom (2001: 71–72) about the highly homoplasious characters in Prendini's (2000) modeling of neobothriotaxy now appears to be quite well-founded. It is clear to us that when cladistic results produce such weakly supported characters as that seen in Prendini's (2000) modeling of neobothriotaxy (the consistency index (CI) for three characters ranged from 0.25 to 0.44), and the implied weighting analysis has significant impact on the "topology of choice", this modeling in particular should have been reevaluated. And, as pointed out by Soleglad & Sissom (2001), since three of the five "synapomorphies" supporting the monophyly of *Heteroscorpion* + *Urodacus* involved these characters, skepticism of this result is certainly warranted. We discuss these issues in detail elsewhere in this paper.

Phylogeny of Prendini (2003b). Reanalyzing a subset of scorpionoid data in his revision of bothriurid genus *Lisposoma*, Prendini (2003b) obtained two alternative topologies concerning these taxa, and selected the "optimal" topology of the monophyletic (*Heteroscorpion* + *Urodacus*) clade over an alternative "suboptimal" one where *Heteroscorpion* formed a sister group to (*Hemiscorpius* + *Opisthacanthus*), and *Urodacus*, to (*Scorpio* + *Nebo*). Prendini (2003b: 155) commented that "...The primary differences between the topologies obtained in the various analyses concern the placement for...families Heteroscorpionidae and Urodacidae. ...The two alternative hypotheses for the positions of *Heteroscorpion* and *Urodacus* were also retrieved in previous analyses under different weighting regimes (Prendini, 2000c) [Prendini, 2000 in our References] and it is clear that additional data from other sources (e.g. DNA sequences) are needed to discriminate among them".

Phylogeny of Coddington et al. (2004). Later, Prendini (in Coddington et al., 2004, p. 310, Fig. 18.5) published a tentative phylogeny of all scorpions; this

paper had been finalized before, but published after the publication of the detailed morphology-based phylogeny by Soleglad & Fet (2003b). Prendini (in Coddington et al., 2004, p. 310) commented that "...Relationships among the katoikogenic scorpionoid families, portrayed in figure 18.5, are well supported, except for the sister group relationship of Malagasy *Heteroscorpionidae* and Australian *Urodacidae*, which warrants additional testing (Prendini, 2000)". It is interesting to note that in this reference, as well as in his *Lisposoma* revision (2003b), Prendini was now subtly questioning his choice of the "optimal topology" as originally established (Prendini, 2000).

Preliminary analysis by Soleglad & Fet (2003b).

Based on many important characters, which genus *Heteroscorpion* uniquely shares with the family Hemiscorpiidae (then treated as Liochelidae), and, likewise, does not share with the genus *Urodacus*, Soleglad & Fet (2003b) investigated Prendini's (2000) original cladistic analysis, which combined *Heteroscorpion* and *Urodacus* as sister groups. This questioning 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). Soleglad & Sissom (2001) pointed out that Prendini considered almost all neobothriotaxic conditions found within the superfamily Scorpionoidea as single derivations within the pedipalp segment surfaces. This approach, in the opinion of Soleglad & Sissom (2001), predictively created severe homoplasy (i.e., Prendini's simplistic model did not reflect true evolutionary events for this complicated set of derivations). As stated in the discussion by Soleglad & Sissom (2001), three of these characters (those involving the chelal ventral surface, and patellar ventral and external surfaces) exhibited the lowest overall character support in Prendini's (2000) entire analysis. Notwithstanding Prendini's recent retort (Prendini, 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 Prendini's neobothriotaxy model. Soleglad & Fet (2003b) digitized Prendini's (2000: Table 3) original data matrix and made the following alterations:

- (1) assigned separate states to Prendini's three neobothriotaxy characters for *Heteroscorpion* and *Urodacus* (but retained the mappings for the other genera with neobothriotaxy);
- (2) changed *Heteroscorpion*'s state to indicate opposing subequal distal denticles on dorsal/ventral edges of cheliceral movable finger;
- (3) updated the modeling of the sternum to that defined by Soleglad & Fet (2003a);
- (4) changed the number of chelal finger median denticle (MD) rows to two for *Heteroscorpion* since two rows are visible on the distal one-third of the finger, although fused into "many rows" basally;
- (5) changed Prendini's mapping of a single state to three disparate genera groups that exhibit a single ventral median carina on metasomal segments I–IV: *Heteroscorpion*, *Urodacus*, and *Hemiscorpius* + *Habibiella*. Each group was assigned its own state, thus removing the assumption of homologous derivation.

The result of these changes to Prendini's data matrix (Soleglad & Fet, 2003b, Fig. 126) generated the same topology as originally proposed by Stockwell (1989: Figs. 251, 259): *Heteroscorpion* forming a sister group to the clade (Liochelinae + Hemiscorpiinae), and *Urodacus* forming a sister group to the clade (Scorpioninae + Diplocentrinae).

Selection of taxa for analysis

Prendini (2000) studied both species of *Heteroscorpion* recognized at that time, *H. opisthacanthoides* (Krapelin, 1896) (type species) and *H. goodmani* Lourenço, 1996. For *Urodacus*, Prendini (2000) used only two "exemplar" species, *U. novaehollandiae* Peters, 1861 (type species) and *U. yaschenkoi* Birula, 1903. Soleglad & Fet (2003b), in their pilot analysis of scorpionoids, studied only *Heteroscorpion opisthacanthoides* and *Urodacus manicatus* (Thorell, 1876) as well as literature data. In this analysis, we had an opportunity to expand our set of taxa. Two more species of *Heteroscorpion* have been described recently (Lourenço & Goodman, 2002, 2004; Lourenço et al., 2003). We examined specimens of *H. goodmani* and *H. opisthacanthoides* as well as *H. raselimananai* Lourenço & Goodman, 2004; in addition, we included information from the description of *H. magnus* Lourenço & Goodman, 2002. For *Urodacus*, we included seven species: *U. armatus*, *U. elongatus*, *U. hoplurus*, *U. manicatus*, *U. novaehollandiae*, *U. planimanus*, and *U. yaschenkoi*.

Methods & Material

Terminology and conventions

Terminology describing chelal finger dentition and pedipalp chelal ornamentation follows that described and illustrated in Soleglad & Sissom (2001). Sternum terminology follows that described and illustrated in Soleglad & Fet (2003a). Terminology for the pedipalp

patella and metasomal carinae, cheliceral dentition, leg tarsus armature, and classification of neobothriotaxy types follows that described in Soleglad & Fet (2003b).

Cladistic analysis software packages

Software package PAUP* Version 4 (beta) (Swofford, 1998) was used for Maximum Parsimony (MP) analysis of morphology-based character codings.

Abbreviations

List of depositories: CAS, California Academy of Sciences, San Francisco, California, USA; FKCP, Personal collection of František Kovařík, Prague, Czech Republic; FMNH, Field Museum Natural History, Chicago, Illinois, USA; GL, Personal collection of Graeme Lowe, Philadelphia, Pennsylvania, USA; MES, Personal collection of Michael E. Soleglad, Borrego Springs, California, USA; USNM, United States National Museum (Smithsonian Institution), Washington, DC, USA; and VF, Personal collection of Victor Fet, Marshall University, Huntington, West Virginia, USA.

Material examined

The following scorpionoid material was examined for analysis and/or illustrations provided in this paper. The list below uses current classification of superfamily Scorpionoidea, most recently modified by Soleglad & Fet (2003b) and Fet et al. (2004a), and therefore does not reflect the taxonomic emendations established in this paper. Refer to this section for locality data of species-level illustrations.

Bothriuridae: Bothriurinae: *Bothriurus araguayae* Vellard, 1934, Minas Gerais, Brazil, ♀ (VF); *Bothriurus burmeisteri* Kraepelin, 1894, Gobernador Costa, Chubut, Argentina (VF); *Bothriurus* sp., Concepción, Chile, ♂ (VF); *Brachistosternus ehrenberghii* (Gervais, 1841), Tarapaca Prov., Valle de Azapa, Chile, ♂ (VF); *Brachistosternus* sp., Antofagasta Prov., 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, 1893, Valdivia Nancul, Fundo El Linque, Chile, ♀ (VF); *Phoniocercus sanmartini* Cekalovic, 1973, Concepción Prov., Estero Nonguen, Chile, ♂ (VF); *Urophonius granulatus* Pocock, 1898, Ultima Esperanza Prov., Laguna Amarga, Chile, ♂ (VF). **Lisposominae:** *Lisposoma elegans* Lawrence, 1928, Königstein, Namibia, subadult ♀ (FKCP), Omaruru, Farm Okosongomingo, Namibia, juvenile ♂ (FKCP); *Lisposoma joseher-*

mana Lamoral, 1979, Waterberg, Namibia, subadult ♀ (CAS).

Liochelidae: Liochelinae: *Cheloctonus* sp., St. Lucia, Kwazulu, Natal, South Africa, ♀ (VF); *Cheloctonus jonesii* Pocock, 1882, Londolozi, Eastern Transvaal, South Africa, ♀ (VF); *Hadogenes troglodytes* (Peters, 1861), Johannesburg, South Africa (MES); *Liocheles australasiae* (Fabricius, 1775), Bali, Indonesia (VF), Papua New Guinea, ♀ (MES); *Liocheles karschii* (Keyserling, 1885), Guadalcanal, Solomon Islands, ♂ (MES); *Opisthacanthus asper* (Peters, 1861), False Bay, Kwazulu, Natal, South Africa, ♀ (VF); *Opisthacanthus lepturus* (Beauvois, 1805), Aguacate, Panama, ♀ (MES).

Urodacidae: Heteroscorpioninae: *Heteroscorpion goodmani* Lourenço, 1996, Reserve Naturelle Integrale d'Andohahela, Toliara Prov., Madagascar, 9 ♂ paratypes (FMNH); *Heteroscorpion opisthacanthoides* (Kraepelin, 1896), Madagascar, ♀ (MES), Nossibe, Madagascar, ♀ (FKCP); *Heteroscorpion raselimananai* Lourenço & Goodman, 2004, Mt. Ambatobe, Fianarantsoa Prov., Madagascar, ♀ holotype (FMNH). **Urodacinae:** *Urodacus armatus* Pocock, 1888, Lake Berlee env., Western Australia, Australia, ♂ (FKCP), Ethabuka Station, Simpson Desert, Queensland, Australia, 2 ♂ (VF), Wallatinna Homestead, Musgrave Ranges, South Australia, Australia, 2 ♂ (GL); *Urodacus elongatus* L. E. Koch, 1977, Mt. Remesheble, South Australia, Australia, ♀ (VF), Mambay Creek, Mt Remarkable National Park, Flinders Ranges, South Australia, Australia, ♂ (GL), Flinders Ranges National Park, South Australia, Australia, ♀ (GL); *Urodacus hoplurus* Pocock, 1898, Lake Berlee env., Western Australia, Australia, 3 ♂ (FKCP), Gill Pinnacle, Schwerin Mural Crescent, Western Australia, Australia, ♀ (GL); *Urodacus manicatus* (Thorell, 1876), Warrumbungle, New South Wales, Australia, ♂ and ♀ (FKCP), Arapils, Victoria, Australia, 2 ♂ and ♀ (FKCP), Canberra, Australia, ♂ and ♀ (VF), Black Mtn., Canberra, Australia, ♀ (USNM), Adelaide, South Australia, Australia, ♀ (USNM), Armidale, New South Wales, Australia, 3 ♂ and 4 ♀ (USNM), New South Wales, Australia, ♂ and 2 ♀ (USNM), Ravine de Casoars, Flinders Chase National Park, Kangaroo Island, South Australia, Australia, ♂ (GL), Queanbeyan, New South Wales, Australia, ♀ and early instar juveniles (GL); *Urodacus novaehollandiae* Peters, 1861, Southern Cross, Western Australia, Australia, ♂ (FKCP), Streaky Bay, Eyre Peninsula, South Australia, Australia, ♀ (GL); *Urodacus planimanus* Pocock, 1893, Darling Range, 50 km E Perth, Western Australia, Australia, ♀ (FKCP), Condobolin, New South Wales, Australia, 5 ♂ (FKCP); *Urodacus yaschenkoi* (Birula, 1903), Hermannsburg, Northern Territory, Australia, ♀ (GL), Strathearn Homestead, South Australia, Australia, 2 ♂ (GL).

Scorpionidae: Diplocentrinae: *Bioculus comondae* Stahnke, 1968, Loreto, Baja California Sur, Mexico, ♂ (MES); *Cazierius gundlachii* (Karsch, 1880), San Juan,

Santiago de Cuba, Cuba, ♂ (VF); *Didymocentrus le-seurii* (Gervais, 1844), Martinique, ♀ (VF); *Diplocentrus ochoterenai* Hoffmann, 1931, Oaxaca, Mexico, ♀ (MES); *Diplocentrus tehuacanus* Hoffmann, 1931, Iguala, Guerrero, Mexico, ♀ (MES); *Diplocentrus whitei* (Gervais, 1844), Cuatro Ciénegas, Coahuila, Mexico, ♀ and ♂ (MES); *Nebo hierichonticus* (Simon, 1872), Israel, subadult ♂ and 2 subadult ♀ (VF). **Scorpioninae:** *Heterometrus longimanus* (Herbst, 1800), Mindanao, Philippines, ♂ (MES); *Heterometrus petersii* (Thorell, 1876), Palawan, Philippines, ♂ (USNM); *Heterometrus swammerdami* Simon, 1872, Chilaw, Sri Lanka, ♀ (MES); *Opisththalmus glabriformis* Peters, 1861, Vaalwater, Waterberg, South Africa, ♀ (VF); *Opisththalmus pugnax* Thorell, 1876, Magalesberg, South Africa, ♀ (VF); *Opisththalmus wahlbergii* (Thorell, 1876), Kalahari Gemsbok Park, Twee Rivieren, South Africa, ♂ and ♀ (VF); *Pandinus imperator* (C. L. Koch, 1841), ♀ (MES); *Scorpio maurus* Linnaeus, 1758, Tel-Yezucham, Israel, ♀ (MES).

Cladistic Analysis

Assumptions

Assumptions in cladistic analysis may occur in several steps in the process of establishing a data matrix: a priori *weighting* of characters, the *ordering* of character states, and the assignment of *homology* of a character state across two or more taxa.

Weighting. In general, a priori weighting is frowned upon in cladistic analysis, even though it is common in molecular analyses where, for example, in DNA sequence comparisons, more weight is sometimes given to the evolutionary event of transversion (i.e., the state change from a purine to a pyrimidine and vice versa) over that of transition (i.e., the state change from a purine to purine or a pyrimidine to pyrimidine). The temptation to assign a priori weights is understandable, however. For example, no scorpologist would consider the relative evolutionary significance of the presence or absence of cheliceral serrulae to be equivalent, for example, to fundamental orthobothriotaxic patterns. Surely the latter is a much more important evolutionary event and any systematist would certainly want it to have more influence on the branching process. Fundamental sternum type versus the number of pectinal teeth is another glaring (highly exaggerated, we admit) example of this blatant inequity in the choice of characters for cladistic analysis, under the assumption that they must have “equal weight”. The first example can be rectified to a degree by considering all the trichobothria comprising the orthobothriotaxic patterns, thus a “single character” is transformed into many characters; this approach was utilized by Soleglad & Fet (2001) in their study of the evolution of orthobothriotaxy. The quantification of fun-

damental sternum types by Soleglad & Fet (2003a) is another example where a “single character” was broken down into several substructures (i.e., its basic type, existence of compression within a type, important morphometric ratios, etc.). Selective a priori weighting can be applied also if the systematist believes there is a numerical imbalance across the character set. Thiele (1993), in his somewhat elegant approach to coding meristic and continuous data in cladistic analysis (i.e., “gap” coding), recommended that all other characters should be weighted accordingly so that they have the same weight as the affected characters (i.e., gap coding of meristic data requires assigning successive increasing weights via a Sankoff character). Soleglad & Fet (2003b), in their analysis that combined the entire set of orthobothriotaxic trichobothria with other morphological characters, also weighted all other characters by 2 to equalize the characters in the data matrix (i.e., statements on the trichobothria existence were implemented with a Sankoff character, which assigned a full trichobothrium the weight of 2). It is interesting to point out here that a posteriori weighting is sometimes applied in cladistic analyses (i.e., successive weighting, the REWEIGHT command in PAUP, and implied weighting, the GOLOBOFF mode in PAUP). In these schemes, the weight of homoplasious characters is reduced based on their degree of homoplasy, effectively giving more weight to the characters exhibiting less homoplasy (or none). These schemes are allegedly thought of as “assumption free” but are, nevertheless, based on artificial mechanisms to obtain their result. This same accusation of artificiality can be made against bootstrap and jackknife algorithms as well, which claim to provide independent support metrics for resulting topologies.

Ordering. The ordering of character states is a common practice in cladistics. Ordering in its simplest form is an assumption of nested evolution, although in general the ordering is not rooted (i.e., there is no assumption as to the primitive state). Stockwell (1989), in his important and highly regarded cladistic analysis of high-level scorpion phylogeny, applied ordering throughout his analysis. Of the 138 single state characters, he formed no less than 24 additive binary complexes comprised of 66 characters—nearly half of his characters were involved in ordering in one form or another. Some of these additive complexes formed complicated “evolutionary trees”, such as that seen in Stockwell’s modeling of neobothriotaxy (see Soleglad & Sissom, 2001: 70–71, for a detailed discussion). Prendini (2000), in his analysis of superfamily Scorpionoidea, ordered 13 characters (out of 115); Soleglad & Sissom (2001), in their revision of the chactoid family Euscorpidae, defined four partially ordered characters and applied one instance of primary-secondary characters (out of 89 characters); and Soleglad & Fet (2003b), in their high-level analysis of the systematics of extant scorp-

ons, employed combinations of ordered (two), partially ordered (five), and primary-secondary characters (three complexes, comprised of two characters each) (out of 105 characters).

Homology argumentation. Another form of assumption is the simple process of assigning homology across two or more taxa for a given character state. Although homology argumentation is usually thought of as identifying a structure found in two taxa as the same structure (the *similarity* test of homology), it also involves establishing that the two instances of this structure state occurred in the same evolutionary lineage (the *congruency* test of homology, a necessary condition for a synapomorphy; see Kitching et al., 1998, for a formal definition of homology). This second and very important step in homology argumentation is where the assumption usually occurs. Often, the systematist does not have that much difficulty in establishing that a structure in one organism is the same as in another. For example, in scorpions, the subdistal denticle(s) (*sd*) of the cheliceral movable finger are easily identified across species. If two species exhibit two *sd* denticles, this is a straightforward observation to make. However, to assign these two instances of paired *sd* denticles to the same character state, or to different states, is a more complicated issue and involves an assumption in either case. This is simply because we do not know for certain whether the observed state in these two taxa occurred in the same evolutionary lineage as a single derivation. Whether we assign the same state to these observed characters or assign different states, both are an assumption since we really do not know the history of their derivation. The question immediately arises, which of the two state mapping alternatives manifests the strongest assumption, that is, the assumption that has the most impact on cladistic analysis (i.e., the “branching process”)? It is clear that the assignment of separate states is the *weaker* of the two assumptions. For example, if these are the only instances of paired *sd* denticles in our dataset, the assignment of two states is autapomorphic for these two taxa, therefore having no impact on the branching process (our metric for determining the impact of an assumption). Assigning two taxa with the same state value will *always* affect the branching process since it implies that these two observed structures indeed occurred in the same evolutionary lineage manifested as a *single derivation*. The more inclusive a character state assignment (i.e., the more taxa assigned this state), the larger the assumption. We are not suggesting that all observed instances of a structure should be assigned different state values to each and every taxon with this structure—this of course would provide us with absolutely no resolution as to the topology of the ingroup. We are suggesting, however, that common sense needs to be employed when making these character state assignments which, in turn, depend on the degree of the cur-

rent knowledge of the ingroup in question. If the ingroup is entirely unknown (scorpions certainly are not an example of this), or the study is aimed at species-level cladistics (e.g., determining the monophyly of a putative genus and its substructure), then the strongest assumptions should be *initially* implemented. On the other hand, if the group is well-known (i.e., the species set is well fleshed out, characters well analyzed, a fossil record is available, etc.) then one should lessen the assumption level, maybe bracketing stated homologies within well-defined putative clades, clades that are supported by other characters. In either case, we believe that cladistics is an iterative process; if a given statement of homology produces extreme homoplasy for a given set of characters, these characters must be reanalyzed and the process repeated. Stockwell (1989) was certainly aware of the nuances in assigning homologous character states since many of his additive binary complexes were implemented for the sole purpose of assigning different states to the “same structure” (i.e., they were *similar*, as in the homology definition) to taxa groups he believed evolved in different lineages with respect to this character state.

Character analysis

It is important to note here that, for the purposes of comparative analyses and the coherent presentation of the material, the taxonomic group names and their relationships as established in this paper are used throughout this discussion, specifically: **Bothriuridae = Bothriurinae + Lisposominae; Scorpionidae = Scorpioninae + Diplocentrinae + Urodacinae; Hemiscorpiidae = Hemiscorpiinae + Heteroscorpioninae + Hormurinae.** See Table 6 for the generic composition of these families and subfamilies. The section on **Systematics** specifies taxonomic changes to officially establish this family-group nomenclature.

We now discuss a subset of Prendini’s (2000: Appendix 3) character set that is germane specifically to the analysis of the genera *Heteroscorpion* and *Urodacus*: characters 2, 9, 11, 20, 21, 28, 33, 43, 45, 49, 50, 55, and 95. In this section, we also introduce three new characters (116, 117, and 118) which further quantify the distinctions between three families and eight subfamilies of superfamily Scorpionoidea. See Table 5 for the data matrix representing these character changes to the original matrix of Prendini (2000).

Trichobothria: neobothriotaxy

Soleglad & Sissom (2001: 70–73) discussed in detail the important issue that neobothriotaxy must be considered as separate evolutionary events in the major scorpion groups that exhibit such a derivation. In this study we adopt this approach as well. In general, the taxonomic level of neobothriotaxy modeling conducted

in this paper is consistent with that presented in Soleglad & Fet (2003b).

Prendini (2000) modeled neobothriotaxy with five characters (see our Table 1): character 43, ventral surface of the patella; character 45, external surface of the patella; character 46, internal surface of chela; character 49, ventral surface of chelal palm; and character 53, external surface of chelal palm. In general, we agree with Prendini's (2000) scope of state assignments for characters 46 and 53, however, these involve just a few isolated genera (i.e., the presence of internal accessory trichobothria found in some species of the scorpionid genus *Pandinus*, and external accessory trichobothria occurring in genera *Urodacus* and some species of *Hadogenes*). Curiously, and in strong contrast and far superior to other modeling approaches utilized by Prendini (2000), he considered the two occurrences of external accessory trichobothria to be separate evolutionary events. Incidentally, Prendini's (2000: 58) claim that *Urodacus* and *Hadogenes* are the only Recent scorpions exhibiting external accessory trichobothria on the chela is incorrect, since these trichobothria have been reported also in iuroid genera *Hadrurus* and *Hoffmannihadrurus* (as *Hadrurus gertschi*) (Soleglad, 1976; Fet et al., 2004b) and in the superstitioniid genus *Alacran*, illustrated by Francke (1982) and identified as such in Soleglad & Fet (2003b: 51).

We take strong exception to Prendini's (2000) modeling of the neobothriotaxy in the patella and the ventral surface of the chelal palm (i.e., characters 43, 45, and 49). It is important that we take a close look at the assumptions of the state assignments to taxa for these three characters (Table 1).

Character 43 (ventral surface of patella): Prendini (2000) recognized two evolutionary instances of neobothriotaxy, accessory trichobothria numbering between one and 17 (state=2) and numbers exceeding 17 (state=3). To the first instance of neobothriotaxy, Prendini (2000) assigned taxa *Heteroscorpion*, *Hadogenes*, *Urodacus*, one species of *Opisththalmus* (*O. holmi*), and a single species of *Timogenes* and *Brachistosternus* (*T. mapuche* and *B. ehrenbergii*). This state mapping encompasses all three scorpionoid families spanning no less than five subfamilies. This is an extremely strong assumption, and certainly one that belies any sense of reasonableness. Even more bizarre is the assumption that only certain species of no less than three genera spanning two families are included in the evolutionary lineage of this character state, the other species being excluded. This certainly makes for an very interesting fragment of evolution: It essentially implies that other non-neobothriotaxic species in genera *Brachistosternus*, *Timogenes*, and *Opisththalmus* evolved separately with respect to this character state. To the second instance of neobothriotaxy, genera *Vachonia* and *Pandinus*

are assigned, again a somewhat questionable evolutionary relationship.

Character 45 (external surface of patella): For this character, Prendini (2000) has one state assignment for a neobothriotaxic condition, one or more accessory trichobothria (state=2). Mapped to this state are genera *Heteroscorpion*, *Habibiella*, *Hadogenes*, *Urodacus*, *Opisththalmus*, *Pandinus*, *Vachonia*, and one species of *Timogenes* (*T. mapuche*), again spanning all three scorpionoid families and six subfamilies. Again, we see the bizarre assumption that the two presumed species of *Timogenes* fall in two separate evolutionary lineages as implied by this character assignment. Since Prendini (2000) ordered this character, are we to assume *T. mapuche* gained accessory trichobothria on this surface and somehow was included in the same evolutionary lineages as the other non-bothriurids assigned this state? Or, possibly, did both species of *Timogenes* have this condition and then *T. dorbignyi* lost the accessory trichobothria?

Character 49 (ventral surface of chelal palm): Two evolutionary instances of neobothriotaxy are hypothesized for this character, one accessory trichobothrium (state=3) and two or more accessory trichobothria (state=4). To the first state, with five ventral trichobothria (one accessory), Prendini (2000) assigned several genera from subfamily Bothriurinae. We consider this a reasonable assignment and therefore take no exception as to the implied assumption of this evolutionary lineage. The state exhibiting the excess of one accessory trichobothrium, however, follows the same bizarre assumption of evolutionary lineage discussed above for the other characters by assigning *Heteroscorpion*, *Hadogenes*, *Urodacus*, two species of *Pandinus* (*P. imperator* and *P. cavimanus*), one species of *Opisththalmus* (*O. holmi*), *Vachonia*, *Timogenes*, and one species of *Brachistosternus* (*B. ferrugineus*) to the same character state. In this case, again, species from the same genus (i.e., *Brachistosternus*) are split between two hypothesized evolutionary lineages.

In summary, we object to this modeling for the reasons discussed elsewhere in this paper, that is, the general assignment of all taxonomic groups to the same state value is by far too inclusive and, therefore, too strong an assumption of evolution. And, as discussed above, the assignments and groupings of taxa within certain genera are nonsensical, defying any reasonable notion of evolution in the superfamily Scorpionoidea. In addition, Prendini's (2000: Table 6) support values for these three characters were the lowest in his analysis (see Soleglad & Sissom, 2001: 72). This fact alone should have been a reason enough for Prendini to re-evaluate his somewhat superficial and, in places, nonsensical modeling of neobothriotaxy.

In addition to objections involving overall philosophy discussed above, we now provide empirical argu-

Bothriuridae		Scorpionidae			Hemiscorpiidae		
Bothriurinae	Lisposominae	Diplocentrinae	Scorpioninae	Urodacinae	Hormurinae	Hemiscorpiinae	Heteroscorpioninae
Patella Ventral (43)							
0: 0 *							
1: 3 (ortho)							
2: 4-20	Brach ¹ , Timo ¹			Opisto ¹	Urod	Hado	Heteros
3: > 20	Vach			Pand			
Patella External (45 ordered)							
0: 7 *							
1: 13 (ortho)							
2: 14+	Timo ¹ , Vach			Opisto, Pand	Urod	Hado	Habi Heteros
Chela Internal (46 ordered)							
0: 1 *							
1: 2 (ortho)							
2: 3+				Pand ¹			
Chela Ventral (49)							
0: 1 *							
1: 2 *							
2: 4 (ortho)							
3: 5	Brach ¹ , Both, Centr, Cerc, Ortho, Phon, Tehu, Urop						
4: 6+	Brach ¹ , Timo, Vach			Opisto ¹ , Pand ¹	Urod	Hado	Heteros
Chela External (53)							
0: 0 (ortho)							
1: 10-15							
2: > 20					Urod	Hado	

Table 1: Neobothriotaxy modeling of superfamily Scorpionioidea by Prendini (2000). This modeling is based entirely on the gross number of trichobothria contained on a pedipalp segment surface. Family and subfamily names reflect taxonomic changes made in Sologlad & Fet (2003b), Fet et al. (2004a), and in this paper. Number inside parentheses refer to the character number in the analysis of Prendini's (2000) (Appendix 3). "ortho" indicates the orthobothriotaxic state for that segment surface (i.e., Type C) and genera complying with this state are not listed as well as references to the outgroup taxa (i.e., *Centruroides* and *Chaerilus*); these character states, if different from the scorpionoids, are marked with an asterisk. Both of these states are shaded with gray. Character 53 refers only to external *accessory* trichobothria, while other characters refer to the total number of orthobothriotaxic and accessory trichobothria on that pedipalp segment surface. Genus name abbreviations: Brach = *Brachistosternus*, Both = *Bothriurus*, Centr = *Centromachetes*, Cerc = *Cercophonius*, Habi = *Habibiella*, Hado = *Hadogenes*, Heteros = *Heteroscorpion*, Opisto = *Opisthophthalmus*, Ortho = *Orthobothrius*, Pand = *Pandinus*, Phon = *Phoniocercus*, Tehu = *Tehuanea*, Timo = *Timogenes*, Urod = *Urodacus*, Urop = *Urophonius*, Vach = *Vachonia*. ¹ = in part, not all ingroup species in genus comply with this state.

ments showing the unlikelihood that neobothriotaxy exhibited in genera *Heteroscorpion* and *Urodacus* occurred in the same evolutionary path as a single derivation. Below, we discuss significant differences in the major neobothriotaxy exhibited in these two genera in the following areas: (1) differences in the degree of variability (i.e., variability in the numbers of accessory trichobothria), (2) comparison of individual trichobothrial series of the patellar external surface, (3) com-

parison of accessory trichobothria on the external surface of the chelal palm, and (4) comparison of the trichobothrial patterns of the ventral surface of the chelal palm.

Variability in neobothriotaxy. Table 2 presents a general overview of the reported variability in the numbers of accessory trichobothria found in genera *Urodacus* and *Heteroscorpion*. All species currently described are included. In *Urodacus*, the variability within

	Chela		Patella	
	Ventral*	External Accessory	Ventral*	External*
<i>U. armatus</i>	7–25	3–17	5–15	19–46
<i>U. carinatus</i>	16–20	9–16	11–16	30–47
<i>U. centralis</i>	17–24	10–12	13–16	38–47
<i>U. elongatus</i>	13–23	7–13	9–15	29–49
<i>U. excellens</i>	13–18	8–12	10–15	28–36
<i>U. giulianii</i>	15–22	11–17	12–16	34–50
<i>U. hartmeyeri</i>	11–22	6–15	11–15	25–38
<i>U. hoplurus</i>	11–22	7–15	10–16	30–43
<i>U. koolanensis</i>	18–25	11–18	14–18	41–62
<i>U. lowei</i>	11–32	8–26	9–21	27–60
<i>U. macrurus</i>	11–21	5–14	9–15	20–41
<i>U. manicatus</i>	8–11	2–5	7–11	17–23
<i>U. mckenziei</i>	6–7	2–3	6–8	15–22
<i>U. megamastigus</i>	11–13	5–10	8–11	22–27
<i>U. novaehollandiae</i>	7–16	3–10	7–12	20–38
<i>U. planimanus</i>	8–11	3–7	6–9	19–25
<i>U. similis</i>	17–21	8–17	12–15	27–38
<i>U. spinatus</i>	12–15	6–9	10–13	22–27
<i>U. varians</i>	16–22	9–13	13–17	32–39
<i>U. yaschenkoi</i>	18–31	6–26	12–19	29–54
<i>H. goodmani</i>	7–9	absent	8–9	17
<i>H. magnus</i>	12–15	1 (?)	14–19	31–40
<i>H. opisthacanthoides</i>	8–9	absent	10–11	17–19
<i>H. raselimananai</i>	6	absent	7–8	16

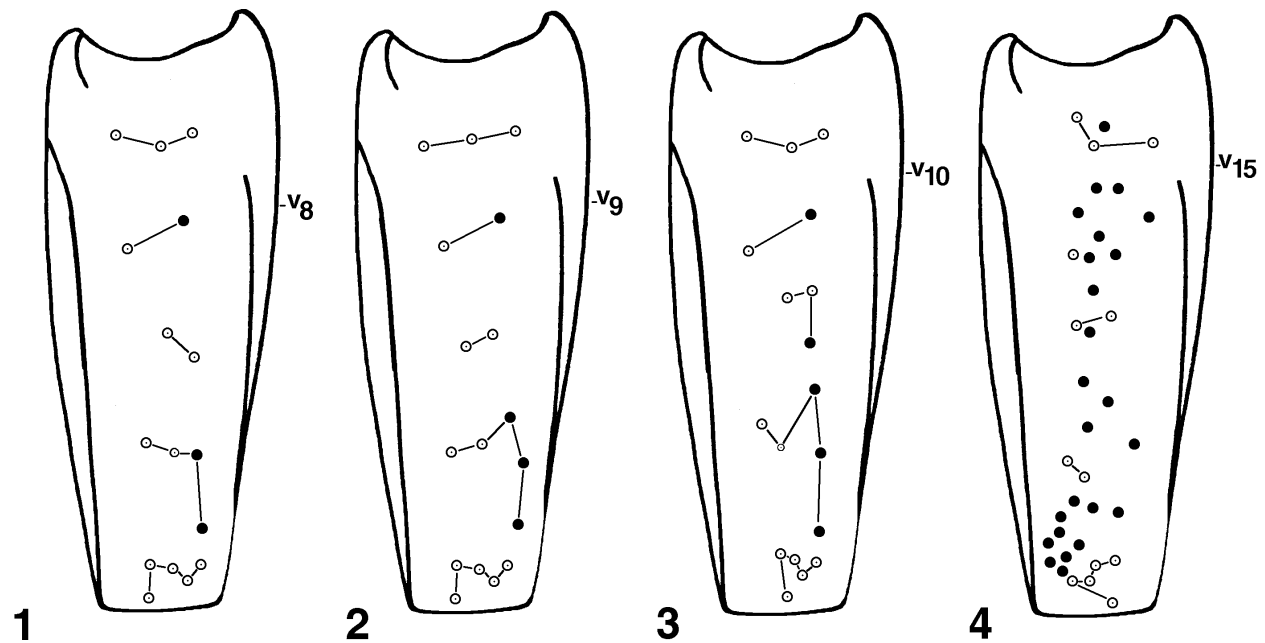
Table 2: General synopsis of neobothriotaxy in genera *Urodacus* (after Koch, 1977, in part; *U. mckenziei* after Volschenk et al. 2000, in part) and *Heteroscorpion* (after Lourenço & Goodman, 2002, 2004, in part). *Counts include orthobothriotaxic trichobothria.

a given species is considerable; for example, the numeric span of the minimum-maximum ranges for the patella external surface (as reported by Koch, 1977) for *U. armatus*, *U. elongatus*, *U. lowei*, *U. macrurus*, and *U. yaschenkoi* exceed twenty accessory trichobothria. Also, this significant variability is found in all four pedipalp surfaces with neobothriotaxy. For example, for these same five species range spans exceed ten for the ventral aspect of the chela, six for the external surface of the chela, and six for the ventral surface of the patella. In stark contrast, the variability in genus *Heteroscorpion* is considerably lower: even in the species with the highest number of accessory trichobothria (*H. magnus*), the relative variability is less than that in species of *Urodacus* with comparable numbers of accessory trichobothria. In *Urodacus* species with the lowest number of accessory trichobothria, *U. mckenziei* and *U. manicatus*, the relative variability in the patellar external series exceeds that seen in *H. opisthacanthoides*, the only other species of *Heteroscorpion* besides *H. magnus* that shows variability on this surface.

External surface of patella. In this analysis, we adopt Vachon's (1974: Figs. 106, 107) trichobothrial

designations for Type C orthobothriotaxy. Two species represented in his figures (*H. opisthacanthoides* and *U. manicatus*) possess relatively simple patterns of neobothriotaxy, thus the determination of individual accessory trichobothria is somewhat straightforward. We show patterns for all four species of *Heteroscorpion* (Figs. 1–4), which can be compared to patterns from eight species of *Urodacus* (Figs. 5–12), spanning the simplest patterns as seen in species *U. manicatus* and *U. mckenziei*, to the highly complex patterns of *U. armatus*, *U. elongatus*, *U. hoplurus*, and *U. yaschenkoi*. Of course the designation of accessory trichobothria in the latter species as well as for *H. magnus* (Fig. 4) is somewhat arbitrary with respect to external series assignments, but in general we believe the designation of orthobothriotaxic trichobothria are reasonable, especially in the species with smaller numbers of accessory trichobothria.

In *Heteroscorpion* (Fig. 1–4), the patellar external terminal trichobothrial series (*et*) is orthobothriotaxic in three species; only *H. magnus* (Fig. 4) is hypothesized as having a single accessory trichobothria. In genus *Urodacus*, all species except *U. mckenziei* (Fig. 6) have at least one accessory *et* trichobothria. The external sub-



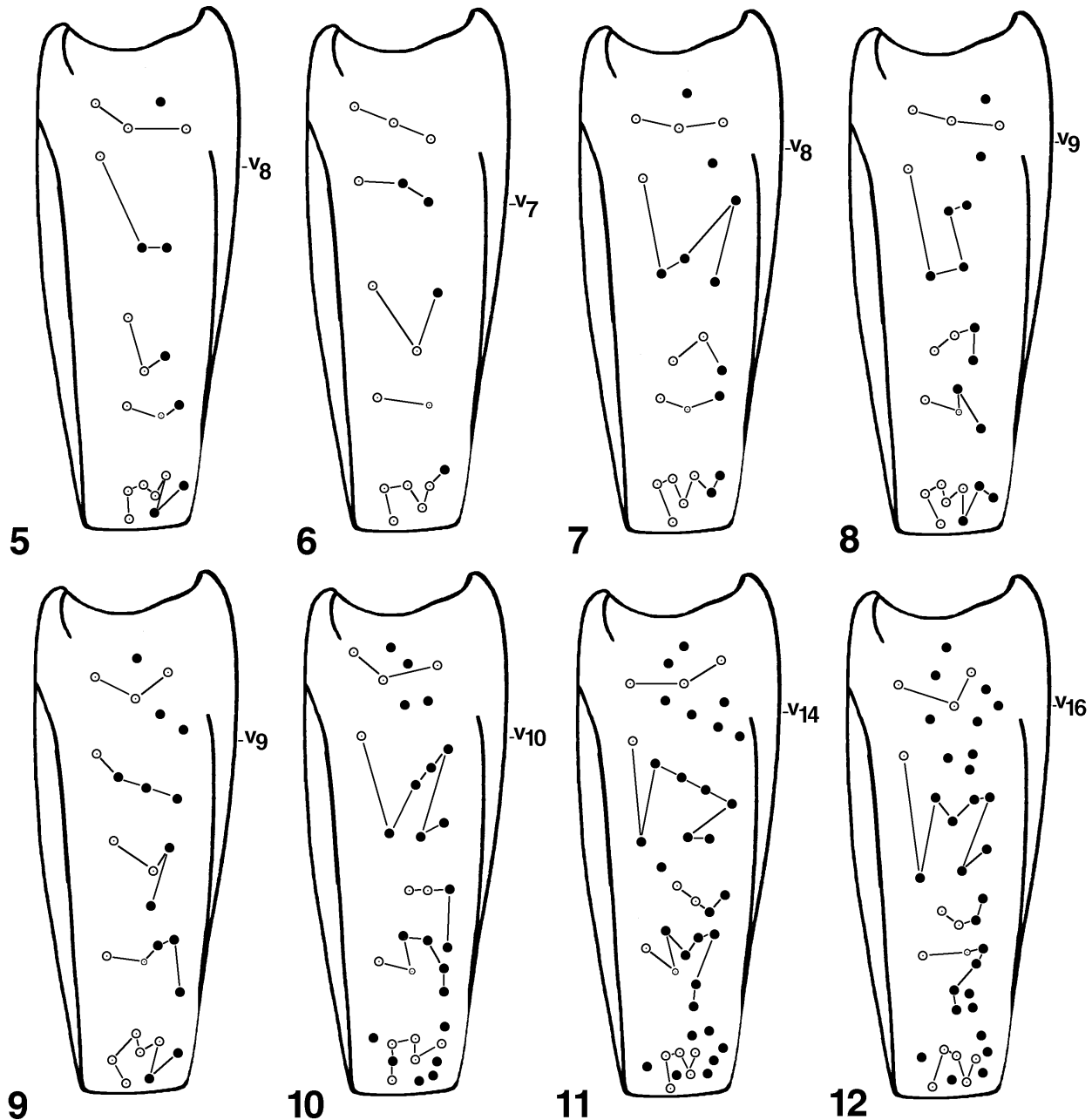
Figures 1-4: Diagrammatic trichobothrial pattern of external surface of patella for genus *Heteroscorpion*. 1. *Heteroscorpion raselimananai*. 2. *H. goodmani*. 3. *H. opisthacanthoides* (after Vachon, 1974, in part) 4. *H. magnus* (after Lourenço & Goodman, 2002, in part). Distal ventral trichobothrium number and position depicted as v_{xx} . Open circles depict orthobothriotaxy based on Vachon (1974: Fig. 106), closed circles depict hypothesized accessory trichobothria.

terminal series (*est*) shows one accessory trichobothrium in three *Heteroscorpion* species (*H. magnus* presumably has considerably more), whereas in *Urodacus* there are two accessory trichobothria in *U. mckenziei* and *U. manicatus* and considerably more in other species. In the external median (*em*) series, *Heteroscorpion raselimananai* (Fig. 1) and *H. goodmani* (Fig. 2) have orthobothriotaxy, and *H. opisthacanthoides* has a single accessory trichobothrium. In contrast, all species of *Urodacus* exhibit neobothriotaxy in the *em* series, with one accessory trichobothrium in more simple patterns, and two or more in more complicated patterns. In the external suprabasal (*esb*) series, neobothriotaxy is expressed in *Heteroscorpion* with at least two accessory trichobothria (usually three or more); in *Urodacus*, *U. mckenziei* (Fig. 6) is orthobothriotaxic and species with more simple patterns have one or two accessory trichobothria. Finally, the external basal (*eb*) series in *Heteroscorpion* is orthobothriotaxic (except for *H. magnus*). In *Urodacus*, this series has at least one accessory trichobothrium, two being typical in species with minimal to medium number of accessory trichobothria; species with massive neobothriotaxy (e.g., *U. armatus*, *U. elongatus*, and *U. yaschenkoi*) have more than five accessory trichobothria in the *eb* series.

This analysis shows that none of the trichobothrial series of the external surface of the patella are similar in variability between these two genera. This is particularly apparent when the two simplest patterns in each genus are compared series by series (*H. raselimananai* (Fig. 1),

H. goodmani (Fig. 2), *U. mckenziei* (Fig. 4), and *U. manicatus* (Fig. 3)): there is no match in numbers of accessory trichobothria (except for the *et* series where *U. mckenziei* is orthobothriotaxic, the only species in *Urodacus* with this condition).

External surface of chela. All 20 species of the genus *Urodacus* have external accessory trichobothria on the chela (Figs. 13–18). As discussed above, the presence of external accessory trichobothria is quite unusual in Recent scorpions being only known in the scorpionoids (i.e., genera *Urodacus* and *Hadogenes*), the iuroids (caraboctonid subfamily Hadrurinae), and in the monotypic chactoid genus *Alacran* (family Superstitioniidae). In the simplest pattern, *U. mckenziei* (Table 2), there are 2–3 accessory trichobothria, and in *U. manicatus*, 2–5 (Fig. 13 and Table 2). Species such as *U. elongatus* (Fig. 16), *U. hoplurus* (Fig. 17), and *U. yaschenkoi* (Fig. 18) exhibit many external accessory trichobothria, up to 26 (this somewhat high number is reported by Koch, 1977). In most cases, the external accessory trichobothria form two irregular rows on the extreme ventral aspect of the external surface of the chelal palm. At the same time, *Heteroscorpion* does not exhibit external accessory trichobothria, with the possible exception of the highly neobothriotaxic species *H. magnus*. Lourenço & Goodman (2002: Fig. 21) do not mention the presence of external accessory chelal trichobothria in this species, but illustrate an apparent single accessory trichobothrium on the medial distal aspect of the chelal palm. In either case, it is clear that *Heteroscorpion* does not in general

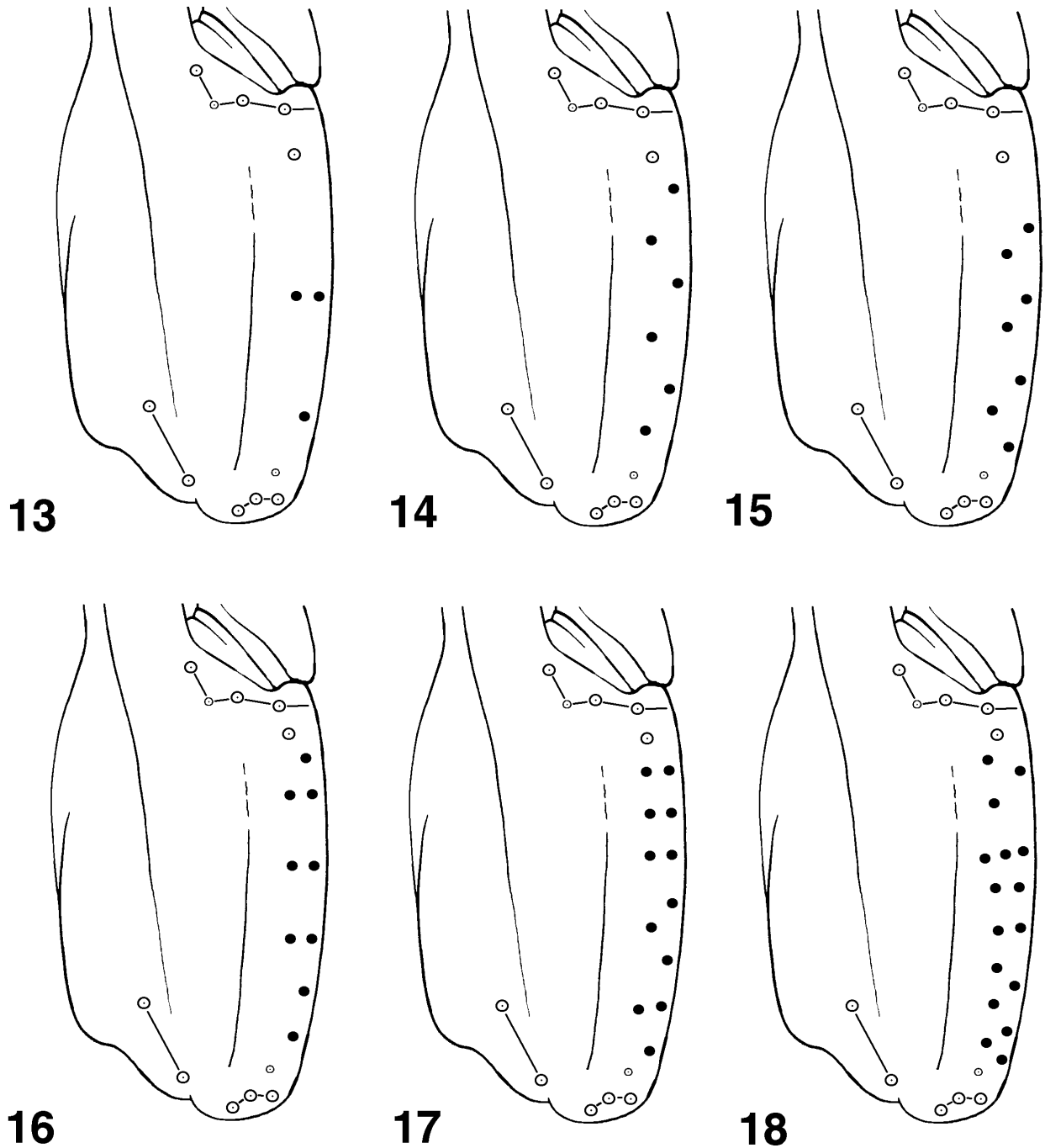


Figures 5-12: Diagrammatic trichobothrial pattern of external surface of patella for genus *Urodacus*. 5. *Urodacus manicatus*. 6. *U. mckenziei* (after Volschenk et al., 2000: Fig. 11, in part). 7. *U. planimanus*. 8. *U. novaehollandiae*. 9. *U. armatus*. 10. *U. elongatus*. 11. *U. hoplurus*. 12. *U. yaschenkoi*. Distal ventral trichobothrium number and position depicted as v_{xx} . Open circles depict orthobothriotaxy based on Vachon (1974: Fig. 107), closed circles depict hypothesized accessory trichobothria.

exhibit external accessory trichobothria whereas we see accessory trichobothria on the external surface of the palm in all species of *Urodacus*, in most cases forming irregular doubled rows and exceeding 15 trichobothria in several species (see Table 2).

Ventral surface of the chela. In Figures 20–23 (*Heteroscorpion*) and 25–28 (*Urodacus*), we illustrate the ventral chelal trichobothria. For both genera, we hypothesize four orthobothriotaxic trichobothria (V_1 – V_4).

In four species of *Heteroscorpion* we see that the ventral series, including hypothesized accessory trichobothria, is essentially inline including the highly neobothriotaxic species *H. magnus*. In contrast, the genus *Urodacus* has an additional basal trichobothrium, clearly accessory, situated between Et_1 and V_1 . Only *U. mckenziei* (the species with the minimal neobothriotaxy) lacks this trichobothrium. In addition, the ventral series of trichobothria in *Urodacus* extends to the exterobasal

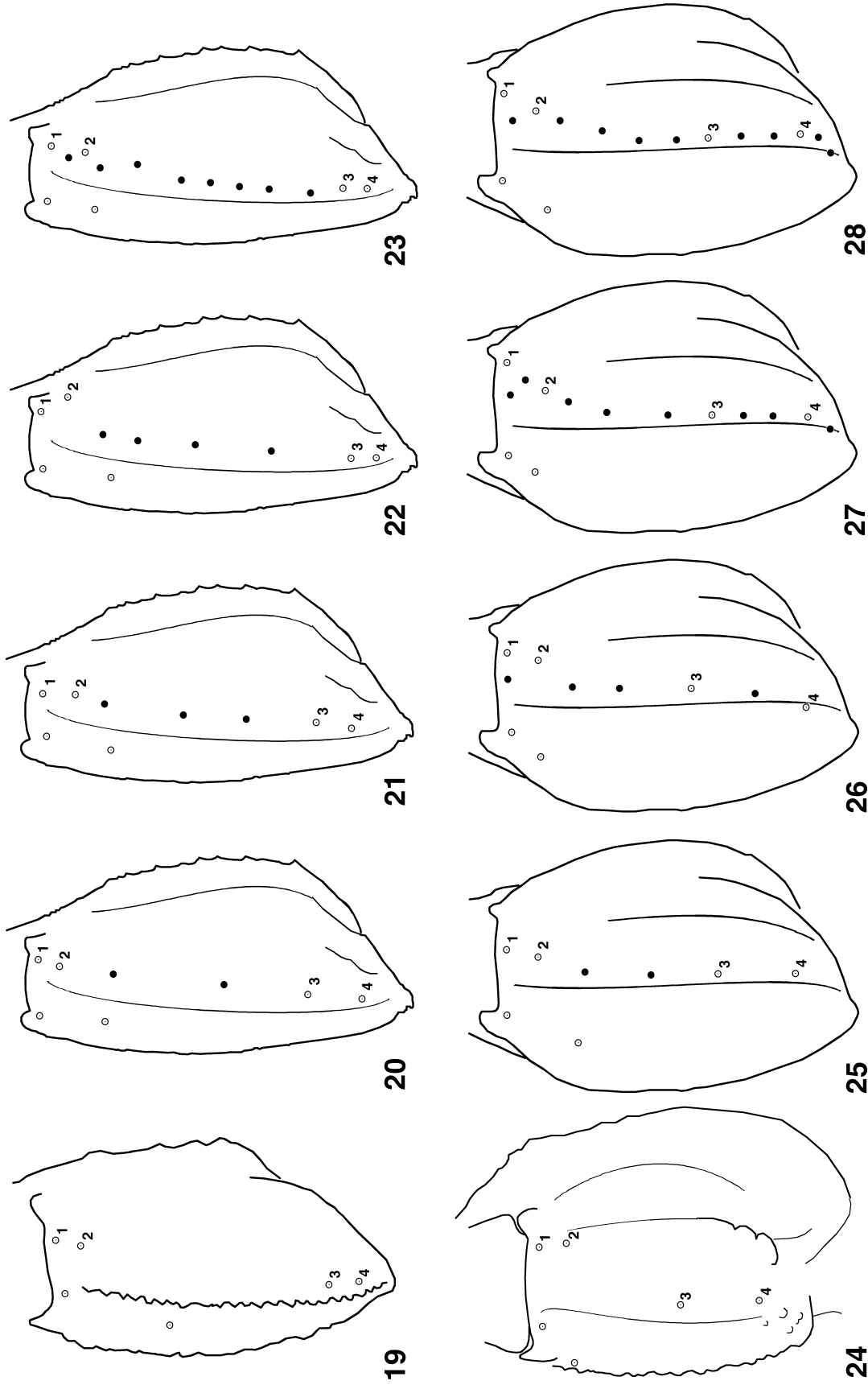


Figures 13-18: Diagrammatic trichobothrial pattern of external surface of chela for genus *Urodacus* showing external accessory trichobothria. **13.** *Urodacus manicatus*. **14.** *U. novaehollandiae*. **15.** *U. armatus*. **16.** *U. elongatus*. **17.** *U. hoplurus*. **18.** *U. yaschenkoi*. Open circles depict orthobothriotaxy, closed circles depict hypothesized external accessory trichobothria. Note, ventral accessory trichobothria located on the extreme basal aspect of the palm are not shown.

surface in species with large numbers of trichobothria in this series (i.e., *U. novaehollandiae* (Fig. 27) and *U. armatus*, etc.). This is not seen in *Heteroscorpion*.

It is clear from the above discussion that the two neobothriotaxic configurations found in genera *Het-*

eroscorpion and *Urodacus* have nothing in common. We can conclude that neobothriotaxy in all likelihood occurred in separate evolutionary lineages, as assumed in this analysis. We would also suggest here that genera from other scorpionoid subfamilies that exhibit neo-



Figures 19-28: Diagrammatic trichothrial pattern of ventral surface of the chela for genera *Heteroscorpion* and *Urodacus* as compared to *Opisthacanthus* and *Scorpio*, respectively. 19. *Opisthacanthus lepturus*. 20. *Heteroscorpion raselimananai*. 21. *Heteroscorpion goodmani*. 22. *Heteroscorpion opisthacanthoides* (after Vachon, 1974: Fig. 129, in part). 23. *Heteroscorpion magnus* (after Lourenço & Goodman, 2002: Fig. 21, in part). 24. *Scorpio maurus*. 25. *Urodacus mckenziei* (after Volschenk, et al., 2000: Fig. 15, in part). 26. *Urodacus manicattus*. 27. *Urodacus novaeollandiae*. 28. *Urodacus armatus*. Open circles depict hypothesized orthobothriotaxy (ventral trichothria are numbered 1-4), closed circles depict hypothesized ventral accessory trichothria. The only external trichothria shown are Et_1 and Est .

bothriotaxy can be distinguished from each other as we demonstrated in this paper for *Urodacus* and *Heteroscorpion* (i.e., *Hadogenes* vs. *Pandinus* vs. *Opisthophthalmus*, etc.).

Data matrix change. For neobothriotaxy we modify three characters in Prendini's data matrix (2000: Table 3) as follows:

Character 43: Neobothriotaxy on patellar ventral surface (*unordered*)

- 0: absent (*Centruroides*)
- 1: three (orthobothriotaxic) (*Chaerilus*, select scorpionoids)
- 2: neobothriotaxic (select bothriurids)
- 3: neobothriotaxic (select hormurines)
- 4: neobothriotaxic (select hemiscorpiines (null))
- 5: neobothriotaxic (Heteroscorpioninae)
- 6: neobothriotaxic (select scorpionines)
- 7: neobothriotaxic (Urodacinae)

The character support for this character is an improvement over that of Prendini's (2000: Table 6) original analysis, Consistency Index (CI)/Retention Index (RI) = 0.667/0.625 vs. 0.37/0.54 (see Kitching et al., 1998, for a definition of these support indices).

Character 45: Neobothriotaxy on patellar external surface (*unordered*)

- 0: seven (orthobothriotaxic) (*Centruroides*, *Chaerilus*)
- 1: thirteen (orthobothriotaxic) (select scorpionoids)
- 2: neobothriotaxic (select bothriurids)
- 3: neobothriotaxic (select hormurines)
- 4: neobothriotaxic (select hemiscorpiines)
- 5: neobothriotaxic (Heteroscorpioninae)
- 6: neobothriotaxic (select scorpionines)
- 7: neobothriotaxic (Urodacinae)

The character support for this character is an improvement over that of Prendini's (2000: Table 6) original analysis, CI/RI = 0.778/0.800 vs. 0.25/0.60.

Character 49: Neobothriotaxy on chelal ventral surface (*unordered*)

- 0: one (orthobothriotaxic) (*Chaerilus*)
- 1: two (orthobothriotaxic) (*Centruroides*)
- 2: four (orthobothriotaxic) (select scorpionoids)
- 3: neobothriotaxic (select bothriurids)
- 4: neobothriotaxic (select hormurines)
- 5: neobothriotaxic (select hemiscorpiines (null))
- 6: neobothriotaxic (Heteroscorpioninae)
- 7: neobothriotaxic (select scorpionines)
- 8: neobothriotaxic (Urodacinae)

The character support for this character is an improvement over that of Prendini's (2000: Table 6) original analysis, CI/RI = 0.857/0.800 vs. 0.44/0.80.

Trichobothria: orthobothriotaxy

Prendini's (2000) character 50 models the relative distance between chelal ventral trichobothria V_2 and V_3 . This character was employed in Stockwell's (1989) analysis as well (character 79). Both of these modeling schemes distinguished the relatively wide gap between these two trichobothria as exhibited in Hemiscorpiidae. They considered other scorpionoids (i.e., bothriurids and scorpionids) to have a "normal" spacing between these trichobothria. In addition, in Prendini's (2000) analysis all taxa exhibiting neobothriotaxy on this chelal surface were coded with an inapplicable value (-); that is, he assumed that V_1-V_4 could not be identified.

We have analyzed this character and believe that the relative spacing between trichobothria V_2 and V_3 can be quantified into *three* basic arrangements using the morphometric ratio V_2-V_3/V_3-V_4 :

- (1) "normal" spacing, where all four ventral trichobothria are essentially equally spaced; approximate ratio value range equals <1–1.2 (mean 1.1) [n=8], as found in the family Bothriuridae.
- (2) the gap between V_2 and V_3 is larger than that between V_3 and V_4 , giving us a ratio value range of 1.2–2.1 (mean 1.61) [n=12], as exhibited in family Scorpionidae.
- (3) the gap between V_2 and V_3 is considerably larger than that between V_3 and V_4 , approximate ratio value range equals 2.3–6.3 (mean 4.04) [n=11], as seen in family Hemiscorpiidae.

By using this ratio, we can see that the relative spacing between trichobothria V_2 and V_3 is both a function of the closeness of V_1 and V_2 as well as the relative closeness between V_3 and V_4 . That is, not only does V_3 appear more proximal on the palm, but V_2 is located quite close to V_1 . For example, we get similar results for the morphometric ratio V_2-V_3/V_1-V_2 : Bothriuridae, 1.07–2.26 (mean 1.76) [n=7]; Scorpionidae, 2.33–5.34 (mean 3.78) [n=7]; and Hemiscorpiidae, 5.17–8.82 (mean 6.95) [n=7].

We believe, using orthobothriotaxic genera as a reference within these three scorpionoid families, that we can distinguish, with some certainty, the V_1-V_4 series from the accessory trichobothria occurring on that surface. For example, for the bothriurids, we agree with Vachon's (1974: Figs. 203, 205–206) designations of V_1-V_4 for genera *Centromachetes*, *Thestylus*, and *Timogenes*, which match favorably in relative spacing of these trichobothria. The same spacing is observed in genera *Brachistosternus*, *Bothriurus*, and *Lisposoma* (Fet et al., 2004a: Figs. 5–8). Using *Lisposoma* and

Thestylus as a basis for orthobothriotaxy, we can see that Vachon's designations of V_1 – V_4 are very likely to be correct for other bothriurid genera. This same approach can be used in the family Scorpionidae. Again referring to Vachon (1974: Figs. 68, 71, 74) for diplocentrine genera *Oichus*, *Diplocentrus*, and *Nebo*; Lamoral (1979: Figs. 362, 384, 396, 404) for four species of genus *Opisthophthalmus*; Kovařík (2004a: Fig. 2) for genus *Heterometrus*; and our Fig. 24 for genus *Scorpio*, we see that the spacing between these three trichobothria, as quantified by our ratio, are similarly spaced and the trichobothria V_2 and V_3 are spaced farther than that seen in the bothriurids. In family Hemiscorpiidae, we see the most exaggerated spacing as indicated by the ratio. This is illustrated by Vachon (1974: Figs. 111, 120, 123) for *Hemiscorpius*, *Liocheles*, and *Iomachus*, and in our Figs. 19–23, for *Opisthacanthus* and *Heteroscorpion*.

In Figures 19–28, we illustrate chelal ventral trichobothria patterns of *Heteroscorpion* and *Urodacus* and, for comparison, of two orthobothriotaxic genera from Hemiscorpiidae and Scorpionidae. By studying the species with the most simple neobothriotaxic patterns in each genus, *H. raselimananai* (Fig. 20) and *H. goodmani* (Fig. 21), and *U. mckenziei* (Fig. 25) and *U. manicatus* (Fig. 26), we can distinguish, with some certainty, the V_1 – V_4 trichobothria in the two genera. In two *Heteroscorpion* species we see two proximal trichobothria that are positioned similarly to those in *Opisthacanthus* (Fig. 19). These two isolated trichobothria are also quite conspicuous in *H. opisthacanthoides* (Fig. 22). Based on these three species of *Heteroscorpion*, we hypothesize the V_1 – V_4 series for the highly neobothriotaxic *H. magnus* (Fig. 23). In contrast, we do not see the two proximal trichobothria in two species of *Urodacus* with the simplest patterns. Consequently, we hypothesize the designation of the V_1 – V_4 series for four species of *Urodacus* (Figs. 25–28). In addition, in *U. manicatus* (Fig. 26), *U. novaehollandiae* (Fig. 27), and *U. armatus* (Fig. 28), we can see an accessory trichobothrium positioned distally between the two condyles of the movable finger. It is not present in *U. mckenziei*, which is presumably the *Urodacus* species exhibiting the least number of accessory trichobothria (see Table 2). This accessory trichobothrium is not present any of the four species of *Heteroscorpion* (Figs. 20–23). We address this issue elsewhere in the discussion of neobothriotaxy.

The relative positioning and/or spacing of the chelal ventral trichobothria series has shown its diagnostic value in other scorpion groups. For example, Soleglad & Fet (2003b) discussed the shortening of this series in general, and the internal location of the V_1 – V_2 – V_3 juncture as diagnostic for most chactoids except for family Vaejovidae. Soleglad & Sissom (2001) emphasized the external position of trichobothrium V_4 in euscorpoid subfamilies Euscorpinae and Megacorminae.

In Prendini's (2000) character 55, the location of the chelal *Est* trichobothrium, we see that inapplicable codes are assigned to genera *Urodacus* and *Hadogenes*. By referencing two *Urodacus* species with minimal neobothriotaxy, *U. manicatus* (Fig. 13) and *U. mckenziei*, we can with reasonable certainty determine the position of trichobothrium *Est*, which in our opinion, is located on the distal aspect of the palm. This conclusion is also supported by Volschenk et al. (2000: Fig. 14). We also think it reasonable to believe that the position of *Est* in other species of *Urodacus* that exhibit massive neobothriotaxy, e.g., *U. yaschenkoi* (Fig. 18), *U. hoplurus* (Fig. 17), and *U. elongatus* (Fig. 16), would be consistent with other species. Consequently we have changed the data matrix accordingly. Since *Hadogenes* is not a subject of this paper, we leave the inapplicable coding as originally established in the data matrix of Prendini (2000), although one would suspect that *Est* is located medially on the palm, showing consistency with the other hormurine genera.

Data matrix change. For orthobothriotaxy we modify two characters in the data matrix of Prendini (2000: Table 3) as follows:

Character 50: Distribution of chelal trichobothria V_1 – V_4 , ratio V_2 – V_3 / V_3 – V_4 (*unordered*)

0: ratio value range, <1 – 1.2 (mean 1.1) (Bothriuridae)

1: ratio value range, 1.2 – 2.1 (mean 1.61) (Scorpionidae)

2: ratio value range, 2.3 – 6.3 (mean 4.04) (Hemiscorpiidae)

(-): (*Centruroides*, *Chaerilus*)

The character support for this character is the same as that of Prendini's (2000: Table 6) original analysis, CI/RI = 1/1.

Character 55: Position of chelal trichobothrium *Est* (*unordered*)

0: distal aspect of palm (other taxa)

1: middle aspect of palm (Hormurinae except *Hadogenes*)

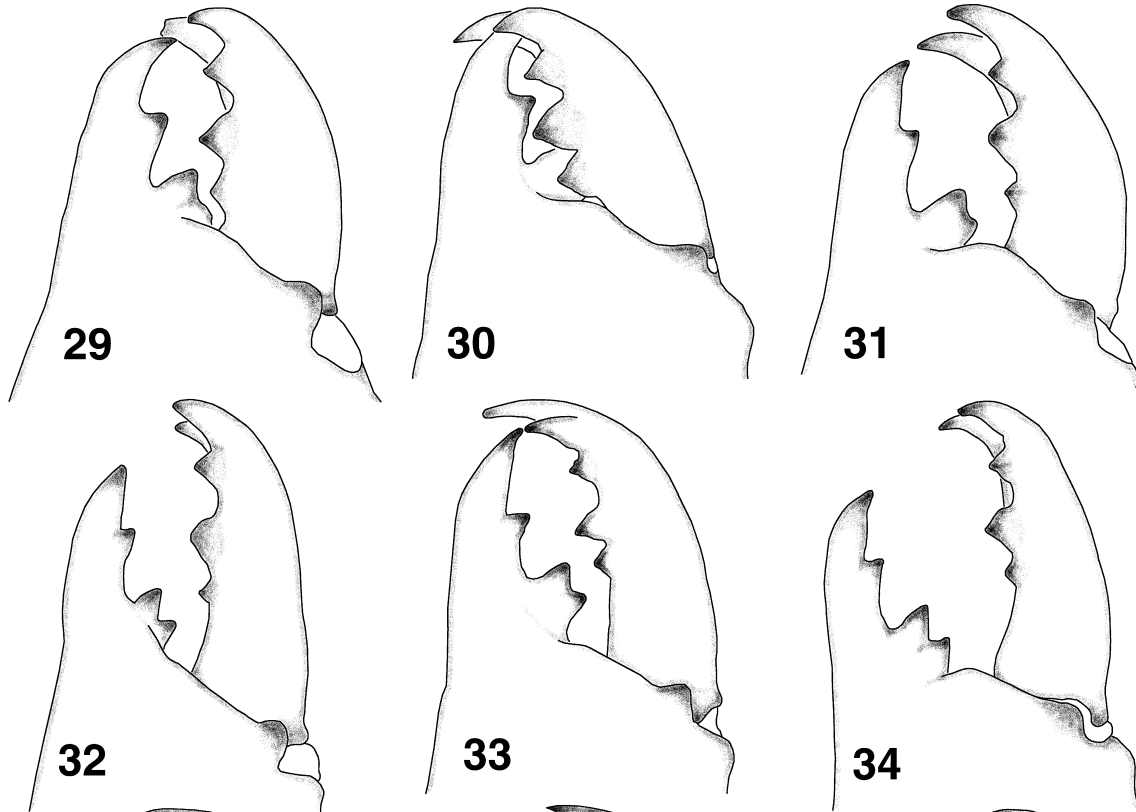
(-): (*Hadogenes*)

The character support for this character is the same as that of Prendini's (2000: Table 6) original analysis, CI/RI = 1/1.

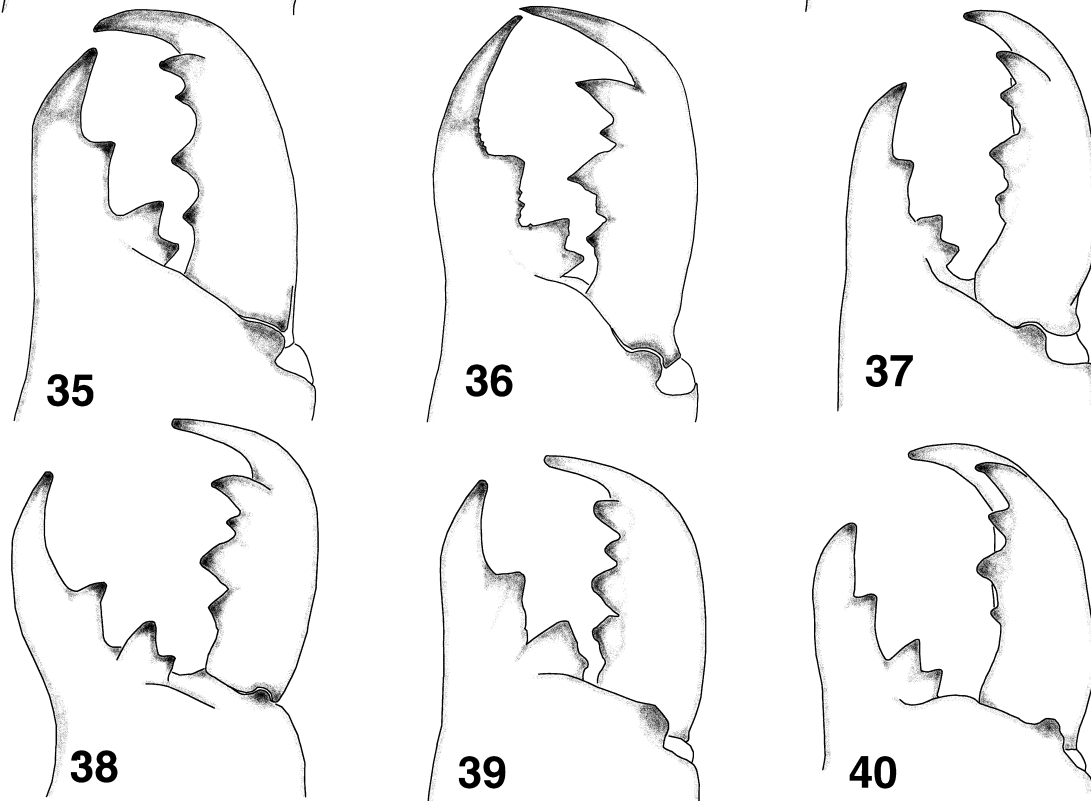
Chelicerae

Prendini's (2000) character 11 deals with the relative development of the distal tines (i.e., dorsal distal (*dd*) and ventral distal (*vd*) denticles) of the cheliceral movable finger. We agree with Prendini's assessment

Hemiscorpiidae



Scorpionidae



Figures 29–40: Chelicerae, dorsal view, of representative genera of families Hemiscorpiidae and Scorpionidae showing the differences between the two families in the relative sizes of the ventral and dorsal distal denticles and the size of the subdistal (*sd*) denticle of the movable finger. **29.** *Heteroscorpion raselimananai*, female holotype. **30.** *Heteroscorpion goodmani*, male paratype. **31.** *Hadogenes troglodytes*. **32.** *Opisthacanthus asper*. **33.** *Liocheles karschii*. **34.** *Opisthacanthus lepturus*. **35.** *Urodacus elongatus*. **36.** *Urodacus yaschenkoii*. **37.** *Heterometrus swammerdami*. **38.** *Scorpio maurus*. **39.** *Opisthophthalmus pugnax*. **40.** *Nebo hierichonticus*.

that subequal *dd* and *vd* (i.e., roughly appposable in alignment) is an important diagnostic character for Hemiscorpiidae, as contrasted with the noticeably unequal denticles exhibited in Scorpionidae and Bothriuridae. Soleglad & Sissom (2001) also used the relative development of these distal denticles in their diagnosis of euscorpoid subfamily Scorpioninae, which has conspicuous appposable denticles.

In Figures 29–40 we illustrate six examples each of this denticle alignment for families Hemiscorpiidae and Scorpionidae, including two species of *Heteroscorpion* and *Urodacus*, the primary subject of this paper. Prendini (2000) stated that the distal denticles in *Heteroscorpion* were unequal (= unappposable). This depiction is clearly incorrect since we see in species *H. raseli-mananai* and *H. goodmani* (Figs. 29–30) that the two distal denticles are appposable, as illustrated for Hemiscorpiidae in our figures. In addition, illustration of *H. magnus* chelicerae by Lourenço & Goodman (2002: Figs. 13–14) also indicates appposable alignment of these denticles.

Within Hemiscorpiidae and Scorpionidae, we see slight variation within “appposable (= subequal)” and “unappposable (= unequal)” distal denticle alignments. In *Urodacus*, we see considerable differences in the relative alignment of these denticles between species *U. elongatus* (Fig. 35) and *U. yaschenkoi* (Fig. 36). In the latter species, the dorsal distal (*dd*) denticle is noticeably smaller than its ventral counterpart, similar to that seen in the scorpionid genus *Scorpio* (Fig. 38). In family Hemiscorpiidae, the denticle alignment of the *Liocheles* as illustrated in Fig. 33, is the same as that in *Heteroscorpion goodmani*, the dorsal tine being slightly smaller than the ventral denticle. In the hemiscorpiid genera *Opisthacanthus* (Figs. 32, 34) and *Hadogenes* (Fig. 31), the dorsal distal denticle is approximately the same size as the ventral denticle.

Also of interest, accompanying these two distal denticle alignments, is the relative size of the single subdistal (*sd*) denticle of the dorsal edge of the cheliceral movable finger. Among Scorpionidae, this denticle is somewhat reduced, being considerably smaller than the adjacent median (*m*) denticle. This, in particular, is quite conspicuous in *Scorpio* (Fig. 38) and *Opisthophthalmus* (Fig. 39); the same is seen in *Urodacus* (Figs. 35–36). Among Hemiscorpiidae, the *sd* denticle is somewhat more robust, e.g. in *Hadogenes* (Fig. 31) and *Opisthacanthus* (Figs. 32, 34); the same is seen in *Heteroscorpion* (Figs. 29–30). We suggest here that the increase in *sd* denticle size in the Hemiscorpiidae may be caused by the longer dorsal edge of the movable finger. This same feature was observed by Soleglad & Sissom (2001) in the euscorpoid subfamily Scorpioninae, which also exhibits substantial *sd* denticles (i.e., two *sd* denticles are present in Euscorpidae) as compared to those found e.g. in genus *Euscorpion*.

Recently, Prendini (2003b), in his revision of the bothriurid genus *Lisposoma*, depicted *L. haringtoni* (referred to as *Brandbergia haringtoni*; see Fet et al., 2004a) as having appposable distal denticles of the cheliceral movable finger. Although, as reported by Prendini (2003b), the distal tines are more unequal in *Lisposoma elegans* and *L. josehermana*, Fet et al. (2004a) disagreed with this depiction as being appposable in the same way as exhibited in Hemiscorpiidae (Figs. 29–34). In fact, the relative alignment of these denticles in *Lisposoma haringtoni* is more unequal than that exhibited in scorpionid genera *Heterometrus* (Fig. 37) and *Nebo* (Fig. 40). The relative alignment differences among three species of *Lisposoma* is similar to that seen in *Urodacus*, as discussed above.

Data matrix change. For the chelicerae we modify one character in Prendini’s data matrix (2000: Table 3) as follows:

Character 11: Alignment of distal denticles (*dd*) and (*vd*) of cheliceral movable finger (*unordered*)

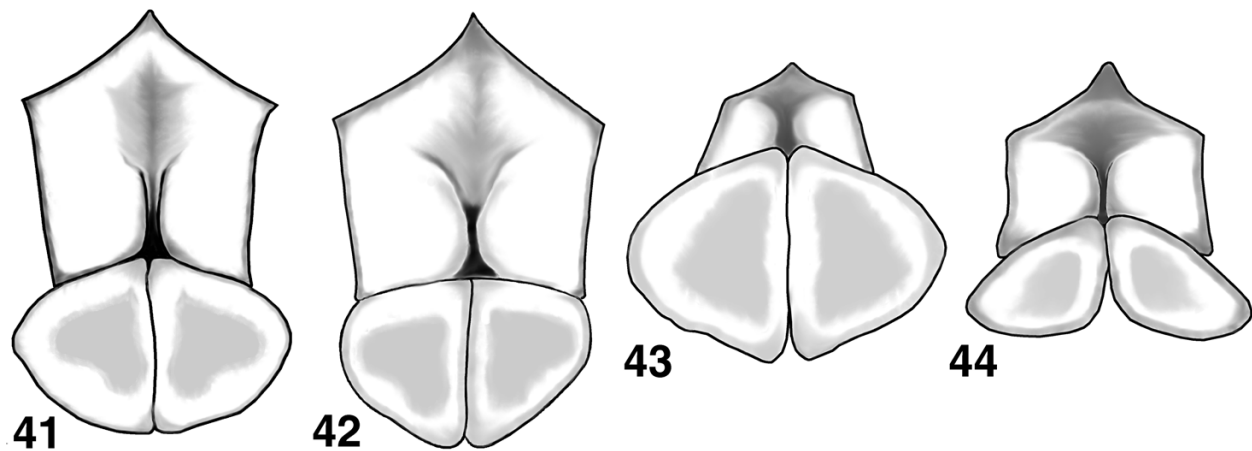
0: subequal (= appposable), $dd \leq vd$ (*Centruroides*, *Chaerilus*, Hemiscorpiidae)

1: unequal, $dd \ll vd$ (Scorpionidae, Bothriuridae)

We changed the state values for *Heteroscorpion* to depict subequal distal denticles (state=0), otherwise this character is as originally specified by Prendini (2000). The character support for this character is slightly better than that of Prendini’s (2000: Table 6) original analysis, CI/RI = 0.500/0.952 vs. 0.500/0.940.

Sternum

Prendini (2000) modeled the sternum (character 9) after three characters proposed by Stockwell (1989) (characters 28–30). This modeling reflected the old interpretation of the sternum based on “shape”, commonly perpetuated by all scorpologists for almost 150 years. Recently, Soleglad & Fet (2003a) reanalyzed the sternum in detail, internally as well as externally, for a large assemblage of Recent scorpion genera. They came to the conclusion that only two basic sternum types exist in Orthostern scorpions: Type 1, attributed to fossil family Palaeopisthacanthidae and three primitive parvorders of Recent scorpions (as defined in Soleglad & Fet, 2003b), Pseudochactida, Buthida, and Chaerilida; and Type 2, attributed to the Recent scorpion parvorder Iurida. Within these two sternum types, Soleglad & Fet (2003a) introduced the notions of horizontal (Type 1) and vertical (Type 2) compression to explain the anteriorly tapered sternum commonly exhibited in parvorder Buthida and the very short and widened sternum of the family Bothriuridae, respectively. Just recently, Fet et al. (2004a: Figs. 17–19) established that the sternum of the



Figures 41–44: Sterna of genera *Heteroscorpion* and *Urodacus*. 41. *H. goodmani*, male paratype. 42. *Heteroscorpion opisthacanthoides*, female. 43. *Urodacus yaschenkoi*, female. 44. *U. elongatus*, male.

primitive bothriurid subfamily Lisposominae exhibits a rudimentary vertical compression with its somewhat shortened sternum. However, in contrast with its sister subfamily Bothriurinae, the sternum of Lisposominae is not as short, nor is there conspicuous separation of the lateral lobes. Consequently, there are three forms of the Type 2 sternum: (1) no vertical compression; (2) rudimentary compression, sternum wider than long, lateral lobes either adjacent or only moderately separated posteriorly; and (3) extensive compression, sternum considerably wider than long, with significant separation between the lateral lobes. In Soleglad & Fet's (2003a: 28–30) discussion concerning the phylogeny of the sternum it was suggested that the Type 2 sternum is derived from the Type 1 sternum, and that the two types of compression described were derivations within these two sternum types. We reflect this hypothesis here by ordering the character representing these sternum types (i.e., character 9). In addition, as suggested by Fet et al. (2004a), we considered the rudimentary form of compression exhibited in Lisposominae as a primitive form of this compression.

Prendini (2000) made an important observation (in part following Stockwell, 1989) that the sterna of certain hemiscorpiid genera, *Liocheles* and *Iomachus* in particular, taper in an anterior to posterior direction (anterior divergence), unusual in scorpions. Unfortunately, Prendini (2000) coupled this observation with the notion of an “equilateral pentagonal” sternum (i.e., state value 3 for his character 9), and therefore only recognized this condition for the two genera mentioned above which complied with both conditions. Soleglad & Fet (2003a: Table 1) reported the anterior divergence for six genera in subfamilies Hormurinae and Hemiscorpiinae. In these cases, the sternum was either roughly equilateral or considerably longer than wide. Since this feature is seen consistently within large aggregates of scorpionoid taxa, and is essentially absent from other scorpion groups, we be-

lieve that this character has diagnostic merit. It can be easily quantified with the morphometric ratio of posterior width (PW) divided by the apex width (AW) (see Figs. 1–2 in Soleglad & Fet (2003a) for sternum terminology and methods of measurement).

Figures 41–44 illustrate the sterna of *Heteroscorpion* and *Urodacus* (for two species of each genus). We see that the sternum of *Heteroscorpion* is longer than wide, with a definite tapering of its posterior portion. In contrast, the sternum of *Urodacus* is either wider than long or subequal, and its posterior portion is wider than the apex width. Table 3 presents morphometric ratio results for seven species of *Urodacus* and three species of *Heteroscorpion* (only *H. magnus* is not included). These data clearly show that in *Heteroscorpion* sternum is longer than wide and diverges anteriorly. Note that Lourenço & Goodman (2002: 60) state for *H. magnus*: “... sternum pentagonal, higher than wider ...”, so for this species we know at least that the sternum is longer than wide, which is consistent with the other three species. It should also be noted that nine paratype specimens of *H. goodmani* were measured for our analysis. In addition to *Heteroscorpion*, these two characters of the sternum are found in hemiscorpiid subfamilies Hormurinae and Hemiscorpiinae. Comparing our Table 3 to that presented by Soleglad & Fet (2003a: Table 1), we see that both morphometric ratios designated here for *Heteroscorpion* are consistent with the same ratios for Hormurinae and Hemiscorpiinae (referred to as Ischnuridae and Hemiscorpiidae in Soleglad & Fet, 2003a), and quite distinct from all other scorpionoid taxa.

Therefore, we consider the sternum of *Heteroscorpion* to be homologous to that present in Hemiscorpiidae. On the other hand, *Urodacus* exhibits the more conventional scorpionid sternum with lateral edges that do not taper posteriorly. These differences are quite apparent in Soleglad & Fet (2003a: Fig. 5) where several hemiscorpiid genera are illustrated, including *Hemiscor-*

	Sternum _L /Sternum _{PW}	Sternum _{PW} /Sternum _{AW}
<i>Urodacus</i>	0.679–1.038 (0.897) [7]	1.019–1.293 (1.109) [7]
<i>Heteroscorpion</i>	1.195–1.436 (1.252) [3*]	0.736–0.906 (0.855) [3]

Table 3: *Sternum* morphometric ratios: minimum, maximum, mean, and number of species. End points of each range is as follows: for *Urodacus*, *U. yaschenkoi* (low) and *U. elongatus* (high); for *Heteroscorpion*, *H. raselimananai* (low) and *H. goodmani* (high). Terminology and method of measurement is based on Soleglad & Fet (2003a: Fig. 1). *The mean of nine male specimens of *Heteroscorpion goodmani* was first calculated and then used in the calculation for the three species.

pius; the sternum of *Urodacus manicatus*, illustrated in the same figure, is consistent with two species of *Urodacus* shown in our Figs. 43–44.

Data matrix change. For the sternum we modify one character in the data matrix of Prendini (2000: Table 3), and create two new characters reflecting two morphometric ratios:

Character 9: Sternum type and substructure (*ordered* (a change))

- 0: Type 1 (*Centruroides*, *Chaerilus*)
- 1: Type 2, no vertical compression (Scorpionidae, Hemiscorpiidae)
- 2: Type 2, sternum exhibits rudimentary *vertical compression* (Lisposominae)
- 3: Type 2, sternum exhibits significant *vertical compression* (Bothriurinae)

The character support for this character is the same as that in the original analysis of Prendini (2000: Table 6), CI/RI = 1/1, although it has been considerably modified.

Character 116: Sternum (Type 2) morphometric ratio: L/PW (*new character, unordered*)

- 0: L << PW (Bothriuridae)
- 1: L <= PW (*Scorpio*, *Pandinus*, *Opisththalmus*, Urodacinae)
- 2: L >> PW (Hormurinae, Hemiscorpiinae, Heteroscorpioninae, Diplocentrinae, *Heterometrus*)
- (-): (*Centruroides*, *Chaerilus*)

The character support for this new character is CI/RI = 0.600/0.935. The encountered homoplasy is due to the longer than wide sternum found independently in Scorpionidae in genus *Heterometrus* and subfamily Diplocentrinae. In other scorpionids, the sternum length is less than, or equal to, its width.

Character 117: Non-compressed sternum (Type 2) morphometric ratio: AW/PW (*new character, unordered*)

- 0: AW <= PW (Scorpionidae)
- 1: AW > PW (Hemiscorpiidae)
- (-): (*Centruroides*, *Chaerilus*, Bothriuridae)

This character exhibits no homoplasy, having a support of CI/RI = 1/1.

Chelal finger dentition

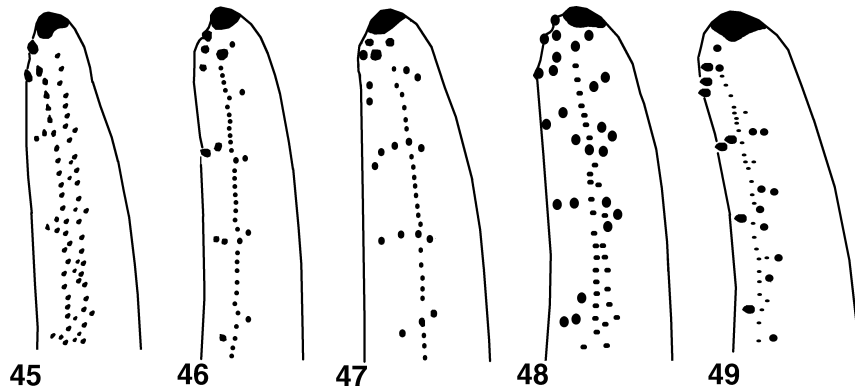
Soleglad & Fet (2003b: 116) questioned the depiction of *Heteroscorpion* by Prendini (2000) as exhibiting “multiple rows” of primary median denticles (MD) (Prendini’s character 33, character state = 2). They countered by stating this genus was equipped with only two MD rows distally, the basal half of the finger exhibiting a more irregular fused collection of denticles (Prendini’s character state value=1). At the time of their analysis, however, Soleglad & Fet (2003b) accepted Prendini’s (2000) assignment of “multiple rows” to genus *Urodacus*.

In the current study, where several species of *Urodacus* were examined, we have concluded that this genus is equipped primarily with two MD rows. In fact, some species, *U. yaschenkoi* (Fig. 46) and *U. novaehollandiae* (Fig. 47), exhibit a single MD row on the distal one-third of the finger. Species *U. elongatus* (Fig. 48) and *U. armatus* (Fig. 49) show traces of a second MD row on the distal aspect of the finger. Also of interest in *Urodacus* is the presence of three or more internal denticles at the extreme distal tip of the movable finger, a condition which reduces usually to two internal denticles further down the finger at denticle group (DG) boundaries (Figs. 46–49). In *Heteroscorpion* (Fig. 45) we see two MD rows at the distal one-third of the finger (verified in two species examined for this paper, plus as illustrated for species *H. opisthacanthoides* by Lourenço, 1996: Fig. 64). Consequently, both genera, *Urodacus* and *Heteroscorpion*, are assigned the same character state (=1) for character 33.

We consider only the bothriurid genera *Urophonius*, *Cercophonius*, and *Centromachetes* as having multiple MD rows (exceeding two) in the scorpionoids (character state value=2 in Prendini, 2000). Other scorpionoid genera usually have some remnant of two rows or less.

Data matrix change. The following changes have been made to character 33:

Character 33: Composition of median denticle (MD) rows of chelal fingers (*unordered*)



Figures 45-49: Diagrammatic pattern of denticle edge of chelal movable finger, distal aspect, showing first three denticle groups (DG). **45.** *Heteroscorpion goodmani*. **46.** *Urodacus yaschenkoi*. **47.** *Urodacus novaehollandiae*. **48.** *Urodacus elongatus*. **49.** *Urodacus armatus*.

0: single MD row (*Centruroides*, *Chaerilus*, Diplocentrinae, Scorpioninae, select hormurines and bothriurids)

1: two MD rows, fused on basal half (Heteroscorpioninae, Hemiscorpiinae, select hormurines, Urodacinae)

2: three or more MD rows (*Urophonius*, *Cercophonius*, *Centromachetes*)

The character support for this new character is CI/RI = 0.333/0.826, as compared to the original result of Prendini (2000: Table 6) of 0.33/0.82.

Chelal carinal configurations

The Hemiscorpiidae have a somewhat distinctive pedipalp chela with a palm that is flat in appearance when viewed laterally. This flat appearance is caused, in part, by the reduction or obsolescence of the dorsosecondary (*D3*) and ventromedian (*V2*) carinae. This same characteristic of the chelal palm was reported for the chactoid family Euscorpidae by Soleglad & Sissom (2001: Fig. 44) where flat appearance, as in Hemiscorpiidae, was caused by the reduction of the *D3* and *V2* carinae. Soleglad & Fet (2004) recently reported a similar flat chela in the chactid subfamily Uroctoninae; again, reduction in carinae *D3* and *V2* was the primary cause of this condition. We analyzed characters 20, 21, and 28 of Prendini (2000), which deal with the development of the *D3* and *V2* carinae. In particular, we were interested in the condition of these carinae in the genera *Urodacus* and *Heteroscorpion*, the subject of this paper.

Characters 20 and 21 model the *D3* carina for male and female, respectively. Prendini (2000) in his modeling characterized *D3* carina in *Heteroscorpion* as distinct. We take exception to this depiction since the two species we studied exhibit a weak, very flat carina with some granulation on its base. Therefore, we have changed the data matrix accordingly. This condition was found on both genders and therefore this data matrix change applies to both characters.

Prendini's (2000) character 28 models the development of the *V2* carina (both genders) where this carina in *Urodacus* was characterized as vestigial to obsolete. We again disagree with this depiction since we see this carina strongly developed, although low-profiled and rounded, in *U. novaehollandiae*, *U. armatus*, *U. hoplurus*, and *U. yaschenkoi*, and at least strongly developed basally in *U. manicatus*. Only in *U. elongatus* the *V2* carina is weak to obsolete. We must stress here that the *V2* carina in *Urodacus* is not as prominent as it is (other) Scorpionidae genera being more rounded, but it certainly is not flat and essentially obsolete as exhibited in Hemiscorpiidae. Therefore, we have changed Prendini's (2000) state assignment for *Urodacus* in the data matrix.

Data matrix changes. We have made alterations to Prendini's (2000) data matrix as discussed above to the three following characters:

Character 20: Development of dorsosecondary (*D3*) carina, male (*unordered*)

0: distinct (*Centruroides*, *Chaerilus*, Bothriuridae, Hemiscorpiinae, Urodacinae, select diplocentrines)

1: obsolete (Hormurinae, Heteroscorpioninae, Scorpioninae, select diplocentrines)

This character exhibits considerable homoplasy, having a support of CI/RI = 0.250/0.786, as compared to Prendini's (2000: Table 6) result of 0.250/0.81.

Character 21: Development of dorsosecondary (*D3*) carina, female (*unordered*)

0: distinct (*Centruroides*, *Chaerilus*, Bothriuridae, Hemiscorpiinae, Urodacinae, select diplocentrines)

1: obsolete (Hormurinae, Heteroscorpioninae, Scorpioninae, select diplocentrines)

This character exhibits considerable homoplasy, having a support of CI/RI = 0.250/0.700, as compared to Prendini's (2000: Table 6) result of 0.250/0.75.

Character 28: Development of ventromedian (*V2*) carina (*unordered*)

0: vestigial to obsolete (Bothriuridae, Hemiscorpiidae, select diplocentrines)

1: distinct (Scorpionidae, select diplocentrines)

(-): (*Centruroides*, *Chaerilus*)

This character exhibits some homoplasy exhibiting a support of $CI/RI = 0.500/0.913$, as compared to Prendini's (2000: Table 6) result of $0.33/0.90$.

Pedipalp patella

In Figures 50–59, we illustrate the dorsal view of the pedipalp patella contrasting representative genera of family Hemiscorpiidae and the genus *Urodacus*. On the basal internal surface of patella are located important Dorsal and Ventral Patellar Spurs (DPS and VPS). As reported by Soleglad & Fet (2003b: 52), this area of the patella surface can sometimes be vaulted, providing a conspicuous projection emanating from the surface. Such a projection for hemiscorpiids (including *Heteroscorpion*) is illustrated in Figs. 50–54. In these genera, not only is the interobasal area of the patella vaulted but significantly developed DPS and VPS are present. Interestingly, these two spurs are connected by an irregular row of granules (illustrated in Soleglad & Fet, 2000b: Fig. 98, for genus *Liocheles*). Further, the base of the projection is lined with granules appearing to be a bifurcation of the dorsoexternal (DE_c) and ventroexternal (VE_c) carinae (i.e., the carinae not only continue on the patellar edge but also branch outward along the projection). An alternative interpretation of these granules is that these are DPS_c and VPS_c carinae shifted more toward the patellar base edges.

In contrast, in *Urodacus* (Figs. 55–59) we see a somewhat flat internal surface of the patella, with a modestly developed DPS and a vestigial VPS. There is no indication of the vaulted projection as found in Hemiscorpiidae. The patella of *Urodacus* is similar to that found in scorpionid subfamilies Diplocentrinae and Scorpioninae.

Prendini (2000) in his character 18 correctly depicts this patellar projection (termed *anterior process* in his paper) as far as the data matrix coding is concerned, so there are no changes in this respect. However, we discuss and illustrate this structure in the hemiscorpiids because it is such an unusual structure exhibiting several novel features as discussed above. We believe this projection as described above provides strong support for the inclusion of *Heteroscorpion* in the family Hemiscorpiidae.

Metasomal ventral median (*VM*) carinae

Prendini (2000) models the number of ventral median (*VM*) carinae for metasomal segments I–IV with his character 95. As common in much of Prendini's (2000) character modeling philosophy, he assigns the same state value to four genera exhibiting a single VM carina, *Urodacus*, *Heteroscorpion*, *Hemiscorpius*, and *Habibiella* (the latter two are in subfamily Hemiscorpiinae). Based on reasons discussed elsewhere in this paper, we consider this mapping much too strong of an assumption of evolution. Although we accept the assignment of the same state to the hemiscorpiine genera to be reasonable, assigning the same state value to the other two genera, each classified under a separate subfamily and family, is by far too strong of an assumption. As a minimum baseline assumption, we believe that assigning different states to the three subfamilies involved is prudent. In the cladistic analysis discussed below, we test this assumption of three individual states. We also consider the situation where *Heteroscorpion* and Hemiscorpiinae are assigned the same state value. This is a stronger assumption, but since they do occupy the same family (i.e., as based on the result where three separate states are assigned), we have some basis for this hypothesis. We compare these two analyses below from a cladistics perspective.

Data matrix change. For the ventral median carinae of the metasoma, we test two changes to Prendini's data matrix (2000: Table 3) as follows:

Character 95 (version 1): Number of *VM* carinae on metasomal segments I–IV (*unordered*)

0: *VM* paired (*Centruroides*, *Chaerilus*, Bothriuridae, Diplocentrinae, Scorpioninae, Hormurinae)

1: *VM* single (Urodacinae)

2: *VM* single (Hemiscorpiinae)

3: *VM* single (Heteroscorpioninae)

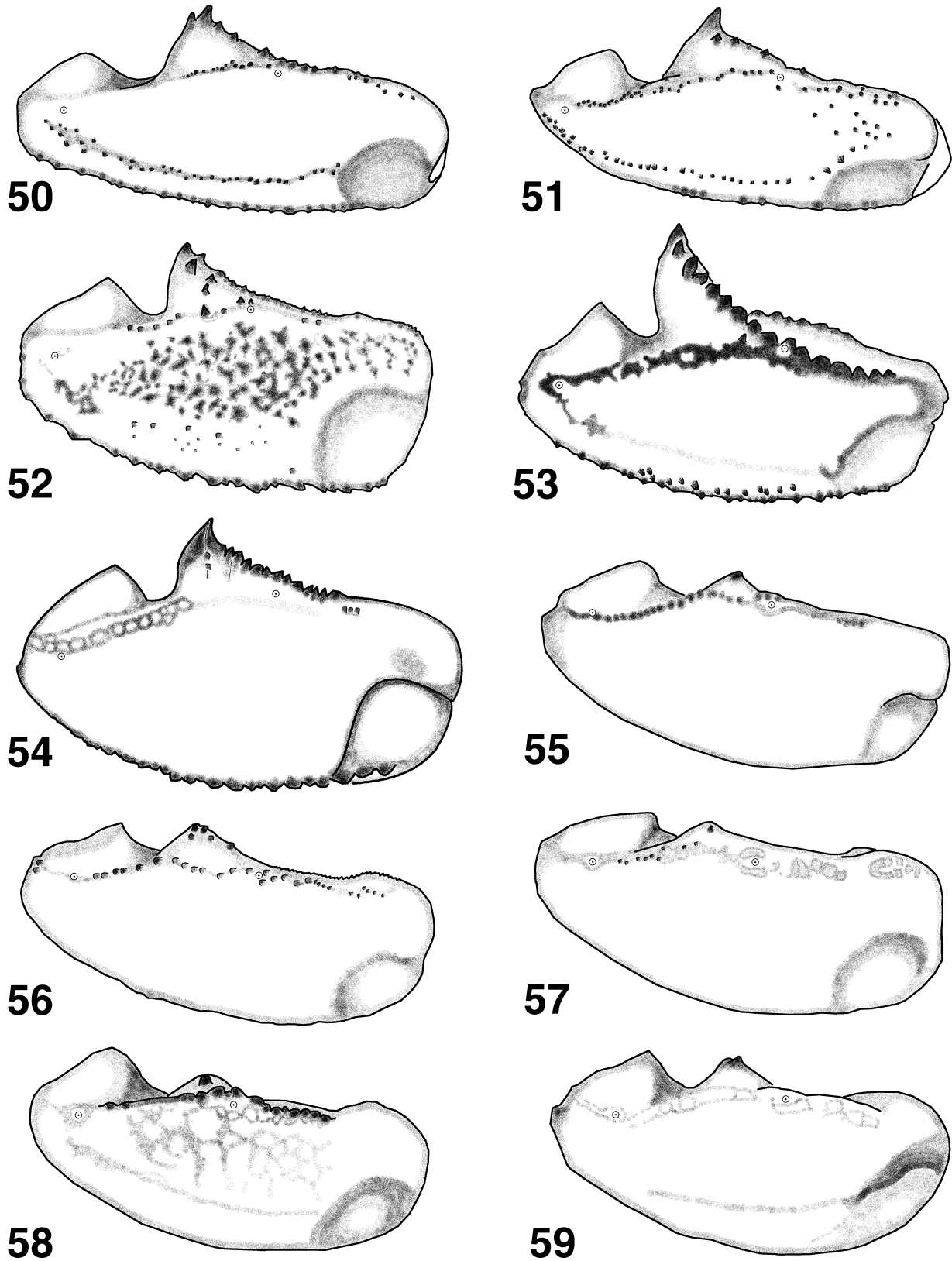
Character 95 (version 2): Number of *VM* carinae on metasomal segments I–IV (*unordered*)

0: *VM* paired (*Centruroides*, *Chaerilus*, Bothriuridae, Diplocentrinae, Scorpioninae, Hormurinae)

1: *VM* single (Urodacinae)

2: *VM* single (Hemiscorpiinae, Heteroscorpioninae)

Neither versions of this character exhibits homoplasy, having a support of $CI/RI = 1/1$ as compared to Prendini's (2000: Table 6) original result, $CI/RI = 0.50/0.83$. In both versions the derivations are unambiguously distributed and constitute a synapomorphy for the respective subfamilies.



Figures 50-59: Pedipalp patella, dorsal view, comparing the development of the internal projection of select hemiscorpiid genera with that of genus *Urodacus*. **50.** *Heteroscorpion raselimananai*, female holotype. **51.** *Heteroscorpion goodmani*, male paratype. **52.** *Opisthacanthus lepturus*. **53.** *Hadogenes troglodytes*. **54.** *Liocheles australasiae*, Papua. **55.** *Urodacus novaehollandiae*. **56.** *Urodacus yaschenkoii*. **57.** *Urodacus hoplurus*. **58.** *Urodacus manicatus*. **59.** *Urodacus armatus*. Note, only dorsal trichobothria, d_1 and d_2 , are shown.

Carapace

Prendini (2000) characterized the height of the median ocular tubercle in his character 2, declaring that Hormurinae and Hemiscorpiinae have a shallow (“flat”) tubercle in contrast to the other scorpionoids whose tubercle was considered “raised”, presumably a primitive condition. Prendini (2000) considered the “flat” ocular tubercle as synapomorphic for his clade Ischnuridae (now Hormurinae) + Hemiscorpiidae (now Hemiscorpiinae). We analyzed this character and found several genera in family Scorpionidae with median ocular tubercle essentially as flat as that commonly seen in some hormurines. For example, the smaller diplocentrine genera, such as *Bioculus* and *Didymocentrus* exhibit very flat ocular tubercles; in two species of *Opisthophthalmus* we also detected very flat ocular tubercles. Consequently, we consider this character questionable due to the inconsistencies spanning no less than two subfamilies in Scorpionidae, and therefore have eliminated it from the analysis.

Leg tarsus

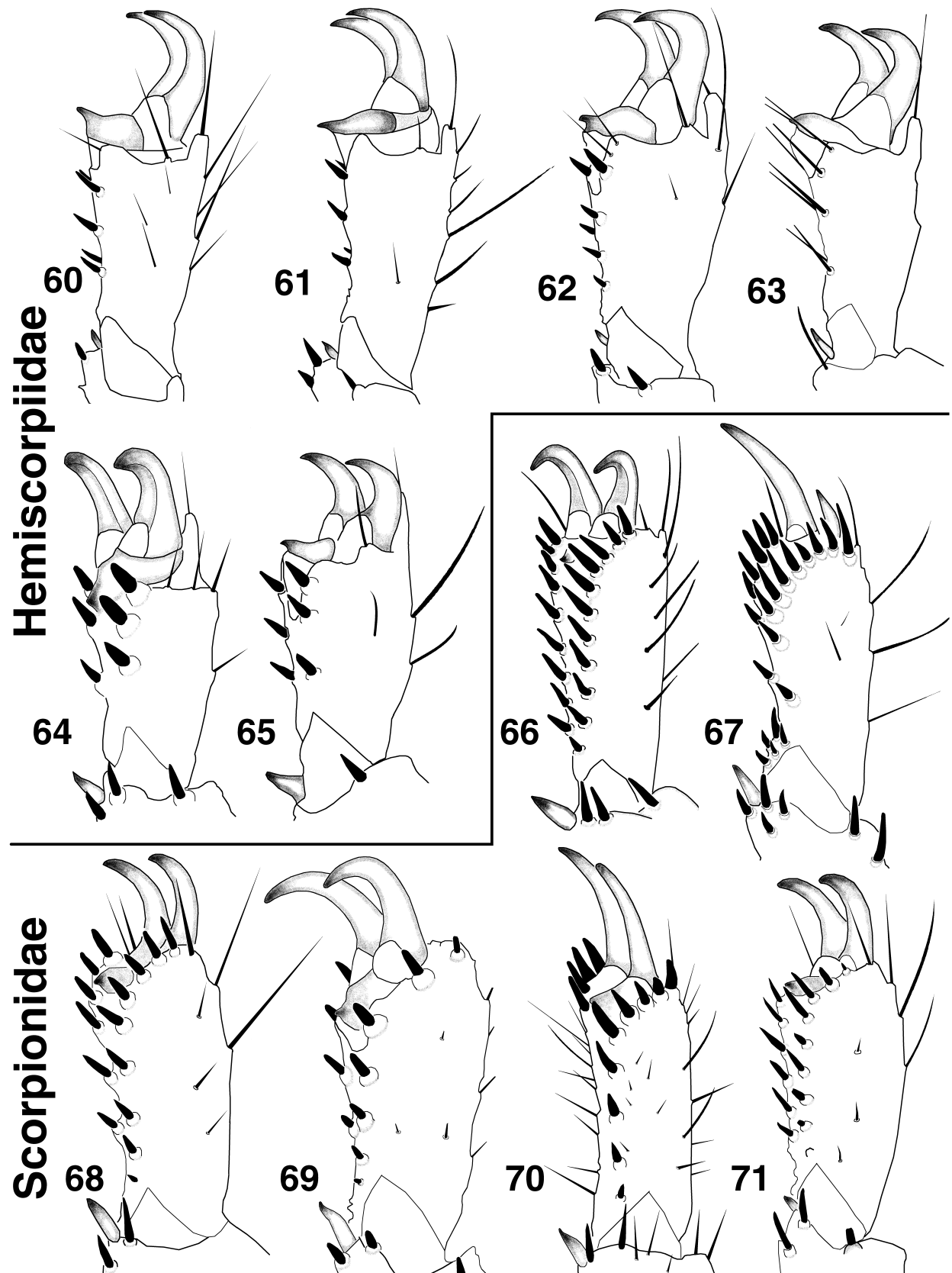
The distal structure of the leg tarsus in the family Scorpionidae (Figs. 66–71) is unprecedented in Recent scorpions, as emphasized already by Birula (1917). Stockwell (1989: 78, Fig. 178) termed the rounded lobe-like tarsus terminus as laterodistal lobes (i.e., occurring on each side, each adjacent to an ungue (= epitarsus)). These lobes extend distally, encasing the base of the unguis and basal aspect of the unguicular spine. The degree of this extension is debatable, however. Stockwell (1989: 78) states “... Of the seven genera of Diplocentridae [note, Soleglad & Fet (2003b) recently downgraded Diplocentridae to a subfamily], only *Nebo* can be said to have laterodistal lobes. Some *Diplocentrus* also have them, but only in the larger species of the genus. ...”. It is our interpretation on Stockwell’s observation that these are only termed lobes if they extend beyond the base of the epitarsus. Prendini (2000), in his character 65, accommodated Stockwell’s interpretation of the diplocentrine tarsus terminus, in part, but ignored Stockwell’s statement that it only applies to the smaller species of *Diplocentrus* (i.e., Stockwell recognized some large *Diplocentrus* species with this condition). Prendini (2000) in his state assignments mapped all diplocentrines, except for the genus *Nebo*, with “truncated” laterodistal lobes. He also ordered this character, suggesting the “truncated laterodistal lobes” in the New World diplocentrines (i.e., tribe Diplocentrini) was derived from the “rounded” lobes.

In either case, whether the lobes extend considerably around the base of the epitarsus as in *Scorpio* (Fig. 68) and *Urodacus* (Figs. 66–67), or do not extend beyond the base of the epitarsus, as seen, for example, in

the small diplocentrine genus *Bioculus* (see Soleglad & Fet, 2003b: Fig. 28), the tarsus terminus is rounded and accommodates lateral setal pairs. In stark contrast in the families Hemiscorpiidae (Figs. 60–65) and Bothriuridae and, incidentally, most other Recent scorpions, we see a truncated “flat” structure of the tarsus terminus where the distal edges do not exhibit setal pairs as that seen in Scorpionidae. We consider this a more precise definition of this unique condition. Consequently, we take exception to Prendini’s terminology of “truncated lobes”, although, in this present paper, we will accept the distinction as well as the ordering of his character 65. The issue concerning which species of *Diplocentrus* have laterodistal lobes similar to those of, for example, *Nebo* will not be addressed here and therefore we left Prendini’s (2000) state mappings for three species of *Diplocentrus* as used in his analysis.

Prendini (2000) adopted Stockwell’s (1989) terminology of ventral median and ventral submedian “setae” in his characters 68–71 and did not discern the important difference between setae and spinules. For example, typically the ventral median row of “setae” found in scorpions is composed of *spinules* (simple extrusions of cuticle), not setae which are socketed (see Soleglad & Fet, 2003b: Fig. 10). This distinction even includes the Iuroidea where the so-called “setaceous tufts” found in the genus *Iurus* and the South American iuroids (*Caraboctonus* and *Hadruroides*) are actually spinule clusters (Soleglad & Fet, 2003b; Fet et al., 2004b). Prendini (2000) used “spiniiform” and “setiform” terminology to distinguish the robustness of the setae: if they were long and thin, they were termed “setiform”, and if short and stout, they were termed “spiniiform”—in either case they are all setae for the “ventral submedian” rows (only the primitive scorpion genus *Pseudochactas* has two rows of ventral submedian spinules).

As stated above, we quantified the leg tarsus terminus structure not only by rounded versus truncated laterodistal lobes, but also by the presence of a large number of paired, socketed stout setae on this terminus in Scorpionidae which are absent in families Hemiscorpiidae and Bothriuridae. Based on this observation, we also see that the number of setal pairs occurring on the entire ventral aspect of the tarsus, including the terminus, is quite different between these families. In Table 4 we show setal counts for a number of major genera spanning families Scorpionidae, Hemiscorpiidae and Bothriuridae, broken down into the prolateral (= internal) and retrolateral (= external) aspects of the tarsus. In many cases, multiple species contributed to this sparse dataset. We see a very reduced number of setal pairs in the hemiscorpiids and bothriurids, typically numbering three. For example, in *Cheloctonus* (two species) we see the lowest number of setae, two prolateral and three retrolateral for all four legs; the same is observed in *Heteroscorpion* (four species). On the other hand, the scor-



Figures 60-71: Leg tarsus (left), ventrolateral view, of representative genera of families Hemiscorpiidae and Scorpionidae. Note differences in the tarsus terminus and the number of paired spinoid setae between the two families. **60.** *Heteroscorpion raselimananai*, female holotype. **61.** *Heteroscorpion goodmani*, male paratype. **62.** *Opisthacanthus lepturus*. **63.** *Liocheles australasiae*, Papua. **64.** *Hadogenes troglodytes*. **65.** *Opisthacanthus asper*. **66.** *Urodacus elongatus*. **67.** *Urodacus yaschenkoi*. **68.** *Scorpio maurus*. **69.** *Heterometrus swammerdami*. **70.** *Opisthophthalmus wahlbergi*. **71.** *Nebo hierichonticus*.

		I	II	III	IV
		Prolateral/ Retrolateral	Prolateral/ Retrolateral	Prolateral/ Retrolateral	Prolateral/ Retrolateral
Scorpionidae	<i>Urodacus</i> (7)	6-9/9-12	6-10/9-12	7-10/9-12	6-10/9-12
	<i>Scorpio</i> (1)	4/8	5/8	6/8	6/8
	<i>Opisththalmus</i> (3)	3-5/7-9	3-5/9	4-5/6-9	4-6/6-9
	<i>Pandinus</i> (1)	–	–	3/5	5/5
	<i>Heterometrus</i> (2)	4-5/6-7	4/5-6	4-5/5-6	4/6
	<i>Nebo</i> (1)	6/8	8/8	8/8	8/9
	<i>Diplocentrus</i> (3)	4-6/5-7	5-7/5-7	6-7/6-8	6-7/6-8
	<i>Bioculus</i> (1)*	3/3	4/4	5/5	5/5
	<i>Cazierius</i> (1)*	3/3	5/5	6/6	6/6
	<i>Didymocentrus</i> (1)*	4/4	4/4	5/5	5/5
Hemiscorpiidae	<i>Heteroscorpion</i> (4)	2/3	2/3	2/3	2/3
	<i>Liocheles</i> (2)	3/3	3/3	3/3-4	3-4/3-5
	<i>Hadogenes</i> (1)	3/3	3/3	3/3	3/3
	<i>Opisthacanthus</i> (2)	2-3/3-4	2-3/3-5	2-3/3-5	2-3/3-5
	<i>Cheloctonus</i> (2)	2/3	2/3	2/3	2/3
Bothriuridae	<i>Bothriurus</i> (3)	0/0	1-2/1-2	3/3	3/3
	<i>Centromachetes</i> (2)	2/2	2-3/2-3	3-4/3-4	3-4/3-4
	<i>Cercophonius</i> (1)	0/0	1/1	2/2	3/2
	<i>Lisposoma</i> (3)	1/1-2	1-2/2-3	3/3	3/3
	<i>Orobothriurus</i> (1)	0/0	2/2	3/3	3/3
	<i>Phoniocercus</i> (2)	0-2/0-1	2-3/2-3	3-4/3	3-4/3
	<i>Urophonius</i> (1)	0/0	2/2	4/4	5/6

Table 4: Lateral ventral setal pair formulae of leg tarsus (I–IV) of representative genera of scorpionoid families Scorpionidae, Hemiscorpiidae and Bothriuridae. Family placements reflect changes made in Soleglad & Fet (2003b) and in this paper. Number in parentheses specifies number of species examined per genus. * Distal rounded tarsal lobes are reduced in this genus.

pionid genus *Urodacus* (Figs. 66–67) has extremely high numbers of setal pairs, the retrolateral edge of the tarsus having as many as twelve on each of the four legs. Even excluding the setal pairs occurring on the laterodistal lobes, we see that the Scorpionidae in general have higher number of setal pairs than families Hemiscorpiidae and Bothriuridae. We consider this clearly increased number of setal pairs in the scorpionids important phylogenetically and therefore have modeled it with a new character. Although there may be some perceived relationship, in part, with the rounded laterodistal lobes found in Scorpionidae (i.e., since setal pairs occur on these lobes and not on the truncated lobes), the higher number of setal pairs found on the basal portion of the tarsus, excluding the terminus, in our opinion, belies this relationship. In addition, the expression of rounded lobes, as perceived by Stockwell (1989) and Prendini (2000), in some Diplocentrinae, further argues against direct relationship.

Also of interest in both *Urodacus* and Scorpionidae is the decreased expression of prolateral tarsus setae and the reduction of the retrolateral ungue in apparently

sand-adapted species. In *Urodacus yaschenkoi* (Fig. 67), the retrolateral ungue is considerably reduced, being less than half the length of the other ungue. Also in this species, the prolateral setae are reduced in number on the main aspect of the tarsus, only showing significant numbers on the terminus. Similarly, *Opisththalmus wahlbergi* (Fig. 70) exhibits a slightly reduced retrolateral ungue and the prolateral setae are only present on the distal terminus of the tarsus, their number being considerably reduced. The asymmetric length of the ungues for psammophilic scorpions is not uncommon, being reported in the vaejovid *Vejovoidus longiunguis* (see Fet et al., 1998: Fig. 8), in certain bothriurid species of *Timogenes*, *Brachistosternus*, and *Vachonia* (L. Acosta, pers. comm.), and the buthid genus *Parabuthus* (Prendini, 2001). Accompanying these unusual configurations in many psammophiles, in part, is a reduction in the setation or spination commonly found on the ventral aspect of the leg tarsus. This is true for *Vejovoidus*, which would normally have a well-developed ventral median row of spinules, and the buthid genus *Liobuthus*, where irregular rows of setae are normally found.

Data matrix change. For the leg tarsus III we create a new character in Prendini's data matrix (2000: Table 3), reflecting the relative number of tarsus ventral setal pairs:

Character 118: Setal/spinule configuration 4: number of ventral setal pairs on leg III (**new character, unordered**)

0: Configuration 4: 2–4 pairs (Hemiscorpiidae, Bothriuridae)

1: Configuration 4: 5–12 pairs (Scorpionidae)

(-): Configurations 2a, 2b (*Centruroides*, *Chaerilus*)

This new character exhibits no homoplasy, having a support of CI/RI = 1/1. The character's distribution is also unambiguous, the increased number of ventral tarsus setae constitutes a synapomorphy for family Scorpionidae.

Results

We conducted two cladistic analyses based on two state value assignment schemes for the modeling of the ventral median (*VM*) carinae found on metasomal segments I–IV (this is discussed above in detail for character 95). The most conservative modeling scheme assumes that a single *VM* carina occurred separately for the three subfamilies exhibiting this condition, Urodacinae, Heteroscorpioninae, and Hemiscorpiinae; that is, we assign a separate state value to each occurrence. Under this scheme, we obtain the topologies depicted in Fig. 73, which resulted in 23,990 Maximum Parsimonious Trees (MPTs) and an overall support of CI/RI/G-Fit = 0.6189/0.9302/-93.451. Under strict consensus of these MPTs, we obtain polytomies within both families Scorpionidae and Hemiscorpiidae, thus providing no resolution for their respective subfamilies. Under majority-rule consensus (i.e., more than 50 % support for any node), the relationships among the subfamilies are resolved, Scorpioninae binding with Urodacinae, and Hemiscorpiinae binding with Hormurinae. However, these two groupings are not fully supported by all 23,990 MPTs, exhibiting 59 % and 69 % support, respectively.

Our second modeling scheme assumes, as a hypothesis, that the single *VM* carina condition on metasomal segments I–IV occurred twice in scorpionoid evolution, for the scorpionid subfamily Urodacinae, and for the hemiscorpiid subfamilies Heteroscorpioninae and Hemiscorpiinae. We can rationalize this modeling scheme, which constitutes a stronger assumption than the previous scheme, by noting that, even under the first scheme, subfamilies Heteroscorpioninae and Hemiscorpiinae group in the same family, Hemiscorpiidae, whereas subfamily Urodacinae is a member of Scorpionidae. In this second scheme we obtain a different topology (Fig. 74) and a much smaller number of MPTs, 992, with an overall support of CI/RI/G-Fit =

0.6189/0.9310/-93.355. In this topology we see a different arrangement of the hemiscorpiid subfamilies, Hemiscorpiinae binding with Heteroscorpioninae rather than Hormurinae. Also of importance is the 100 % support of this topology by all MPTs for each node. Therefore, based on the smaller, more resolved collection of resulting MPTs and the complete support of all nodes by these trees, we consider the topology based on the second scheme to be the most likely one to represent the correct phylogeny of these subfamilies. In either modeling scheme the overall result of this paper, absence of Heteroscorpioninae + Urodacinae monophyly, and placement of Urodacinae in Scorpionidae and Heteroscorpioninae in Hemiscorpiidae, is endorsed by 100 % of MPTs.

The following clades below subfamily level also exhibited 100 % support in all 992 MPTs: **Bothriurinae:** (*Thestylus* + (*Phoniocercus* + ((*Cercophonius* + *Urophonius*) + (... (*Timogenes* + *Vachonia*) ...))); **Diplocentrinae:** (*Nebo* + ((*Bioculus* + *Cazierius* + *Oiclus*) ... (*Diplocentrus* + *Didymocentrus*) ... (*Heteronebo* + *Tarsoporosus*)); **Scorpioninae:** (... (*Heterometrus* + *Pandinus*) ...); **Hormurinae:** (*Opisthacanthus validus* + (*Cheloctonus* + (*Hadogenes* + (... (*Opisthacanthus elatus* + *Iomachus* + *Liocheles*) ... (*Opisthacanthus mada-gascariensis* + *Palaeocheloctonus pauliani*))).

Unresolved clades involve relationships among genera and/or subclades such as *Brachistosternus*, *Bothriurus*, *Orobothriurus*, *Centromachetes*, *Tehuanka*, *Timogenes* + *Vachonia* for subfamily Bothriurinae; subclades listed under Diplocentrinae; *Scorpio* and *Opisthophthalmus* for subfamily Scorpioninae; *Chiomachetes*, *Chiromachus* and subclades listed under **Hormurinae**. One would suspect that if more species were used in each genus that many of these unresolved clades would be rectified (typically, only two species per genus were considered under the "exemplar approach" by Prendini (2000), i.e. less than 20 % of all known species assigned to superfamily Scorpionoidea).

Bootstrap support. In Fig. 72, the resulting topology is presented along with the topologies of Stockwell (1989) and Prendini (2000). For the latter two topologies, bootstrap support is depicted. The topology proposed in this paper has a strong bootstrap support (> 82 %) in all clades except Scorpionidae and Scorpioninae + Urodacinae, which exhibited medium support (57 %), and Heteroscorpioninae + Hemiscorpiinae with low support (33 %). In Prendini's (2000) result, clades of Bothriuridae and Urodacidae + (Scorpionidae + Hemiscorpiidae) showed strong support (74–100 %), Scorpionidae and Hemiscorpiidae exhibited medium to low support (41–47 %), and Scorpionidae + Hemiscorpiidae as a sister group to Heteroscorpioninae + Urodacinae, showed very low support of 18 %.

Observations. Based on the discussions and cladistic results presented in this paper, it is clear to us that the

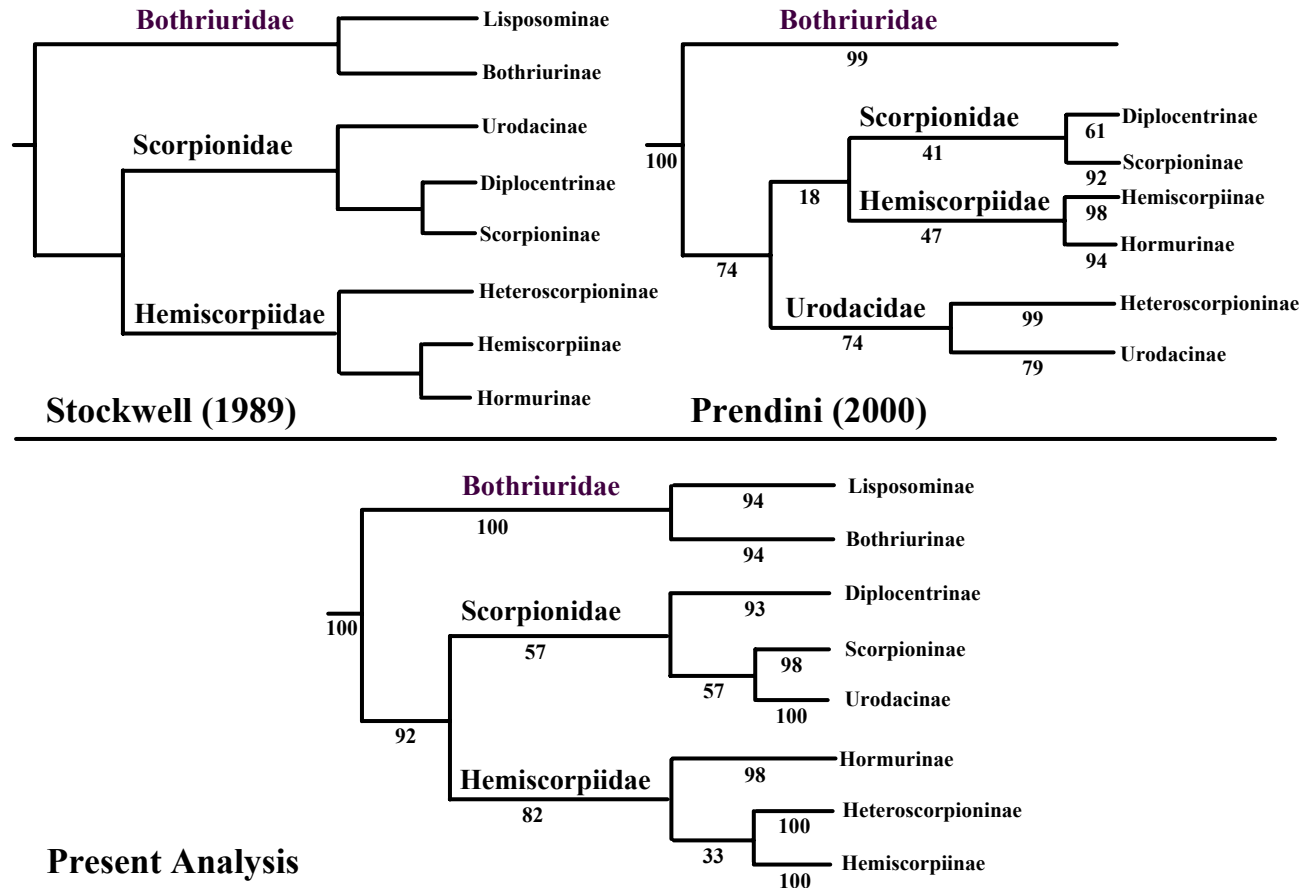


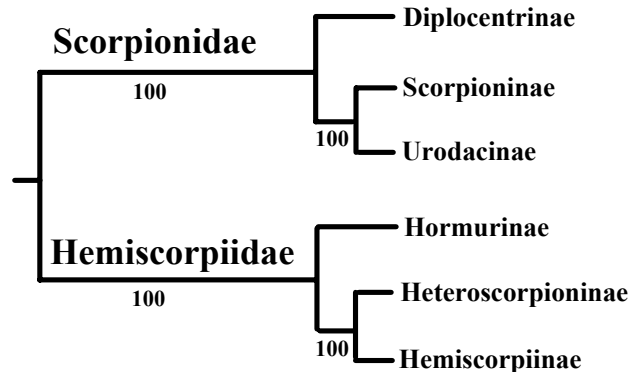
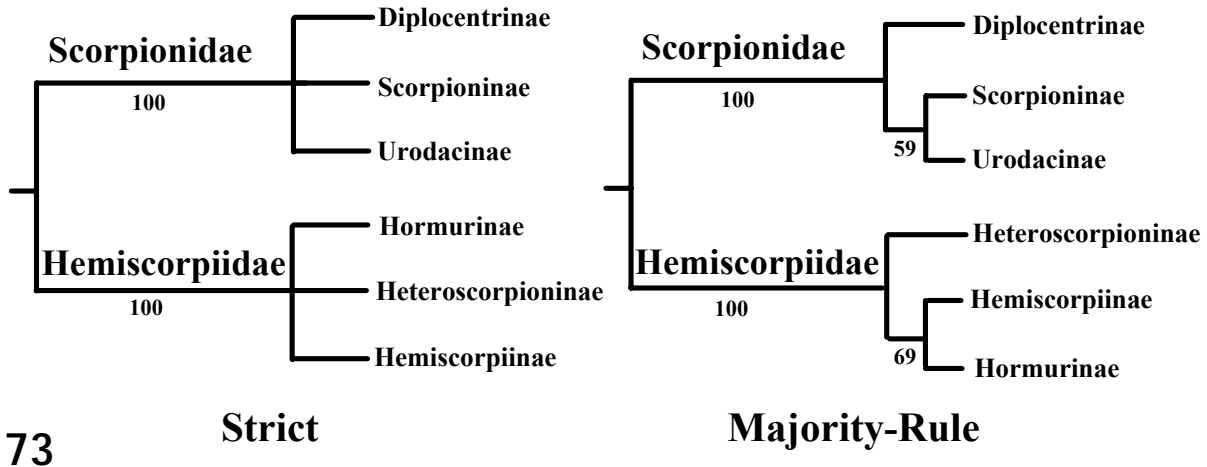
Figure 72: Phylogenies based on Stockwell (1989), Prendini (2000), and the results of our analysis for superfamily Scorpionoidea showing families and subfamilies. Family-group names are those established in this paper and not necessarily levels used by other authors. For Prendini's (2000: Fig. 2) phylogeny, overall support data is CI/RI = 0.55/0.92, and bootstrap results are shown below the branches and are based on a single sequence of 10,000 pseudoreplicates. For the results of our analysis, all nodes are supported by all (100 %) 992 MPTs. Overall support data for our analysis: CI/RI/G-Fit = 0.6189/0.9310/-93.355; bootstrap values are indicated below the branches and represent the mean value of three 1,000 pseudoreplicate sequences.

overall results of Prendini's (2000) analysis of superfamily Scorpionoidea is lacking in many areas and, therefore, one cannot consider it a serious proof of the monophyly of superfamily Scorpionoidea (albeit, we are not questioning this monophyly). There is a tendency in Prendini's (2000, 2003a, 2003b) analytic methodology to approach cladistic analysis in a somewhat rote, cookbook manner—the choice of two or three species per genus regardless of the genus size or complexity (adherence to the “exemplar method”), homology argumentation is always formed around the strongest assumption, characters once defined are never questioned or revised (a desire for “repeatability”). For example, in his revision of *Lisposoma*, Prendini (2003b) used a subset of his scorpionoid dataset from Prendini (2000) without re-evaluating any characters or defining new ones, which, as demonstrated by Fet et al. (2004a), was clearly required. Stockwell's (1989) original analysis, in contrast, which much of Prendini's (2000) characters were based

on, is a much stronger demonstration of monophyly of superfamily Scorpionoidea. This is due in most part to the comprehensive set of outgroups considered in the analysis—all major clades of Recent scorpions were included by Stockwell (1989). In Prendini's (2000) analysis, only the primitive superfamilies of Buthoidea and Chaeriloidea were used (one species each per superfamily), with a complete omission of Scorpionoidea's closest sister groups, the superfamilies Iuroidea and Chactoidea. To demonstrate a monophyly for any in-group, it is mandatory that putative sister groups be included as outgroups.

Character distribution

We present the distribution of character derivations of superfamily Scorpionoidea for 14 nodes of interest, down to the subfamily level (see cladogram in Fig. 72 for location of these nodes). Each derivation (a synapo-



Figures 73-74: Alternative topologies and support for scorpionoid families Scorpionidae and Hemiscorpiidae based on the character state assignments of a single ventromedian (*VM*) carina found on metasomal segments I–IV (character 95). **73.** Subfamilies Urodacinae, Heteroscorpioninae, and Hemiscorpiinae are assigned different state values: Note that for majority-rule consensus of 23,990 MPTs, clades **Scorpioninae + Urodacinae** and **Hemiscorpiinae + Hormurinae** show only 59 % and 69 % support, respectively. **74.** Subfamily Urodacinae is assigned a different state value than subfamilies Heteroscorpioninae and Hemiscorpiinae: Note that all clades are supported by all (100 %) 992 MPTs, both for strict and majority-rule consensus.

morphy) is described as follows: *character_number* (*old_state* = *value1* → *new_state* = *value2*, *U(nambiguous)* | *A(mambiguous)* | *AC(CTRAN only)* | *DE(LTRAN only)*) followed by a brief verbal description. *Value1* and *value2* = 0 - n|(-) = integer|inapplicable. Consult Prendini (2000: Appendix 3) and the discussion above on modified and/or new characters for a detailed description of referenced characters and their state values.

Bothriuridae. Character 9 (state=1 → state=2, U): sternum type 2, rudimentary vertical compression; character 10 (state=0 → state=1, U): dorsal edge of cheliceral movable finger with two subdistal (*sd*) denticles; character 23 (state=0 → state=1, U): digital (*DI*) carina of chela obsolete; character 26 (state=0 → state=1, U):

ventroexternal (*VI*) carina of chela obsolete; character 27 (state=1 → state=3, U): ventroexternal (*VI*) carina of chela oblique to horizontal axis of palm; character 50 (state=(-) → state=0, DE): chelal trichobothria V_2-V_3/V_3-V_4 ratio equals <1 - 1.2 (1.1); character 56 (state=0 → state=1, U): chelal trichobothrium Et_2 located on ventral surface; character 58 (state=0 → state=1, U): chelal trichobothrium *db* located on distal aspect of palm; character 60 (state=(-) → state=0 DE): chelal trichobothrium *dsb* below *db-dst* axis; character 62 (state=(-) → state=0, DE): chelal trichobothrium *eb* proximal of articulation membrane and below *esb-est-et* axis; character 68 (state=0 → state=1, U): ventromedian row of “setae” on leg tarsus “setiform”; character 85 (state=0 → state=1, U): internal wall of sperm duct of

paraxial organ with semilunar shelf; character 99 (state=0 ↔ state=(-), A): distal portion of ventromedian (*VM*) carina of metasomal segment V straight; character 111 (state=0 → state=2, AC): ventral surface of telson vesicle smooth; character 116 (state=(-) → state=0, DE): sternum, length (L) << posterior width (PW).

Lisposominae. Character 44 (state=0 → state=1, U): patellar trichobothrium v_3 located on external surface; character 89 (state=0 → state=1, U): hemispermatophore lamellar hook located distally; character 111 (state=0 → state=2, DE): ventral surface of telson vesicle smooth.

Bothriurinae. Character 9 (state=2 → state=3, U): sternum type 2, significant vertical compression; character 16 (state=0 → state=1, U): external (*E*) carina of chela obsolete; character 80 (state=2 → state=1, U): sclerites of genital operculum of female loosely joined; character 81 (state=0 → state=1, U): sclerites of genital operculum of male loosely joined; character 86 (state=0 → state=1, U): distal lamina of hemispermatophore with prominent crest; character 96 (state=0 → state=1, AC): metasomal carinae of segments I–IV are more prominently developed on segments I–II than on segments III–IV.

Scorpionidae + Hemiscorpiidae. Character 3 (state=0 → state=2, U): median notch of carapace anterior edge deeply developed; character 4 (state=0 → state=1, U): median longitudinal furrow of carapace narrowly suturiform; character 7 (state=0 → state=1, U): posterior sutures of carapace present; character 50 (state=0 → state=1, AC): chelal trichobothria V_2-V_3/V_3-V_4 ratio equals 1.2 – 2.1 (mean 1.61); character 52 (state=0 → state=1, U): chelal trichobothrium *Dt* positioned at midpoint of palm; character 59 (state=0 → state=1, U): chelal trichobothrium *db* positioned on internal surface; character 60 (state=0 → state=1, A): chelal trichobothrium *dsb* inline with *db-dst* axis; character 62 (state=0 → state=1, A): chelal trichobothrium *eb* positioned midway on fixed finger inline with *esb-est-et* axis; character 77 (state=0 → state=1, U): embryonic development katoikogenic; character 78 (state=0 → state=1, U): ovariuterine follicles stalked; character 105 (state=0 → state=1, AC): telson aculeus short, sharply curved; character 110 (state=0 → state=1, AC): anterodorsal lateral lobes of telson vesicle absent; character 116 (state=0 → state=2, A): sternum length(L) > posterior width (PW); character 117 (state=(-) → state=0, AC): sternum anterior width (AW) <= posterior width (PW).

Scorpionidae. Character 11 (state=0 → state=1, DE): cheliceral dorsal distal (*dd*) denticle of movable finger considerably shorter than ventral distal (*vd*) denticle; character 16 (state=0 → state=1, AC): external (*E*) carina of chela obsolete; character 28 (state=0 →

state=1, AC): ventromedian (*V2*) carina of chela distinct; character 50 (state=(-) → state=1, DE): chelal trichobothria V_2-V_3/V_3-V_4 ratio equals 1.2 – 2.1 (mean 1.61); character 52 (state=1 → state=2, AC): chelal trichobothrium *Dt* positioned at distal aspect of palm near base of fixed finger; character 65 (state=0 → state=1, U): laterodistal lobes of leg tarsus rounded; character 117 (state=(-) → state=0, DE): sternum anterior width (AW) <= posterior width (PW); character 118 (state=0 → state=1, U): 5–12 ventral setal pairs on leg tarsus.

Diplocentrinae. Character 16 (state=0 → state=1, DE): external (*E*) carina of chela obsolete; character 52 (state=2(1) → state=3(3), A): chelal trichobothrium *Dt* positioned proximal end of fixed finger; character 88 (state=0 → state=1, U): lamellar hook and median lobe of hemispermatophore fused; character 89 (state=0 → state=(-), U): hemispermatophore lamellar hook position inapplicable; character 90 (state=0 → state=(-), U): hemispermatophore lamellar hook composition inapplicable; character 105 (state=0 → state=1, DE): telson aculeus short abruptly curved; character 106 (state=0 → state=1, U): telson subaculear tubercle distinct; character 110 (state=1 → state=0, AC): anterodorsal lateral lobes of telson vesicle present; character 114 (state=0 → state=1, U): venom pigment is reddish.

Scorpioninae + Urodacinae. Character 28 (state=0 → state=1, DE): ventromedian (*V2*) carina of chela distinct; character 68 (state=0 → state=2, U): ventromedian row of spinules on leg tarsus absent; character 72 (state=0 → state=1, U): retrolateral row of macrochaete setae on basitarsus I–II spiniform; character 73 (state=(-) → state=0, U): reduction of retrolateral row of macrochaete setae on basitarsus I–II from three or more to two is absent; character 105 (state=1 → state=0, AC): telson aculeus long and slightly curved; character 110 (state=0 → state=1, DE): anterodistal lobes of telson vesicle absent; character 116 (state=2 → state=1, U): sternum posterior width (PW) >= length (L).

Scorpioninae. Character 15 (state=0 → state=1, U): dorsal surface of pedipalp patella convex; character 16 (state=0 → state=1, DE): dorsoexternal (*DE_c*) carina of pedipalp patella obsolete; character 22 (state=0 → state=1, U): dorsosecondary (*D3*) carina of chela extending part way across dorsal surface, subdigital (*D2*) carina extending part way across in opposite direction; character 34 (state=0 → state=1, U): dentate margins of chelal fingers noticeably scalloped; character 41 (state=0 → state=1, U): patellar trichobothrium *d₂* located on internal surface; character 51 (state=0 → state=1, U): chelal trichobothrium *Db* located on dorsal surface; character 52 (state=1 → state=2, DE): chelal trichobothrium *Dt* positioned at distal half of palm near base of fixed finger; character 75 (state=(-) → state=0, AC): stridulatory

mechanism formed as a “rasp” on pedipalpal coxae and a “scraper” on coxae of legs I.

Urodacinae. Character 1 (state=1 → state=2, U): lateral eyes two per side; character 16 (state=1 → state=0, AC): external (*E*) of chela distinct; character 20 (state=1 → state=0, U): dorsosecondary (*D3*) carina of chela distinct (male); character 21 (state=1 → state=0, U): dorsosecondary (*D3*) carina of chela distinct (female); character 29 (state=1 → state=0, U): ventrointernal (*V3*) carina of chela more strongly developed than interomedian (*I*) carina which may be obsolete; character 33 (state=0 → state=1, U): two rows of median denticles (MD) are found on chelal fingers; character 43 (state=1 → state=7, U): major neobothriotaxy present on ventral surface of patella (state = 7); character 45 (state=1 → state=7, U): major neobothriotaxy present on external surface of patella (state = 7); character 49 (state=2 → state=8, U): major neobothriotaxy present on ventral surface of chela (state = 8); character 52 (state=2(1) → state=0, A): chelal trichobothrium *Dt* positioned at proximal aspect of palm; character 53 (state=0 → state=1, U): major neobothriotaxy present on external surface of chela (state = 1); character 59 (state=1 → state=0, U): chelal trichobothrium *db* positioned on dorsal surface; character 72 (state=1 → state=2, U): retrolateral row of macrochaete setae on basitarsi I–II setiform, in form of a “sand comb”; character 92 (state=0 → state=1, U): sclerotized mating plug of hemispermatophore present; character 95 (state=0 → state=1, U): ventral median (*VM*) carinae of metasomal segments I–IV is single (state = 1); character 99 (state=0 → state=1, U): distal aspect of ventral median (*VM*) carina of metasomal segment V bifurcated.

Hemiscorpiidae. Character 8 (state=0 → state=1, U): nongranular surfaces of prosoma, mesosoma, metasoma and legs punctate; character 11 (state=1 → state=0, AC): cheliceral dorsal distal (*dd*) denticle of movable finger subequal in length to the ventral distal (*vd*) denticle; character 33 (state=0 → state=1, U): two rows of median denticles (MD) are found on chelal fingers; character 50 (state=1(-) → state=2, A): chelal trichobothria V_2-V_3/V_3-V_4 ratio equals 2.3 – 6.3 (mean 4.04); character 107 (state=0 → state=1, U): telson vesicle of male is laterally flattened; character 108 (state=0 → state=1, AC): telson vesicle of female is laterally flattened; character 110 (state=0 → state=1, DE): anterolateral distal lobes of telson vesicle absent; character 113 (state=0 → state=1, U): venom glands simple; character 117 (state=0 → state=1, A): sternum anterior width (AW) wider than posterior width (PW).

Hormurinae. Character 3 (state=2 → state=1, U): median notch of carapace shallow; character 30 (state=0 → state=1, U): ventrointernal (*V3*) carina of chela less developed than interomedian (*I*) carina, sometimes obso-

lete; character 35 (state=0 → state=1, U): lobe of chelal movable finger, which is rounded dorsally and without a tooth, is well-developed on the male; character 55 (state=0 → state=1, U): chelal trichobothrium *Est* is located medially on the palm; character 61 (state=0 → state=1, U): chelal trichobothrium *esb* located on palm proximal of articulation membrane of movable finger; character 62 (state=1 → state=0, U): chelal trichobothrium *eb* located on palm proximal of articulation membrane of movable finger and below *esb-est-et* axis; character 76 (state=0 → state=1, U): anterior aspect of maxillary lobes I extend beyond lobes II and taper inward.

Heteroscorpioninae + Hemiscorpiinae. Character 18 (state=0 → state=1, U): anterior process well developed on internal surface of pedipalp patella; character 29 (state=1 → state=0, U): ventrointernal (*V3*) carina of chela more developed than interomedian (*I*) carina which may be obsolete; character 95 (state=0 → state=2, U): ventral median (*VM*) carinae of metasomal segments I–IV is single (state=2).

Heteroscorpioninae. Character 1 (state=1 → state=2, U): lateral eyes two per side; character 43 (state=1 → state=5, U): major neobothriotaxy present on ventral surface of patella (state=5); character 45 (state=1 → state=5, U): major neobothriotaxy present on external surface of patella (state=5); character 49 (state=2 → state=6, U): major neobothriotaxy present on ventral surface of chela (state=6); character 52 (state=1 → state=0, U): chelal trichobothrium *Dt* located on proximal aspect of palm; character 59 (state=1 → state=0, U): chelal trichobothrium *db* located on dorsal surface of fixed finger; character 105 (state=1 → state=0, AC): telson aculeus long and shallowly curved; character 108 (state=0 → state=1, DE): telson vesicle laterally flattened in female.

Hemiscorpiinae. Character 20 (state=1 → state=0, U): dorsosecondary (*D3*) carina of chela (male) distinct; character 21 (state=1 → state=0, U): dorsosecondary (*D3*) carina of chela (female) distinct; character 48 (state=0 → state=1, U): chelal trichobothria *ib-it* positioned medially on fixed finger; character 51 (state=0 → state=1, U): chelal trichobothrium *Db* located on dorsal surface of palm; character 52 (state=1 → state=3, U): chelal trichobothrium *Dt* located on base of fixed finger; character 70 (state=0 → state=1, U): ventrosulmedian setae of leg tarsus slender and spiniform; character 105 (state=0 → state=1, DE): telson aculeus short and abruptly curved; character 108 (state=1 → state=0, AC): telson vesicle not laterally flattened in female; character 109 (state=0 → state=1, U): telson vesicle of male elongated with a pair of distal lobes.

Systematics

Comments on family-group nomenclature

The name of scorpion family Ischnuridae Simon, 1879, which has been commonly used in the recent decades (Fet, 2000b) has been found to be a senior homonym of a damselfly subfamily Ischnurinae Fraser, 1957 (Insecta, Odonata) (Fet & Bechly, 2000, 2001). The case was addressed to the International Commission for Zoological Nomenclature, which ruled (ICZN, 2003) that the substitute name Liochelidae Fet et Bechly, 2001, will have precedence over Ischnuridae Simon, 1879. This ruling, however, did *not* award the name Liochelidae precedence over the available junior synonyms of Ischnuridae. Therefore, Soleglad & Fet (2003b) were incorrect in interpreting the name Liochelidae as a valid family name, since several senior synonyms were available. Of these, the priority belongs to Hormurini Laurie, 1896. Although this name has not been used for 80 years (Fet, 2000b) and is based on *Hormurus* Thorell, 1876, which is a junior synonym of *Liocheles* Sundevall, 1833, Hormurini still has the priority (Article 40.1 of the Code). In fact, the same principle applies here as has been applied to Ischnuridae before its replacement: *Ischnurus* C. L. Koch, 1837 has been a junior synonym of *Liocheles* Sundevall, 1833, which did not affect the family name.

It follows that Soleglad & Fet (2003b), when they first merged Liochelidae and Hemiscorpiidae, should have used subfamily name Hormurinae as an available senior synonym instead of Liochelinae, and should have accepted Hemiscorpiidae as a senior family name.

As a result of this current revision, we restore by priority the valid family name Hemiscorpiidae Pocock, 1893, with three subfamilies: Hemiscorpiinae Pocock, 1893; Heteroscorpioninae Kraepelin, 1905; and Hormurinae Laurie, 1896. The latter replaces the subfamily name Liochelinae Fet & Bechly, 2001.

The amended definitions of families Hemiscorpiidae and Scorpionidae are presented below. The current taxonomy of Recent scorpions, including the changes established in this paper, is shown in Table 6.

Family Hemiscorpiidae Pocock, 1893 (amended composition)

Type Genus. *Hemiscorpius* Peters, 1861.

Synonyms.

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

Liochelidae Fet et Bechly, 2001 (1879), **new synonymy**; type genus *Liocheles* Sundevall, 1833

Other available family names used.

Heteroscorpionidae Kraepelin, 1905 (valid as subfamily name); type genus *Heteroscorpion* Birula, 1903.

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. As recognized here, family Hemiscorpiidae includes three subfamilies (Hemiscorpiinae, Heteroscorpioninae, and Hormurinae) and 11 genera, predominantly from the Old World (only some species of *Opisthacanthus* are found in the New World).

The content of Hemiscorpiidae is dramatically changed here compared to that of Prendini (2000), who was last to use this family name. We accept this name as the oldest available family-group synonym of Liochelidae Fet & Bechly, 2001 (1879). The subordinate subfamily name Hormurinae Laurie, 1896, is restored from synonymy; it includes all eight genera listed by Soleglad & Fet (2003b) under Liochelinae Fet & Bechly, 2001 (Table 6). We also transfer to Hemiscorpiidae the monotypic subfamily Heteroscorpioninae (from the abolished scorpionoid family Urodacidae), which includes one endemic Madagascan genus, *Heteroscorpion* (four species; Fet, 2000a; Lourenço & Goodman, 2002, 2004). See Soleglad & Fet (2003b) for the detailed taxonomic history.

Distribution. Asia, Africa (with Madagascar), Australia, Oceania, Caribbean, Central and South America.

Biogeographic history. Inclusion of Heteroscorpioninae adds an endemic, monotypic Madagascan subfamily to Hemiscorpiidae but does not dramatically change biogeographic patterns of this family as outlined (under the name Liochelidae) by Soleglad & Fet (2003b). Lourenço (1996a, 1996b, 2001) discussed *Heteroscorpion* in the context of endemic fauna of Madagascar, which generally is related to the African fauna, diverging with the split of Gondwanaland. Assuming the phylogeny of Hemiscorpiidae as shown at Fig. 72, Heteroscorpioninae represents the sister group of Hemiscorpiinae. Separation of the block including Madagascar and India from Africa is dated 165–121 Mya (late Jurassic-early Cretaceous) (Vences et al., 2001; Chakrabarty, 2004). In our scenario, Heteroscorpioninae lineage appears to have been isolated on Madagascar during this split. At the same time, the arid-adapted taxa of Hemiscorpiinae now survive only in the East Africa and Middle East. The common ancestor of these two subfamilies, therefore, could have been present in the African portion of Gondwanaland prior to Jurassic.

The subfamily Hormurinae in our topology forms an outgroup to the Heteroscorpioninae + Hemiscorpiinae clade, and thus represents the most ancient hemiscorpiid lineage. Therefore, the split between Hormurinae and Heteroscorpioninae + Hemiscorpiinae lineages should have occurred *long before* Gondwanaland fragmentation (otherwise the monophyly of Hormurinae would be challenged). Genera of Hormurinae survived across the

Parvorder	Superfamily	Family	Subfamily	Tribe	Genus
Pseudochactida Buthida	Pseudochactoidea Buthoidea	Pseudochactidae			<i>Pseudochactas</i>
		Buthidae			<i>Afroisometrus, Akenirobuthus, Alayoityyus, Ananiteris, Androctonus, Anomalobuthus, Apistobuthus, Australobuthus, Babycurus, Balloorthochirus, Birulatus, Buthacus, Butheloidea, Butholus, Buthus, Darche-cus, Buthoscorpio, Buthus, Centruroides, Charmus, Cicileus, Compsobuthus, Congobuthus, Darche-lia, Egyptobuthus, Grosphus, Hemibuthus, Hemilychias, Himalayoityyobuthus, Hottentotta, Iranobut-hus, Isometroides, Isometrus, Karasbergia, Kraepelinia, Lanzatus, Leiurus, Liobuthus, Lissothus, Lychas, Lychastioides, Mesobuthus, Mesoitoyus, Microbuthus, Microityyus, Neogrosphus, Odontobut-hus, Odonturus, Orthochiroidea, Orthochirus, Parabuthus, Paraorthochirus, Pectinibuthus, Ple-siobuthus, Polisius, Psammobuthus, Pseudolissothus, Pseudolychias, Pseudouroplectes, Razianus, Rhopalurus, Sabinebuthus, Sassanidothus, Simonoidea, Somalibuthus, Somalicharmus, Thaicharmus, Tityobuthus, Tityopsis, Tityus, Troglorhopalurus, Troglotyobuthus, Uroplectes, Uroplectoidea, Yachoniolus, Yachonus, Zabius</i>
Chaerilida Iurida	Chaeriloidea Iuroidea	Microcharmidae			<i>Microcharmus, Neoprotobuthus</i>
		Chaerilidae	Chaerilinae		<i>Chaerilus</i>
		Iuridae			<i>Calchas, Iurus</i>
		Caraboctonidae	Caraboctoninae Hadruirinae		<i>Caraboctonus, Hadruroides Hadurus, Hoffmannihadurus</i>
		Scorpionidae	Scorpioninae Urodacinae Diplocentrinae	Diplocentrimi Nebini	<i>Heterometrus, Opistophthalmus, Pandinus, Scorpio Urodacus Bioculus, Cazierius, Didymocentrus, Diplocentrus, Heteronebo, Oiclus, Tarsoporosus Nebo</i>
		Hemiscorpiidae	Hormurinae		<i>Chelocentrus, Chironachetes, Chironachus, Hadogenes, Iomachus, Liocheles, Opisthacanthus, Palaeochelocentrus</i>
			Hemiscorpiinae Heteroscorpioninae		<i>Habibiella, Hemiscorpius Heteroscorpion</i>
		Bothriuridae	Bothriurinae Lisposominae		<i>Bothriurus, Brachistosternus Brazilobothriurus, Centromachetes, Cercophonius, Orobothriurus, Pachakutej, Phonicercus, Tehuankea, Thesylus, Timogenes, Urophonius, Yachonia Lisposoma</i>
		Chactidae	Chactinae	Chactini Nullibrotheimi Brotheimi Belisarini	<i>Chactas, Teuthraustes, Yachoniochactas Nullibrotheas Subtribe Brotheina: Broteo-chactas, Brotheas, Hadrurochactas Subtribe Neochactina: Neochactas Belisarius Anuroctonus, Uroctonus</i>
		Euscorpidae	Euscorpinae Megacorminae	Megacormini Chactopsini Scorpiopini Trogllocormini	<i>Euscorpius Megacormus, Plestiochactas Chactopsis Alloscorpions, Dasyscorpions, Euscorpions, Neoscorpions, Parascorpions, Scorpiops Trogllocormus</i>
		Supersittioniidae	Supersittioniinae Typhlochactinae		<i>Supersittionia, Troglotayosicus Alacran, Sotano-chactas, Typhlochactas</i>
		Vaejovidae			<i>Paravaejovis, Paruroctonus, Pseudouroctonus, Serradigitus, Smeringurus, Syntropis, Uroctonites, Vaejovis, Vaejovoides</i>

Table 6: Taxonomy of Recent Scorpions (Order Scorpiones, Suborder Neoscorpionina, Infraorder Orthostemi). After Soleglad & Fet (2003b), with amendments from Fet et al. (2004a, 2004b), Kovařík (2004b), Lourenço et al. (2004), and the present paper.

Gondwanaland fragments (Africa, Madagascar, India, and South America); presence of the genus *Liocheles* in Australasia and Oceania is probably due to secondary dispersal from India. The scorpion fauna of Madagascar includes two endemic hormurine genus-group taxa, genus *Palaeocheloctonus* Lourenço, 1996 and subgenus *Monodopisthacanthus* Lourenço, 2001 (Lourenço, 1996a, 1996b, 2001). Their ancestors appear to have been also captured on Madagascar after its Jurassic split, along with distantly related Heteroscorpioninae.

Thus, the common ancestor of Hemiscorpiidae as a group could have an early Gondwanaland origin; there is no biogeographic or fossil data to confirm hemiscorpiid presence in Laurasia (compare below with Scorpionidae).

The most ancient scorpionoid fossil is the genus *Protoischnurus* Carvalho & Lourenço, 2001 (extinct family Protoischnuridae Carvalho & Lourenço, 2001) from the Lower Cretaceous of Brazil (Crato Formation). Carvalho & Lourenço (2001) commented that *Protoischnurus* shows some affinities to the modern families Scorpionidae and Ischnuridae (now Hemiscorpiidae). Additional data from Crato fossils (our observations; F. Menon and P. Selden, pers. comm.) allow suggesting that *Protoischnurus* can be placed closer to Hemiscorpiidae than to Scorpionidae. By most recent estimates, the split of South America from Africa is dated 101–86 Mya (mid-Cretaceous) (Vences et al., 2001; Chakraborty, 2004), which is close to the actual age of *Protoischnurus* (ca. 110 Mya); the separation of three extant hemiscorpiid subfamilies clearly preceded this geological event. *Protoischnurus*, which is known from a number of specimens with various degree of preservation, is an important fossil since modern presence of Hemiscorpiidae in Central and South America is limited only to five species of *Opisthacanthus* (Lourenço, 1985, 1989; Fet, 2000b).

Diagnosis. Nongranular surfaces of prosoma, mesosoma, metasoma and legs punctate; cheliceral dorsal distal (*dd*) denticle of movable finger subequal in length to the ventral distal (*vd*) denticle; two rows of median denticles (MD) are found on chelal fingers; chelal trichobothria V_2-V_3/V_3-V_4 ratio equals 2.3–6.3 (mean 4.04); telson vesicle of male is laterally flattened; telson vesicle of female is laterally flattened; anterolateral distal lobes of telson vesicle absent; venom glands simple; sternum anterior width (AW) wider than posterior width (PW). See discussion above on character distribution for the breakdown of synapomorphies and important symplesiomorphies.

Family Scorpionidae Latreille, 1802 (amended composition).

Type Genus. *Scorpio* Linnaeus, 1758.

Composition. As recognized here, the family includes three subfamilies (Diplocentrinae, Scorpioninae,

and Urodacinae) and 13 extant genera. Soleglad & Fet (2003b) demonstrated that Diplocentridae should be considered a subfamily of Scorpionidae. The content of Scorpionidae is further changed here compared to that in Fet (2000c) and the later revisions (Prendini, 2000; Prendini et al., 2003; Soleglad & Fet, 2003b). As the result of present study, the scorpionoid family Urodacinae is abolished; its nominotypic subfamily Urodacinae is transferred to Scorpionidae. Urodacinae includes only one genus, *Urodacus* (20 species; Koch, 1977; Fet, 2000c; Volschenk et al., 2000). See Soleglad & Fet (2003b) for detailed taxonomic history.

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

Biogeographic history. Inclusion of Diplocentrinae (Soleglad & Fet, 2003b), extended geographic distribution of Scorpionidae to all continents (except Australia). With current addition of endemic Australian Urodacinae, the family has worldwide distribution. The Miocene genus *Mioscorpio* is known from Europe (Fet, 2000c) where scorpionids are currently not found. Assuming the phylogeny of Scorpionidae as shown at Fig. 72, Urodacinae represents the sister group of Scorpioninae (the latter is notably absent from Australia). The isolation of Urodacinae, therefore, could be assigned to the separation of India from the Australian/Antarctic block, i.e. late Jurassic (Veevers, 1991). See Prendini et al. (2003) for a detailed discussion on the biogeographic history of four genera of Scorpioninae (*Heterometrus*, *Opisthophthalmus*, *Pandinus*, and *Scorpio*); these authors concur with a hypothesis of eastern Gondwanaland origin of Scorpioninae (Sissom, 1990). While both subfamilies Scorpioninae and Urodacinae can be interpreted as Gondwanaland groups, the same might not be true for Diplocentrinae with their bizarre disjunct range. The common ancestor of Scorpionidae could have been present in Pangean times (Permian–Triassic) (compare above with Hemiscorpiidae). Koch (1977) discussed systematics, biogeographic distribution, and desert adaptations of the diverse Australian genus *Urodacus*.

Diagnosis. Cheliceral dorsal distal (*dd*) denticle of movable finger considerably shorter than ventral distal (*vd*) denticle; external (*E*) carina of chela obsolete; ventromedian (*V2*) carina of chela distinct; chelal trichobothria V_2-V_3/V_3-V_4 ratio equals 1.2–2.1 (mean 1.61); chelal trichobothrium *Dt* positioned at distal aspect of palm near based of fixed finger; laterodistal lobes of leg tarsus rounded; sternum anterior width (AW) <= posterior width (PW); 5–12 ventral setal pairs on leg tarsus. See discussion above on character distribution for the breakdown of synapomorphies and important symplesiomorphies.

Taxonomic Changes

Below, we list taxonomic changes at the family-group level resulting from this study as compared to the nomenclature listed in Soleglad & Fet (2003b).

Hemiscorpiidae Pocock, 1893, **new status** (a valid family name) = Hadogenidae Lourenço, 1999, **new synonymy**; = Liochelidae Fet & Bechly, 2001, **new synonymy**.

Hormurinae Laurie, 1896 (a valid subfamily name) = Opisthacanthinae Kraepelin, 1905, **new synonymy**; = Hadogeninae Lourenço, 1999, **new synonymy**; = Liochelinae Fet & Bechly, 2001, **new synonymy**.

Heteroscorpioninae Kraepelin, 1905 (a valid subfamily name): transferred to Hemiscorpiidae Pocock, 1893.

Urodacidae Kraepelin, 1905: abolished as a family.

Urodacinae Kraepelin, 1905 (a valid subfamily name): transferred to Scorpionidae Latreille, 1802.

Conclusions

Our present reanalysis of the position of *Heteroscorpion* and *Urodacus* among other scorpionoids does not support monophyly of the lineages representing these genera, either as two monotypic families proposed by Prendini (2000, 2003b) and Prendini in Coddington et al. (2004), or as two subfamilies of Urodacidae retained by Soleglad & Fet (2003b). Instead, our study confirms the phylogeny suggested by Stockwell (1989). At the same time, the family rank for Urodacidae (first suggested by Stockwell, 1989) is abolished here. Subfamily Urodacinae is transferred to Scorpionidae, and subfamily Heteroscorpioninae, to Hemiscorpiidae. As a result, the superfamily Scorpionoidea now includes three families: Bothriuridae (with two subfamilies, Lisposominae and Bothriurinae; Fet et al., 2004a), Hemiscorpiidae (with three subfamilies, Hemiscorpiinae, Heteroscorpioninae, and Hormurinae), and Scorpionidae (with three subfamilies, Diplocentrinae, Scorpioninae, and Urodacinae).

It is interesting to note that two scorpionoid families, Scorpionidae and Hemiscorpiidae, as accepted here, fit very well with the infrafamilial division first proposed by A. Birula almost 90 years ago (1917). Birula (1917: 161–162) separated scorpion family Scorpionidae into two “tribes” (“tribus”): Scorpionaria and Ischnuraria. This category *does not* correspond to the modern family-group category of tribe, which is subordinate to subfamily; in fact, modern classification does not use any ranks between family and subfamily. The *only* char-

acter by which Birula defined these “tribes” was presence or absence of rounded lateral distal tarsal lobes, present in Scorpionaria but lacking in Ischnuraria, which is indeed a very unique and unprecedented character in scorpions (Soleglad & Fet, 2003b; see also discussion above). Each “tribe” of Birula was subdivided into subfamilies: Scorpionaria included Scorpioninae and Urodacinae; Ischnuraria included Ischnurinae (now synonym of Hormurinae), Hormurinae, Hemiscorpiinae, and Heteroscorpioninae. This arrangement (with addition of Diplocentrinae as a subfamily of Scorpionidae; Soleglad & Fet, 2003b) corresponds exactly to the phylogeny proposed here.

Acknowledgments

We thank Jim Boone, Matt Braunwalder, Philip Brownell, Tomas Cekalovic, Jonathan Coddington, Graeme Lowe, Lorenzo Prendini, Rolando Teruel, Darrell Ubick, Michael Warburg, and Gary Wilson for the gifts and/or loans of scorpion material. We are grateful to Günther Bechly, Pat Craig, Wilson Lourenço, Federica Menon, and Paul Selden, for sharing information and ideas on the Crato fossil scorpions from Brazil, and especially to Luis Acosta for his thoughtful review of this paper. We also thank Luis Acosta and Izyaslav Kerzhner for their valuable advice on the family-group nomenclatural problems.

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