

ISSN 0748-3007
Volume 16, Number 1, March 2000

Cladistics

The International Journal
of the Willi Hennig Society



ACADEMIC PRESS

A Harcourt Science and Technology Company

<http://www.academicpress.com/cladistics>

Phylogeny and Classification of the Superfamily Scorpionoidea Latreille 1802 (Chelicerata, Scorpiones): An Exemplar Approach

Lorenzo Prendini

Percy FitzPatrick Institute, University of Cape Town, Rondebosch 7701, South Africa

Accepted November 11, 1999

S. A. Stockwell (1989, "Revision of the Phylogeny and Higher Classification of Scorpions (Chelicerata)." Univ. of California, Berkeley) proposed a cladogram and revised classification for the superfamily Scorpionoidea Latreille 1802 (comprising the families Bothriuridae, Diplocentridae, Heteroscorpionidae, Ischnuridae, and Scorpionidae), based on 47 morphological characters and 35 supraspecific terminal taxa, representing genera whose monophyly was implicitly assumed. Given the widespread practice of defining scorpion genera on the basis of plesiomorphic character states, the assumption of monophyly implicit in supraspecific terminal taxa reduces confidence in Stockwell's cladistic findings and, consequently, his revised suprageneric classification. A re-investigation of scorpionoid phylogeny is presented here, based on 115 morphological characters (including the characters used by Stockwell) and 71 exemplar species. The criterion of "maximal morphological diversity" was employed for exemplar selection. This approach provides a stronger test of monophyly than random exemplar selection. Sixteen cladistic analyses were performed on the scorpionoid data matrix, which varied in the use of equal, successive, or implied weights and in the additive or nonadditive treatment of multistate characters. The preferred hypothesis, a single most parsimonious tree obtained by analysis with equal weights and 13 ordered

multistate characters, yielded the scheme of relationships: (Bothriuridae ((Heteroscorpionidae Urodacinae) ((Hemiscorpiinae Ischnuridae) (Diplocentridae Scorpioninae))). On the basis of these results, revisions are proposed to the existing suprageneric classification of the Scorpionoidea, including new diagnoses, new descriptions, and an illustrated key to the families and subfamilies. Familial status is provided for the scorpionoid subfamilies Hemiscorpiinae and Urodacinae. © 2000

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INTRODUCTION

The "Catalog of the Scorpions of the World (1758–1998)" (Fet *et al.*, 2000) lists 1259 currently valid extant (Recent) scorpion species in 155 genera and 16 families. This approximately fourfold increase in the number of species listed 100 years ago in Kraepelin's (1899) survey of the world scorpion fauna is the result of a plethora of taxonomic revisions and regional studies undertaken by modern workers. Unfortunately, comparatively little progress has been made in our understanding of scorpion higher classification since the early works of Peters (1861), Thorell (1876, 1877), Karsch (1879a,b), Simon (1879, 1880), Pocock (1893a), Laurie

(1896a,b), Kraepelin (1891, 1894, 1899, 1905), and Birula (1917a,b). Indeed, the suprageneric classification of Recent scorpions has reached a state in which familial assignment of specimens may require prior identification to genus (Stockwell, 1989, 1992). This situation can largely be attributed to the infrequent application of modern systematic techniques (in particular, cladistics) by contemporary workers.

The first quantitative cladistic analysis of Recent scorpions, excluding buthids, was undertaken by Stockwell (1989), who proposed a revised higher classification, based upon the resulting cladogram. His analysis incorporated all currently recognised non-buthid genera, a single buthid terminal taxon (a composite of the 50 buthid genera recognised at the time), and seven fossil terminals, in a matrix of 89 taxa and 138 binary morphological characters. The Eurypterida, the Xiphosura, and the Arachnida (a composite of the 10 non-scorpion arachnid orders) were used as outgroups. Aside from the empirical difficulties of combining morphological evidence from taxa as diverse as mites and amblypygids into a single terminal taxon (viz. "Arachnida"), doing so rests upon the assumption that the Scorpiones are basal to all other arachnids (Pocock, 1893b; Weygoldt and Paulus, 1979; Weygoldt, 1986, 1998). This view has been questioned on the basis of embryological (Yoshikura, 1975), morphological (Van der Hammen, 1977a,b, 1986; Shultz, 1990), and molecular evidence (Wheeler *et al.*, 1993; Wheeler and Hayashi, 1998).

Stockwell (1989) recognised four major clades of Recent scorpions, for which he proposed superfamilial status: Buthoidea Simon 1879 [*sic*; the correct author is C. L. Koch 1837 (V. Fet, pers. comm.)], Chactoidea Pocock 1893, Scorpionoidea Peters 1862 [*sic*; the correct author is Latreille 1802 (V. Fet, pers. comm.)], and Vaejovoidea Thorell 1876. However, Stockwell (1992) published only his proposed revisions to the suprageneric classification of North American Chactoidea and Vaejovoidea. Lourenço (1998a,b) recently implemented some of Stockwell's unpublished revisions to the Chactoidea and Vaejovoidea. The remaining superfamily for which Stockwell proposed revisions, i.e., the Scorpionoidea (Table 1), has been ignored until now.

Within the scorpionoid clade, Stockwell (1989) obtained limited cladistic resolution below the familial level (Fig. 1a). This may be partly explained by his use of "intuitive" ground-plan analysis (*sensu* Yeates,

TABLE 1

Current Classification of the Superfamily Scorpionoidea
Latreille 1802

Classification based on Lourenço (1989) and Sissom (1990)

Family Bothriuridae Simon 1880

Subfamily Bothriurinae Simon 1880

Bothriurus Peters 1861; *Centromachetes* Lönnberg 1897; *Cerco-phonius* Peters 1861; *Orobthriurus* Maury 1976; *Phoniocercus* Pocock 1893; *Tehuanka* Cekalovic 1973; *Thestylus* Simon 1880; *Timogenes* Simon 1880; *Urophonius* Pocock 1893

Subfamily Brachistosterninae Maury 1973

Brachistosternus Pocock 1893

Subfamily Vachonianinae Maury 1973

Vachonia Abalos 1954

incertae sedis

Lisposoma Lawrence 1928

Family Diplocentridae Pocock 1893

Subfamily Diplocentrinae Pocock 1893

Cazierius Francke 1978; *Didymocentrus* Kraepelin 1905; *Diplo-centrus* Peters 1861; *Heteronebo* Pocock 1899; *Oiclus* Simon 1880; *Tarsoporosus* Francke 1978

Subfamily Nebinae Kraepelin 1905

Nebo Simon 1878

Family Ischnuridae Simon 1879

Cheloctonus Pocock 1892; *Chiromachus* Pocock 1893; *Hadogenes* Kraepelin 1894; *Heteroscorpion* Birula 1903; *Iomachus* Pocock 1893; *Liocheles* Sundevall 1833; *Opisthacanthus* Peters 1861

Family Scorpionidae Latreille 1802

Subfamily Hemiscorpiinae Pocock 1893

Habibiella Vachon 1974; *Hemiscorpius* Peters 1861

Subfamily Scorpioninae Latreille 1802

Heterometrus Ehrenberg 1828; *Opisththalmus* C. L. Koch 1837; *Pandinus* Thorell 1876; *Scorpio* Linnaeus 1758

Subfamily Urodacinae Pocock 1893

Urodacus Peters 1861

Recent emendations to the classification (Lourenço, 1996a, 1997)

Family Heteroscorpionidae Kraepelin 1905

Heteroscorpion Birula 1903

Family Ischnuridae Simon 1879

Cheloctonus Pocock 1892; *Chiromachetes* Pocock 1899; *Chiromachus* Pocock 1893; *Hadogenes* Kraepelin 1894; *Iomachus* Pocock 1893; *Liocheles* Sundevall 1833; *Opisthacanthus* Peters 1861; *Palaeo-cheloctonus* Lourenço 1996

1995), in which hypothetical terminal taxa were used to represent genera for which monophyly was implicitly assumed. Stockwell's assumption that scorpion genera are monophyletic superficially appears reasonable. However, it appears less reasonable in view of the long tradition in scorpion systematics of defining genera, and even subfamilies and families, on the basis of plesiomorphic states, a practice of which Stockwell (1989:47–52) was well aware. Typically, for any particular binary character, one taxon will be defined by the presence of state 0 and another taxon by the presence

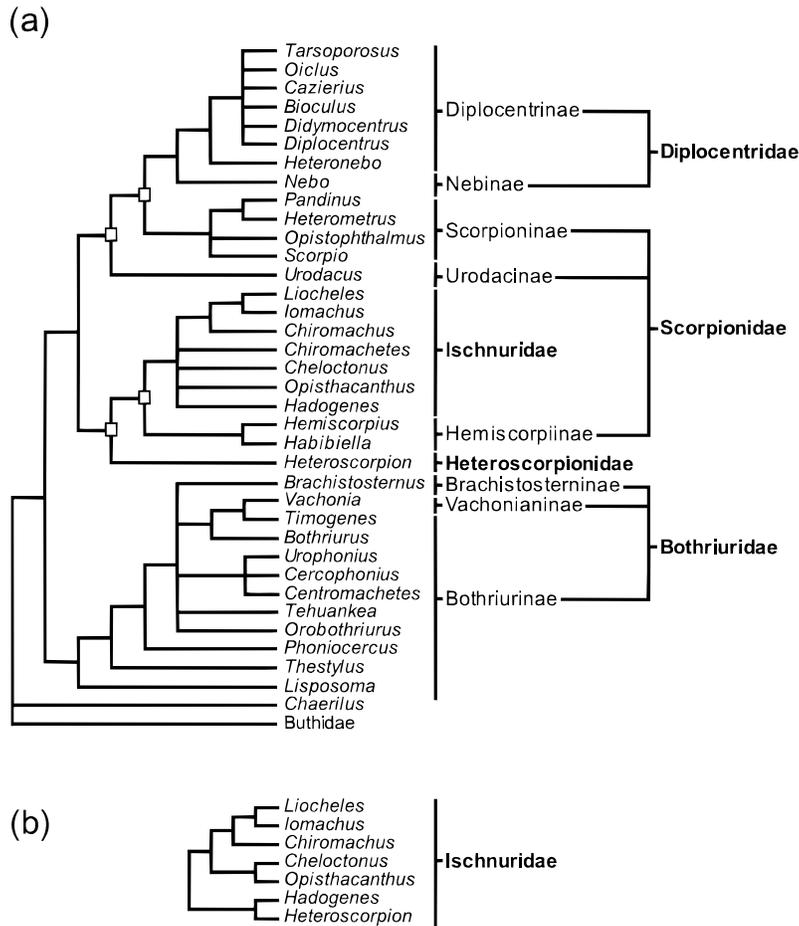


FIG. 1. Previous hypotheses of relationship among scorpionoid genera. Scorpionoid higher taxa, indicated in boldface for families and lightface for subfamilies, reflect the current classification (Table 1). (a) The scorpionoid section of Stockwell's (1989) unpublished cladogram for the non-buthid genera of Recent scorpions. This tree is part of the strict consensus of 456 most parsimonious trees (unweighted length 208 [sic]; CI 66; RI 92) obtained by Stockwell after successive character weighting on 1799 trees (length 221; CI 62; RI 90). Nodes which collapsed in the strict consensus of Stockwell's 1799 trees obtained with equal weights are indicated with open squares. This tree is derived from a matrix of 47 binary characters (listed in Appendix 2), bearing on scorpionoid relationships, that were extracted from Stockwell's unpublished matrix and reproduced in Table 4. The outgroup taxon, "Buthidae," is a hypothetical representative of 50 genera in the family Buthidae. (b) Lourenço's (1985, 1989, 1996a) "cladogram" for the genera of Ischnuridae. This tree is not based upon any empirical evidence that has been presented.

of state 1. One need look no further than the family Ischnuridae, distinguished by means of truncated laterodistal lobes of the telotarsi and smooth venom glands from the family Scorpionidae, with rounded laterodistal lobes and folded venom glands (Lourenço, 1989; Sissom, 1990). If the states assigned to the Ischnuridae both happened to be plesiomorphic, the family could be paraphyletic with respect to the Scorpionidae.

Cladistic theory assumes that the terminal taxa in an analysis are monophyletic (Gaffney, 1979). The consequences of erroneous assumptions of monophyly on

the resultant cladograms can be severe (Bininda-Emonds *et al.*, 1998; Wiens, 1998). Accordingly, the assumption of monophyly implicit in Stockwell's supra-specific terminal taxa reduces confidence in his cladistic findings and his revised higher classification (Table 2). This is ironic when one considers Stockwell's (1989:52) comments on Lamoral's (1980) cladogram and the "cladogram" proposed by Lourenço (1985, 1989): "Part of the problem with both of these analyses is that they utilize the currently recognized families [as terminal taxa], many of which are not monophyletic.

TABLE 2

Stockwell's (1989) Unpublished Classification of the Superfamily Scorpionoidea Latreille 1802

Family Bothriuridae Simon 1880
Subfamily Bothriurinae Simon 1880
<i>Bothriurus</i> Peters 1861; <i>Brachistosternus</i> Pocock 1893; <i>Centromachetes</i> Lönnberg 1897; <i>Cercophonius</i> Peters 1861; <i>Orobothriurus</i> Maury 1976; <i>Phoniocercus</i> Pocock 1893; <i>Tehuanka</i> Cekalovic 1973; <i>Thestylus</i> Simon 1880; <i>Timogenes</i> Simon 1880; <i>Urophonius</i> Pocock 1893; <i>Vachonia</i> Abalos 1954
Subfamily Lisposominae Lawrence 1928
<i>Lisposoma</i> Lawrence 1928
Family Diplocentridae Pocock 1893
Subfamily Diplocentrinae Pocock 1893
<i>Bioculus</i> Stahnke 1968; <i>Cazierius</i> Francke 1978; <i>Didymocentrus</i> Kraepelin 1905; <i>Diplocentrus</i> Peters 1861; <i>Heteronebo</i> Pocock 1899; <i>Oiclus</i> Simon 1880; <i>Tarsoporus</i> Francke 1978
Subfamily Nebinae Kraepelin 1905
<i>Nebo</i> Simon 1878
Family Ischnuridae Simon 1879
Subfamily Hemiscorpiinae Pocock 1893
<i>Habibiella</i> Vachon 1974; <i>Hemiscorpius</i> Peters 1861
Subfamily Heteroscorpioninae Kraepelin 1905
<i>Heteroscorpion</i> Birula 1903
Subfamily Ischnurinae Simon 1879
<i>Cheloctonus</i> Pocock 1892; <i>Chiromachetes</i> Pocock 1899; <i>Chiromachus</i> Pocock 1893; <i>Hadogenes</i> Kraepelin 1894; <i>Iomachus</i> Pocock 1893; <i>Liocheles</i> Sundevall 1833; <i>Opisthacanthus</i> Peters 1861
Family Scorpionidae Latreille 1802
<i>Heterometrus</i> Ehrenberg 1828; <i>Opisthophthalmus</i> C. L. Koch 1837; <i>Pandinus</i> Thorell 1876; <i>Scorpio</i> Linnaeus 1758
Family Urodacidae Pocock 1893
<i>Urodacus</i> Peters 1861

There is little purpose to carrying out a cladistic analysis when the terminal taxa are not monophyletic." Stockwell was referring to the use of families as terminal taxa, but the same problems beset the use of genera as terminal taxa in his analysis.

Associated with a recent cladistic analysis of the species-level relationships among southern African burrowing scorpions of the scorpionid genus *Opisthophthalmus* (Prendini, manuscript in preparation), I embarked on a study of cladistic relationships among the genera within the family Scorpionidae, intending to test Stockwell's (1989) finding that the Scorpionidae is polyphyletic and to resolve relationships among the scorpionid genera. Initial investigations indicated that the character states traditionally used to include the genera *Habibiella*, *Hemiscorpius*, and *Urodacus* within the Scorpionidae are plesiomorphic and therefore provide no evidence of phylogenetic relationship.

Moreover, these genera share several potential synapomorphies with taxa from other scorpionoid families such as the Ischnuridae and the enigmatic Heteroscorpionidae, whose phylogenetic positions are also currently equivocal. In the face of general uncertainty about the relationships among these and other scorpionoid taxa, it became evident that a reanalysis of the 36 genera in the superfamily Scorpionoidea (*sensu* Stockwell, 1989, comprising the families Bothriuridae, Diplocentridae, Heteroscorpionidae, Ischnuridae, and Scorpionidae) was required, the results of which are presented here.

The approach implemented in the current analysis differs from Stockwell's in that each genus was represented by two or three species (except for monotypic genera), instead of a single hypothetical supraspecific taxon. I adopted the "exemplar" approach (*sensu* Mishler, 1994; Yeates, 1995) with the expectation that it would assist in resolving the relationships within groups such as the family Ischnuridae, in which certain genera (e.g., *Opisthacanthus* and *Iomachus*) were doubtfully monophyletic.

The aims of this investigation were therefore (1) to resolve relationships among the major clades within the superfamily Scorpionoidea, with particular emphasis on the placement of the abovementioned genera; (2) to test the monophyly of the scorpionoid families and subfamilies and the internal relationships among their component genera; and (3) to provide revisions to the existing suprageneric classification, based on the Hennigian principle of monophyly.

MATERIAL AND METHODS

Taxa

All 35 scorpionoid genera included in Stockwell's (1989) analysis, together with Lourenço's (1996a) recently described ischnurid genus, *Palaeocheloctonus*, were included as ingroup taxa in the present analysis (Table 3). Each genus was represented by at least two exemplar species in the analysis, except for *Thestylus*, for which an additional species could not be obtained for morphological examination, and the monotypic genera *Chiromachus*, *Habibiella*, *Oiclus*, *Palaeocheloctonus*, *Tehuanka*, and *Vachonia*. Two of the 19 currently

recognised subspecies of the monotypic *Scorpio maurus* were included as putative phylogenetic species (Nelson and Platnick, 1981; Cracraft, 1983, 1989; Wheeler and Nixon, 1990; Nixon and Wheeler, 1990). In addition, 4 large genera with considerable interspecific “polymorphism” (see Wiens, 1998:397) in character states were represented by a third exemplar species: *Brachistosternus*, *Opisthacanthus*, *Opisthophthalmus*, and *Pandinus*. By means of this approach, all known applicable character states could be scored unambiguously with the exception of one, which is intraspecifically polymorphic in *Opisthacanthus validus*.

Contingent upon the availability of specimens for examination, exemplar species were chosen so as to provide the strongest test of monophyly for the higher taxa they represent. Accordingly, exemplar species were selected so as to reflect maximal morphological diversity within the genera and thereby allow groupings largely independent of *a priori* assumptions encapsulated in the current taxonomy (Appendix 1). Type species were included as exemplars in 34 of the 36 genera. Exemplars representing the 2 genera for which type species could not be included (*Hadogenes* and *Timogenes*) were considered congeneric with the type species on the basis of the available morphological evidence. Several methods were used to estimate the morphological divergence for selection of the remaining exemplars. First, formally published subgenera and species groups were included wherever possible, as these represent current estimates of morphological diversity. Second, in the absence of subgenera or species groups, species from disjunct geographical locations were chosen to represent genera with widespread distributions, on the assumption that geographical disjunction may be correlated with morphological divergence. Third, species whose taxonomic status within particular genera had been disputed in the past (usually on the premise of morphological divergence), and species whose phylogenetic position with respect to their own, or other, closely related genera had been speculated about by previous authors, were included to provide a test of such hypotheses.

Trees were rooted using the outgroup method (Watrous and Wheeler, 1981; Farris, 1982; Nixon and Carpenter, 1993). *Centruroides gracilis* and *Chaerilus granosus* were chosen as exemplar species for the families Buthidae and Chaerilidae, to be used as outgroup taxa (Appendix 1). The buthids and chaerilids are generally

considered basal to all other Recent scorpions (Lamoral, 1980; Lourenço, 1985; Stockwell, 1989), although there is debate as to whether the Chaerilidae are the sister taxon of the other Recent scorpions (Lamoral, 1980; Lourenço, 1985) or the sister taxon of the Buthidae (Stockwell, 1989). Selection of a representative for the diverse family Buthidae was based on the criterion that the exemplar species should have distinct pedipalpal carinae (which are often obsolete in buthids) to facilitate homology assessment for the carinal characters, which would otherwise be scored with missing entries.

Characters

An investigation of adult morphology was undertaken for the cladistic analysis, in which 115 characters (including a single behavioural character) were scored across the 71 species chosen as exemplar taxa (Table 3). Forty-one of these characters were compiled from 47 binary characters that bear on scorpionoid relationships in Stockwell’s (1989) original data matrix (Table 4; Appendix 2). Thirteen were reduced to six multistates (Appendix 3), in order to decrease redundancy (Pimentel and Riggins, 1987). One character, for which additional states were recognised, was split into two characters (Appendix 3). A further 12 of Stockwell’s characters were corrected or otherwise modified, based on new information (including the addition of previously missing data for *Chiromachus* and *Heteroscorpion*) or reinterpretation. Twenty-one characters remain unaltered. The remaining 74 characters in the data matrix are new or were collated from the literature (Appendix 3). Several of the latter were explicitly omitted by Stockwell (1989). In an effort to ensure consistent treatment and repeatability, most characters used in the analysis (except 67, 77–79, 83–85, and 114–115) were critically examined across all terminal taxa (except *Chiromachetes tirupati* and the monotypic genera *Habibiella*, *Tehuankea*, and *Vachonia*). In a few cases, this necessitated a reinterpretation of putative homologies. Missing entries for *Chiromachetes* are attributed to the fact that adult males of both described species have never been discovered. Trichobothrial terminology follows Vachon (1974). All other terminology follows Stockwell (1989) and Sissom (1990), except for pedipalpal carinae (Stahnke, 1970) and tarsi (Couzijn, 1976; Lamoral, 1979).

1.5 (Farris, 1988), and PAUP version 3.1.1 (Swofford, 1991). The data matrices were analysed on a 133-MHz Pentium computer (64 Mb RAM) for NONA and Hennig86 and on a Power Macintosh 7600/132 (32 Mb RAM) for PAUP. Heuristic search strategies were adopted since exhaustive searches, which obtain the complete set of most parsimonious trees, proved too time consuming. In Hennig86, the heuristic branch breaking routine (command sequence "mh*; bb*;") was used. This algorithm generates multiple trees and then applies branch swapping to select the set of most parsimonious trees. In PAUP, the heuristic TBR option was employed, again because the exhaustive branch-and-bound option was too computer-intensive. This algorithm generates an initial tree(s) by stepwise addition and then subjects this tree to trial rearrangements to obtain the set of most parsimonious trees (Platnick, 1989b), a process referred to as tree-bisection-reconnection (TBR) branch swapping (Swofford, 1991). TBR branch swapping was conducted on 100 random addition replicates, with MULPARS in effect and max-trees set to 1000. In NONA, the heuristic analysis was run with the following command sequence: "hold10000; hold/1000; mult*1000;" (hold 10,000 trees in memory; hold 1000 starting trees in memory; perform TBR branch swapping on 1000 random addition replicates). Additional swapping on up to 1000 trees that are up to 5% longer than the shortest trees (command sequence "jump 50;") was performed to help the swapper move between multiple "islands" of trees (Goloboff, 1997). Trees found with the jump command were again swapped. All trees obtained with Hennig86 and NONA were submitted to TBR branch swapping in PAUP and vice versa.

The relative degree of support for each node in the trees obtained with equal weights was assessed with branch support indices (Bremer, 1994) and bootstrap percentages (Felsenstein, 1985; Sanderson, 1989). The branch support or decay index for a given node in the shortest unconstrained tree is the number of extra steps required in the shortest trees that are inconsistent with that node, i.e., the number of steps required to collapse the node. The bootstrap percentage for each node reflects the frequency with which that node is retrieved from randomly sampled data sets with replacement. Although there is widespread debate regarding the value of bootstrapping as a statistical test of the robustness of a cladogram (Sanderson, 1989, 1995; Linder,

1991; Hillis and Bull, 1993; Kluge and Wolf, 1993; Carpenter, 1996), bootstrap values may provide some indication of the resistance of nodes to perturbation. Branch support indices up to 100 extra steps (setting the maximum number of trees held in memory to 10,000) were calculated with NONA, by means of the command sequence "h10000; bsupport 100;". Bootstrap percentages were calculated in PAUP from 10,000 bootstrap replicates (setting the maximum number of trees held in memory to 500).

Successive approximations character weighting (Farris, 1969) was conducted in NONA, using the squared consistency index as weighting function, by means of the swt.run file (command sequence "run] swt hold10000 hold/1000 mult*1000 jump50;"). Methods of *a posteriori* character weighting, such as successive weighting, are generally used to find topologies supported by the most consistent characters, thus facilitating the choice of a preferred tree(s) from the initial set obtained with analysis under equal weights (Carpenter, 1988, 1994; Carpenter *et al.*, 1993). As such, they are seldom applied if a single most parsimonious tree is obtained with equal weights. However, in the present context, *a posteriori* weighting was undertaken to assess the effects of weighting against homoplastic characters, irrespective of the number of trees obtained with equal weights, and may be viewed as a type of "sensitivity analysis" (Wheeler, 1995). Sensitivity analysis is concerned with assessing the relative robustness of clades to different parameters, in this case, character weights (note that branch support indices, bootstrap percentages, and the unordering of all multistate characters may be viewed as other parameters that were varied in these analyses). If a group is monophyletic only under a very specific combination of parameters, less confidence may be placed in the supposition that the data robustly support its monophyly than may be placed in a group which is monophyletic under a wider range and combination of parameters (Whiting *et al.*, 1997). For example, Griswold *et al.* (1998) argued in support of their single most parsimonious tree on the grounds that it was stable under analysis with equal, successive, and implied weights.

The effects of implied character weighting (Goloboff, 1993a) were explored for the same reason as successive weighting, using Pee-Wee version 2.5.1 (Goloboff, 1993b), with the command sequence "hold10000; hold/1000; mult*1000; jump50;". Pee-Wee searches for trees

which maximise total fit, $F = \sum f_i$, where f_i , the fit of character i , is obtained with $f_i = k/(k + ES_i)$; k is a constant of concavity which can be varied between 1 and 6 with the “conc N” command (to allow homoplastic characters to have less or more influence, respectively); and ES_i is the number of extra steps for character i . Strongly concave functions (low values of k) weight more heavily against homoplastic characters than less concave functions (i.e., functions approaching linearity) in which homoplastic characters are allowed more influence. Consequently, results obtained with high values of k should approach those of analysis with equal weights. There is currently no theoretical justification for selecting a particular k value (Turner and Zandee, 1995). However, the use of very mild or very strong functions is contraindicated (Goloboff, 1993a, 1995): very mild functions do not differ appreciably from analysis with equal weights, whereas very strong functions cannot be defended. Published studies (e.g., Goloboff, 1993c; De Jong *et al.*, 1996; Griswold *et al.*, 1998) made use of the default, $k = 3$. In the context of a sensitivity analysis, the effects of varying the concavity function on the scorpionoid topology were assessed by analysis with six k values, spanning the input range permitted by Pee-Wee.

Alternative hypotheses of scorpionoid evolution were investigated in NONA (commands “force +N; max/;”, “ref;”, and “cmp;”) by constraining clades, proposed in the literature or obtained by the analyses with *a posteriori* weighting, on the topology of the tree located by the analysis with equal weights, swapping on the other terminals, and calculating the difference in length and fit. Although they should be longer than the tree obtained with equal weights, constraint trees were expected to have a better total fit for some groups located in the weighted analyses. Constraint analyses also allowed length and fit differences to be determined for characters supporting these alternative hypotheses.

RESULTS

Parsimony analysis of the 112 informative characters in NONA, Hennig86, and PAUP located a single tree with equal weights (Table 5; Fig. 2). This tree is presented as the preferred hypothesis of scorpionoid relationships (Fig. 7).

Six trees, each nine steps shorter than the tree obtained with the 13 ordered multistate characters, were located when all multistate characters were unordered (Table 5; collapsed nodes indicated on Fig. 2). The topology of one of these trees was identical to that in Fig. 2, except for a single node, which was collapsed (indicated with a solid square). Unordering caused the CIs and RIs to increase for 3 characters and decrease for 9 (Table 6). Four of the ordered multistate characters decreased in length (increased in fitness), whereas 1 of the unordered multistate characters increased (Tables 7 and 8).

Bootstrap percentages for the nodes obtained in the analyses with equal weights were mostly >50%, except for some of the nodes supporting the internal relationships of the Bothriuridae, Ischnuridae, and Diplocentrinae (Fig. 2). The lowest bootstrap value was obtained for an internal node of the Bothriuridae, which collapsed in all analyses with unordered multistates (indicated with a solid square in Fig. 2). All except three higher taxon groupings received bootstrap values of >50%. However, the node grouping all non-bothriurids except *Heteroscorpion* and *Urodacus* received a comparatively high branch support value despite the low bootstrap. Aside from occasional inconsistencies between the bootstrap and the branch support values obtained for such nodes, the values obtained were generally comparable inasmuch as most groupings with high bootstrap values also received high branch support values. High bootstrap values obtained for some groupings with relatively lower branch support values (primarily genera such as *Tarsoporosus*, *Opisthophthalmus*, and *Timogenes*) reflect the presence of one or two unique synapomorphies supporting those nodes. A general decrease in the bootstrap and branch support values of most nodes occurred as a result of unordering all multistate characters.

The successive weighting routine located a single tree, which was slightly longer (unweighted length) than, but topologically congruent with, the trees obtained in the analyses with equal weights, except for relationships within the Diplocentrinae and Ischnuridae (Table 5; Figs. 4 and 5). Relative to the analysis with equal weights, the CIs and RIs of 2 characters increased in length, whereas 4 decreased, as a result of successive weighting (Table 6). A single tree was again obtained with successive weighting when all multistate characters were unordered and differed

TABLE 5
Summary of Statistical and Topological Differences among the Most Parsimonious Trees (MPTs) Obtained by Analysis with Equal Weights (EW), Successive Weights (SW), and Implied Weights (IW) with Six Values for the Concavity Constant (k)

	MPTs	Steps	Fit(F_i)	Rescaled fit	CI	RI	Fig. 3	Fig. 4	Fig. 5
EW _o	1	263	913.9	72	55	92	a	a	a
SW _o	1	265	915.0	73	83	97	a	b	b
IW _o : $k = 6$	1	267	986.3	78	—	—	c	b	b
IW _o : $k = 5$	2	267	969.3	77	—	—	d	b	b
IW _o : $k = 4$	2	268	948.3	75	—	—	d	b	b
IW _o : $k = 3$	1	268	918.1	73	—	—	e	b	b
IW _o : $k = 2$	3	270	871.9	70	—	—	f	c	b
IW _o : $k = 1$	15	272	797.6	65	—	—	f	d	c
EW _u	6	254	899.7	73	56	91	b	a	a
SW _u	1	258	900.9	73	83	97	a	e	b
IW _u : $k = 6$	1	258	970.9	79	—	—	f	a	b
IW _u : $k = 5$	1	258	954.9	78	—	—	f	a	b
IW _u : $k = 4$	1	258	934.1	76	—	—	f	a	b
IW _u : $k = 3$	1	258	904.5	73	—	—	f	a	b
IW _u : $k = 2$	1	258	858.1	70	—	—	f	a	b
IW _u : $k = 1$	6	261	782.5	65	—	—	f	f	c

Note. Analyses with multistates ordered and unordered are indicated, respectively, by subscripts “o” and “u”. Unweighted length is reported for SW trees. Letters refer to the alternative topologies for the following groups, as presented in Figs. 3–5: Heteroscorpionidae, Scorpioninae, and Urodacinae (Fig. 3); Diplocentrinae (Fig. 4); Ischnuridae (Fig. 5).

from the tree obtained in the successive weighting analysis with ordered multistates only in the diplocentrine relationships (Table 5; Fig. 4). The CIs and RIs increased for 13 characters and decreased for 4, relative to the successive weighting analysis with ordered multistates (Table 6). Unordering caused a decrease in the length of 3 ordered multistate characters, 1 unordered multistate character, and 2 binary characters (Tables 7 and 8). One unordered multistate character and 1 binary character increased in length.

Results of the analyses with implied weights under six k values are summarised in Table 5. As expected, the trees located by these analyses were longer than the trees from the analyses with equal weights. They were also longer than the unweighted length of the trees obtained with successive weighting, except when all multistate characters were unordered, in which case only the trees obtained with $k = 1$ were longer. However, only analyses with $k \geq 3$ located trees fitter than those with equal weights. Trees obtained with lower values of k were less fit than those obtained with equal weights, a trend also noted by Turner and Zandee (1995). For example, the trees obtained by analyses with $k = 1$ were eight or nine steps longer and 7–8% less fit than the trees obtained with equal weights. By comparison, the trees obtained by analyses with $k =$

6 were only 4 four steps longer, but 6% more fit. The analyses with $k = 1$ also located three clades (two for Diplocentrinae and one for Ischnuridae) not obtained in any other analysis (Figs. 4 and 5). In contrast, the topologies obtained by the analyses with $k = 2$ –6 differed from each other, and from the topologies obtained with successive weighting, only in the relative positions of the Heteroscorpionidae, Scorpioninae, and Urodacinae (Fig. 3). The analysis with $k = 2$ also differed slightly in the internal resolution of the Diplocentrinae (Fig. 4). None of the trees obtained in the analyses with implied weights under $k = 2$ –6 differed with regard to the positions of the Heteroscorpionidae, Scorpioninae, and Urodacinae when all multistate characters were unordered, although their positions differed consistently from the analyses with equal weights and successive weights (Fig. 3).

The effects of the k value on the length and fit of the characters are evident in Table 7. Ten characters decreased in length (increased in fitness) and 15 characters increased, relative to the analysis with equal weights, in at least one of the six analyses in which k was varied. The length and fit of the characters were identical in the analyses with $k = 3$ –4 and the analyses with $k = 5$ –6. However, when all multistates were unordered, the length and fit of the characters were

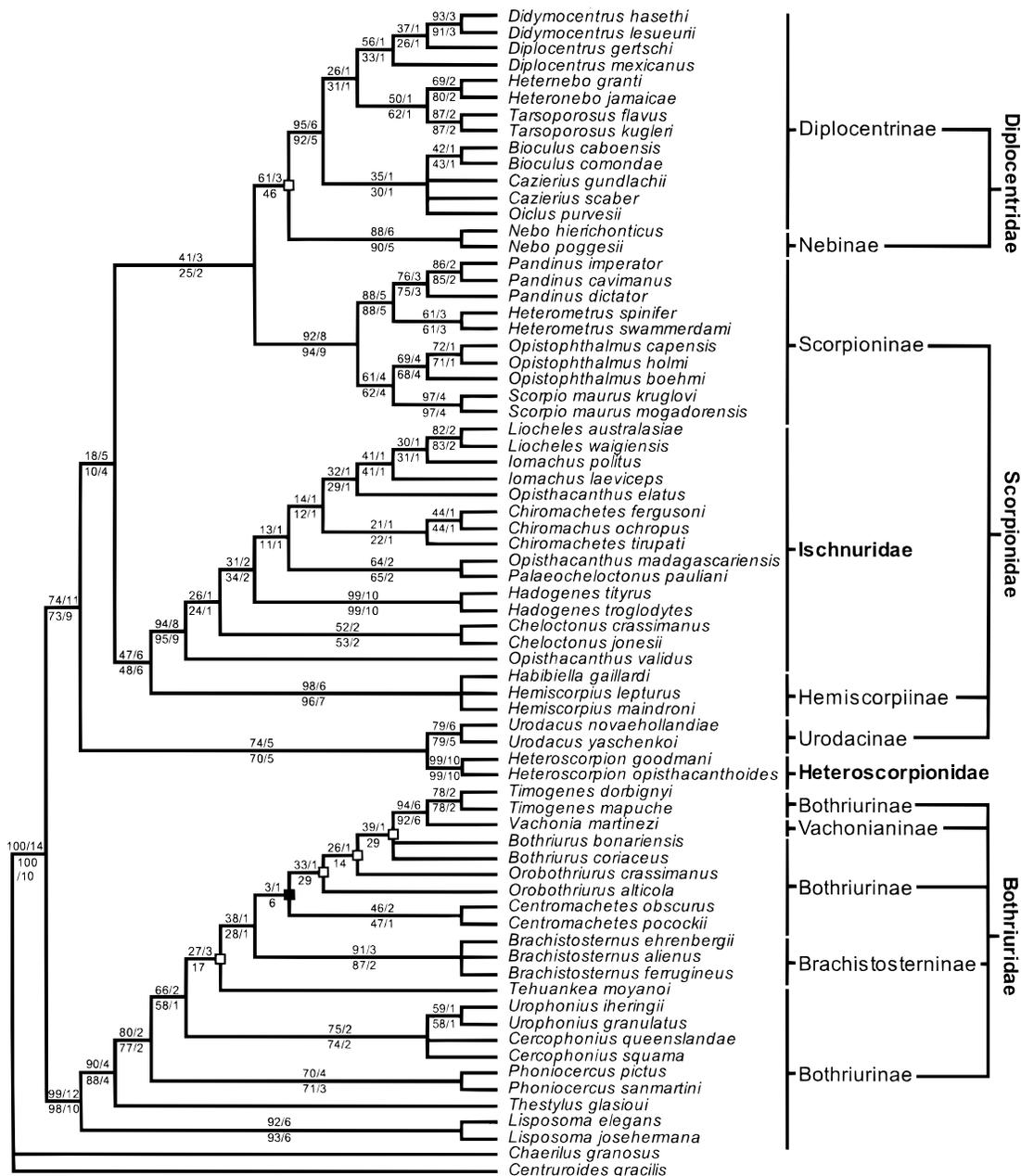


FIG. 2. The single most parsimonious tree (length 263; CI 55; RI 92) obtained from the analysis with equal weights in which 13 multistate characters were ordered. Zero-length branches are collapsed. Nodes which collapsed in the strict consensus of six most parsimonious trees (length 254; CI 56; RI 91) obtained when these multistate characters were unordered are indicated with squares. The solid square indicates a node which also collapsed in the analyses with *a posteriori* weighting, as a result of unordering. Further topological differences between the trees obtained with equal weights and those obtained with *a posteriori* weighting are indicated in Figs. 3–5. Bootstraps and branch support values of nodes are indicated above branches for the analysis in which 13 multistate characters were ordered and below branches for the analysis in which these multistate characters were unordered. The bootstrap percentage is listed first in each case. Scorpionoid higher taxa, indicated in bold-face for families and lightface for subfamilies, reflect the current classification (Table 1). Refer to Fig. 7 for a summary of this tree in which the revised familial classification is portrayed.

TABLE 6
Consistency Indices (CI), Retention Indices (RI), and Final Weights of Informative Characters (Including 13 Ordered Multistates) in the Analyses with Equal Weights (EW) and Successive Weights (SW)

Char	CI _{EW}	CI _{SW}	RI _{EW}	RI _{SW}	Weight _{SW}	Char	CI _{EW}	CI _{SW}	RI _{EW}	RI _{SW}	Weight _{SW}
<u>1</u>	33	33 (40)	42	42 (57)	3.3	58	100	100	100	100	10.0
2	100	100	100	100	10.0	59	33	33	93	93	3.3
<u>3</u>	50	66	93	96	5.0	60	100	100	100	100	10.0
4	50	50	96	96	5.0	61	100	100	100	100	10.0
<u>5</u>	100 (33)	100	100 (66)	100	10.0	62	50	50	96	96	5.0
6	100	100	100	100	10.0	63	33	33	88	88	3.3
7	50	50	96	96	5.0	65	66	66	97	97	6.7
<u>8</u>	25	25 (16)	87	87 (79)	2.5	66	100	100	100	100	10.0
9	100	100	100	100	10.0	67	100	100	100	100	10.0
<u>10</u>	50 (25)	50	93 (81)	93	5.0	68	40	40	91	91	4.0
11	50	50	94	94	5.0	69	33	33 (40)	77	77 (76)	3.3
13	100	100	100	100	10.0	<u>70</u>	75	75	85	85	7.5
14	50	50	0	0	5.0	71	100	100	100	100	10.0
15	25	25	91	91	2.5	72	28	28	83	83	2.9
<u>16</u>	25	20	80	73	2.5	73	100	100	100	100	10.0
17	100	100	100	100	10.0	74	100	100	100	100	10.0
18	25	25	80	80	2.5	75	100	100	100	100	10.0
19	100	100	100	100	10.0	76	100	100	100	100	10.0
<u>20</u>	25	20	81	75	2.0	77	100	100	100	100	10.0
<u>21</u>	25	20 (25)	75	66 (75)	2.0	78	100	100	100	100	10.0
22	100	100	100	100	10.0	79	100	100	100	100	10.0
23	25	25	90	90	2.5	80	66	66	95	95	6.7
24	100	100	100	100	10.0	81	100	100	100	100	10.0
25	100	100	100	100	10.0	82	100	100	100	100	10.0
26	100	100	100	100	10.0	83	100	100	100	100	10.0
27	60 (75)	60 (75)	95 (96)	95 (96)	6.0	84	100	100	100	100	10.0
28	33	33 (50)	90	90 (95)	3.3	85	100	100	100	100	10.0
29	25	25	66	66	2.5	86	100	100	100	100	10.0
30	100	100	100	100	10.0	87	100	100	100	100	10.0
31	100	100	100	100	10.0	<u>88</u>	100 (50)	100	100 (92)	100	10.0
<u>32</u>	100 (50)	100	100 (80)	100	10.0	89	50	50	83	83	5.0
33	33	33	82	82	3.3	90	100	100	100	100	10.0
34	50	50	90	90	5.0	91	100	100	100	100	10.0
35	50	50	88	88	5.0	92	100	100	100	100	10.0
36	33	33	60	60	3.3	93	100	100	100	100	10.0
37	33	33	50	50	3.3	94	100	100	100	100	10.0
38	50	50	0	0	5.0	95	50	50	83	83	5.0
39	66	66	0	0	6.7	96	20	20	84	84	2.0
40	100	100	100	100	10.0	98	100	100	100	100	10.0
41	50	50	95	95	5.0	99	50	50	71	71	5.0
42	100	100	100	100	10.0	<u>100</u>	100 (50)	100	100 (50)	100	10.0
43	37	37	54	54	3.8	<u>101</u>	66 (100)	100	95 (100)	100	10.0
44	100	100	100	100	10.0	102	50	50	50	50	5.0
45	25	25	60	60	2.5	103	50	50	75	75	5.0
46	100	100	100	100	10.0	<u>104</u>	50 (33)	50	60 (20)	60	5.0
47	100	100	100	100	10.0	105	50	50	96	96	5.0
48	100	100	100	100	10.0	<u>106</u>	100 (50)	100	100 (92)	100	10.0
49	44	44	80	80	4.4	107	50	50	94	94	5.0
50	100	100	100	100	10.0	108	50	50	93	93	5.0
51	50	50	91	91	5.0	109	100	100	100	100	10.0
52	50 (75)	50 (75)	95 (97)	95 (97)	5.0	<u>110</u>	50 (33)	50	96 (93)	96	5.0
53	100	100	100	100	10.0	<u>111</u>	33	28 (22)	80	75 (65)	3.3
54	100	100	100	100	10.0	<u>112</u>	100	100	100	100	10.0
55	100	100	100	100	10.0	113	33	33	90	90	3.3
56	100	100	100	100	10.0	<u>114</u>	100 (50)	100	100 (92)	100	10.0
57	100	100	100	100	10.0	115	100	100	100	100	10.0

Note. Numbers in parentheses indicate the CIs and RIs that changed when all multistate characters were unordered. The CIs and RIs of underlined characters differed between the EW and the SW analyses.

TABLE 7
 Length and Fit (f_i) of Informative Characters (Including 13 Ordered Multistates) in the Analyses with Equal Weights (EW), Successive Weights (SW), and Implied Weights (IW) with Six Values for the Concavity Constant (k)

Char	EW	SW	IW				Char	EW	SW	IW			
			$k = 5-6$	$k = 3-4$	$k = 2$	$k = 1$				$k = 5-6$	$k = 3-4$	$k = 2$	$k = 1$
<u>1</u>	6/4.2	6/4.2	7/3.7	7/3.7	7/3.7	7/3.7	58	1/10.0	1/10.0	1/10.0	1/10.0	1/10.0	1/10.0
<u>2</u>	1/10.00	1/10.0	1/10.0	1/10.0	1/10.0	1/10.0	59	3/6.0	3/6.0	4/5.0	4/5.0	5/4.2	5/4.2
<u>3</u>	4/6.0	3/7.5	3/7.5	3/7.5	3/7.5	3/7.5	60	1/10.0	1/10.0	1/10.0	1/10.0	1/10.0	1/10.0
<u>4</u>	2/7.5	2/7.5	2/7.5	2/7.5	2/7.5	2/7.5	61	1/10.0	1/10.0	1/10.0	1/10.0	1/10.0	1/10.0
<u>5</u>	1/10.00	1/10.0	1/10.0	1/10.0	1/10.0	1/10.0	62	2/7.5	2/7.5	2/7.5	2/7.5	2/7.5	2/7.5
<u>6</u>	1/10.00	1/10.0	1/10.0	1/10.0	1/10.0	1/10.0	63	3/6.0	3/6.0	3/6.0	3/6.0	3/6.0	3/6.0
<u>7</u>	2/7.5	2/7.5	2/7.5	2/7.5	2/7.5	2/7.5	65	3/7.5	3/7.5	3/7.5	2/10.0	3/7.5	3/7.5
<u>8</u>	4/5.0	4/5.0	3/6.0	3/6.0	3/6.0	2/7.5	66	1/10.0	1/10.0	1/10.0	1/10.0	1/10.0	1/10.0
<u>9</u>	3/10.0	3/10.0	3/10.0	3/10.0	3/10.0	3/10.0	67	1/10.0	1/10.0	1/10.0	1/10.0	1/10.0	1/10.0
<u>10</u>	2/7.5	2/7.5	2/7.5	2/7.5	2/7.5	2/7.5	68	5/5.0	5/5.0	5/5.0	5/5.0	5/5.0	6/4.2
<u>11</u>	2/7.5	2/7.5	2/7.5	2/7.5	2/7.5	2/7.5	69	6/4.2	6/4.2	6/4.2	6/4.2	6/4.2	6/4.2
<u>12</u>	1/10.00	1/10.0	1/10.0	1/10.0	1/10.0	1/10.0	70	4/7.5	4/7.5	4/7.5	4/7.5	4/7.5	4/7.5
<u>14</u>	2/7.5	2/7.5	2/7.5	2/7.5	2/7.5	2/7.5	71	1/10.0	1/10.0	1/10.0	1/10.0	1/10.0	1/10.0
<u>15</u>	4/5.0	4/5.0	4/5.0	4/5.0	4/5.0	4/5.0	72	7/3.7	7/3.7	7/3.7	7/3.7	7/3.7	7/3.7
<u>16</u>	4/5.0	5/4.2	5/4.2	5/4.2	6/3.7	6/3.7	73	1/10.0	1/10.0	1/10.0	1/10.0	1/10.0	1/10.0
<u>17</u>	1/10.00	1/10.0	1/10.0	1/10.0	1/10.0	1/10.0	74	2/10.0	2/10.0	2/10.0	2/10.0	2/10.0	2/10.0
<u>18</u>	4/5.0	4/5.0	3/6.0	3/6.0	3/6.0	3/6.0	75	1/10.0	1/10.0	1/10.0	1/10.0	1/10.0	1/10.0
<u>19</u>	1/10.00	1/10.0	1/10.0	1/10.0	1/10.0	1/10.0	76	1/10.0	1/10.0	1/10.0	1/10.0	1/10.0	1/10.0
<u>20</u>	4/5.0	5/4.2	5/4.2	5/4.2	5/4.2	6/3.7	77	1/10.0	1/10.0	1/10.0	1/10.0	1/10.0	1/10.0
<u>21</u>	4/5.0	5/4.2	6/4.2	6/4.2	6/4.2	6/4.2	78	1/10.0	1/10.0	1/10.0	1/10.0	1/10.0	1/10.0
<u>22</u>	1/10.00	1/10.0	1/10.0	1/10.0	1/10.0	1/10.0	79	1/10.0	1/10.0	1/10.0	1/10.0	1/10.0	1/10.0
<u>23</u>	4/5.0	4/5.0	4/5.0	4/5.0	4/5.0	5/4.2	80	3/7.5	3/7.5	3/7.5	3/7.5	3/7.5	3/7.5
<u>24</u>	1/10.00	1/10.0	1/10.0	1/10.0	1/10.0	1/10.0	81	1/10.0	1/10.0	1/10.0	1/10.0	1/10.0	1/10.0
<u>25</u>	1/10.00	1/10.0	1/10.0	1/10.0	1/10.0	1/10.0	82	2/10.0	2/10.0	2/10.0	2/10.0	2/10.0	2/10.0
<u>26</u>	1/10.00	1/10.0	1/10.0	1/10.0	1/10.0	1/10.0	83	1/10.0	1/10.0	1/10.0	1/10.0	1/10.0	1/10.0
<u>27</u>	5/6.0	5/6.0	5/6.0	5/6.0	5/6.0	6/5.0	84	1/10.0	1/10.0	1/10.0	1/10.0	1/10.0	1/10.0
<u>28</u>	3/6.0	3/6.0	3/6.0	3/6.0	3/6.0	3/6.0	85	1/10.0	1/10.0	1/10.0	1/10.0	1/10.0	1/10.0
<u>29</u>	4/5.0	4/5.0	4/5.0	4/5.0	4/5.0	4/5.0	86	1/10.0	1/10.0	1/10.0	1/10.0	1/10.0	1/10.0
<u>30</u>	1/10.0	1/10.0	1/10.0	1/10.0	1/10.0	1/10.0	87	1/10.0	1/10.0	1/10.0	1/10.0	1/10.0	1/10.0
<u>31</u>	2/10.0	2/10.0	2/10.0	2/10.0	2/10.0	2/10.0	88	1/10.0	1/10.0	1/10.0	1/10.0	1/10.0	1/10.0
<u>32</u>	1/10.0	1/10.0	1/10.0	1/10.0	1/10.0	1/10.0	89	2/7.5	2/7.5	2/7.5	2/7.5	2/7.5	2/7.5
<u>33</u>	6/4.2	6/4.2	6/4.2	7/3.7	6/4.2	6/4.2	90	1/10.0	1/10.0	1/10.0	1/10.0	1/10.0	1/10.0
<u>34</u>	2/7.5	2/7.5	2/7.5	2/7.5	2/7.5	2/7.5	91	1/10.0	1/10.0	1/10.0	1/10.0	1/10.0	1/10.0
<u>35</u>	4/6.0	4/6.0	4/6.0	4/6.0	4/6.0	4/6.0	92	1/10.0	1/10.0	1/10.0	1/10.0	1/10.0	1/10.0
<u>36</u>	3/6.0	3/6.0	3/6.0	3/6.0	3/6.0	4/5.0	93	1/10.0	1/10.0	1/10.0	1/10.0	1/10.0	1/10.0
<u>37</u>	3/6.0	3/6.0	3/6.0	3/6.0	3/6.0	2/7.5	94	1/10.0	1/10.0	1/10.0	1/10.0	1/10.0	1/10.0
<u>38</u>	2/7.5	2/7.5	2/7.5	2/7.5	2/7.5	2/7.5	95	2/7.5	2/7.5	2/7.5	3/6.0	2/7.5	2/7.5
<u>39</u>	3/7.5	3/7.5	3/7.5	3/7.5	3/7.5	3/7.5	96	5/4.2	5/4.2	5/4.2	5/4.2	5/4.2	5/4.2
<u>40</u>	1/10.0	1/10.0	1/10.0	1/10.0	1/10.0	1/10.0	98	1/10.0	1/10.0	1/10.0	1/10.0	1/10.0	1/10.0
<u>41</u>	2/7.5	2/7.5	2/7.5	2/7.5	2/7.5	2/7.5	99	4/6.0	4/6.0	4/6.0	4/6.0	4/6.0	4/6.0
<u>42</u>	2/10.0	2/10.0	2/10.0	2/10.0	2/10.0	2/10.0	100	2/10.0	2/10.0	2/10.0	2/10.0	2/10.0	2/10.0
<u>43</u>	8/3.7	8/3.7	9/3.3	9/3.3	9/3.3	9/3.3	101	3/7.5	2/10.0	2/10.0	2/10.0	2/10.0	2/10.0
<u>44</u>	1/10.0	1/10.0	1/10.0	1/10.0	1/10.0	1/10.0	102	2/7.5	2/7.5	2/7.5	2/7.5	2/7.5	2/7.5
<u>45</u>	8/3.3	8/3.3	9/3.0	9/3.0	9/3.0	9/3.0	103	2/7.5	2/7.5	2/7.5	2/7.5	2/7.5	2/7.5
<u>46</u>	2/10.0	2/10.0	2/10.0	2/10.0	2/10.0	2/10.0	104	4/6.0	4/6.0	4/6.0	4/6.0	4/6.0	4/6.0
<u>47</u>	1/10.0	1/10.0	1/10.0	1/10.0	1/10.0	1/10.0	105	2/7.5	2/7.5	2/7.5	2/7.5	2/7.5	2/7.5
<u>48</u>	1/10.0	1/10.0	1/10.0	1/10.0	1/10.0	1/10.0	106	1/10.0	1/10.0	1/10.0	1/10.0	1/10.0	1/10.0
<u>49</u>	9/3.7	9/3.7	10/3.3	10/3.3	10/3.3	10/3.3	107	2/7.5	2/7.5	1/10.0	1/10.0	1/10.0	1/10.0
<u>50</u>	1/10.0	1/10.0	1/10.0	1/10.0	1/10.0	1/10.0	108	2/7.5	2/7.5	2/7.5	2/7.5	2/7.5	2/7.5
<u>51</u>	2/7.5	2/7.5	2/7.5	2/7.5	2/7.5	2/7.5	109	1/10.0	1/10.0	1/10.0	1/10.0	1/10.0	1/10.0
<u>52</u>	6/5.0	6/5.0	7/4.2	7/4.2	9/3.3	9/3.3	110	2/7.5	2/7.5	2/7.5	2/7.5	1/10.0	1/10.0
<u>53</u>	2/10.0	2/10.0	2/10.0	2/10.0	2/10.0	2/10.0	111	6/4.2	7/3.7	7/3.7	7/3.7	7/3.7	6/4.2
<u>54</u>	1/10.0	1/10.0	1/10.0	1/10.0	1/10.0	1/10.0	112	1/10.0	1/10.0	1/10.0	1/10.0	1/10.0	1/10.0
<u>55</u>	1/10.0	1/10.0	1/10.0	1/10.0	1/10.0	1/10.0	113	3/6.0	3/6.0	2/7.5	2/7.5	2/7.5	2/7.5
<u>56</u>	1/10.0	1/10.0	1/10.0	1/10.0	1/10.0	1/10.0	114	1/10.0	1/10.0	1/10.0	1/10.0	1/10.0	1/10.0
<u>57</u>	1/10.0	1/10.0	1/10.0	1/10.0	1/10.0	1/10.0	115	1/10.0	1/10.0	1/10.0	1/10.0	1/10.0	1/10.0

Note. Underlined characters differed in length and fit between at least two analyses.

TABLE 8

Length and Fit (f) of Informative Characters Which Changed When All Multistate Characters Were Unordered in the Analyses with Equal Weights (EW), Successive Weights (SW), and Implied Weights (IW) with Six Values for the Concavity Constant (k)

Char	EW	SW	IW	
			$k = 2-6$	$k = 1$
<u>1</u>	6/4.2	5/5.0	7/3.7	7/3.7
<u>8</u>	4/5.0	6/3.7	3/6.0	4/5.0
<u>16</u>	4/5.0	5/4.2	6/3.7	6/3.7
<u>20</u>	4/5.0	5/4.2	4/5.0	5/4.2
<u>21</u>	4/5.0	4/5.0	4/5.0	4/5.0
<u>23</u>	4/5.0	4/5.0	4/5.0	4/5.0
<u>27</u>	4/7.5	4/7.5	4/7.5	4/7.5
<u>28</u>	3/6.0	2/7.5	3/6.0	2/7.5
<u>32</u>	2/7.5	1/10.0	1/10.0	1/10.0
<u>33</u>	6/4.2	6/4.2	6/4.2	6/4.2
<u>52</u>	4/7.5	4/7.5	5/6.0	5/6.0
<u>59</u>	3/6.0	3/6.0	5/4.2	5/4.2
<u>65</u>	3/7.5	3/7.5	3/7.5	3/7.5
<u>69</u>	4/4.2	5/5.0	5/5.0	5/5.0
<u>95</u>	2/7.5	2/7.5	2/7.5	2/7.5
<u>101</u>	2/10.0	2/10.0	2/10.0	2/10.0
<u>110</u>	2/7.5	2/7.5	1/10.0	1/10.0
<u>111</u>	6/4.2	9/3.0	7/3.7	8/3.3

Note. Underlined characters differed in length and fit between at least two analyses.

identical in all analyses except $k = 1$ (Table 8). Three ordered multistate characters, 1 unordered multistate character, and 6 binary characters decreased in length as a result of unordering. One ordered multistate character, 1 unordered multistate character, and 3 binary characters increased in length.

Topological results of the sensitivity analysis in which 16 combinations of weighting regime and character transformation (multistates ordered vs unordered) were analysed are summarised, in the manner of Whiting *et al.* (1997), by means of a majority rule (>50%) consensus (Fig. 6).

Table 9 presents the results of constraining groups obtained in the weighted analyses, or proposed by previous authors (Lourenço, 1985, 1989; Stockwell, 1989; Sissom and Walker, 1992), on the topology of the tree located by the analysis with equal weights and ordered multistates. In all cases, constraint trees required one or more steps than the tree located with equal weights, although a better fit was obtained for five groups (reflecting the effects of weighting against homoplastic characters in the analyses with *a posteriori*

weighting). Better fit was obtained with most alternative placements of Heteroscorpionidae, Scorpioninae, and Urodacinae proposed by the implied weighting analyses (Fig. 3), but these cost up to seven extra steps on the equal-weights tree. However, one alternative topology for the internal relationships of the Diplocentrinae (Fig. 4) and another for the internal relationships of the Ischnuridae (Fig. 5) had a better fit at the cost of only one extra step. Only one extra step was required to constrain three genera (*Chiromachetes*, *Iomachus*, and *Orobothriurus*) for monophyly, at a slight fitness cost. In contrast, constraining *Opisthacanthus* (or the subgenus *Nepabellus*) for monophyly cost six extra steps and 9.6 loss in fitness. The greatest number of extra steps and loss of fitness occurred when the ischnurid generic relationships proposed by Lourenço (1985, 1989, 1996a) were constrained or when the monophyly of the Scorpionidae was constrained.

DISCUSSION

Scorpionoid Relationships

All the trees produced in the present analyses are congruent with Stockwell's (1989) tree (Fig. 1a) as regards the monophyly of the superfamily Scorpionoidea and its major clades (Fig. 6). The Scorpionoidea was supported by characters 11, 63, 69, 80, and 84 in all analyses (Appendix 4). Stockwell's basal dichotomy between the Bothriuridae and the remaining scorpionoid families (Diplocentrinae, Heteroscorpionidae, Ischnuridae, and Scorpionidae) was also supported in all analyses. Placement of the Bothriuridae as the sister taxon of the remaining Scorpionoidea differs from previously proposed topologies (Lamoral, 1980; Lourenço, 1985) and requires the hypothesis that characters 63, 69, and 80 (Appendix 4) are reversed in most bothriurids (Stockwell, 1989). The second monophyletic group of the basal scorpionoid dichotomy, comprising the remaining genera, conforms to the traditional superfamily Scorpionoidea (i.e., excluding Bothriuridae) and is supported by characters 3, 77, and 78 in all analyses (Appendix 4). High bootstrap and branch support values were obtained on the equal-weights tree for the Scorpionoidea, the Bothriuridae, and the monophyletic group comprising the remaining (non-bothriurid) genera (Fig. 2).

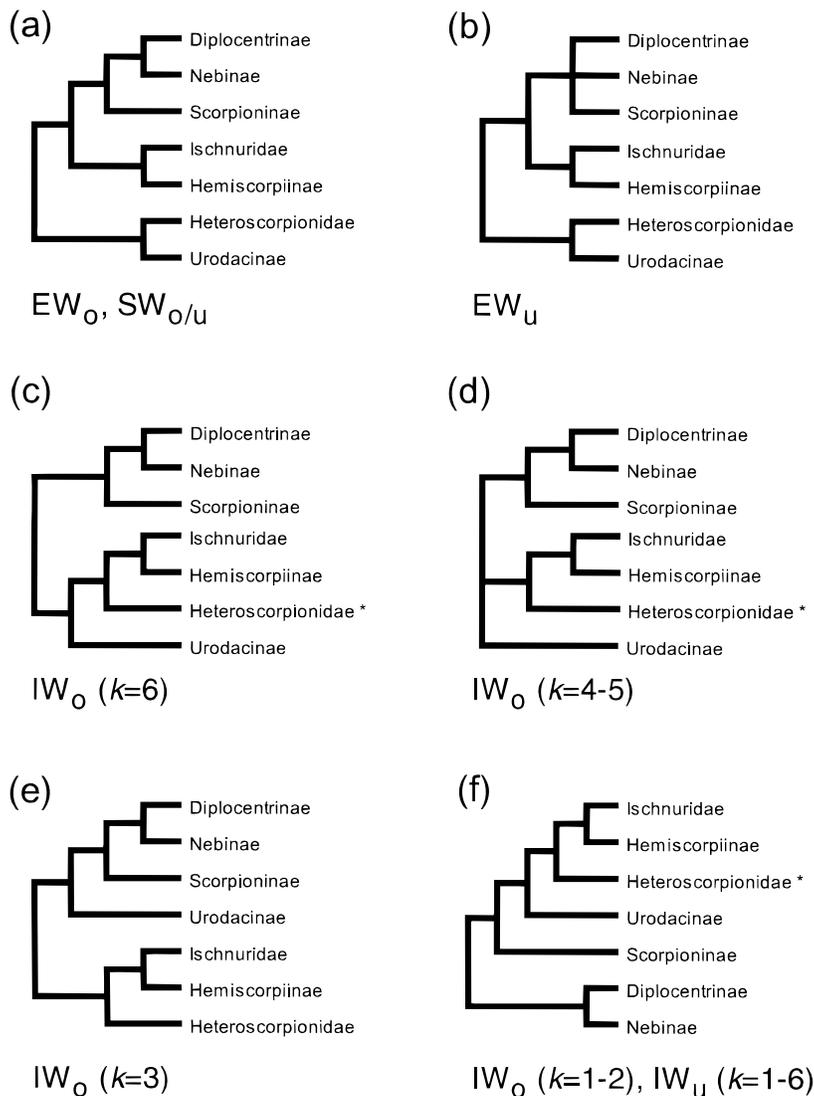


FIG. 3. Results of “sensitivity analysis” showing alternative hypotheses for the relationships among the major clades of Scorpionoidea obtained with equal weights (EW), successive weights (SW), and implied weights (IW) with six values for the concavity constant (k). Analyses with multistates ordered and unordered are indicated, respectively, by the subscripts “o” and “u”. Higher taxa reflect the current classification (Table 1) and correspond to Figs. 1 and 2. The asterisk indicates topologies in which monophyly of the two exemplar species of Heteroscorpionidae was unsupported. Tree statistics are provided in Table 5.

The primary differences between the topologies obtained in the various analyses concern the relationships within this second monophyletic group. All analyses supported the monophyly of (Hemiscorpiinae + Ischnuridae), on the basis of characters 2 and 11 (Appendix 4), thus confirming Stockwell’s (1989) topology. In addition, eight monophyletic groups, conforming to currently recognised families and subfamilies, were

retrieved in most analyses (Fig. 6): Diplocentridae, Diplocentrinae, Hemiscorpiinae, Heteroscorpionidae, Ischnuridae, Nebinae, Scorpioninae, and Urodacinae [diplocentrid monophyly was not supported in the analysis with equal weights and multistates unordered (Fig. 2) and heteroscorpionid monophyly was not supported in most of the analyses with implied weights (Figs. 3c, 3d, and 3f)]. In most cases, these higher taxa

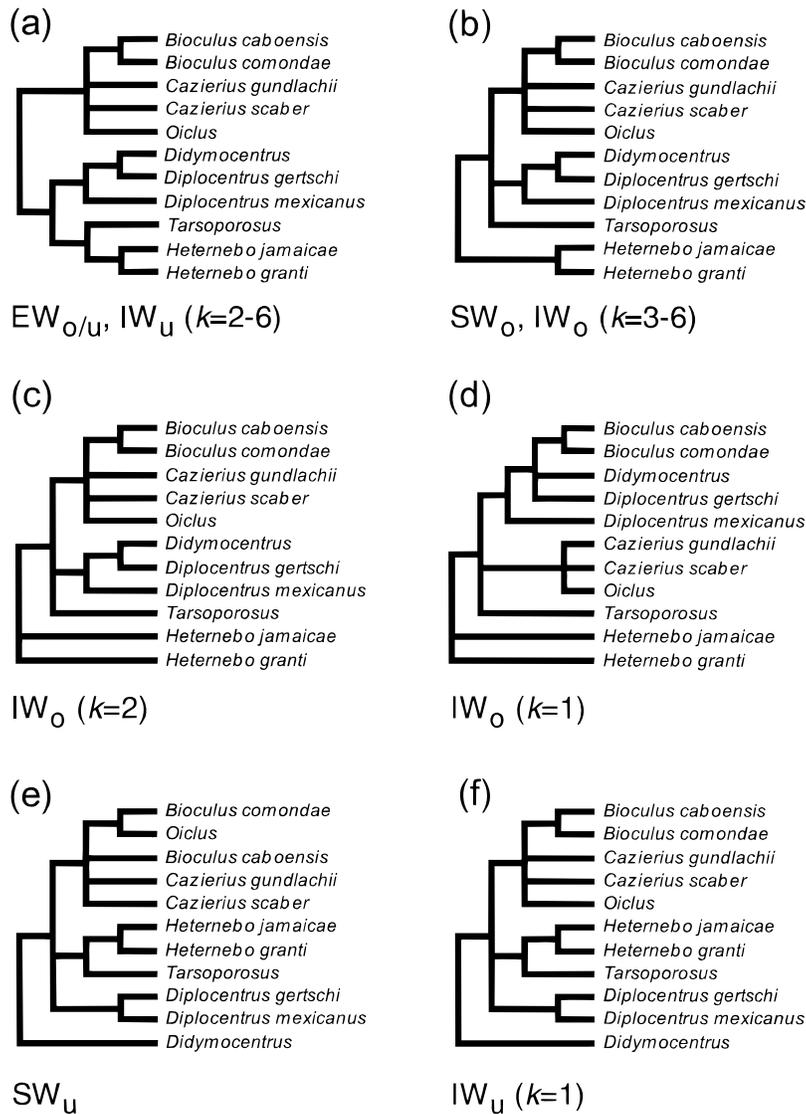


FIG. 4. Results of sensitivity analysis showing alternative hypotheses for the internal relationships of the Diplocentrinae obtained with EW, SW, and IW with six values for the concavity constant k . Analyses with multistates ordered and unordered are indicated, respectively, by the subscripts “o” and “u”. Genera which were consistently monophyletic (and monotypic genera) are indicated by a single terminal. Zero-length branches are collapsed. Tree statistics are provided in Table 5.

received fairly high bootstrap and branch support values on the equal-weights trees (Fig. 2). Their internal relationships are discussed further below. Topological differences among them concern the relative positions of the Heteroscorpionidae (*Heteroscorpion*), Urodacinae (*Urodacus*), and Scorpioninae.

The analyses with equal weights and successive weights were unanimous in the finding that *Heteroscorpion* and *Urodacus* form a monophyletic sister group

to the remaining taxa as follows (Fig. 3a): ((*Heteroscorpion* + *Urodacus*) ((*Hemiscorpiinae* + *Ischnuridae*) (*Diplocentridae* + *Scorpioninae*))). The (*Diplocentridae* + *Scorpionidae*) clade was first proposed by Lammoral (1980). However, the (*Heteroscorpion* + *Urodacus*) clade, supported by characters 33, 43, 45, 49, and 95 (Appendix 4), is novel and recalls the early views of Laurie (1896a,b) who considered *Urodacus* to be the most basal of the katoikogenic scorpions (the clade

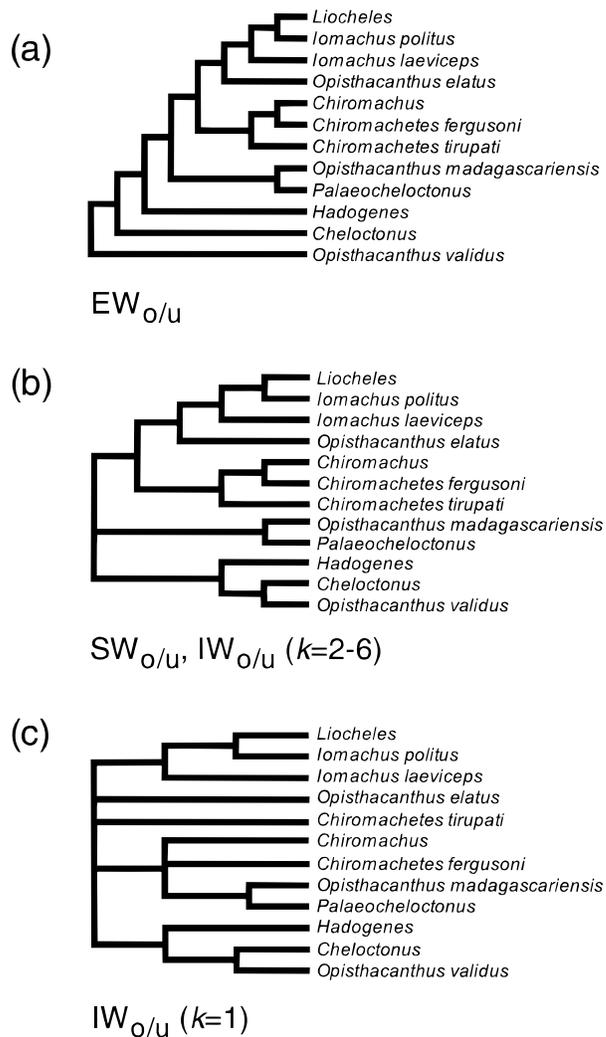


FIG. 5. Results of sensitivity analysis showing alternative hypotheses for the internal relationships of the Ischnuridae obtained with EW, SW, and IW with six values for the concavity constant k . Analyses with multistates ordered and unordered are indicated, respectively, by the subscripts "o" and "u". Genera which were consistently monophyletic (and monotypic genera) are indicated by a single terminal. Zero-length branches are collapsed. Tree statistics are provided in Table 5.

comprising all scorpionoids except the Bothriuridae). Stockwell (1989) omitted four of the characters supporting this group.

The (*Heteroscorpion* + *Urodacus*) clade was not obtained in any of the analyses with implied weights (Figs. 3c–3f), all of which supported Stockwell's (1989) placement of *Heteroscorpion* as sister group of the (Hemiscorpiinae + Ischnuridae) clade, on the basis of charac-

ters 8, 18, 107, and 113 (Appendix 4). The position of *Urodacus* was unresolved in the analyses with $k = 4-5$ and ordered multistates (Fig. 3d). *Urodacus* grouped basal to *Heteroscorpion* in most of the remaining analyses with implied weights, resulting in a (*Urodacus* (*Heteroscorpion* (Hemiscorpiinae + Ischnuridae))) clade, supported consistently by characters 33 and 95 (Appendix 4). However, in the analysis with $k = 3$ and ordered multistates (Fig. 3e), *Urodacus* grouped as the sister genus of the (Diplocentridae + Scorpioninae) clade, on the basis of character 65 (Appendix 4). This relationship was also obtained by Stockwell (Fig. 1a). Although the (*Heteroscorpion* (Hemiscorpiinae + Ischnuridae)) clade required five extra steps and a loss in fitness of 0.4 when constrained in isolation on the tree obtained with equal weights, additionally constraining *Urodacus* into either of the abovementioned positions decreased the number of extra steps to four, and increased the fit by up to 3.7 (Table 9). The increase in fitness was slightly greater for the (*Urodacus* (*Heteroscorpion* (Hemiscorpiinae + Ischnuridae))) clade than for the (*Urodacus* (Diplocentridae + Scorpioninae)) clade (Table 9).

Two alternative hypotheses for the position of the Scorpioninae were obtained in the analyses with implied weighting: ((Diplocentridae + Scorpioninae) (Hemiscorpiinae + Ischnuridae)) vs (Diplocentridae (Scorpioninae (Hemiscorpiinae + Ischnuridae))). The first group, which was also obtained in the analyses with equal weights and successive weights (Figs. 3a and 3b), conforms to the traditional view proposed by Vachon (1965, 1974) and later by Lamoral (1980), Lourenço (1985), and Stockwell (1989). It was restricted to implied weighting analyses in which moderate to mild concavity functions ($k = 3-6$) were applied when multistates were ordered (Figs. 3c–3e) and was consistently supported by characters 16, 52, and 59 (Appendix 4). The second group, in which the Scorpioninae were located basal to (*Urodacus* (*Heteroscorpion* (Hemiscorpiinae + Ischnuridae))), was obtained in analyses with unordered multistates or when strong concavity functions ($k = 1-2$) were applied in analyses with ordered multistates (Fig. 3f). This group was supported by character 110 (Appendix 4) and corresponds to the traditional family Scorpionidae (Kraepelin, 1894), before the subfamilies Ischnurinae and Heteroscorpioninae were elevated to familial status by Lourenço (1989, 1996a). It required seven extra steps when constrained

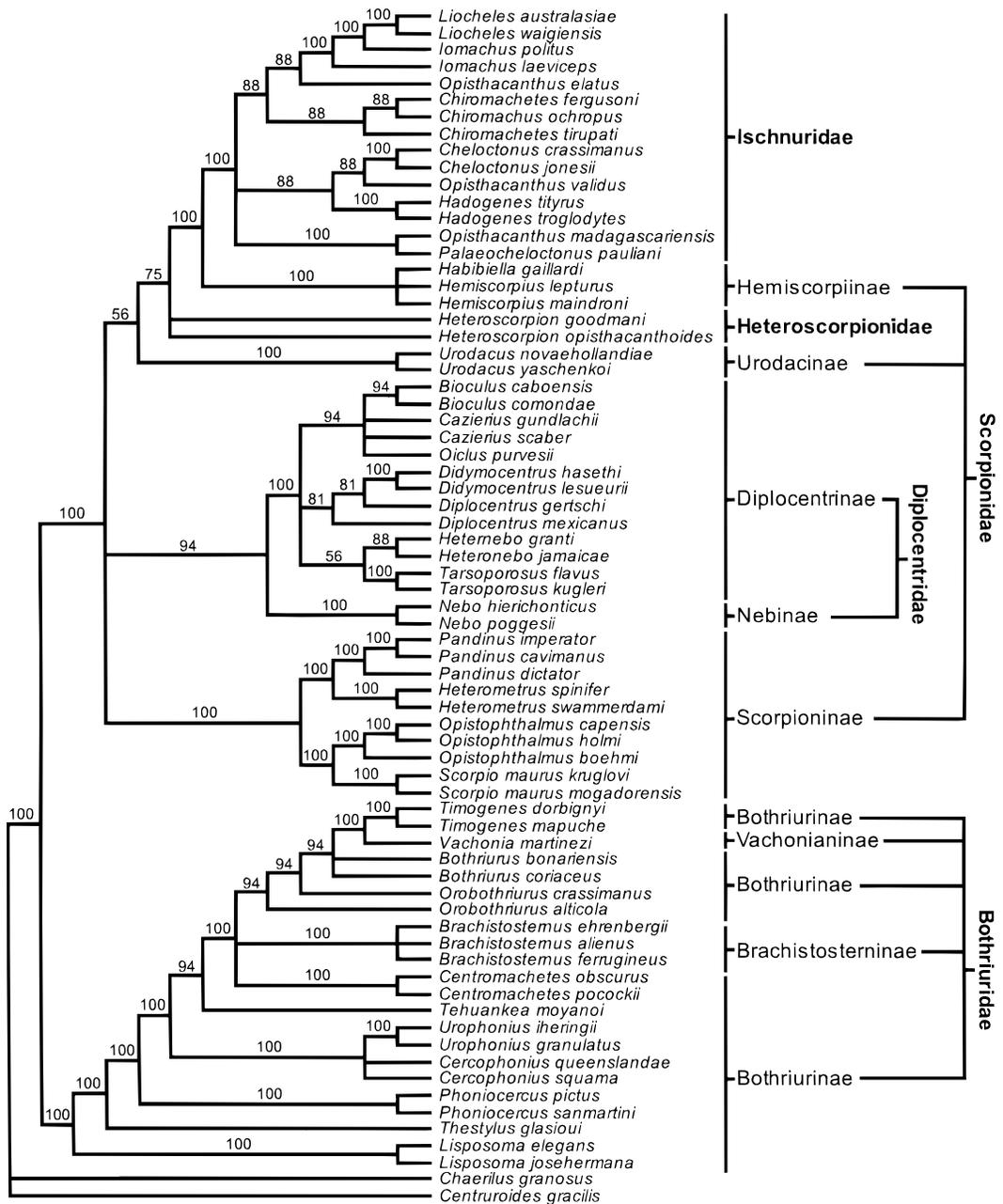


FIG. 6. Majority rule (>50%) consensus of the trees obtained by the 16 analyses (Table 5) in which weighting regime and multistate character transformation were varied. The frequencies with which nodes were retrieved are indicated above the branches (nodes with frequencies <100% are collapsed in the strict consensus).

on the equal-weights tree, but caused an increase in fitness of 4.0 (Table 9).

It is clear from these findings that the basal relationships of the second major scorpionoid lineage (the non-bothriurids) are somewhat less certain than implied

by Stockwell's (1989) results. Indeed, only 1 in 16 topologies is entirely concordant with his in this regard (Fig. 3e). However, choosing a preferred hypothesis necessitates philosophical arguments for or against the method of character transformation and the method

TABLE 9
Comparison of Alternative Hypotheses of Scorpionoid Evolution

Constrained topology	Figure	Step diff.	Fit diff.
Lourenço (1989): ischnurid generic relationships	1b	22	24.7
Monophyletic Scorpionidae, i.e., (Hemiscorpiinae + Scorpioninae + Urodacinae)		18	17.0
Lourenço (1989): (<i>Heteroscorpion</i> + <i>Hadogenes</i>)	1b	14	17.5
Lourenço (1989): (<i>Cheloctonus</i> + <i>Opisthacanthus</i>), with monophyletic <i>Opisthacanthus</i>	1b	9	9.6
(Scorpioninae (Urodacinae (Heteroscorpionidae (Hemiscorpiinae + Ischnuridae))))	3f	7	<u>4.0</u>
Monophyletic <i>Opisthacanthus</i>		6	9.6
Monophyletic <i>Nepabellus</i>		6	9.6
(Heteroscorpionidae (Hemiscorpiinae + Ischnuridae))	3c–3f	5	0.4
Stockwell (1989): (<i>Cercophonius</i> + <i>Urophonius</i> + <i>Centromachetes</i>)	1a	4	4.4
(Urodacinae (Heteroscorpionidae (Hemiscorpiinae + Ischnuridae)))	3c	4	<u>3.7</u>
Stockwell (1989): ((Urodacinae (Diplocentridae + Scorpioninae)) (Heteroscorpionidae (Hemiscorpiinae + Ischnuridae)))	1a, 3e	4	<u>2.1</u>
(<i>Bioculus</i> + <i>Didymocentrus</i> + <i>Diplocentrus gertschi</i>)	4d	3	0.4
Sissom and Walker (1992): (<i>Bioculus</i> + <i>Diplocentrus</i>)		2	1.8
Monophyletic <i>Orobothriurus</i>		1	2.5
Monophyletic <i>Iomachus</i>		1	1.0
Monophyletic <i>Chiromachetes</i>		1	1.0
Stockwell (1989): <i>Heteronebo</i> basal in Diplocentrinae	1a, 4b–4d	1	<u>0.9</u>
Monophyletic <i>Diplocentrus</i>		1	0.8
(<i>Chiromachus Chiromachetes fergusonii</i> (<i>O. madagascariensis</i> + <i>Palaeocheloctonus</i>))	5c	1	0.3
(<i>Hadogenes</i> (<i>Cheloctonus</i> + <i>Opisthacanthus validus</i>))	5b–5c	1	<u>0.2</u>

Note. Alternative topologies proposed in the literature or obtained by the analyses with a *posteriori* weighting are compared with the tree located by the analysis with equal weights (multistate characters ordered). Trees constrained for the corresponding monophyletic group required one or more steps than the tree obtained with equal weights, although in some cases a better total fit was obtained (underlined).

and intensity of weighting or arguments based upon the resultant character optimisation. Some of these arguments may be weaker (see above), but the choice among most will be arbitrary. In the present context, the tree obtained by the analysis with equal weights and ordered multistates (Fig. 2) is presented as the preferred hypothesis of scorpionoid relationships (Fig. 7) because equal weighting is the most general form of weighting (Kluge, 1989) and is therefore “preferable on philosophical grounds as the least assumption-laden approach” (Brower, 1999:202). However, additional data from other sources (e.g., molecular), applied in a “total evidence” framework (Kluge, 1989), will be required to confirm these relationships. The placement of *Heteroscorpion* and *Urodacus*, in particular, appears to be critical in resolving the higher level phylogeny of the Scorpionoidea.

Bothriurid Relationships

Although the monophyly of the Bothriuridae has never been contested, the position of *Lisposoma* has

been the focus of some attention. *Lisposoma* was originally placed in a separate subfamily, Lisposominae, of the Scorpionidae (Lawrence, 1928). Vachon (1974:940) discussed trichobothrial similarities between *Lisposoma* and the Bothriuridae (refer to Appendix 3), but merely considered these to support Lawrence’s (1928) placement of the genus in a unique subfamily of the Scorpionidae. However, Francke (1982a) realised that these, and other characters (discussed in Appendix 3), were synapomorphic and suggested that *Lisposoma* should be transferred to the Bothriuridae, where it has remained since, without definite placement (Sissom, 1990). Stockwell’s (1989) analyses placed *Lisposoma* in a monophyletic group with the remaining genera of the Bothriuridae (Fig. 1a), thus confirming Francke’s view, and this group was supported in all present analyses (Fig. 6) by characters 10, 23, 26, 56, 58, 68, and 85 (Appendix 4).

All analyses supported Stockwell’s (1989) pectinate arrangement of *Lisposoma*, *Thestylus*, and *Phoniocercus* (Fig. 1a), which branched off sequentially from the base of the bothriurid clade, and his (*Timogenes* + *Vachonia*)

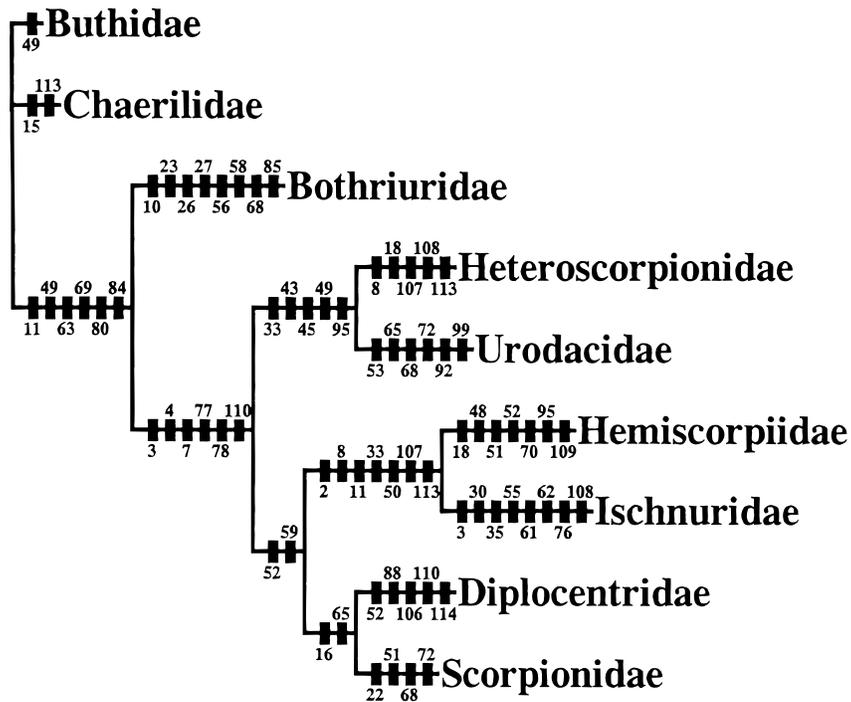


FIG. 7. Preferred hypothesis of relationships among the families of Scorpionoidea (summary of Fig. 2), with unambiguous synapomorphies optimised.

and (*Cercophonius* + *Urophonius*) clades (Fig. 6). The bootstrap and branch support values of these nodes, especially the (*Timogenes* + *Vachonia*) clade, were fairly high in the analyses with equal weights (Fig. 2). Most analyses also supported Stockwell's (*Bothriurus* (*Timogenes* + *Vachonia*)) clade, but this collapsed in the strict consensus of the analysis with equal weights and multistates unordered (Fig. 2). The analyses offered more resolution of the relationships among the remaining bothriurid genera and conflicted with Stockwell's findings on the position of *Centromachetes* (Fig. 1a), which formed a monophyletic group with the remaining genera, rather than with (*Cercophonius* + *Urophonius*). Nine extra steps (9.6 decrease in fitness) were required to constrain the monophyly of (*Centromachetes* + *Cercophonius* + *Urophonius*) on the tree obtained by the unweighted analysis with ordered multistates (Table 9). The phylogenetic positions of *Brachistosternus*, *Orobothriurus*, and *Tehuanka* were also resolved in most analyses, resulting in the following pectinate clade, which formed the sister group of (*Cercophonius* + *Urophonius*): (*Tehuanka* (*Brachistosternus* (*Centromachetes*

(*Orobothriurus* (*Bothriurus* (*Timogenes* + *Vachonia*))))). However, these nodes had low bootstrap and branch support values and the first five of them collapsed in the strict consensus of the analysis with equal weights when multistates were unordered (Fig. 2). The node grouping *Centromachetes* with the remaining genera received the lowest bootstrap value of all and remained unsupported in the weighted analyses with multistate characters unordered.

As discussed by Stockwell (1989), the phylogenetic positions of *Vachonia* and *Brachistosternus* pose problems for continued recognition of Maury's (1973a) subfamilies Vachonianinae and Brachistosterninae, which are clearly unjustified. Even if subfamilial status were provided for any clade basal to (*Timogenes* + *Vachonia*), it would take the name Bothriurinae, as would any clade basal to *Brachistosternus*. Accordingly, I support Stockwell's proposal to place the Brachistosterninae and Vachonianinae in synonymy with the Bothriurinae. However, there is no obvious justification for Stockwell's proposal to retain *Lisposoma* in a unique subfamily, Lisposominae.

The monophyly of three bothriurid genera, *Bothriurus*, *Orobothriurus*, and *Cercophonius*, was not supported in the current analyses. *Orobothriurus* was rendered paraphyletic by *O. crassimanus*, which formed a monophyletic group with (*Bothriurus* (*Timogenes* + *Vachonia*)), to the exclusion of *O. alticola* (Fig. 2). However, only one extra step was required to constrain *Orobothriurus* for monophyly (Table 9). *Cercophonius* appears to be separable from *Urophonius* on meristic grounds, e.g., counts of the telotarsal spiniform setae (Koch, 1977; Acosta, 1990), but the difficulties of scoring such data into discrete states for cladistic analysis (Farris, 1990) prevented their use in the current analyses. Consequently, it is unknown whether these characters are apomorphic in *Cercophonius*. However, it is clear that *Bothriurus* is defined entirely by plesiomorphic states, relative to *Timogenes* and *Vachonia*. *Timogenes* and *Vachonia* may have to be placed in synonymy with *Bothriurus* (which has nomenclatural priority), unless *Bothriurus*, with 33 currently recognised species (Lowe and Fet, 2000), can be split into more than one genus. Nevertheless, I refrain from suggesting any further emendations to the current status of these genera until a more comprehensive phylogenetic analysis of the Bothriuridae, incorporating a larger number of exemplar taxa and additional characters, has confirmed the relationships revealed in the present analyses.

Diplocentrid Relationships

The monophyly of the Diplocentridae was supported by characters 88, 106, and 114 (Appendix 4) in all present analyses except the analysis with equal weights and unordered multistates. This analysis obtained a polytomy between the Diplocentrinae, the Nebinae (*Nebo*), and the Scorpioninae in the strict consensus (Fig. 2), attributed to the grouping of the Diplocentrinae with the Scorpioninae, to the exclusion of *Nebo*, in three of the six equal length trees. The monophyly of the Diplocentridae has never previously been disputed, and the consistent grouping of *Nebo* with the Diplocentrinae in the remaining 15 analyses presented here (Fig. 6) argues strongly in its support. Both the Diplocentrinae and the Nebinae were consistently monophyletic (Fig. 6), on the basis of characters 65, 96, and 101 and character 47 (Appendix 4), respectively. The bootstrap and branch support values for the two

subfamilies were higher than those for the Diplocentridae (Fig. 2).

In contrast to the monophyly of the Diplocentridae and its subfamilies, the internal relationships among the genera of Diplocentrinae are less certain. This is reflected in the low bootstrap and branch support values of many internal diplocentrine nodes, of which the monophyly of *Didymocentrus* received highest support (Fig. 2). Stockwell's (1989) analyses provided no internal resolution of diplocentrine relationships, aside from the basal position of *Heteronebo* (Fig. 1a). Among the present analyses, Stockwell's placement of *Heteronebo* was confirmed only in the weighted analyses with ordered multistates (Figs. 4b–4d). In the analyses with equal weights and the weighted analyses with unordered multistates, *Heteronebo* consistently grouped as the sister genus of *Tarsoporosus* (Fig. 4a, 4e, and 4f). However, only one extra step was required to constrain Stockwell's placement of *Heteronebo* on the equal-weights tree with the alternative topology and this resulted in an increase in fitness of 0.9 (Table 9). The monophyly of *Heteronebo* was supported in all analyses except with implied weights under strong concavity ($k = 1-2$), when multistates were ordered (Figs. 4c and 4d).

Stockwell's failure to resolve the internal relationships of the Diplocentrinae is not particularly surprising. Most diplocentrine genera are defined principally on meristic or morphometric criteria (e.g., Francke, 1977a, 1978) which were not employed in Stockwell's analysis or in the present analyses, because of the difficulties of scoring such data into discrete states (Farris, 1990). Despite this, several monophyletic groups were consistently retrieved in the present analyses (Fig. 6), based upon the evidence of the limited number of qualitative characters available for the diplocentrine taxa. Several of these groups call into question the monophyly of existing diplocentrine genera, which would not have been revealed without the application of an exemplar approach.

Cazierius formed a monophyletic group with *Oiclus* in all analyses (Fig. 4). However, the monophyly of *Cazierius* was consistently unsupported, which may be expected since Francke (1978:32) considered *Cazierius* to be ancestral to *Oiclus* and, hence, defined it on the basis of plesiomorphic states relative to the latter. In

contrast, *Oiclus* is autapomorphic for character 64 (Appendix 4). *Cazierius* should probably be placed in synonymy with *Oiclus* (which has nomenclatural priority). However, this cannot be implemented until the position of *Bioculus* is confirmed.

Most analyses supported the monophyletic grouping of the two exemplar species of *Bioculus* and their placement in a monophyletic group with *Cazierius* and *Oiclus* (Fig. 6). These novel findings may ease or add to the controversy that has surrounded the genus *Bioculus* since its inception. *Bioculus* was originally proposed by Stahnke (1968) for 14 species from Baja California Sur (México) and adjacent islands. After extensive field study, resulting in the accumulation of hundreds of additional specimens, Williams and Lee (1975) synonymised the genus with *Didymocentrus* and recognised only four species from the region. Several years later, Francke (1978) emended the diagnoses for the genera *Didymocentrus* and *Diplocentrus* and transferred the four species to *Diplocentrus*, but Francke (1979) subsequently listed one of them, *Diplocentrus comondae*, in combination with *Didymocentrus*. Williams (1980) continued to recognise the four species as belonging to *Didymocentrus* in his monograph on the scorpions of Baja California. Stockwell (1988) proposed several similarities with *Didymocentrus* (refer to Appendix 3 for further discussion), but did not decide on the placement of the four species. Sissom and Walker (1992) recently described *Diplocentrus gertschi* as the first record of a species of *Diplocentrus* from the western (i.e., Baja) side of the Sierra Madre Occidental and proposed several characters (also discussed further in Appendix 3), some of which they admitted to be plesiomorphic, shared by the latter species and *Bioculus*, but not by *Didymocentrus*. (This provided the rationale for the choice of *D. gertschi* as one of the exemplars in the present analysis, as discussed in Appendix 1.) Sissom and Walker concluded that *Bioculus* should not be placed in *Didymocentrus*, but they refrained from placing *Bioculus* formally in *Diplocentrus*, pending the discovery of new characters or new diplocentrids from México. In the most recent development, *Bioculus* was reinstated by Stockwell (1992) in a key to the families and genera of North American scorpions, leading Sissom and Fet (2000) to question its validity on the grounds that no empirical evidence of monophyly was presented.

In the present context, the monophyly of the two

exemplar species of *Bioculus* represented here was supported by all analyses except successive weighting with multistates unordered (Fig. 4e). Given that these two exemplar species provide a reasonable estimate of morphological diversity among the four Baja diplocentrids (Appendix 1), there appears to be less cause to question the taxonomic status of *Bioculus* on the grounds of synapomorphy. However, additional data will be required to place the *Bioculus* clade unambiguously within the Diplocentrinae. The monophyletic grouping of *Bioculus* with *Cazierius* and *Oiclus*, as opposed to *Didymocentrus* and *Diplocentrus*, was supported in most of the analyses (Fig. 6). Only in analyses with a very strong weighting function (implied weighting with $k = 1$) did *Bioculus* group with *D. gertschi* (Fig. 4d). Since this monophyletic group also included *Didymocentrus*, to the exclusion of *Diplocentrus mexicanus*, Sissom and Walker's (1992) hypothesis is not supported. The (*Bioculus* + *Didymocentrus* + *D. gertschi*) clade required three extra steps (loss in fitness of 0.4) when constrained for monophyly on the equal-weights tree (Table 9) and was not retrieved when the implied weighting analysis with $k = 1$ was conducted with multistates unordered (Fig. 4f). Constraining the monophyly of *Bioculus* and *Diplocentrus*, to the exclusion of *Didymocentrus*, in accordance with Sissom and Walker's hypothesis, required two extra steps and a loss in fitness of 1.8 (Table 9).

The final difference between the diplocentrine topologies obtained in the various analyses concerns the placement of *Didymocentrus* and *Diplocentrus*. All except two analyses supported the paraphyly of *Diplocentrus* with respect to *Didymocentrus* (Fig. 6), as follows: (*D. mexicanus* (*D. gertschi* (*Didymocentrus*))). The analyses with unordered multistates retrieved a monophyletic *Diplocentrus* with successive weighting and with implied weighting under a strong concavity of $k = 1$ (Figs. 4e and 4f). Notably, *Diplocentrus* monophyly was supported only as a result of the basal placement of *Didymocentrus* in the Diplocentrinae, in which case the position of *Diplocentrus* was unresolved with respect to the remaining diplocentrines. One extra step (loss in fitness of 1.0) was required to constrain the monophyly of *Diplocentrus* on the tree obtained with equal weights and ordered multistates (Table 9).

The widespread finding of *Diplocentrus* paraphyly casts doubt on the possibility that *Didymocentrus* can

be upheld. In order to retain the monophyly of *Diplocentrus* (which has nomenclatural priority), *Didymocentrus* may have to be placed in synonymy with the latter. Alternatively, *Diplocentrus*, estimated to include at least 50 species, many of which are undescribed (Francke, 1978), could be split into several genera (W. D. Sissom, pers. comm.). In lieu of the large number of species recognised in *Diplocentrus*, and the apparent morphological diversity within this genus (e.g., see Francke, 1977b; Stockwell, 1988; Sissom and Walker, 1992), it would be premature to suggest revisions to the generic status of the species currently recognised in *Didymocentrus* until further analysis of the species-level relationships of both genera, incorporating additional characters, has been conducted. Indeed, a more comprehensive analysis of diplocentrine relationships is also needed to confirm or reject the topological positions of *Bioculus*, *Heteronebo*, *Tarsoporosus*, and the (*Cazierius* + *Oiclus*) clade with respect to *Diplocentrus* and *Didymocentrus*. The paucity of discrete morphological characters in the Diplocentrinae suggests that molecular data would provide a more productive avenue for future research into the relationships within this group (Prendini and Wheeler, manuscript in preparation).

Ischnurid Relationships

Until recently, the family Ischnuridae comprised genera that were formerly assigned to the subfamilies Ischnurinae and Heteroscorpioninae, in the Scorpionidae (Sissom, 1990). The familial name Ischnuridae was used in a more restricted sense (i.e., not including *Heteroscorpion*) by several previous authors (Pocock, 1900; Kraepelin, 1913; Tikader and Bastawade, 1983; Bastawade, 1986). However, it was redefined and formally removed from the Scorpionidae by Lourenço (1985, 1989), who also provided a hypothetical “cladogram” of the relationships among the genera (Fig. 1b). This tree does not appear to be derived from any empirical evidence (i.e., no data matrix has been presented and no characters are mapped onto the tree). Lourenço (1985, 1989) based his resurrection of the Ischnuridae principally upon the morphology of the venom glands, despite asserting that Ischnuridae possessed the plesiomorphic state for this character and was therefore paraphyletic (Lourenço, 1985:169): “La position des Ischnuridae, groupe paraphylétique, dont les éléments

partagent le caractère ‘glandes à venin simples’ (plésiomorphe) . . .” [Note that this assertion was fallacious—the occurrence of simple venom glands in *Heteroscorpion* and the Ischnuridae is apomorphic, based on outgroup comparison with the Bothriuridae (Stockwell, 1989; this analysis).] Sissom (1990) reiterated that the characters used by Lourenço (1985, 1989) to separate the Ischnuridae from the Scorpionidae were plesiomorphic and, hence, that there were no synapomorphies for the family, but continued to recognise it. More recently, Lourenço (1996a) elevated *Heteroscorpion* to familial status, although he had not retained its subfamilial status under the Ischnuridae (Table 1).

In the present analyses, monophyly of the Ischnuridae, corresponding here with Lourenço’s (1996a) most recent treatment and Stockwell’s (1989) subfamily Ischnurinae, was consistently supported (Fig. 6) by characters 30, 35, 53, 59, 60, and 75 (Appendix 4) and received high bootstrap and branch support values on the equal-weights trees (Fig. 2). The monophyly of *Heteroscorpion* was supported in the analyses with equal weights and successive weights (Figs. 3a and 3b), by characters 8, 18, 107, 108, and 113 (Appendix 4), and received higher bootstrap and branch support values than all families except the Bothriuridae on the equal-weights trees (Fig. 2). Despite this, *Heteroscorpion* monophyly was unsupported in all analyses with implied weights, except with intermediate concavity ($k = 3$) and ordered multistates (Fig. 3e), in which it was supported by characters 43, 45, and 49 (Appendix 4).

As discussed above, two alternative hypotheses for the position of *Heteroscorpion* were obtained in the present analyses, corresponding to the use of equal weights or successive weights vs the use of implied weights (Fig. 3): (*Heteroscorpion* + *Urodacus*) vs (*Heteroscorpion* (Hemiscorpiinae + Ischnuridae)). These findings, as those of Stockwell, refute Lourenço’s (1985, 1989) hypothesis that *Heteroscorpion* is the sister genus of *Hadogenes* (Fig. 1b). Fourteen extra steps (17.5 decrease in fitness) were required to constrain these genera to be monophyletic on the tree obtained by the analysis with equal weights and ordered multistates (Table 9). Moreover, these results call into question Lourenço’s (1985, 1989) initial placement of *Heteroscorpion* in the Ischnuridae (Table 1) and Stockwell’s (1989) proposed retention of the genus as a subfamily of the Ischnuridae (Table 2). In light of the trees obtained with equal weights and successive weights, I support Lourenço’s (1996a)

more recent view that the unique phylogenetic and biogeographical position of this endemic Malagasy genus is justification for its recognition at the familial level.

The internal relationships of the Ischnuridae were weakly supported in the present analyses and received low bootstrap and branch support values on the equal-weights trees (Fig. 2). The monophyly of *Hadogenes* and *Liocheles* were notable exceptions. Two areas of incongruence can be identified among the trees obtained (Fig. 5). The first involved the positions of *Hadogenes*, *Opisthacanthus validus*, and *Cheloctonus*, for which there are two alternative hypotheses. In the analyses with equal weights, these taxa grouped basal to the remaining ischnurids in a pectinate arrangement (Fig. 5a). However, in the analyses with *a posteriori* weighting, they formed a monophyletic group in which *Hadogenes* was basal to (*O. validus* + *Cheloctonus*), thus creating a polytomy by collapsing the monophyletic grouping of (*Opisthacanthus madagascariensis* + *Palaeocheloctonus*) with the remaining genera (Figs. 5b and 5c). The (*Hadogenes* (*O. validus* + *Cheloctonus*)) clade required only one extra step when constrained to be monophyletic on the equal-weights tree and resulted in an increase in fitness of 0.2 (Table 9).

The second area of conflict among the analyses regards the position of the (*O. madagascariensis* + *Palaeocheloctonus*) clade, which grouped basal to ((*Chiromachetes tirupati* (*Chiromachetes fergusonii* + *Chiromachus*)) (*Opisthacanthus elatus* (*Iomachus* + *Liocheles*))) in most analyses (Fig. 6). However, the analyses with implied weights under a strong concavity ($k = 1$) supported a monophyletic grouping of (*O. madagascariensis* + *Palaeocheloctonus*) with *Chiromachus* and *C. fergusonii*, resulting in the collapse of the first three nodes in the latter clade (Fig. 5c). This hypothesis also required one extra step when constrained for monophyly, but resulted in a 0.3 loss in fitness (Table 9).

Although the results of these analyses are far from unanimous as regards the internal relationships of the Ischnuridae, they nevertheless refute Lourenço's (1985, 1989) hypotheses (Fig. 1b) that *Hadogenes* comprises a sister group (together with *Heteroscorpion*) of the remaining ischnurid genera and that (*Opisthacanthus* + *Cheloctonus*) are the sister group of the (*Chiromachus* (*Iomachus* + *Liocheles*)) clade. The placement of *O. validus* in a monophyletic group with *Cheloctonus* in the weighted analyses is congruent with Lourenço's (1985,

1989) hypothesis that *Opisthacanthus* and *Cheloctonus* are sister genera. However, nine extra steps (loss in fitness of 9.6) were required to force the monophyly of *Opisthacanthus* with *Cheloctonus* on the equal-weights tree (Table 9).

A total of 22 extra steps (loss in fitness of 24.7) were required to constrain the monophyly of all the groups postulated by Lourenço (1985, 1989, 1996a) in Fig. 1b (Table 9). Many of these extra steps can be attributed to the fact that two of the genera, *Chiromachetes* and *Iomachus*, were found to be paraphyletic, while a third, *Opisthacanthus*, was polyphyletic. For example, 6 of the 9 extra steps required to constrain the monophyly of (*Opisthacanthus* + *Cheloctonus*) are attributed to constraining the monophyly of *Opisthacanthus* (Table 9). This finding, and indeed, the generally equivocal nature of relationships within the Ischnuridae, is merely a reflection on the unfortunate state of ischnurid systematics, in which genera have been repeatedly defined by plesiomorphic states or overall similarity. Cladistic analyses with supraspecific terminal taxa, which assume these genera to be monophyletic, cannot be expected to obtain much resolution of the internal relationships in this family.

All present analyses supported the monophyletic grouping of (*Chiromachetes fergusonii* + *Chiromachus ochropus*) and most analyses (implied weights with $k = 1$ excepted) placed these taxa in a monophyletic group with Lourenço's (1997) recently described *Chiromachetes tirupati* (Fig. 6). The current taxonomic status of *Chiromachetes* is problematic. The genus was originally created by Pocock (1899) for *C. fergusonii*, known only from a single female specimen. Tikader and Bastawade (1983) recognised the monotypic genus in their monograph on the scorpions of India, but Lourenço (1983a, 1985, 1989) suggested that the characters used to separate it from *Iomachus* were not legitimate at the generic level. Stockwell (1989) continued to recognise *Chiromachetes* and included it in his analysis and classification, but Sissom (1990) followed Lourenço's (1985) view and did not include it in his key to the genera of Ischnuridae. Recently, Lourenço (1997) re-evaluated *Chiromachetes* and described a second species, *C. tirupati*, from a single female specimen. However, the character states provided for *Chiromachetes* by Lourenço (1997) are plesiomorphic and the genus was found to be paraphyletic in all of the present analyses (Fig. 6), one extra step (loss in fitness of 1.0) being required to constrain its

monophyly (Table 9). These findings cast doubt on the validity of *Chiromachetes* as currently defined (*Chiromachus* has nomenclatural priority). However, further analysis of ischnurid relationships is needed before a conclusive decision can be taken regarding the taxonomic status of the genus.

Stockwell's analyses supported a single monophyletic group within the Ischnuridae, comprising the genera *Chiromachus*, *Iomachus*, and *Liocheles*, placed in a pectinate arrangement (Fig. 1a). This relationship was originally postulated by Lourenço (1985, 1989) in his hypothetical cladogram (Fig. 1b). Most of the present analyses [implied weights with $k = 1$ (Fig. 5c) excepted] also retrieved this monophyletic group (Fig. 6), but differed in the inclusion of *Chiromachetes* as the paraphyletic sister group of *Chiromachus* and in the inclusion of the Neotropical *Opisthacanthus elatus* as the sister taxon of the (*Iomachus* + *Liocheles*) clade. The monophyletic grouping of *Iomachus* and *Liocheles* was obtained in all analyses (Fig. 6). However, *Iomachus* was consistently paraphyletic, on account of the Afrotropical species, *Iomachus politus*, forming a monophyletic group with *Liocheles*, to the exclusion of the Indian species, *Iomachus laeviceps*. One extra step (loss in fitness of 1.0) was required to constrain *Iomachus* to be monophyletic (Table 9).

In a series of papers on the species of *Iomachus*, Sreenivasa-Reddy (1968a,b,c,d) neglected to address the relationships of the Indian species with their Afrotropical counterparts, thus failing to address the diagnosis of the genus *sensu lato*. Sreenivasa-Reddy (1968d) omitted the Afrotropical *I. borana* (Caporiacco 1939) altogether. The diagnostic character states provided for *Iomachus* by Sreenivasa-Reddy (1968d), and subsequently adopted by Lourenço (1985) and Sissom (1990), are plesiomorphic, as with *Chiromachetes*, and a reevaluation of the taxonomic status of the genus is in order.

Perhaps the most significant finding of the present analyses for ischnurid phylogenetic relationships is the discovery that the largest ischnurid genus, *Opisthacanthus*, is a polyphyletic assemblage. Although the topologies obtained from the analyses with equal weights differed from the topologies obtained with *a posteriori* weighting as regards the placement of *O. validus* (Fig. 5), all analyses demonstrated that *Opisthacanthus* is polyphyletic (Fig. 6). Furthermore, all analyses indicated that the Afrotropical subgenus *Nepabellus* (originally afforded generic status by Francke, 1974) is also

polyphyletic. The Malagasy member of *Nepabellus*, *Opisthacanthus madagascariensis*, consistently grouped with the recently described Malagasy genus, *Palaeocheloctonus* (Lourenço, 1996a). The African member of *Nepabellus*, *Opisthacanthus validus*, grouped basal to the rest of the Ischnuridae in the analyses with equal weights (Fig. 5a), but formed a monophyletic group with the two exemplars of *Cheloctonus*, another African genus, in the weighted analyses (Figs. 5b and 5c). The Neotropical *Opisthacanthus elatus*, placed in the nominal subgenus, consistently grouped as the sister taxon of the monophyletic group (*Iomachus* + *Liocheles*), except in the analyses with implied weights in which $k = 1$, in which its position was unresolved (Fig. 5c). Six extra steps (loss in fitness of 9.6) were required to constrain the monophyly of *Opisthacanthus* and the monophyly of *Nepabellus* (Table 9).

A more comprehensive phylogenetic analysis, incorporating a larger number of exemplar taxa and additional characters, including molecular data (Prendini and Wheeler, manuscript in preparation), is evidently required in order to clarify the internal relationships of the major clades of Ischnuridae and establish whether certain genera that are suspected to be nested within others (e.g., *Cheloctonus*) can be upheld. Nonetheless, some general suggestions can be offered to enhance the stability of the existing ischnurid classification. First, a new genus should be created for the two Afrotropical species of *Iomachus* (the Indian species have nomenclatural priority). Second, in the case of *Opisthacanthus*, the Afrotropical subgenus *Nepabellus*, originally assigned generic status by Francke (1974), should be raised, but the Malagasy species should be excluded from it. Although a new genus could be created for the Malagasy species, it would be more sensible to transfer them to Lourenço's recently created genus, *Palaeocheloctonus*. This would leave the Neotropical species (and the Afrotropical *Opisthacanthus lecomtei*) in *Opisthacanthus*, with which the nominal subgenus would then be synonymous.

Scorpionid Relationships

As will be apparent from the above discussions, Scorpionidae, as currently defined, is polyphyletic in all analyses presented here, on account of the positions of the scorpionid genera *Urodacus*, *Hemiscorpius*, and *Habibiella*. Eighteen extra steps (17.0 loss in fitness)

were required to constrain the monophyly of the Scorpionidae on the tree obtained by the analysis with equal weights and ordered multistates (Table 9). The finding of scorpionid polyphyly confirms Stockwell's (1989) results. However, I propose to deal with the problem somewhat differently.

On the basis of the evidence obtained in this study, I support Stockwell's view (adopted also by Lourenço, 1996a) that the endemic Australian *Urodacus*, comprising the subfamily Urodacinae, should be provided familial status on the grounds of its unique phylogenetic and biogeographic position. Although the exact phylogenetic placement of *Urodacus* is still contestable, its basal position within the Scorpionoidea is fairly certain. Its monophyly, supported in all analyses by characters 53, 92, and 99 (Appendix 4) and consequently by high bootstrap and branch support values on the equal-weights trees (Fig. 2), remains undisputed (Fig. 6). A similar rationale (see above) was provided by Lourenço (1996a), based on Stockwell's (1989) cladogram, for proposing familial status for the endemic Malagasy genus, *Heteroscorpion*.

Recognition of both *Heteroscorpion* and *Urodacus* at the familial level provides the further justification for elevating the remaining two enigmatic scorpionids, *Hemiscorpius* and *Habibiella* (subfamily Hemiscorpiinae), to familial level. Sissom (1990) admitted that the Hemiscorpiinae could not be separated from the Ischnuridae by means of the characters discussed by Lourenço (1985, 1989), and doubted their placement in the Scorpionidae, but did not suggest an alternative. Stockwell (1989) proposed transferring the Hemiscorpiinae directly from the Scorpionidae to the Ischnuridae, where he retained their subfamilial status (Table 2). However, it is logically inconsistent to apply different ranking criteria to these subfamilies in the face of similar cladistic interpretations: the basal phylogenetic position of the Hemiscorpiinae and their disjunct distribution in the Middle East (Pocock, 1894; Kraepelin, 1905; Birula, 1917b) also warrants the assignment of familial status. Monophyly of the Hemiscorpiinae was supported in all analyses by characters 48, 51, 70, and 109 (Appendix 4). High bootstrap and branch supports were obtained for the group on the equal-weights trees (Fig. 2). It should be noted that the monophyly of *Hemiscorpius* was not supported in any of the present

analyses (Fig. 6) and continued recognition of the generic status of *Habibiella* may thus be unwarranted (*Hemiscorpius* has nomenclatural priority).

Assigning familial status to the Urodacinae and Hemiscorpiinae would restore monophyly to the family Scorpionidae. The Scorpionidae would then be recognised in accordance with Stockwell (1989) as comprising the monophyletic group of genera traditionally referred to as the subfamily Scorpioninae: *Heterometrus*, *Opisthophthalmus*, *Pandinus*, and *Scorpio* (Table 1). This group was supported in all present analyses by characters 22 and 51 (Appendix 4) and consequently received high bootstrap and branch support values on the equal-weights trees (Fig. 2). All the analyses also supported the sister-group relationship of *Heterometrus* and *Pandinus*, postulated originally by Couzijn (1981) and confirmed by Stockwell (1989), and the novel sister-group relationship of *Opisthophthalmus* and *Scorpio* (Fig. 6). These internal relationships received fairly high bootstrap and branch support values (Fig. 2).

CONCLUSION

Stockwell (1989:243) concluded his contribution with a plea for "particular, detailed studies at the generic level." It is clear that such studies will be essential to clarify the internal relationships of groups such as the Bothriuridae, Diplocentrinae, and Ischnuridae. However, these relationships should be investigated by means of an exemplar approach, as argued here. The taxonomic insights revealed by the present cladistic analysis of suprageneric relationships within the superfamily Scorpionoidea bear testament to the advantages of this approach. The classification scheme derived from it is presented in Table 10. Revised diagnoses and descriptions for the families and subfamilies are presented below. Future research on the Scorpionoidea should be directed towards confirming the phylogenetic positions of the Heteroscorpionidae, Scorpionidae and Urodacidae, resolving the generic relationships within the Bothriuridae, Diplocentrinae and Ischnuridae, and addressing the monophyly of the unsupported genera.

TABLE 10

Proposed Classification of the Superfamily Scorpionoidea
Latreille 1802

Family Bothriuridae Simon 1880
Bothriurus Peters 1861; *Brachistosternus* Pocock 1893; *Centromachetes* Lönnberg 1897; *Cercophonius* Peters 1861; *Lisposoma* Lawrence 1928; *Orobthriurus* Maury 1976; *Phoniocercus* Pocock 1893; *Tehuanka* Cekalovic 1973; *Thestylus* Simon 1880; *Timogenes* Simon 1880; *Urophonius* Pocock 1893; *Vachonia* Abalos 1954

Family Diplocentridae Pocock 1893
 Subfamily Diplocentrinae Pocock 1893:
Bioculus Stahnke 1968; *Cazierius* Francke 1978; *Didymocentrus* Kraepelin 1905; *Diplocentrus* Peters 1861; *Heteronebo* Pocock 1899; *Oiclus* Simon 1880; *Tarsoporus* Francke 1978

Subfamily Nebinae Kraepelin 1905
Nebo Simon 1878

Family Hemiscorpiidae Pocock 1893
Habibiella Vachon 1974; *Hemiscorpius* Peters 1861

Family Heteroscorpionidae Kraepelin 1905
Heteroscorpion Birula 1903

Family Ischnuridae Simon 1879
Cheloctonus Pocock 1892; *Chiromachetes* Pocock 1899; *Chiromachus* Pocock 1893; *Hadogenes* Kraepelin 1894; *Iomachus* Pocock 1893; *Liocheles* Sundevall 1833; *Opisthacanthus* Peters 1861; *Palaeocheloctonus* Lourenço 1996

Family Scorpionidae Latreille 1802
Heterometrus Ehrenberg 1828; *Opisththalmus* C. L. Koch 1837; *Pandinus* Thorell 1876; *Scorpio* Linnaeus 1758

Family Urodacidae Pocock 1893
Urodacus Peters 1861

TAXONOMIC EMENDATIONS

Family Bothriuridae Simon 1880

Telegonini Peters 1861:509 (family); type genus *Telegonus* C. L. Koch 1837 (= *Thestylus* Simon 1880), a junior homonym of *Telegonus* Hübner 1816 (Lepidoptera).

Bothriuridae Simon 1880:392–393; type genus *Bothriurus* Peters 1861.

Acanthochiroidea Karsch 1880:408; type genus *Acanthochirus* Peters 1861 (= *Cercophonius* Peters 1861).

Lisposominae Lawrence 1928:281; type genus *Lisposoma* Lawrence 1928, NEW SYNONYMY.

Brachistosterninae Maury 1972:30–31; type genus *Brachistosternus* Pocock 1893, NEW SYNONYMY.

Vachonianinae Maury 1972:30–32; type genus *Vachonia* Abalos 1954, NEW SYNONYMY.

Diagnosis. The Bothriuridae can be separated from all other scorpionoid taxa by each of the following characters: carapace without median notch in anterior

margin; pedipalp chela with ventroexternal carina obsolete; pedipalp chela with trichobothrium *db* located on dorsal surface of manus and trichobothrium *Et₂* located on ventral surface of manus; sternum width greater than twice its length (reduced to a narrow transverse sclerite in all genera except *Lisposoma*, in which it is pentagonal); paraxial organ with semilunar shelf on internal wall of sperm duct invagination; ovariuterine follicles without diverticula.

Description. Carapace without median notch in anterior margin; median longitudinal furrow broad and shallow, without suture, or obsolete; posterior carapacial sutures absent. Three pairs of lateral ocelli (two in *Vachonia*). Median ocular tubercle raised. Nongranular surfaces of prosoma, mesosoma, metasoma, and legs smooth. Cheliceral movable finger with two subdistal teeth (one in *Bothriurus*, *Timogenes*, and *Vachonia*); distal external and distal internal teeth unequal, distal external tooth considerably smaller than distal internal tooth, not closely apposed. Pedipalp patella with anterior process and dorsoexternal carina obsolete (dorsoexternal carina distinct in *Lisposoma*). Pedipalp chela dorsal secondary, subdigital, digital, and ventroexternal carinae obsolete; ventroexternal carina oblique to longitudinal axis of chela, with distal edge directed toward and almost connecting with internal movable finger condyle; ventrointernal and internomedian carinae equally developed, obsolete. Pedipalp chela fingers with a single primary row of denticles (multiple rows in *Centromachetes*, *Cercophonius*, and *Urophonius*). Pedipalps neobothriotaxic major, with accessory trichobothria in the femur (*Vachonia*), the *v* series of the patella (*Vachonia*, *Brachistosternus* (*Brachistosternus*), and some *Timogenes*), the *e* series of the patella (*Vachonia* and some *Timogenes*), and the *V* series of the chela (all genera except *Lisposoma* and *Thestylus*); rarely neobothriotaxic minor, with loss of trichobothria from the *e* series of the patella in *Brachistosternus* (*Ministernus*). Pedipalp patella with trichobothrium *d₂* located on dorsal surface. Pedipalp chela with trichobothria *ib* and *it* located basally on fixed finger; *db* located on dorsal surface of manus; *eb* and *esb* located proximally on fixed finger, *esb* below the *eb-est-et* axis and near articulation of fixed and movable fingers; *Db* located on external surface of manus; *Dt* located proximally on manus; *Est* located distally on manus; *Et₂* located on ventral surface of manus; *V₂* and *V₃* not widely separated (in *Lisposoma* and *Thestylus*). Sternum width

greater than twice its length (reduced to a narrow transverse sclerite in all genera except *Lisposoma*, in which it is pentagonal). Basitarsi I–II each with a retrolateral row of macrochaete setae (spiniform setae in *Bothriurus*, *Centromachetes*, and *Orobothriurus*; setiform setae in *Brachistosternus*, *Timogenes*, and *Vachonia*) or without (*Cercophonius*, *Lisposoma*, *Phoniocercus*, *Thestylus*, *Urophonius*). Telotarsi III–IV (I–IV in *Lisposoma*, *Thestylus*, *Phoniocercus*, and *Centromachetes*) each with paired ventrosubmedian rows of spiniform setae (I–IV setiform in *Brachistosternus*) and a ventromedian row of setiform setae; laterodistal lobes truncated, flush with base of median dorsal lobe; retrolateral pedal spurs present (absent in *Lisposoma*, *Phoniocercus*, *Thestylus*, and *Vachonia*). Metasomal segments I–IV each with paired ventrosubmedian carinae (obsolete in *Brachistosternus*, *Timogenes*, *Vachonia*, and some *Bothriurus* and *Orobothriurus*), more strongly developed on segments I–II than III–IV (equally developed on I–IV in *Lisposoma* and *Phoniocercus*); segment V with a transverse carina in *Bothriurus*, *Timogenes*, *Vachonia*, and some *Orobothriurus*, with distal portion of ventromedian carina bifurcating in *Cercophonius* and *Urophonius*; telson vesicle not laterally compressed, with anterodorsal lateral lobes; aculeus long, shallowly curved, without subaculear tubercle. Venom glands complex; venom pigment opalescent. Genital opercula of female loosely joined (fused in *Lisposoma*). Paraxial organ with semilunar shelf on internal wall of sperm duct invagination. Hemispermaphore with lamellar hook and median lobe separate; distal lamina with a prominent sclerotised crest (absent in *Lisposoma*). Ovariuterine follicles without diverticula. Embryonic development apoirogenic.

Included taxa. Twelve genera: *Bothriurus* Peters 1861, *Brachistosternus* Pocock 1893, *Centromachetes* Lönnerberg 1897, *Cercophonius* Peters 1861, *Lisposoma* Lawrence 1928, *Orobothriurus* Maury 1976, *Phoniocercus* Pocock 1893, *Tehuanka* Cekalovic 1973, *Thestylus* Simon 1880, *Timogenes* Simon 1880, *Urophonius* Pocock 1893, *Vachonia* Abalos 1954.

Distribution. Africa (Namibia), Asia (India), Australia (including Tasmania), South America (Argentina, Bolivia, Brazil, Chile, Ecuador, Paraguay, Perú, Uruguay).

Family Diplocentridae Karsch 1880

Diplocentrini Karsch 1880:408 (subfamily; part); type genus *Diplocentrus* Peters 1861.

Diagnosis. The Diplocentridae can be separated from all other scorpionoid taxa by each of the following characters: telson vesicle with a subaculear tubercle and hemispermaphore with fusion of the lamellar hook and median lobe.

Description. Carapace with median notch in anterior margin; median longitudinal furrow broad and shallow, without suture (Diplocentrinae) or narrow, suturiform, with anterior furcation (Nebinae); posterior carapacial sutures absent (Diplocentrinae) or present (Nebinae). Three pairs of lateral ocelli (two pairs in some Diplocentrinae). Median ocular tubercle raised. Nongranular surfaces of prosoma, mesosoma, metasoma, and legs usually smooth (distinctly punctate in some Diplocentrinae). Cheliceral movable finger with one subdistal tooth; distal external and distal internal teeth unequal, distal external tooth considerably smaller than distal internal tooth, but moderately apposed in Nebinae and some Diplocentrinae. Pedipalp patella with anterior process obsolete and dorsoexternal carina usually obsolete (dorsoexternal carina distinct in some Diplocentrinae). Pedipalp chela dorsal secondary carina distinct (most Diplocentrinae), in which case extending full way across dorsal surface of manus, or obsolete (Nebinae and some Diplocentrinae); subdigital carina vestigial; digital carina distinct or obsolete (some Diplocentrinae); ventroexternal carina distinct, usually parallel to longitudinal axis of chela, with distal edge directed toward a point between external and internal movable finger condyles, but closer to external condyle (oblique to longitudinal axis of chela in some Diplocentrinae, with distal edge directed toward a point between external and internal condyles, but closer to internal condyle, or directed toward and almost connecting with internal condyle); ventrointernal and internomedian carinae equally developed (often obsolete), with ventromedian carina more strongly developed (Diplocentrinae) or ventrointernal carina more strongly developed than ventromedian and internomedian carinae (Nebinae). Pedipalp chela fingers with a single primary row of denticles. Pedipalps orthobothriotaxic. Pedipalp patella with trichobothrium *d₂* located on internal surface (Diplocentrinae) or external surface (Nebinae). Pedipalp chela with trichobothria *ib* and *it* located basally on fixed finger (Diplocentrinae) or trichobothrium *ib* located basally on fixed finger and *it* located distally (Nebinae); *db* located on internal surface of fixed finger;

eb located proximally on fixed finger; *esb* located midway along fixed finger, in line with the *eb-est-et* axis; *Db* located on external surface of manus; *Dt* located at proximal end of fixed finger; *Est* located distally on manus; *Et₂* located on external surface of manus; *V₂* and *V₃* not widely separated. Sternum longer than wide, pentagonal. Basitarsi I–II without retrolateral rows of macrochaete setae. Telotarsi I–IV each with ventromedian and paired ventrosubmedian rows of spiniform setae; laterodistal lobes not flush with base of median dorsal lobe, secondarily truncated (Diplocentrinae) or rounded (Nebinae); retrolateral pedal spurs absent. Metasomal segments I–IV each with paired ventrosubmedian carinae, more strongly developed on segments I–II than III–IV (Diplocentrinae) or equally developed on all segments (Nebinae); segment V usually with a transverse carina (but partially developed in some Diplocentrinae, absent in Nebinae); telson vesicle not laterally compressed, with anterodorsal lateral lobes; aculeus short, sharply curved, with a rounded, broad-based subaculear tubercle. Venom glands complex; venom pigment reddish. Paraxial organ without semilunar shelf on internal wall of sperm duct invagination; internobasal reflection well developed. Hemispermatophore with lamellar hook and median lobe fused; distal lamina without a prominent sclerotised crest. Ovariuterine follicles with diverticula. Embryonic development katoikogenic.

Included taxa. Two subfamilies: Diplocentrinae Karsch 1880, Nebinae Kraepelin 1905.

Distribution. Africa (Egypt (Sinai)), Asia (Iran (Henjam Island), Israel, Jordan, Lebanon, Oman, Syria, Yemen), Caribbean (Antigua, Bahamas, Barbados, Barbuda, Bonaire, Cayman Islands, Cuba, Curaçao, Dominican Republic, Grenada, Haiti, Iles de Saintes (Guadeloupe), Jamaica, Klein Bonaire, Martinique, Monserrat, Nevis, Puerto Rico, Saba, St. Kitts, St. Lucia, St. Vincent, Virgin Islands), Central America (Belize, Costa Rica, El Salvador, Guatemala, Honduras, Nicaragua), North America (Mexico, United States (Arizona, New Mexico, Texas)), South America (Colombia, Venezuela).

Subfamily Diplocentrinae Karsch 1880

Diplocentrini Karsch 1880:408 (subfamily; part); type genus *Diplocentrus* Peters 1861.

Diagnosis. The Diplocentrinae can be separated from the Nebinae by each of the following characters:

carapace with median longitudinal furrow broad and shallow, without suture, and posterior carapacial sutures absent; pedipalp chela with ventromedian carina more strongly developed than ventrointernal and internomedian carinae; ventrointernal and internomedian carinae equally developed (often obsolete); pedipalp patella with trichobothrium *d₂* located on internal surface; pedipalp chela with trichobothria *ib* and *it* located basally on fixed finger; telotarsi I–IV with laterodistal lobes secondarily truncated, not flush with base of median dorsal lobe; metasomal segments I–IV with paired ventrosubmedian carinae more strongly developed on segments I–II than III–IV; segment V with a transverse carina (partially developed in *Heteronebo*).

Description. Carapace with median longitudinal furrow broad and shallow, without suture; posterior carapacial sutures absent. Three pairs of lateral ocelli (two in *Oiclus* and three species of *Bioculus*). Median ocular tubercle raised. Nongranular surfaces of prosoma, mesosoma, metasoma, and legs smooth (distinctly punctate in *Bioculus*, *Didymocentrus*, and some species of *Diplocentrus*). Cheliceral movable finger with distal external and distal internal teeth moderately apposed in *Didymocentrus*, *Heteronebo*, *Cazierius*, and some *Diplocentrus*. Pedipalp patella with dorsoexternal carina obsolete (distinct in *Heteronebo*). Pedipalp chela dorsal secondary carina obsolete or distinct (in *Heteronebo*, *Tarsoporosus*, male *Diplocentrus* and male *Didymocentrus*), in which case extending full way across dorsal surface of manus; digital carina distinct (obsolete in *Bioculus*, *Cazierius*, and *Oiclus*); ventroexternal carina distinct, usually parallel to longitudinal axis of chela, with distal edge directed toward a point between external and internal movable finger condyles, but closer to external condyle (oblique to longitudinal axis of chela in *Diplocentrus* and *Didymocentrus*, with distal edge directed toward a point between external and internal condyles, but closer to internal condyle in *Diplocentrus* or directed toward and almost connecting with internal condyle in *Didymocentrus*); ventrointernal and internomedian carinae equally developed (often obsolete). Pedipalp patella with trichobothrium *d₂* located on internal surface. Pedipalp chela with trichobothria *ib* and *it* located basally on fixed finger. Telotarsi I–IV each with laterodistal lobes secondarily truncated.

Metasomal segments I–IV with paired ventro-submedian carinae more strongly developed on segments I–II than III–IV; segment V with a transverse carina (partially developed in *Heteronebo*).

Included taxa. Seven genera: *Bioculus* Stahnke 1968, *Cazierius* Francke 1978, *Didymocentrus* Kraepelin 1905, *Diplocentrus* Peters 1861, *Heteronebo* Pocock 1899a, *Oiclus* Simon 1880, *Tarsoporosus* Francke 1978.

Distribution. Asia (Yemen (Abd-al-Kuri Island), Socotra Island), Caribbean (Antigua, Bahamas, Barbados, Barbuda, Bonaire, Cayman Islands, Cuba, Curaçao, Dominican Republic, Grenada, Haiti, Iles de Saintes (Guadeloupe), Jamaica, Klein Bonaire, Martinique, Monserrat, Nevis, Puerto Rico, Saba, St. Kitts, St. Lucia, St. Vincent, Virgin Islands), Central America (Belize, Costa Rica, El Salvador, Guatemala, Honduras, Nicaragua), North America (Mexico, United States (Arizona, New Mexico, Texas)), South America (Colombia, Venezuela).

Subfamily Nebinae Kraepelin 1905

Nebinae Kraepelin 1905:342, 345, 348; type genus *Nebo* Simon 1878.

Diagnosis. The Nebinae can be separated from the Diplocentrinae by each of the following characters: carapace with median longitudinal furrow narrow, suturiform, and anteriorly furcated; posterior carapacial sutures present; pedipalp chela with ventrointernal carina more strongly developed than ventromedian and internomedian carinae; pedipalp patella with trichobothrium d_2 located on dorsal surface; pedipalp chela with trichobothrium *ib* located basally on fixed finger and *it* located distally; telotarsi I–IV with laterodistal lobes rounded, not flush with base of median dorsal lobe; metasomal segments I–IV with paired ventrosubmedian carinae equally developed on all segments; metasomal segment V without a transverse carina.

Description. Carapace with median longitudinal furrow narrow, suturiform; posterior carapacial sutures present. Three pairs of lateral ocelli. Nongranular surfaces of prosoma, mesosoma, metasoma, and legs smooth. Cheliceral movable finger distal external and distal internal teeth moderately apposed. Pedipalp patella dorsoexternal carina obsolete. Pedipalp chela dorsal secondary carina obsolete; digital and ventroexternal carinae distinct; ventroexternal carina parallel to

longitudinal axis of chela, with distal edge directed toward a point between external and internal movable finger condyles, but closer to external condyle; ventrointernal carina more strongly developed than ventromedian and internomedian carinae. Pedipalp patella with trichobothrium d_2 located on dorsal surface. Pedipalp chela with trichobothrium *ib* located basally on fixed finger and *it* located distally. Telotarsi I–IV each with laterodistal lobes rounded. Metasomal segments I–IV with paired ventrosubmedian carinae equally developed on all segments; segment V without a transverse carina, distal portion of ventromedian carina not bifurcating or breaking up into granules.

Included taxa. One genus: *Nebo* Simon, 1878.

Distribution. Africa (Egypt (Sinai)), Asia (Iran (Henjam Island), Israel, Jordan, Lebanon, Oman, Syria, Yemen).

Family Hemiscorpiidae Pocock 1893, NEW RANK

Hemiscorpiini Pocock 1893:306, 308; type genus *Hemiscorpius* Peters 1861.

Diagnosis. The Hemiscorpiidae can be separated from all other scorpionoid taxa by the following character: pedipalp chela with trichobothria *ib* and *it* located midway along fixed finger. They can also be separated from all other scorpionoid taxa, except the Heteroscorpionidae and Urodacidae, by the following character: metasomal segments I–IV each with a single ventromedian carina, equally developed on all segments.

They can be separated from the Heteroscorpionidae and Urodacidae by each of the following characters: three pairs of lateral ocelli; median ocular tubercle shallow; cheliceral movable finger with distal external and distal internal teeth approximately equal in size and closely apposed; pedipalp chela fingers with two primary rows of denticles, often becoming fused at the base; trichobothrium *db* located on internal surface of fixed finger; trichobothrium *Db* located on dorsal surface of manus; trichobothrium *Dt* located at proximal end of fixed finger; no accessory trichobothria in the *v* series of the patella, or the *V* series of the chela; telson vesicle of male elongated and laterally compressed, with a pair of distal lobes; aculeus short, sharply curved.

Description. Carapace with median notch in anterior margin; median longitudinal furrow narrow, suturiform, with anterior furcation; posterior carapacial

sutures present. Three pairs of lateral ocelli. Median ocular tubercle shallow. Nongranular surfaces of prosoma, mesosoma, metasoma, and legs distinctly punctate. Cheliceral movable finger with one subdistal tooth; distal external and distal internal teeth approximately equal in size and closely apposed. Pedipalp patella with anterior process well developed; dorsoexternal carina distinct. Pedipalp chela dorsal secondary carina distinct, extending full way across dorsal surface of manus; subdigital carina vestigial; digital carina distinct; ventroexternal carina distinct, parallel to longitudinal axis of chela, with distal edge directed toward a point between external and internal movable finger condyles, but closer to external condyle; ventrointernal carina more strongly developed than ventromedian and internomedian carinae. Pedipalp chela fingers with two primary rows of denticles, often becoming fused at the base. Pedipalps orthobothriotaxic in *Hemiscorpius*, neobothriotaxic major in *Habibiella*, with accessory trichobothrium in the *e* series of the patella. Pedipalp patella with trichobothrium d_2 located on dorsal surface. Pedipalp chela with trichobothria *ib* and *it* located midway along fixed finger; *db* located on internal surface of fixed finger; *eb* located proximally on fixed finger; *esb* located midway along fixed finger, in line with the *eb-est-et* axis; *Db* located on dorsal surface of manus; *Dt* located at proximal end of fixed finger; *Est* located distally on manus; *Et₂* located on external surface of manus; V_2 and V_3 widely separated. Sternum longer than wide, pentagonal. Basitarsi I–II without retrolateral rows of macrochaete setae. Telotarsi I–IV each with ventromedian and paired ventrosubmedian rows of spiniform setae; laterodistal lobes truncated, flush with base of median dorsal lobe; retrolateral pedal spurs absent. Metasomal segments I–IV each with a single ventromedian carina, equally developed on all segments; segment V without a transverse carina, distal portion of ventromedian carina not bifurcating or breaking up into granules; telson vesicle without anterodorsal lateral lobes, elongated and laterally compressed, with a pair of distal lobes in male, not elongated or compressed and without distal lobes in female; aculeus short, sharply curved, without subaculear tubercle. Venom glands simple; venom pigment opalescent. Genital opercula of female fused. Paraxial organ without semilunar shelf on internal wall of sperm duct invagination; internobasal reflection

moderately developed. Hemispermatophore with lamellar hook and median lobe separate; distal lamina without a prominent sclerotised crest. Ovariuterine follicles with diverticula. Embryonic development katoikogenic.

Included taxa. Two genera: *Habibiella* Vachon 1974, *Hemiscorpius* Peters 1861.

Distribution. Africa (Eritrea, Somalia); Asia (Iran, Iraq, Oman, Pakistan, Saudi Arabia, Samha Island, Socotra Island, United Arab Emirates, Yemen).

Family *Heteroscorpionidae* Kraepelin 1905

Heteroscorpioninae Kraepelin 1905:332; type genus *Heteroscorpion* Birula 1903.

Diagnosis. The Heteroscorpionidae can be separated from all other scorpionoid taxa, except the Hemiscorpiidae and Urodacidae, by the following character: metasomal segments I–IV each with a single ventromedian carina, equally developed on all segments.

They can be separated from the Hemiscorpiidae by the following characters: two pairs of lateral ocelli; median ocular tubercle raised; cheliceral movable finger with distal external and distal internal teeth unequal, distal external tooth considerably smaller than distal internal tooth, not closely apposed; pedipalp chela fingers with multiple primary rows of denticles; trichobothria *ib* and *it* located basally on fixed finger; trichobothrium *db* located on dorsal surface of fixed finger; trichobothrium *Db* located on external surface of manus; trichobothrium *Dt* located at proximal end of manus; accessory trichobothria in the *v* series of the patella and the *V* series of the chela; aculeus long, shallowly curved.

They can be separated from the Urodacidae by the following characters: nongranular surfaces of prosoma, mesosoma, metasoma, and legs distinctly punctate; pedipalp patella with anterior process well developed; no accessory trichobothria in the *e* series of the patella or the *E* series of the chela; telotarsi I–IV each with ventromedian row of spiniform setae; laterodistal lobes of telotarsi I–IV truncated, flush with base of median dorsal lobe; basitarsi I–II without retrolateral rows of macrochaete setae; metasomal segment V without bifurcation in distal portion of ventromedian carina; telson vesicle laterally compressed.

Description. Carapace with median notch in anterior margin; median longitudinal furrow narrow, suturiform, with anterior furcation; posterior carapacial sutures present. Two pairs of lateral ocelli. Median ocular tubercle raised. Nongranular surfaces of prosoma, mesosoma, metasoma, and legs distinctly punctate. Cheliceral movable finger with one subdistal tooth; distal external and distal internal teeth unequal, distal external tooth considerably smaller than distal internal tooth, not closely apposed. Pedipalp patella with anterior process well developed; dorsoexternal carina distinct. Pedipalp chela dorsal secondary carina distinct, extending full way across dorsal surface of manus; subdigital carina vestigial; digital carina distinct; ventroexternal carina distinct, parallel to longitudinal axis of chela, with distal edge directed toward a point between external and internal movable finger condyles, but closer to external condyle; ventrointernal carina more strongly developed than ventromedian and internomedian carinae. Pedipalp chela fingers with multiple primary rows of denticles. Pedipalps neobothriotaxic major, with accessory trichobothria in the *v* and *e* series of the patella and the *V* series of the chela. Pedipalp patella with trichobothrium *d*₂ located on dorsal surface. Pedipalp chela with trichobothria *ib* and *it* located basally on fixed finger; *db* located on dorsal surface of fixed finger; *eb* located proximally on fixed finger; *esb* located midway along fixed finger, in line with the *eb-est-et* axis; *Db* located on external surface of manus; *Dt* located at proximal end of manus; *Est* located distally on manus; *Et*₂ located on external surface of manus. Sternum longer than wide, pentagonal. Basitarsi I–II without retrolateral rows of macrochaete setae. Telotarsi I–IV each with ventromedian and paired ventrosubmedian rows of spiniform setae; laterodistal lobes truncated, flush with base of median dorsal lobe; retrolateral pedal spurs absent. Metasomal segments I–IV each with a single ventromedian carina, equally developed on all segments; segment V without a transverse carina, distal portion of ventromedian carina not bifurcating or breaking up into granules; telson vesicle laterally compressed, without anterodorsal lateral lobes; aculeus long, shallowly curved, without subaculear tubercle. Venom glands simple; venom pigment opalescent. Genital opercula of female fused. Paraxial organ without semilunar shelf on internal wall of sperm duct invagination; internobasal reflection

moderately developed. Hemispermaphore with lamellar hook and median lobe separate; distal lamina without a prominent sclerotised crest. Ovariuterine follicles with diverticula. Embryonic development katoikogenic.

Included taxa. One genus: *Heteroscorpion* Birula 1903.

Distribution. Africa (Madagascar).

Family Ischnuridae Simon 1879

Ischnuridae Simon 1879:92 (part); type genus *Ischnurus* C. L. Koch 1837 (= *Liocheles* Sundevall 1833).

Hormurini Laurie 1896:128 (subfamily); type genus *Hormurus* Thorell 1876 (= *Liocheles* Sundevall 1833).

Opisthacanthinae Kraepelin 1905:343; type genus *Opisthacanthus* Peters 1861.

Diagnosis. The Ischnuridae can be separated from all other scorpionoid taxa by each of the following characters: pedipalp chela with trichobothrium *eb* located on manus, near articulation of fixed finger and movable fingers; *Dt* located approximately midway, to slightly less than midway, along manus (except in *Opisthacanthus* (*Opisthacanthus*), where located at proximal end of manus); *Est* located midway along manus.

Description. Carapace with median notch in anterior margin, shallowly excavated in *Cheloctonus*, *Hadogenes*, and *Opisthacanthus* (*Nepabellus*); median longitudinal furrow narrow, suturiform, with anterior furcation; posterior carapacial sutures present. Three pairs of lateral ocelli [Lourenço's (1989:170) report of the occurrence of two pairs of lateral ocelli in *Hormiops* Fage 1933, which he placed in synonymy with *Liocheles* Sundevall 1833, could not be confirmed: all five species of *Liocheles* examined displayed three pairs of lateral ocelli]. Median ocular tubercle shallow. Nongranular surfaces of prosoma, mesosoma, metasoma, and legs distinctly punctate. Cheliceral movable finger with one subdistal tooth; distal external and distal internal teeth approximately equal and closely apposed. Pedipalp patella with anterior process well developed (obsolete in *Cheloctonus*, *Opisthacanthus* (*Nepabellus*), and some *Iomachus*); dorsoexternal carina obsolete, but distinct in *Cheloctonus* and *Opisthacanthus* (*Nepabellus*). Pedipalp chela dorsal secondary carina obsolete; subdigital carina vestigial; digital and ventroexternal carinae distinct; ventroexternal carina parallel to longitudinal axis

of chela, with distal edge directed toward a point between external and internal movable finger condyles, but closer to external condyle; ventromedian carina obsolete; ventrointernal carina less strongly developed than internomedian carina, which may also be obsolete. Pedipalp chela fingers with two primary rows of denticles, often becoming fused at the base (single row in *Cheloctonus* and *Palaeocheloctonus pauliani* Lourenço 1996). Pedipalps orthobothriotaxic, but neobothriotaxic major in *Hadogenes*, some *Opisthacanthus* (*Opisthacanthus*), and *Liocheles penta* Francke and Lourenço 1991, with accessory trichobothria in the *v* series of the patella (*Hadogenes* and *L. penta*), the *e* series of the patella (*Hadogenes* and *Opisthacanthus* (*Opisthacanthus*)), and the *V* and *E* series of the chela (*Hadogenes*). Pedipalp patella with trichobothrium *d*₂ located on dorsal surface. Pedipalp chela with trichobothria *ib* and *it* located basally on fixed finger; *db* located on internal surface of fixed finger (located on dorsal surface in *Hadogenes*, *Liocheles*, and some *Iomachus*); *eb* located on manus, near articulation of fixed finger and movable fingers; *esb* located proximally on fixed finger, below the *eb-est-et* axis and near articulation of fixed finger and movable fingers; *Db* located on external surface of manus; *Dt* located approximately midway, to slightly less than midway, along manus (located at proximal end of manus in *Opisthacanthus* (*Opisthacanthus*)); *Est* located midway along manus; *Et*₂ located on external surface of manus; *V*₂ and *V*₃ widely separated. Sternum longer than wide, pentagonal. Basitarsi I–II without retrolateral rows of macrochaete setae. Teltarsi I–IV each with ventromedian and paired ventro-submedian rows of spiniform setae (ventromedian rows absent in *Chiromachetes*, *Chiromachus*, and *Liocheles*; setiform setae in *Chiromachus*, *Iomachus*, and *Liocheles*); laterodistal lobes truncated, flush with base of median dorsal lobe; retrolateral pedal spurs absent. Metasomal segments I–IV each with paired ventro-submedian carinae (occasionally obsolete), equally developed on all segments; segment V without a transverse carina, distal portion of ventromedian carina not bifurcating or breaking up into granules; telson vesicle laterally compressed, without anterodorsal lateral lobes; aculeus short, sharply curved, without subaculear tubercle. Venom glands simple; venom pigment opalescent. Genital opercula of female fused (loosely joined in *Hadogenes*). Paraxial organ without semilunar

shelf on internal wall of sperm duct invagination; internobasal reflection moderately developed. Hemispermatophore with lamellar hook and median lobe separate; distal lamina without a prominent sclerotised crest. Ovariuterine follicles with diverticula. Embryonic development katoikogenic.

Included taxa. Eight genera (see *Note added in proof*): *Cheloctonus* Pocock 1892, *Chiromachetes* Pocock 1899b, *Chiromachus* Pocock 1893, *Hadogenes* Kraepelin 1894, *Iomachus* Pocock 1893, *Liocheles* Sundevall 1833, *Opisthacanthus* Peters 1861, *Palaeocheloctonus* Lourenço 1996.

Distribution. Africa (Angola, Botswana, Central African Republic, Cameroon, Congo, Democratic Republic of Congo, Equatorial Guinea (including Bioko Island), Ethiopia, Gabon, Guinea, Kenya, Lesotho, Madagascar, Malawi, Mozambique, Namibia, Sierra Leone, South Africa, Swaziland, Tanzania, Uganda, Zimbabwe, Indian Ocean islands (Mascarene Islands, Seychelles, Zanzibar)), Asia (Aru Islands, Bangladesh, ?Cambodia, China, India (including Andaman Islands and Nikobar Islands), Indonesia, Japan (south), Korea, Laos, Malaysia, Moluccas, Myanmar, ?Nepal, New Guinea, Philippines, Sri Lanka, Thailand, Timor, Vietnam), Australia (including Christmas Island and Cocos Islands), Oceania (Federated States of Micronesia, Fiji, French Polynesia, Key Islands, Marianas, Marshall Islands, New Britain, New Caledonia, Palau, Ponape, Tuvalu (Funafuti), Samoa, Solomon Islands, Tonga, Vanuatu (New Hebrides)), Caribbean (Dominican Republic, Haiti), Central America (Costa Rica (Isla del Coco), Panama), South America (Brazil (Pará), Colombia, French Guiana, Perú, Venezuela).

Family Scorpionidae Latreille 1802

Scorpionides Latreille 1802:46–47 (part); type genus *Scorpio* Linnaeus 1758.

Centrurides C. L. Koch 1837:38 (part); type genus *Centrurus* Ehrenberg 1829 (= *Heterometrus* Ehrenberg 1828).

Pandinoidae Thorell 1876:11 (part); type genus *Pandinus* Thorell 1876.

Heterometridae Simon 1879:92, 115; type genus *Heterometrus* Ehrenberg 1828 (part) (= *Scorpio* Linnaeus 1758).

Diagnosis. The Scorpionidae can be separated from all other scorpionoid taxa by the following character:

pedipalp chela with dorsal secondary carina partially developed, extending part way across dorsal surface of manus, and subdigital carina partially developed, extending part way across in opposite direction. They can also be separated from all other scorpionoid taxa, except the Diplocentrinae, by the following characters: pedipalp chela with ventromedian carina more strongly developed than ventrointernal and internomedian carinae; ventrointernal and internomedian carinae equally developed (often obsolete); pedipalp patella with trichobothrium d_2 located on internal surface.

Description. Carapace with median notch in anterior margin; median longitudinal furrow narrow, suturiform, often with anterior furcation; posterior carapacial sutures present (absent in some *Opisthophthalmus*). Three pairs of lateral ocelli (rarely two in some *Opisthophthalmus*). Median ocular tubercle raised. Non-granular surfaces of prosoma, mesosoma, metasoma, and legs smooth. Cheliceral movable finger with one subdistal tooth; distal external and distal internal teeth unequal, distal external tooth considerably smaller than distal internal tooth, moderately apposed in some *Heterometrus* and *Pandinus*. Pedipalp patella with anterior process and dorsoexternal carina obsolete. Pedipalp chela dorsal secondary carina partially developed, extending part way across dorsal surface of manus; subdigital carina partially developed, extending part way across in opposite direction; digital carina distinct (*Opisthophthalmus* and *Scorpio*) or obsolete (*Heterometrus* and *Pandinus*); ventroexternal carina distinct, parallel to longitudinal axis of chela, with distal edge directed toward a point between external and internal movable finger condyles, but closer to external condyle; ventromedian carina more strongly developed than ventrointernal and internomedian carinae; ventrointernal and internomedian carinae equally developed (usually obsolete). Pedipalp chela fingers with a single primary row of denticles. Pedipalps orthobothriotaxic (*Heterometrus* and *Scorpio*) or neobothriotaxic major (*Opisthophthalmus* and *Pandinus*), with accessory trichobothria in the *v* and *e* series of the patella, the *V* series of the chela, and the *i* series of the chela (some *Pandinus* only). Pedipalp patella with trichobothrium d_2 located on internal surface. Pedipalp chela with trichobothria *ib* and *it* located basally on fixed finger; *db* located on internal surface of fixed finger; *eb* located proximally on fixed finger; *esb* located midway along fixed finger, in line with the *eb-est-et* axis; *Db* located on dorsal surface

of manus; *Dt* located distally on manus, near base of fixed finger; *Est* located distally on manus; *Et₂* located on external surface of manus; *V₂* and *V₃* not widely separated. Sternum longer than wide, pentagonal. Basitarsi I–II each with a retrolateral row of spiniform setae (setiform in some *Opisthophthalmus*). Telotarsi I–IV each with paired ventrosubmedian rows of spiniform setae (prolateral row absent in many *Opisthophthalmus*), but without a ventromedian row; laterodistal lobes rounded, not flush with base of median dorsal lobe; retrolateral pedal spurs absent. Metasomal segments I–IV each with paired ventrosubmedian carinae (obsolete in some *Opisthophthalmus* and *Pandinus*), usually equally developed on all segments, but more strongly developed on segments III–IV in most *Opisthophthalmus* and more strongly developed on segments I–II in *Scorpio* and *Opisthophthalmus boehmi* (Kraepelin 1896); segment V without a transverse carina and with distal portion of ventromedian carina breaking up into numerous granules in *Scorpio* and *O. boehmi*; telson vesicle not laterally compressed, without anterodorsal lateral lobes; aculeus long, shallowly curved, without subaculear tubercle. Venom glands complex; venom pigment opalescent. Genital opercula of female fused. Paraxial organ without semilunar shelf on internal wall of sperm duct invagination; internobasal reflection well developed. Hemispermaphore with lamellar hook and median lobe separate; distal lamina without a prominent sclerotised crest. Ovariuterine follicles with diverticula. Embryonic development katoikogenic.

Included taxa. Four genera: *Heterometrus* Ehrenberg 1828, *Opisthophthalmus* C. L. Koch 1837, *Pandinus* Thorell 1876, *Scorpio* Linnaeus 1758.

Distribution. Africa (Algeria, Angola, Botswana, Burkina Faso, Cameroon, Congo, Côte d'Ivoire, Democratic Republic of Congo, Egypt, Equatorial Guinea (including Bioko Island), Eritrea, Ethiopia, Gabon, Gambia, Ghana, Guinea, Guinea-Bissau, Kenya, Lesotho, Libya, Malawi, Mauritania, Morocco, Mozambique, Namibia, Nigeria, Senegal, Somalia, South Africa, Sudan, Swaziland, Tanzania, Togo, Tunisia, Zambia, Zimbabwe), Asia (Brunei, Cambodia, India, Indonesia, Iran, Iraq, Israel, Jordan, Kuwait, Laos, Lebanon, Malaysia, Myanmar, Philippines, Qatar, Saudi Arabia, Sri Lanka, Syria, Thailand, Turkey, Vietnam, Yemen).

Family Urodacidae Pocock 1893, NEW RANK

Urodacini Pocock 1893:306, 308; type genus *Urodacus* Peters 1861.

Diagnosis. The Urodacidae can be separated from all other scorpionoid taxa by the following character: paraxial organ with internobasal reflection modified into a mating plug. They can also be separated from all other scorpionoid taxa, except the Hemiscorpiidae and Heteroscorpionidae, by the following character: metasomal segments I–IV each with a single ventromedian carina, equally developed on all segments.

They can be further separated from the Hemiscorpiidae by the following characters: two pairs of lateral ocelli; median ocular tubercle raised; nongranular surfaces of prosoma, mesosoma, metasoma, and legs smooth; cheliceral movable finger with distal external and distal internal teeth unequal, distal external tooth considerably smaller than distal internal tooth, not closely, or at most moderately, apposed; pedipalp patella with anterior process obsolete; pedipalp chela fingers with multiple primary rows of denticles; trichobothria *ib* and *it* located basally on fixed finger; trichobothrium *db* located on dorsal surface of fixed finger; trichobothrium *Db* located on external surface of manus; trichobothrium *Dt* located at proximal end of manus; accessory trichobothria in the *v* series of the patella and the *V* and *E* series of the chela; basitarsi I–II each with a retrolateral row of spiniform setae (setiform in some species); telotarsi I–IV without ventromedian row of spiniform setae; laterodistal lobes of telotarsi I–IV rounded, not flush with base of median dorsal lobe; metasomal segment V with distal portion of ventromedian carina bifurcating; telson vesicle usually not elongated or laterally compressed (exception in *Urodacus megamastigus* L. E. Koch 1977); aculeus long, shallowly curved.

They can be further separated from the Heteroscorpionidae by the following characters: nongranular surfaces of prosoma, mesosoma, metasoma, and legs smooth; pedipalp patella with anterior process obsolete; accessory trichobothria in the *e* series of the patella and the *E* series of the chela; basitarsi I–II each with a retrolateral row of spiniform setae (setiform in some species); telotarsi I–IV without ventromedian row of spiniform setae; laterodistal lobes of telotarsi I–IV rounded, not flush with base of median dorsal lobe;

metasomal segment V with distal portion of ventromedian carina bifurcating; telson vesicle usually not laterally compressed (exception in *U. megamastigus*).

Description. Carapace with median notch in anterior margin; median longitudinal furrow narrow, suturiform, with anterior furcation; posterior carapacial sutures present. Two pairs of lateral ocelli. Median ocular tubercle raised. Nongranular surfaces of prosoma, mesosoma, metasoma, and legs smooth. Cheliceral movable finger with one subdistal tooth; distal external and distal internal teeth unequal, distal external tooth considerably smaller than distal internal tooth, usually not closely apposed, but moderately apposed in some (e.g., *Urodacus planimanus* Pocock 1893). Pedipalp patella with anterior process obsolete; dorsoexternal carina distinct. Pedipalp chela dorsal secondary carina distinct, extending full way across dorsal surface of manus; subdigital carina vestigial; digital carina distinct; ventroexternal carina distinct, parallel to longitudinal axis of chela, with distal edge directed toward a point between external and internal movable finger condyles, but closer to external condyle; ventrointernal carina more strongly developed than ventromedian and internomedian carinae. Pedipalp chela fingers with multiple primary rows of denticles. Pedipalps neobothriotaxic major, with accessory trichobothria in the *v* and *e* series of the patella and the *V* and *E* series of the chela. Pedipalp patella with trichobothrium *d*₂ located on dorsal surface. Pedipalp chela with trichobothria *ib* and *it* located basally on fixed finger; *db* located on dorsal surface of fixed finger; *eb* located proximally on fixed finger; *esb* located midway along fixed finger, in line with the *eb-est-et* axis; *Db* located on external surface of manus; *Dt* located at proximal end of manus; *Est* located distally on manus; *Et*₂ located on external surface of manus. Sternum longer than wide, pentagonal. Basitarsi I–II each with a retrolateral row of spiniform setae (setiform in some, e.g., *Urodacus yaschenkoi* (Birula 1903)). Telotarsi I–IV each with paired ventrosubmedian rows of spiniform setae, but without a ventromedian row; laterodistal lobes rounded, not flush with base of median dorsal lobe; retrolateral pedal spurs absent. Metasomal segments I–IV each with a single ventromedian carina, equally developed on all segments; segment V without a transverse carina, distal portion of ventromedian carina bifurcating; telson vesicle not elongated or laterally compressed (exception in *Urodacus megamastigus*),

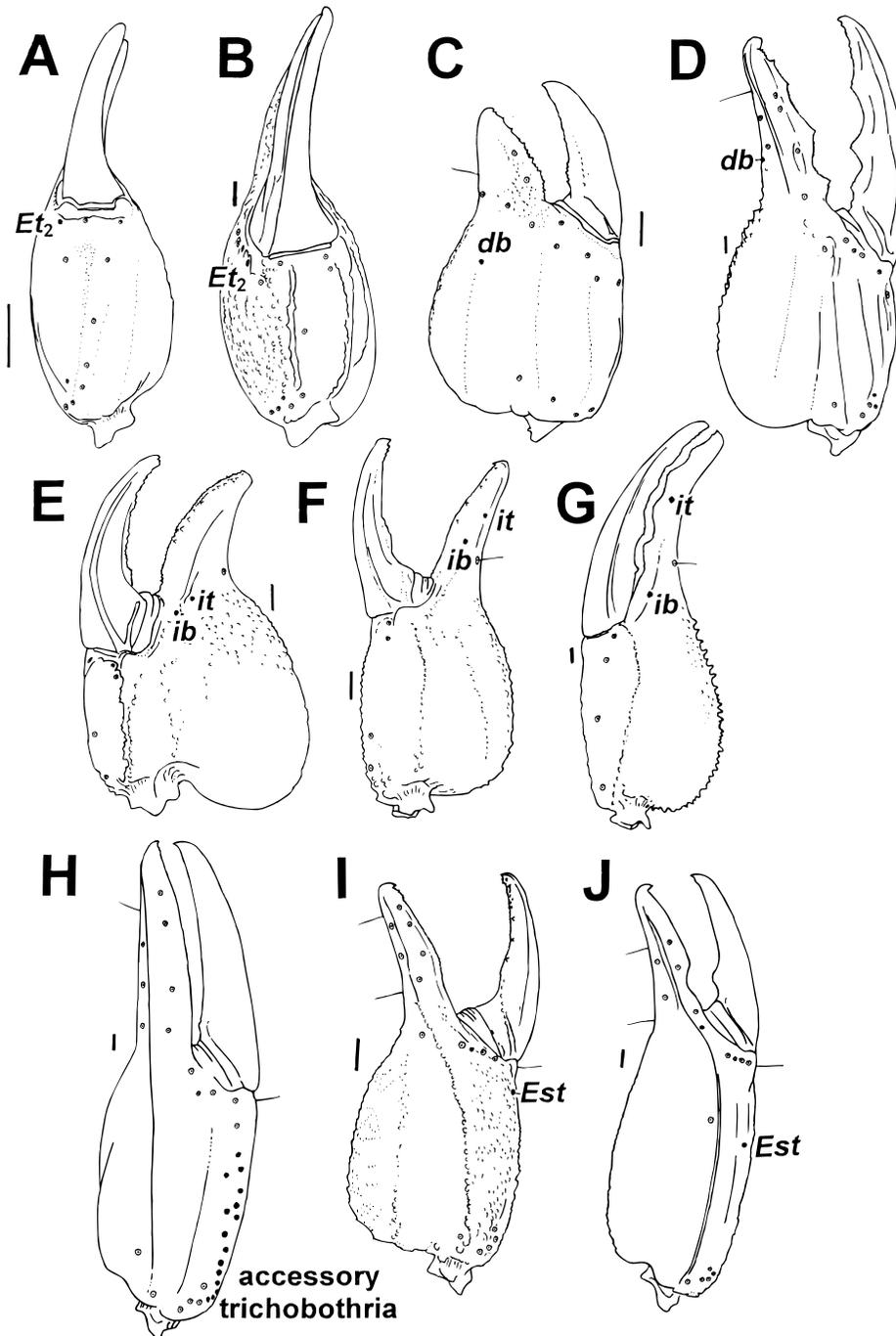


FIG. 8. Right pedipalp chela of selected scorpionoid taxa, illustrating diagnostic trichobothrial patterns [A–F and I and J modified from Stockwell (1989), G and H modified from Vachon (1974)]. Ventral aspect: (A) *Lisposoma josehermana*, (B) *Scorpio maurus*. External aspect: (C) *Bothriurus bonariensis*, (D) *Pandinus* sp., (H) *Urodacus yaschenkoi*, (I) *Hemiscorpius* sp., (J) *Opisthacanthus madagascariensis*. Internal aspect: (E) *Scorpio maurus*, (F) *Hemiscorpius* sp., (G) *Nebo hierichonticus*. Relevant trichobothria are indicated with a solid circle and abbreviated as follows (after Vachon, 1974): *db*, dorsal basal; *Est*, external subterminal; *Et*, external terminal; *ib*, internal basal; *it*, internal terminal. Scale bar, 1 mm.

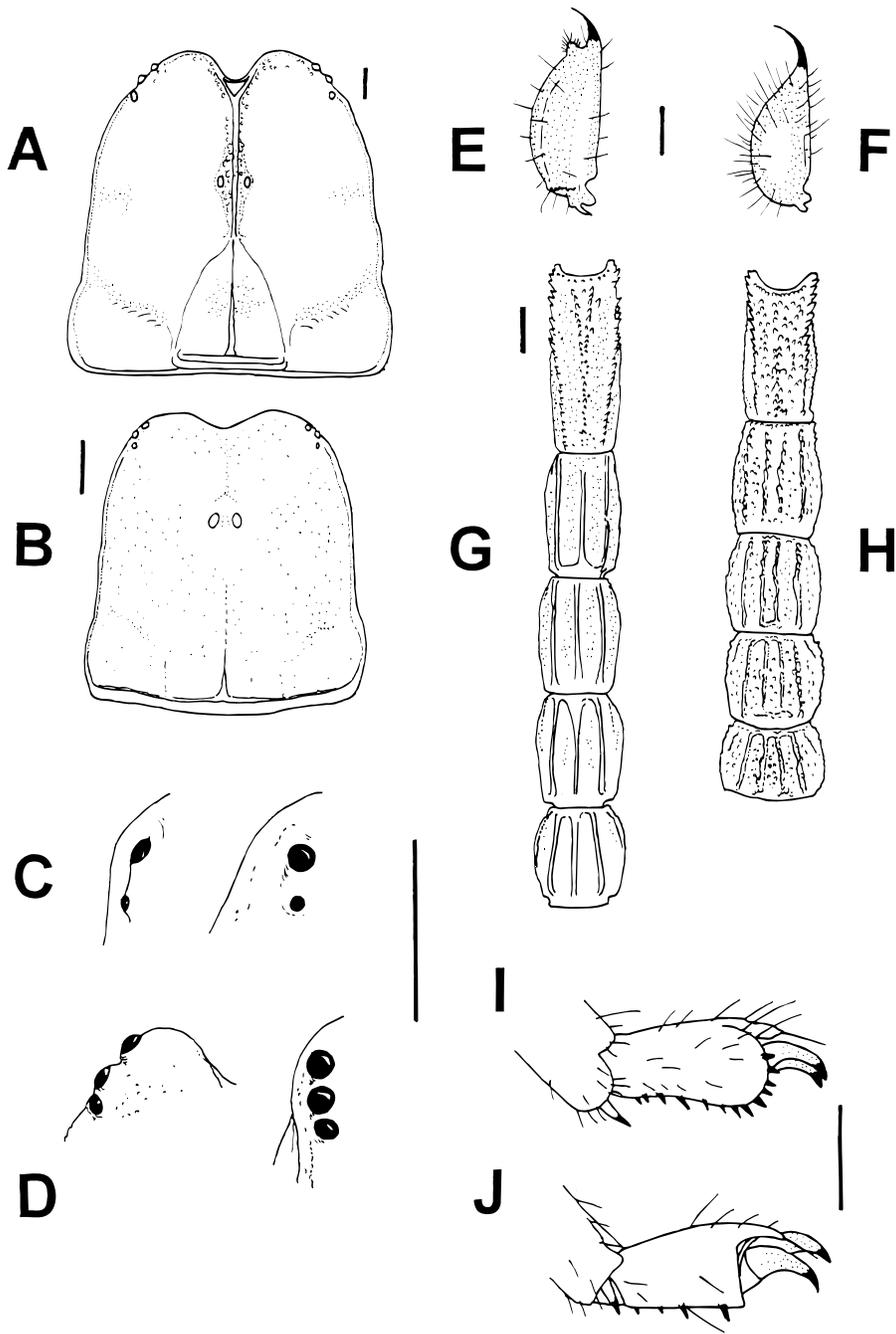


FIG. 9. Diagnostic characters of selected scorpionoid taxa [A, B, and E modified from Stockwell (1989), C, D, and F–H modified from Lourenço (1989), I and J modified from Sissom (1990)]. Carapace: (A) *Nebo hierichonticus*, (B) *Diplocentrus coddingtoni*. Lateral ocelli: (C) *Urodacus novaehollandiae*, (D) *Opisthacanthus lepturus*. Telson, lateral aspect: (E) *Diplocentrus* sp., (F) *Chiromachus ochropus*. Metasomal segments I–V, ventral aspect: (G) *Urodacus novaehollandiae*, (H) *Scorpio maurus*. Telotarsus of leg IV: (I) *Opisththalmus* sp., (J) *Opisthacanthus lepturus*. Scale bar, 1 mm.

without anterodorsal lateral lobes; aculeus long, shallowly curved, without subaculear tubercle. Venom glands complex; venom pigment opalescent. Genital opercula of female fused. Paraxial organ without semilunar shelf on internal wall of sperm duct invagination; internobasal reflection well developed, modified into a mating plug. Hemispermaphore with lamellar hook and median lobe separate; distal lamina without a prominent sclerotised crest. Ovariuterine follicles with diverticula. Embryonic development katoikogenic.

Included taxa. One genus: *Urodacus* Peters 1861.

Distribution. Australia.

Illustrated Key to the Families and Subfamilies of the Superfamily Scorpionoidea

1. Trichobothrium *Et*₂ located on ventral surface of pedipalp chela (Fig. 8A); *db* located on manus (Fig. 8C) Bothriuridae
Trichobothrium *Et*₂ located on external surface of pedipalp chela (Fig. 8B); *db* located on fixed finger (Fig. 8D) 2
2. Metasomal segments I–IV with paired ventro-submedian carinae (Fig. 9H) 3
Metasomal segments I–IV with single ventromedian carinae (Fig. 9G) 6
3. Telson with distinct subaculear tubercle (Fig. 9E) 4 (Diplocentridae)
Telson without subaculear tubercle (Fig. 9F) 5
4. Carapace with median longitudinal and anterior furcated sutures (Fig. 9A); trichobothrium *it* located in distal half of fixed finger (Fig. 8G) Nebinae
Carapace without median longitudinal and anterior furcated sutures (Fig. 9B); trichobothrium *it* located near base of fixed finger (Fig. 8E) ... Diplocentrinae
5. Laterodistal lobes of telotarsi truncate (Fig. 9J); trichobothrium *Est* located midway along chela manus (Fig. 8J) Ischnuridae
Laterodistal lobes of telotarsi rounded (Fig. 9I); trichobothrium *Est* located distally on chela manus (Fig. 8I) Scorpionidae
6. Three pairs of lateral ocelli (Fig. 9D); trichobothria *ib* and *it* located midway along fixed finger (Fig. 8F) Hemiscorpiidae
Two pairs of lateral ocelli (Fig. 9C); trichobothria *ib* and *it* located near base of fixed finger (Fig. 8E) ... 7

7. Laterodistal lobes of telotarsi rounded (Fig. 9I); external surface of chela with accessory trichobothria (Fig. 8H) Urodacidae
Laterodistal lobes of telotarsi truncate (Fig. 9J); external surface of chela without accessory trichobothria (Fig. 8I) Heteroscorpionidae

APPENDIX 1

Exemplar Taxa Chosen for Cladistic Analysis of the Superfamily Scorpionoidea

Depositories for specimens examined are abbreviated as follows (*denotes private collections): AMNH, American Museum of Natural History (New York, NY); BMNH, The Natural History Museum (London, UK); CAS, California Academy of Sciences (San Francisco, CA); FMNH, Field Museum of Natural History (Chicago, IL); JF, *Julio Ferrer, Naturhistoriska Riksmuseet (Stockholm, Sweden); MCZ, Museum of Comparative Zoology, Harvard University (Cambridge, MA); MRAC, Musée Royal de l'Afrique Centrale (Tervuren, Belgium); NM, Natal Museum (Pietermaritzburg, South Africa); SAM, South African Museum (Cape Town, South Africa); SMN, National Museum of Namibia (Windhoek, Namibia); TM, Transvaal Museum (Pretoria, South Africa); USNM, National Museum of Natural History, Smithsonian Institution (Washington, DC); WDS, *W. David Sissom, West Texas A&M University (Canyon, TX); ZMA, Zoologisch Museum, Universiteit van Amsterdam (Amsterdam, The Netherlands); ZMB, Zoologisches Museum, Universität Humboldt (Berlin, Germany).

The buthids and chaerilids are generally considered basal to all other Recent scorpions (Lamoral, 1980; Lourenço, 1985; Stockwell, 1989). However, there is debate as to whether the Chaerilidae are the sister taxon of the other Recent scorpions (Lamoral, 1980; Lourenço, 1985) or the sister taxon of the Buthidae (Stockwell, 1989). A representative outgroup taxon was thus chosen from both families.

1. *Centruroides* Marx 1889: This genus, comprising 46 species (Fet and Lowe, 2000), is one of 72 extant genera in the diverse family Buthidae Simon 1880, according to the most recent published list (Fet and Lowe,

1999). *Centruroides gracilis* (Latreille 1804) was selected as a representative buthid outgroup taxon for this analysis because it has distinct pedipalpal carinae, compared with many other buthid taxa in which the carinae are obsolete, thus facilitating homology assessment for the carinal characters. Specimens that were examined are deposited in the AMNH, CAS, and MCZ collections.

2. *Chaerilus* Simon 1877: A single genus, with 21 recognised species (Fet, 2000a), comprises the family Chaerilidae Pocock 1893. *Chaerilus granosus* Pocock 1900 was included in this analysis as a representative chaerilid outgroup taxon. Specimens that were examined are deposited in the AMNH and MCZ collections.

Bothriuridae

3–4. *Bothriurus* Peters 1861: Two subgenera and 33 species were recognised in this bothriurid genus by Lowe and Fet (2000), following Maury (1981), as opposed to Cekalovic (1983) who listed the following species in synonymy without formal justification: *Bothriurus asper* Pocock 1893, *Bothriurus asymmetricus* Pessôa 1935, *Bothriurus bonariensis* (C. L. Koch 1842), and *Bothriurus karschi* Mello-Leitão 1934 = *Bothriurus vittatus* (Guérin-Méneville 1838); *Bothriurus rochai* Mello-Leitão 1932 = *Bothriurus coriaceus* Pocock 1893; *Bothriurus signatus* Pocock 1893 = *Bothriurus chilensis* (Molina 1782). Two species, representing both of the recognised subgenera, were chosen for this analysis: *Bothriurus* (*Bothriurus*) *bonariensis* (C. L. Koch 1842) and *Bothriurus* (*Andibothriurus*) *coriaceus* Pocock 1893. The first of these is the type species of *Bothriurus*. Specimens of *B. bonariensis* that were examined are deposited in the AMNH and MCZ collections, of *B. coriaceus* in the AMNH collection.

5–6. *Centromachetes* Lönnberg 1897: Three species are recognised in this bothriurid genus (Sissom, 1990; Lowe and Fet, 2000), two of which were represented in this analysis: *Centromachetes obscurus* Mello-Leitão 1932 and *Centromachetes pocockii* (Kraepelin 1894). The second of these is the type species of *Centromachetes*. Specimens examined are deposited in the AMNH, CAS, and MCZ collections.

7–8. *Cercophonius* Peters 1861: Seven species were recognised by Lowe and Fet (2000) in this formerly monotypic Australian bothriurid genus (Koch, 1977), after including Acosta's (1990) revision and Lourenço's

(1996b) description of a new species from the Himalayas. Two of the Australian species were represented in this analysis, as the holotype of *Cercophonius himalayensis* Lourenço 1996 could not be obtained for examination: *Cercophonius queenslandae* Acosta 1990 and *Cercophonius squama* (Gervais 1843). The second of these is the type species of *Cercophonius*. Specimens of *C. queenslandae* that were examined are deposited in the MCZ collection, of *C. squama* in the AMNH, CAS, and MCZ collections.

9–10. *Lisposoma* Lawrence 1928: This genus was originally placed in the Scorpionidae, in the separate subfamily Lisposominae Lawrence 1928. Francke (1982a) suggested that it should be transferred to the Bothriuridae. Accordingly, Sissom (1990) listed the genus under the Bothriuridae as *incertae sedis*, since there were no characters to distinguish the subfamily Lisposominae from the Bothriurinae. Both recognised species were represented in this analysis: *Lisposoma elegans* Lawrence 1928; *Lisposoma josehermana* Lamoral 1979. The first of these is the type species of *Lisposoma*. Specimens of *L. elegans* that were examined are deposited in the NM, SMN, and TM collections, of *L. josehermana* in the AMNH and CAS collections.

11–12. *Orobothriurus* Maury 1976: Eight species, seven of which were removed from *Bothriurus* by Maury (1976), are recognised in this bothriurid genus (Sissom, 1990; Lowe and Fet, 2000). Two of these were represented in this analysis: *Orobothriurus alticola* (Pocock 1899) and *Orobothriurus crassimanus* Maury 1976. The first is the type species of *Orobothriurus*. The second is the only member of the genus with a distinct transverse carina on the ventral surface of metasomal segment V (illustrated by Maury 1976:23), a possible synapomorphy with *Bothriurus*, the absence of which has been used as a diagnostic character for *Orobothriurus* (Maury, 1976; Stockwell, 1989). Specimens of *O. alticola* that were examined are deposited in the BMNH collection, of *O. crassimanus* in the USNM collection.

13–14. *Phoniocercus* Pocock 1893: Two species are recognised in this bothriurid genus (Sissom, 1990; Lowe and Fet, 2000), both of which were represented in this analysis: *Phoniocercus pictus* Pocock 1893 and *Phoniocercus sanmartini* Cekalovic 1968. The first of these is the type species of *Phoniocercus*. Specimens of *P. pictus* that were examined are deposited in the AMNH, CAS, and MCZ collections, of *P. sanmartini* in the MCZ collection.

15. *Tehuanka* Cekalovic 1973: This monotypic bothriurid genus was represented in the analysis by the type species, *Tehuanka moyanoi* Cekalovic 1973. The types of this species could not be obtained for examination, hence character entries were based on the literature.

16. *Thestylus* Simon 1880: Two species are recognised in this bothriurid genus (Sissom, 1990; Lowe and Fet, 2000), only one of which could be obtained for examination: *Thestylus glasioui* (Bertkau 1880). This is the type species of *Thestylus*. Specimens that were examined are deposited in the AMNH and MCZ collections.

17–18. *Timogenes* Simon 1880: Five species are recognised in this bothriurid genus (Sissom, 1990; Lowe and Fet, 1999), after Maury's (1982) revision, in which the two subgenera were placed in synonymy. Two species, representing both of these formerly recognised subgenera, were chosen for this analysis: *Timogenes dorbignyi* (Guérin-Méneville 1843) and *Timogenes mapuche* Maury 1976. These species differ in trichobothrial and metasomal gland characters (among others) which provide potential synapomorphies with *Brachistosternus* Pocock 1893 and *Vachonia* Abalos 1954. Specimens of the type species, *Timogenes sumatranus* Simon 1880, could not be obtained for examination. However, the exemplar species included here are considered congeneric with the type species on the basis of the morphological evidence presented by Maury (1982). *T. mapuche* was previously placed in the same subgenus as the type species. Specimens that were examined are deposited in the AMNH, CAS, and USNM collections.

19–20. *Urophonius* Pocock 1893: Nine species, in three species groups (except for one that has not been allocated to a species group), are currently recognised in this bothriurid genus (Lowe and Fet, 2000). Two species, representing the *brachycentrus* and *granulatus* groups, respectively, were included in this analysis: *Urophonius iheringii* Pocock 1893 and *Urophonius granulatus* Pocock 1898. The first of these is the type species of *Urophonius*. Specimens that were examined are deposited in the AMNH, CAS, and MCZ collections.

21–23. *Brachistosternus* Pocock 1893: Three subgenera and 17 species (one of which has not been allocated to subgenus) are recognised in this bothriurid genus (Lowe and Fet, 2000), for which a separate subfamily, *Brachistosterninae* Maury 1973, was created. Three

species, representing each of the subgenera, were included in this analysis, to reflect the varied trichobothrial character states within the genus: *Brachistosternus (Brachistosternus) ehrenbergii* (Gervais 1841), *Brachistosternus (Leptosternus) alienus* Lönnberg 1898, and *Brachistosternus (Ministernus) ferrugineus* (Thorell 1877). The first of these is the type species of *Brachistosternus*. Specimens that were examined are deposited in the AMNH, CAS, MCZ, and USNM collections.

24. *Vachonia* Abalos 1954: This monotypic bothriurid genus was placed into a separate subfamily, *Vachoniainae* Maury 1973, on the basis of an array of autapomorphic character states. It was represented in this analysis by the type species, *Vachonia martinezi* Abalos 1954. Specimens of this species could not be obtained for examination, hence character entries were based on the literature.

Diplocentridae

25–26. *Bioculus* Stahnke 1968: Four species are currently recognised in this diplocentrid genus which was recently reinstated by Stockwell (1992). Two species were represented in this analysis: *Bioculus caboensis* (Stahnke 1968) and *Bioculus comondae* Stahnke 1968. The first species is the only member of the genus with three pairs of lateral ocelli, which has been suggested to be plesiomorphic in the genus (Williams and Lee, 1975). The second is the type species of *Bioculus*. Specimens that were examined are deposited in the AMNH, CAS, MCZ, and WDS collections.

27–28. *Cazierius* Francke 1978: Three species are recognised in this diplocentrid genus (Sissom, 1990; Sissom and Fet, 2000), two of which were represented in this analysis: *Cazierius gundlachii* (Karsch 1880) and *Cazierius scaber* (Pocock 1893). The first of these is the type species of *Cazierius*. Specimens of *C. gundlachii* that were examined are deposited in the AMNH and MCZ collections. The holotype of *C. scaber* was examined in the BMNH collection.

29–30. *Didymocentrus* Kraepelin 1905: Eight species have been recognised in this diplocentrid genus by Sissom and Fet (2000), since the generic status of *Bioculus* was reinstated by Stockwell (1992). Two species, *Didymocentrus hasethi* Kraepelin 1896 and *Didymocentrus lesueurii* (Gervais 1844), were represented in this analysis. The second of these is the type species of *Didymocentrus*. Specimens that were examined are

deposited in the CAS, FMNH, MCZ, and ZMA collections.

31–32. *Diplocentrus* Peters 1861: Thirty-three species are currently recognised in this diplocentrid genus (Sissom and Fet, 2000), although Francke (1978) estimated that there are at least 50 (more than two-thirds of them undescribed). Two species were represented in this analysis: *Diplocentrus gertschi* Sissom and Walker 1992 and *Diplocentrus mexicanus* Peters 1863. Sissom and Walker (1992) maintained that the first species displays character states (primarily concerning pedipalp ornamentation) intermediate between the diplocentrids of the North American mainland and those from Baja California Sur (now recognised under *Bioculus*), lending support to their hypothesis that the species of *Bioculus* are more closely related to *Diplocentrus* than to the Central American *Didymocentrus*. The second species, *D. mexicanus*, which is the type species of *Diplocentrus*, is at the opposite extreme of this hypothetical continuum in morphological variation. Specimens of *D. gertschi* that were examined are deposited in the AMNH, CAS, and MCZ collections, of *D. mexicanus* in the MCZ and USNM collections.

33–34. *Heteronebo* Pocock 1899: Fourteen species are currently recognised in this diplocentrid genus (Sissom and Fet, 2000). Two species, representing the disjunct Arabian and Caribbean species, respectively, were included in this analysis: *Heteronebo granti* Pocock 1899 and *Heteronebo jamaicae* Francke 1978. The first of these is the type species of *Heteronebo*. The syntypes of *H. granti* were examined in the BMNH collection. Specimens of *H. jamaicae* that were examined are deposited in the AMNH collection.

35. *Oiclus* Simon 1880: This monotypic diplocentrid genus was represented in the analysis by the type species, *Oiclus purvesii* (Becker 1880). Specimens that were examined are deposited in the AMNH, CAS, and MCZ collections.

36–37. *Tarsoporosus* Francke 1978: Four species are recognised in this diplocentrid genus by Sissom and Fet (2000), although González-Sponga (1983, 1984, 1996) continues to recognise *Tarsoporosus flavus* González-Sponga 1983, *Tarsoporosus kugleri* (Schenkel 1932), and *Tarsoporosus yustizi* González-Sponga 1983 in combination with *Diplocentrus* Peters 1861. The first two species were represented in this analysis, the second of which is the type species of *Tarsoporosus*. Specimens

that were examined are deposited in the FMNH, MCZ, and WDS collections.

38–39. *Nebo* Simon 1878: Nine species were recognised in this diplocentrid genus by Sissom and Fet (2000), after Francke's (1980) revision and the new species described by Vachon (1980a) and Sissom (1994). The genus is traditionally placed in a subfamily, Nebinae Kraepelin 1905, separate from the remaining diplocentrid genera. Two species were represented in this analysis: *Nebo hierichonticus* (Simon 1872) and *Nebo poggessii* Sissom 1994. The first of these, which is the type species of *Nebo*, is distributed in Egypt (Sinai), Israel, Jordan, Lebanon, and Syria, disjunct from the remaining species on the Arabian Peninsula, of which the second species is representative. Specimens of *N. hierichonticus* that were examined are deposited in the AMNH, CAS, FMNH, JF, MCZ, and NM collections, of *N. poggessii* in the WDS collection.

Heteroscorpionidae

40–41. *Heteroscorpion* Birula 1903: This formerly monotypic genus was originally placed in the Heteroscorpioninae Kraepelin 1905, a separate subfamily of the Scorpionidae, until Lourenço (1989) transferred it to the Ischnuridae (Fet, 2000b). Lourenço (1996a) recently elevated the genus to familial status and described a second species. Both recognised species were represented in this analysis: *Heteroscorpion goodmani* Lourenço 1996 and *Heteroscorpion opisthacanthoides* (Kraepelin 1896). The second of these is the type species of *Heteroscorpion*. Specimens of *H. opisthacanthoides* that were examined are deposited in the AMNH and BMNH collections, of *H. goodmani* in the FMNH collection.

Ischnuridae

42–43. *Cheloctonus* Pocock 1892: Five species are recognised in this ischnurid genus (Lawrence, 1955; Sissom, 1990; Fet, 2000c), two of which were represented in this analysis: *Cheloctonus crassimanus* (Pocock 1896) and *Cheloctonus jonesii* Pocock 1892. The first species displays several possible synapomorphies with *Nepabellus* Francke 1974, the Afrotropical subgenus of *Opisthacanthus* Peters 1861, and was placed in combination with *Opisthacanthus* in the original description.

The second is the type species of *Cheloctonus*. Specimens of *C. crassimanus* that were examined are deposited in the AMNH, BMNH, MCZ, and MRAC collections, of *C. jonesii* in the AMNH, CAS, MCZ, NM, and TM collections.

44–45. *Chiromachetes* Pocock 1899: The status of this formerly monotypic ischnurid genus, which was described from a single type specimen, is uncertain (Fet, 2000c). Lourenço (1983a, 1985, 1989) doubted its validity and Sissom (1990) did not include it in his key to the genera of Ischnuridae. However, Lourenço (1997) recently reevaluated the genus and described a second species from a single type specimen. Both species were included in this analysis: *Chiromachetes fergusonii* Pocock 1899 and *Chiromachetes tirupati* Lourenço 1997. The first of these is the type species of *Chiromachetes*. The holotype of *C. fergusonii* was examined in the BMNH collection. The holotype of *C. tirupati* could not be obtained for examination, hence character entries were based on the literature.

46. *Chiromachus* Pocock 1893: This monotypic ischnurid genus was represented in the analysis by the type species, *Chiromachus ochropus* (C. L. Koch 1837). Specimens that were examined are deposited in the MCZ, MRAC, and USNM collections.

47–48. *Hadogenes* Kraepelin 1894: Fourteen species were recognised in this ischnurid genus by Newlands and Cantrell (1985), one of which was recently re-described by Newlands and Prendini (1997). Fet (2000c) listed two additional dubious species. Two species, representing the morphological and chromosomal extremes in the genus, were included in this analysis: *Hadogenes tityrus* (Simon 1888) and *Hadogenes troglodytes* (Peters 1861). The type species of the genus, *Hadogenes trichiurus* (Gervais 1843), which includes seven described subspecies (including the nominal subspecies), appears to be a species complex on the basis of morphological and chromosomal evidence presented by Newlands (1980) and Newlands and Cantrell (1985). However, this species complex has yet to be revised taxonomically. In light of this, and due to the fact that the holotype of the nominal subspecies could not be obtained for examination, the type species was excluded from this analysis. Nevertheless, the exemplar species included here are considered congeneric with the type species on the basis of the morphological evidence presented by Newlands (1980) and Newlands and Cantrell (1985). Specimens of *H. tityrus* that were

examined are deposited in the AMNH, SAM, and TM collections, of *H. troglodytes* in the AMNH, CAS, MCZ, NM, SAM, and TM collections.

49–50. *Iomachus* Pocock 1893: Six species are currently recognised in this ischnurid genus by Fet (2000c), including the new species described by Bastawade (1986). Two of these, representing the disjunct Indian and African species, respectively, were included in this analysis: *Iomachus laeviceps* (Pocock, 1890) and *Iomachus politus* Pocock, 1896. The first is the type species of *Iomachus*. Specimens of *I. laeviceps* that were examined are deposited in the BMNH collection, of *I. politus* in the BMNH, CAS, and MCZ collections.

51–52. *Liocheles* Sundevall 1833: Six species are currently recognised in this ischnurid genus by Fet (2000c), including the new species described by Francke and Lourenço (1991) and Locket (1995). Two of these, representing the Indo-Pacific and Australasian species groups, respectively, were included in this analysis: *Liocheles australasiae* (Fabricius 1775) and *Liocheles wai-giensis* (Gervais 1843). The first of these is the type species of the genus. Specimens that were examined are deposited in the AMNH, CAS, JF, MCZ, and NM collections.

53–55. *Opisthacanthus* Peters 1861: Two subgenera [for which generic status was originally proposed by Francke (1974)] and 19 species are currently recognised in this ischnurid genus (Fet, 2000c), based on the work of Lourenço (1979a,b, 1980, 1981a,b,c,d, 1982, 1983b,c, 1987, 1988, 1991, 1995, 1996a) and Armas and Marcato Fondeur (1992). Three species, representing both of the subgenera, were included in this analysis: *Opisthacanthus* (*Opisthacanthus*) *elatus* (Gervais, 1844), *Opisthacanthus* (*Nepabellus*) *madagascariensis* Kraepelin 1894, and *Opisthacanthus* (*Nepabellus*) *validus* Thorell 1877. The first species, which is the type species of *Opisthacanthus*, is Neotropical, whereas the second two species are Afrotropical. Both a Malagasy and an African species of the subgenus *Nepabellus* Francke 1974 were included in this analysis, to reflect the varied carinal character states (among others) within this subgenus. Specimens of *O. elatus* that were examined are deposited in the AMNH, CAS, and MCZ collections, of *O. madagascariensis* in the AMNH and BMNH collections, and of *O. validus* in the AMNH, CAS, MCZ, and SAM collections.

56. *Palaeocheloctonus* Lourenço 1996: This recently described monotypic ischnurid genus was represented

in the analysis by the type species, *Palaeocheloctonus pauliani* Lourenço 1996. Specimens that were examined are deposited in the USNM collection.

Scorpionidae

57. *Habibiella* Vachon 1974: This monotypic scorpionid genus was represented in the analysis by the type species, *Habibiella gaillardi* Vachon 1974. It is traditionally placed in the subfamily Hemiscorpiinae Pocock 1893, with *Hemiscorpius* Peters 1861. The holotype of this species could not be obtained for examination, hence character entries were based on the literature.

58–59. *Hemiscorpius* Peters 1861: Six species are recognised in this scorpionid genus (Sissom, 1990; Fet, 2000d), for which the subfamily Hemiscorpiinae Pocock 1893 was created. Two species were represented in this analysis: *Hemiscorpius lepturus* Peters 1861 and *Hemiscorpius maindroni* (Kraepelin 1900). The first of these is the type species of *Hemiscorpius*. Specimens of *H. lepturus* that were examined are deposited in the AMNH, CAS, FMNH, MCZ, and NM collections, of *H. maindroni* in the WDS collection.

60–61. *Heterometrus* Ehrenberg 1828: Five subgenera and 30 species are recognised in this scorpionid genus by Fet (2000d), after Couzijn's (1981) revision and the new species described by Tikader and Bastawade (1983). Two species, representing one of the Southeast Asian subgenera and one of the Indian subgenera, respectively, were included in this analysis: *Heterometrus (Heterometrus) spinifer* (Ehrenberg 1828) and *Heterometrus (Gigantometrus) swammerdami* Simon 1872. The first of these is the type species of *Heterometrus*. Couzijn (1981) suggested that the second was the most basal species of the genus, based on outgroup comparison with *Pandinus*, whereas the first was relatively more derived. Specimens of *H. spinifer* that were examined are deposited in the AMNH, CAS, JF, MCZ, and USNM collections, of *H. swammerdami* in the CAS and MCZ collections.

62–64. *Opisththalmus* C. L. Koch 1837: This is the largest scorpionid genus, with 50 described species (one of which is dubious) listed by Fet (2000d). The actual number is closer to 80 (Prendini, manuscript in preparation). Three species were included in this analysis, to reflect the varied trichobothrial and carinal character states within the genus: *Opisththalmus boehmi* (Kraepelin 1896). *Opisththalmus capensis*

(Herbst 1800), and *Opisththalmus holmi* (Lawrence 1969). Preliminary analysis of cladistic relationships among the species of *Opisththalmus* (Prendini, manuscript in preparation) suggests that the first species, which Kraepelin (1896) described as a species of *Heterometrus* Ehrenberg 1828 and subsequently transferred to *Scorpio* Linnaeus 1758 (Kraepelin, 1899), is relatively basal in the genus. The second species is the type species of *Opisththalmus*. The third species displays an array of derived psammophilous character states and was originally placed in a separate genus, *Protophthalmus* Lawrence 1969 [placed in synonymy with *Opisththalmus* by Newlands (1972)]. Specimens of *O. boehmi* that were examined are deposited in the AMNH, TM, and ZMB collections, of *O. capensis* in the AMNH, NM, SAM, and TM collections, and of *O. holmi* in the AMNH, NM, and TM collections.

65–67. *Pandinus* Thorell 1876: Five subgenera and 24 species (one of which has not been allocated to subgenus) were recognised in this scorpionid genus by Fet (2000d), following Vachon (1967, 1974) and Lamoral and Reynders (1975). Three species, representing three of the subgenera, were included in this analysis, to reflect the varied trichobothrial character states within the genus: *Pandinus (Pandinus) imperator* (C. L. Koch 1841), *Pandinus (Pandinoidea) cavimanus* (Pocock 1888), and *Pandinus (Pandinopsis) dictator* (Pocock 1888). The first of these is the type species of *Pandinus*. Vachon (1974) suggested that the last species, which he placed in a monotypic subgenus, was the most basal member of the genus. Specimens of *P. imperator* that were examined are deposited in the AMNH, BMNH, CAS, MCZ, and MRAC collections, of *P. cavimanus* in the AMNH, BMNH, CAS, MCZ, MRAC, and NM collections, and of *P. dictator* in the AMNH, BMNH, MCZ, and MRAC collections.

68–69. *Scorpio* Linnaeus 1758: One species, with 19 official subspecies listed by Fet (2000d), is currently recognised in this scorpionid genus. Two of the recognised subspecies were included in this analysis: *Scorpio maurus kruglovi* Birula 1910 and *Scorpio maurus mogadorensis* (Birula 1910). These taxa represent extremes in the morphological variation subsumed into this monotypic species and may be viewed as phylogenetic species (Nelson and Platnick, 1981; Cracraft, 1983, 1989; Wheeler and Nixon, 1990; Nixon and Wheeler, 1990). The former occurs in the Arabian Peninsula and the latter in Morocco. Specimens of *S. m. mogadorensis* that

were examined are deposited in the AMNH, MCZ, and SAM collections, of *S. m. kruglovi* in the FMNH collection.

70–71. *Urodacus* Peters 1861: Nineteen species, in five species groups, were recognised in Koch's (1977) revision of this scorpionid genus, which is traditionally placed in a separate subfamily, Urodacinae Pocock 1893. Two species, representing the *armatus* and *yaschenkoi* groups, respectively, were included in this analysis: *Urodacus novaehollandiae* Peters 1861, and *Urodacus yaschenkoi* (Birula 1903). The first of these is the type species of *Urodacus*. The second displays an array of psammophilous character states and was formerly placed in a monotypic genus, *Hemihoplopus* Birula 1903 [placed in synonymy with *Urodacus* by Kraepelin (1908a)]. Specimens of *U. novaehollandiae* that were examined are deposited in the CAS and TM collections, of *U. yaschenkoi* in the CAS collection.

APPENDIX 2

Characters Bearing on Scorpionoid Relationships Extracted from Stockwell's (1989) Unpublished Analysis

Numbers in parentheses correspond to Stockwell's (1989:147–153) character list. Seven uninformative characters are indicated with an asterisk.

Carapace

- 1 (26). Median longitudinal furrow (a): broad, shallow (0); suturiform (1).
 2 (27). Median longitudinal furrow (b): suturiform (0); broad, shallow—reversal (1).

Sternum

- 3 (28). Shape (a): subpentagonal (0); subtriangular (1).
 4 (29). Shape (b): subpentagonal (0); transverse (1).
 5 (30). Shape (c): subpentagonal (0); equilateral pentagonal (1).

Chelicerae

- 6 (31). Number of subdistal teeth: 1 (0); 2 (1).

Pedipalp Ornamentation

- 7 (43). Chela, male (a): no secondary sexual structures (0); with secondary sexual structures (1).
 8 (44). Chela, male (b): with hook-like structure (0); with rimmed depression (1).
 9 (45). Number of primary finger rows: single (0); multiple (1).

Trichobothria (τ)

- 10 (49). Femur, number of $e \tau$: one (0); two or more (1).
 11 (51). Patella, position of τd_2 : dorsal (0); internal (1).
 12 (52). Patella, $v \tau$ (a): absent (0); three or more retrolaterals present (1).
 13 (53). Patella, $v \tau$ (b): all ventral (0); one or more positioned externally (1).
 14 (60). Patella, $e \tau$: 7 (0); 13 or more (1).
 15 (69). Chela, number of $i \tau$: two (0); one (1).
 16 (70). Chela, position of τit : basal (0); distal (1).
 17 (72). Chela, positions of $i \tau$: basal (0); midfinger—hemiscorpiines (1).
 18 (75). Chela, number of $V \tau$: four (0); five or more (1).
 19 (79). Chela, distance between τV_2 and V_3 : normal (0); widely separated (1); unknown/inapplicable (?).
 20 (84). Chela, position of τDt (b): basal (0); distal—scorpionoids (1).
 21 (85). Chela, position of τDt (c): distal (0); midpalm (1).
 22 (86). Chela, position of τEst : distal (0); midpalm (1); unknown/inapplicable (?).
 23 (87). Chela, position of τEt_2 : external (0); ventral (1).

Legs

- 24 (90). Retrolateral pedal spurs: present (0); absent—scorpionoids (1).
 25 (92). Laterodistal lobes of telotarsi: truncated (0); rounded (1).

26 (93). Ventrosubmedian setae on telotarsi (a): setiform (0); spiniform (1).

27 (94). Ventrosubmedian setae on telotarsi (b): spiniform (1); secondarily setiform (1).

28 (95). Stridulatory organ: mostly lacking (0); on coxae of first leg and pedipalp (1).

29 (96). Length of first pair of maxillary lobes: equal to second pair (0); longer than second pair (1); unknown/inapplicable (?).

Reproductive Anatomy

30 (101). Type of embryonic development: apoikogenic (0); katoikogenic (1).

31 (103). Position of follicles on ovariuterus: sessile (0); stalked (1).

32 (104). Testis: straight (0); coiled (1); unknown/inapplicable (?).

33 (105). Genital opercula, female (a): separated (0); loosely joined (1).

34 (107). Genital opercula, female (c): loosely joined (0); fused (1).

35 (109). Genital opercula, male: separated (0); loosely joined (1).

Hemispermatophore and Paraxial Organ

36 (110). Hemispermatophore type (a): fusiform (0); flagelliform (1).*

37 (111). Hemispermatophore type (b): fusiform (0); lamelliform (1).

38 (114). Truncal flexure (a): lacking (0); mostly developed (1); unknown/inapplicable (?).

39 (117). Mating plug (a): gelatinous (0); sclerotised (1).*

40 (120). Internobasal reflection of sperm duct: lacking (0); well developed (1); unknown/inapplicable (?).

41 (121). Internal outer wall of sperm duct: simple (0); with semilunar shelf (1); unknown/inapplicable (?).

42 (122). Distal lamina: smooth (0); with prominent crest (1); unknown/inapplicable (?).

43 (123). Lamellar hook and median lobe: separate (0); fused (1).

Metasoma

44 (132). Ventral keels of segments I–IV (a): paired (0); single—scorpionoids (1).

45 (134). Transverse ventral keel on segment V: lacking (0); well developed (1).

46 (135). Subaculear tubercle: lacking (0); well developed (1).

47 (136). Venom gland type: complex (0); simple (1).

APPENDIX 3

Characters and Character States Used for Cladistic Analysis of the Superfamily Scorpionoidea

Character states were scored 0 to 4, ? for unknown, – for inapplicable, or * for polymorphic. Multistate characters were treated nonadditively, except where indicated. Three characters indicated with an asterisk are autapomorphies that were excluded from all analyses. Characters corresponding to Stockwell's (1989: 147–153) list (Appendix 2) are noted.

Carapace

1. Lateral ocelli, number of pairs: more than three (0); three (1); two (2). Most Recent scorpion genera have three pairs of lateral ocelli, which is hypothesised to be plesiomorphic on the basis of outgroup comparison with the fossil scorpions *Palaeopisthacanthus* and *Compsoscorpis* (Stockwell, 1989). Two pairs of lateral ocelli are found in *Chaerilus*, most Chactidae, and the scorpionoid genera *Bioculus*, *Heteroscorpion*, *Oiclus*, *Urodacus*, and *Vachonia*, whereas more than three pairs are found in many buthid genera, e.g. *Centruroides*; some iurid genera, e.g., *Anuroctonus*, *Caraboctonus*, and *Iurus*; and some chactoid genera, e.g., *Nullibrotheas* and *Vachonichactas* (Kraepelin, 1894, 1913; Abalos, 1954; Stahnke, 1968; Gertsch and Soleglad, 1972; Maury, 1973a; Williams and Lee, 1975; Koch, 1977; González-Sponga, 1977, 1978, 1984; Lourenço, 1985, 1989; Stockwell, 1989, 1992). Some species of *Opisthophthalmus*, e.g., *Opisthophthalmus jenseni* (Lamoral 1972), also display the condition of two ocelli (Prendini, manuscript in preparation). Lourenço's (1989:170) report of the occurrence of two pairs of lateral ocelli in *Hormiops* Fage 1933, which he placed in synonymy with *Liocheles* Sundevall 1833, could not be confirmed. All species of

Liocheles examined displayed three pairs of lateral ocelli. The distribution of the apomorphic states of this character prompted Stockwell (1989:84–85) to dismiss it as being “nearly useless at the family level.” A similar argument was put forward by Lourenço (1989:164). However, the occurrence of two pairs of lateral ocelli was included as a potential synapomorphy for *Heteroscorpion* and *Urodacus* in the present analysis. Two pairs of lateral ocelli also provided a potential synapomorphy for the diplocentrid genera *Bioculus* and *Oiclus*. However, only three of the four species of *Bioculus* display the apomorphic state of this character: *B. caboensis* has three pairs of lateral ocelli, which has been suggested to be plesiomorphic in the genus (Williams and Lee, 1975).

2. Median ocular tubercle: raised (0); shallow (1). The ocular tubercle is distinctly raised above the carapace in all scorpionoid taxa, except the Ischnuridae and Hemiscorpiinae, for which the shallow ocular tubercle is considered synapomorphic.

3. Median notch: absent (0); shallow (1); strongly excavated (2). The absence of a median notch in the anterior carapace margin is hypothesised to be plesiomorphic for the Bothriuridae (Maury and San Martín, 1973; Lamoral, 1979; Acosta, 1990) on the basis of outgroup comparison with *Chaerilus* and *Centruroides* (Kraepelin, 1913). The presence of a median notch is potentially synapomorphic for the remaining scorpionoid genera. The median notch is shallowly excavated in the ischnurid genera *Cheloctonus* and *Hadogenes* (Newlands, 1970; Lourenço, 1985) and the African species of *Opisthacanthus* (*Nepabellus*) (Lourenço, 1981c, 1982, 1983c, 1985, 1987, 1991), represented here by *O. validus*, for which it provides a potential synapomorphy. The shallowly excavated notch also occurs in the scorpionid genera *Opisthophthalmus* and *Scorpio*, for which it is hypothesised to be synapomorphic.

4. Median longitudinal furrow: broad, shallow, without suture (0); narrow, suturiform (1). This character is an amalgamation of Stockwell’s (1989) characters 26 and 27. The median longitudinal furrow of all scorpionoid taxa, except the Bothriuridae and Diplocentrinae, is suturiform, often with an anterior furcation (Lamoral, 1980; Stockwell, 1989). The presence of a broad, shallow furrow, without a suture, is hypothesised to be plesiomorphic in the Bothriuridae, based on outgroup comparison with *Chaerilus* and *Centruroides*, whereas in the Diplocentrinae it is hypothesised to be a reversal.

Stockwell (1989) coded this putative reversal as a separate character (27), thus preventing this hypothesis from being tested in his analysis.

5. Median longitudinal furrow: well-developed (0); obsolete (1). Obsolescence of the median longitudinal furrow is hypothesised to be synapomorphic for the bothriurid genera *Bothriurus*, *Orobothriurus*, *Timogenes*, and *Vachonia*.

6. Antero-ocular depression: absent (0); present (1). The presence of an antero-ocular depression is hypothesised to be synapomorphic for some species of the scorpionid genus *Opisthophthalmus* (*O. capensis* and *O. holmi* in this analysis).

7. Posterior sutures: absent (0); present (1). Posterior carapacial sutures occur in all scorpionoid taxa except the Bothriuridae and the Diplocentrinae. The absence of posterior sutures is hypothesised to be plesiomorphic in the Bothriuridae, based on outgroup comparison with *Chaerilus* and *Centruroides*, and the presence of sutures synapomorphic for the remaining scorpionoid taxa. The absence of sutures in the Diplocentrinae is hypothesised to be a reversal.

8. Nongranular surfaces of prosoma, mesosoma, metasoma, and legs: smooth (0); distinctly punctate (1). Although the cuticular surfaces of most Recent scorpions are predominantly granular, areas without granulation occur, especially on the ventral surfaces. These nongranular areas are usually smooth, but are distinctly punctate in the Heteroscorpionidae, Hemiscorpiinae, and Ischnuridae (Kraepelin, 1894; Pocock, 1900; Sreenivasa-Reddy, 1968a,b,c,d), providing a potential synapomorphy for these taxa. The occurrence of the punctate condition in two diplocentrid genera, *Bioculus* and *Didymocentrus*, and at least one species of the genus *Diplocentrus*, *D. gertschi* (Francke, 1978; Stockwell, 1988; Sissom and Walker, 1992), is considered to be independently derived from the condition in the Heteroscorpionidae, Hemiscorpiinae, and Ischnuridae and potentially synapomorphic for these diplocentrids.

Sternum

9. Sternum shape: subtriangular (0); subpentagonal (1); transverse (2); equilateral pentagonal (3). This character is an amalgamation of Stockwell’s (1989) characters 28, 29, and 30, in which the apomorphic states were treated as separate characters. The sternum of

most Recent scorpion genera is roughly pentagonal, with sides parallel and apex pointed anteriorly. This shape is retained at maturity and is thus hypothesised to be plesiomorphic (Stockwell, 1989). In the Buthidae, represented here by *Centruroides*, the sides of the sternum converge anteriorly, resulting in a subtriangular appearance (Petrunkevitch, 1916). Lamoral (1980) and Stockwell (1989) considered the subtriangular sternum synapomorphic for the bothrid genera. The sternum of all bothriurids, except *Lisposoma*, is reduced to a narrow sclerite, many times wider than long, and referred to as “transverse” (Werner, 1934; Lamoral, 1980; Francke, 1982a; Stockwell, 1989; Sissom, 1990). This condition is also hypothesised to be apomorphic, based on out-group comparison with *Chaerilus* and the Chactoidea. Stockwell (1989) considered the sternum of *Lisposoma*, which is slightly wider than long, to be homologous with the transverse sternum of the remaining bothriurids. However, the sternum of *Lisposoma* is clearly sub-pentagonal, as indicated by Lamoral (1979) and Francke (1982a). Consequently, *Lisposoma* is assigned the hypothesised plesiomorphic state in the present analysis, and the transverse sternum is considered synapomorphic for the remaining bothriurid genera. The sternum of the ischnurid genera *Liocheles* and *Iomachus* is an equilateral pentagon, with the sides diverging anteriorly, and is hypothesised to be synapomorphic for these genera (Stockwell, 1989). The sternum of *Chir-omachus* is not an equilateral pentagon, as suggested by Stockwell (1989:87).

Chelicerae

10. Cheliceral movable finger, number of subdistal teeth: one (0); two (1). Stockwell’s (1989) character 31. Nine of the 12 genera of Bothriuridae, including *Lisposoma*, have two subdistal teeth on the cheliceral movable finger, which is considered synapomorphic for these genera. However, the genera *Bothriurus*, *Timogenes*, and *Vachonia* have only one subdistal tooth (San Martín, 1972; San Martín and Cekalovic, 1972; Stockwell, 1989), which is hypothesised to be a reversal in these genera.

11. Cheliceral movable finger, distal external and distal internal teeth: subequal, with distal external tooth only slightly smaller than distal internal tooth, and apposable, i.e., forming a bicuspid (0); unequal, with distal external tooth considerably smaller than distal

internal tooth, aligned longitudinally and usually not apposable or, at most, moderately apposable (1). Lamoral (1980) hypothesised that subequal, apposable distal teeth on the cheliceral movable finger were plesiomorphic in Recent scorpions, based on their occurrence in *Chaerilus* and the Buthidae, whereas unequal, longitudinally aligned teeth were synapomorphic for the chactoid family Vaejoidea. Stockwell (1989:90) disagreed with Lamoral’s interpretation, erroneously stating that unequal, longitudinally aligned teeth should be considered plesiomorphic, and rejected the character because it did “not distribute neatly among the groups.” Stockwell (1989:90–91) supported his assertion by invoking Francke’s (1977a) finding that this character was useless for distinguishing among the genera of Diplocentridae as proposed by Werner (1934). Although this character may be of limited value with regard to relationships among the diplocentrid genera, there is no reason to disregard it from an analysis of relationships among the higher taxa of Scorpionoidea. Given the occurrence of subequal, apposable teeth in *Chaerilus* and the Buthidae (represented here by *Centruroides*), the occurrence of unequal, longitudinally aligned teeth is hypothesised to be synapomorphic for other Recent scorpions such as the Scorpionoidea (the apomorphic state is not restricted to the Vaejoidea as proposed by Lamoral). Consequently, the occurrence of subequal, apposable teeth in the Hemiscorpiinae and Ischnuridae (Hewitt, 1925; Lourenço, 1985, 1989) is hypothesised to be a reversal for these taxa.

12. Cheliceral fingers, secondary serrations: absent (0); present (1). The presence of secondary serrations in some species of *Urodacus* (Koch, 1977) is uninformative in this analysis, since it occurs only in *U. yaschenkoi*.*

13. Cheliceral coxae, scaphotrix (stridulatory setae) on dorsointernal surfaces: absent (0); present (1). The presence of an area of stridulatory setae (scaphotrix) on the dorsointernal surfaces of the cheliceral coxae is hypothesised to be autapomorphic for the scorpionid genus *Opisthophthalmus* (Pocock, 1896a; Pavlovsky, 1924a; Werner, 1934; Alexander, 1958, 1960; Vachon et al., 1958, 1960; Dumortier, 1964; Acosta and Maury, 1990).

14. Cheliceral coxae, trichopae (chemoreceptive lamelliform setae) on internal surfaces: absent (0); present (1). The presence of chemoreceptive lamelliform

setae (trichopae) on the internal surfaces of the cheliceral coxae is hypothesised to be synapomorphic for some species of the scorpionid genus *Opisthophthalmus* (Pocock, 1896a; Purcell, 1899; Pavlovsky, 1924a; Werner, 1934; Alexander and Ewer, 1957; Alexander, 1958, 1960; Vachon *et al.*, 1958, 1960; Dumortier, 1964; Sissom, 1990), represented in this analysis by *O. boehmi* and *O. capensis*.

Pedipalp Ornamentation

15. Patella, dorsal surface: flat, dorsomedian, and dorsoexternal carinae in same axis (0); convex, dorsoexternal carina raised above horizontal axis of dorsoexternal carina (1). This character is difficult to polarise due to the presence of one state in *Centruroides* and the other in *Chaerilus*. Nonetheless, the widespread occurrence of the flat condition in many buthid and chactoid genera suggests that it is plesiomorphic in the scorpionoids. Among the latter, the convex condition is hypothesised to be synapomorphic for the bothriurid genera *Bothriurus*, *Brachistosternus*, *Centromachetes*, *Orobothriurus*, *Timogenes*, and *Vachonia*; for the Diplocentriinae; and for the Scorpioninae.

16. Patella, dorsoexternal carina: distinct (0); obsolete (1). The presence of a distinct dorsoexternal carina on the patella is considered plesiomorphic on the basis of outgroup comparison with *Chaerilus* and *Centruroides*. Among the Bothriuridae, the genus *Lisposoma* exhibits the plesiomorphic condition, all other genera being synapomorphic for the obsolete condition. The plesiomorphic condition also occurs in *Heteroscorpion*, *Urodacus*, the Hemiscorpiinae, *Heteronebo*, *Cheloctonus*, and the African species of *Opisthacanthus* (*Nepabellus*), represented by *O. validus*. The obsolete condition provides a potential synapomorphy for most of the genera of Ischnuridae, being independently derived and synapomorphic for the Diplocentridae and Scorpioninae. The occurrence of a distinct dorsoexternal carina in the diplocentrid genus *Heteronebo* is attributed to a reversal.

17. Patella, externomedian carina: continuous from proximal to distal edges (0); discontinuous, interrupted two-thirds along (1). The discontinuous externomedian carina of the patella occurs in all Recent scorpions (represented here by the Scorpionioidea) except the Buthidae and *Chaerilus*. However, since the disposition of this character is unknown in the fossil taxa, the

polarity of its states cannot be determined. The continuous externomedian carina could be synapomorphic for the Buthidae and Chaerilidae, or the discontinuous carina could be synapomorphic for all other Recent scorpions.

18. Patella, anterior process: absent (0); present (1). A well-developed anterior process occurs on the patella of *Heteroscorpion*, the Hemiscorpiinae, and most genera of Ischnuridae (Lourenço, 1985, 1987, 1991), for which it is potentially synapomorphic. However, the anterior process is absent in the ischnurid taxa *Cheloctonus*, the African species of *Opisthacanthus* (*Nepabellus*), represented here by *O. validus*, and the African species of *Iomachus*, represented by *I. politus*, which may be interpreted as reversals.

19. Chela, number of carinae: 8 (0); 10 (1). Stockwell (1989:92) stated that the basic number of carinae on the pedipalp chela is 8 in most Recent scorpions, a corollary of which is that reduction in the number of carinae is apomorphic. In a reinvestigation of pedipalp carinal homology in Recent scorpions, in which setal patterns were used to assess the positions of obsolete carinae (Prendini, manuscript in preparation), I concluded that Stockwell's basic number of 8 carinae occurs only in the Chaerilidae and Buthidae (although simultaneous obsolescence is common in many buthids). All other Recent scorpions have 10 chelal carinae as the basic number, although this is only expressed in a few taxa (e.g., *Diplocentrus*), due to the obsolescence of at least 1 carina in most taxa. The lower number of carinae postulated by Stockwell and previous authors (e.g., Sissom, 1990) is attributed to the fact that vestigial carinae (e.g., the subdigital carina, which is reduced to a vestigial granule at the proximal margin of the chela in all taxa except the four genera of Scorpioninae) have not been counted in the past. The presence of 10 chelal carinae is hypothesised to be synapomorphic for all Recent scorpions (represented here by the Scorpionioidea) except the Chaerilidae and Buthidae.

20. Chela (male), dorsal secondary carina: distinct (0); obsolete (1). A distinct dorsal secondary carina on the pedipalp chela of the adult male is hypothesised to be plesiomorphic in the Scorpionioidea on the basis of its occurrence in *Chaerilus* and *Centruroides*. The apomorphic obsolete condition occurs in the following

scorpionoid taxa: Bothriuridae, Ischnuridae, Scorpioninae, and all diplocentrid genera except *Didymocentrus*, *Diplocentrus*, *Heteronebo*, and *Tarsoporosus*. Obsolescence is hypothesised to be synapomorphic for the Bothriuridae and for the Ischnuridae, but independently derived in the Diplocentridae and Scorpioninae, for which it is considered synapomorphic. The occurrence of a distinct dorsal secondary carina in the diplocentrid genera *Didymocentrus*, *Diplocentrus*, *Heteronebo*, and *Tarsoporosus* is hypothesised to be a reversal. Compared with *Heteronebo* and *Tarsoporosus*, development of the dorsal secondary carina of the adult male varies from moderate to weak among species of *Didymocentrus* and *Diplocentrus* (W. D. Sissom, pers. comm.). Nevertheless, the dorsal secondary carina is distinctly discernible in all these taxa, compared with *Bioculus*, *Cazierius*, *Oiclus*, and *Nebo*, hence they are scored with the hypothesised plesiomorphic state.

21. Chela (female), dorsal secondary carina: distinct (0); obsolete (1). A distinct dorsal secondary carina on the pedipalp chela of the adult female is hypothesised to be plesiomorphic in the Scorpionoidea on the basis of its occurrence in *Chaerilus* and *Centruroides*. The apomorphic obsolete condition occurs in the following scorpionoid taxa: Bothriuridae, Ischnuridae, Scorpioninae, and all diplocentrid genera except *Heteronebo* and *Tarsoporosus*. Obsolescence is hypothesised to be synapomorphic for the Bothriuridae and for the Ischnuridae, but independently derived in the Diplocentridae and Scorpioninae, for which it is considered synapomorphic. The occurrence of a distinct dorsal secondary carina is hypothesised to be a reversal in the diplocentrid genera *Heteronebo* and *Tarsoporosus*.

22. Chela, dorsal secondary carina: extending full way across dorsal surface, subdigital carina vestigial (0); dorsal secondary carina extending part way across dorsal surface, subdigital carina extending part way across in opposite direction (1). The dorsal secondary carina of most Recent scorpions extends full way across the dorsal surface of the chela. This condition is hypothesised to be plesiomorphic, on the basis of outgroup comparison with *Chaerilus* and the Buthidae (represented here by *Centruroides*). In addition, Recent scorpions other than the Buthidae and Chaerilidae (in which only eight chelal carinae are present) display a greatly reduced subdigital carina, visible only as a vestigial granule at the proximal margin of the chela. This condition is considered plesiomorphic in the Scorpionoidea

due to its occurrence in the Chactoidea. However, in the scorpionid genera *Heterometrus*, *Opisthophthalmus*, *Pandinus*, and *Scorpio*, the dorsal secondary carina extends only partially across the dorsal surface, becoming obsolete proximally, whereas the subdigital carina, which is unusually well-developed, extends partially across in the opposite direction, becoming obsolete distally. This condition is hypothesised to be synapomorphic for the Scorpioninae.

23. Chela, digital carina: distinct (0); obsolete (1). Obsolescence of the digital carina is hypothesised to be apomorphic, based on outgroup comparison with *Chaerilus* and most other Recent scorpions. Among the Scorpionoidea, obsolescence of the digital carina occurs in all bothriurid genera; the diplocentrid genera *Bioculus*, *Cazierius*, and *Oiclus* (Francke, 1978; Stockwell, 1988; Sissom and Walker, 1992); the scorpionid genera *Heterometrus* (Couzijn, 1981; Tikader and Bastawade, 1983) and *Pandinus*; and the ischnurid genus *Hadogenes*. Obsolescence is hypothesised to be independently derived in the Bothriuridae, Diplocentridae, Scorpionidae, and *Hadogenes*. A tendency towards obsolescence of the digital carina also occurs in *Didymocentrus* and a few species of *Diplocentrus*, e.g., *D. gertschi* (Sissom and Walker, 1992). However, as with the dorsal secondary carina of the adult male (character 20), the digital carina is distinctly discernible in these taxa, compared with *Bioculus*, *Cazierius*, and *Oiclus*, hence they are scored with the hypothesised plesiomorphic state.

24. Chela, disproportionate development of dorsal secondary and external secondary carinae, relative to digital carina: absent (0); present (1). Disproportionate development of both the dorsal secondary and the external secondary carinae, relative to the digital carina, is hypothesised to be autapomorphic for the diplocentrid genus *Didymocentrus* (Francke, 1978; Stockwell, 1988; Sissom and Walker, 1992). Stockwell (1988) suggested that disproportionate development of the dorsal secondary and external secondary carinae occurs also in *Bioculus*. However, Sissom and Walker (1992) considered the relative development of the digital and external secondary carinae to vary intraspecifically in *Bioculus*, thus weakening the utility of this character as a potential synapomorphy with *Didymocentrus*. In general, the dorsal secondary and external secondary carinae are very weakly developed in *Bioculus*, compared

to other diplocentrids such as *Didymocentrus*, *Diplocentrus*, and *Heteronebo*, and are considered obsolete, a potential synapomorphy with *Cazierius* and *Oiclus* (refer to above discussion of character 20).

25. Chela, disproportionate development of external secondary carina only, relative to digital carina: absent (0); present (1). Disproportionate development of the external secondary carina, relative to the digital carina (which is completely absent) is autapomorphic for the ischnurid genus *Hadogenes*.

26. Chela, ventroexternal carina: distinct (0); obsolete (1). Obsolescence of the ventroexternal carina is hypothesised to be synapomorphic for the genera of Bothriuridae, including *Lisposoma*, on the basis of outgroup comparison with *Chaerilus*, the Buthidae (represented here by *Centruroides*), and most other Recent scorpions.

27. Chela, ventroexternal carina: parallel to longitudinal axis of chela, distal edge connected to external movable finger condyle (0); parallel to longitudinal axis of chela, distal edge disconnected from external movable finger condyle and directed towards a point between external and internal movable finger condyles, but closer to external condyle (1); oblique to longitudinal axis of chela, distal edge disconnected from external movable finger condyle and directed towards a point between external and internal movable finger condyles, but closer to internal condyle (2); oblique to longitudinal axis of chela, distal edge disconnected from external movable finger condyle and directed towards (almost connecting) internal movable finger condyle (3) (additive). The ventroexternal carina of most Recent scorpions is oriented roughly parallel to the longitudinal axis of the chela and, in *Chaerilus* and the Buthidae (represented here by *Centruroides*), the distal edge connects with the external movable finger condyle. This condition is hypothesised to be plesiomorphic in Recent scorpions, based on outgroup comparison with the fossil scorpion *Palaepisthacanthus* (Kjellesvig-Waering, 1986). In all other Recent scorpion genera, the distal edge of the ventroexternal carina is disconnected from the external movable finger condyle and directed inwards of it, leaving what appears to be an additional, short carina at the condyle (interpreted here as the remaining distal portion of the ventroexternal carina). This condition is hypothesised to be synapomorphic for all Recent scorpion genera except bothriurids and chaerilids. Although the orientation of the

ventroexternal carina is usually parallel to the longitudinal axis of the chela in the remaining genera, it is oblique to the longitudinal axis in certain scorpionoid taxa, a condition that is considered to be derived from the parallel condition. This derived oblique condition occurs in the Bothriuridae and the diplocentrid genera *Didymocentrus* and *Diplocentrus* and is hypothesised to have evolved independently in the two families. The oblique orientation has resulted in the distal edge of the ventroexternal carina being directed towards, and almost connecting with, the internal movable finger condyle in the bothriurids and *Didymocentrus*. However, the orientation of the ventroexternal carina in *Diplocentrus* is intermediate between the orientation in *Didymocentrus* or the bothriurids and that in the remaining scorpionoids and chactoids, in which the distal edge is directed inwards of, but closer to, the external condyle. Accordingly, an ordered transformation series has been postulated for this character, such that the oblique orientation in *Diplocentrus* is derived from the parallel orientation and synapomorphic with the oblique orientation in *Didymocentrus*, which is considered to be further derived. The oblique orientation of the ventroexternal carina was first used as a diagnostic character for *Didymocentrus* by Francke (1978) and adopted by subsequent authors (Stockwell, 1988; Sissom, 1990; Sissom and Walker, 1992). *Bioculus* displays the relatively plesiomorphic parallel orientation (Stockwell, 1989; Sissom and Walker, 1992). The length of this character decreased in all analyses as a result of unordering.

28. Chela, ventromedian carina: vestigial or obsolete (0); distinct (1); inapplicable (-). The position of the ventromedian carina on the pedipalp chela cannot be determined in the outgroups, *Chaerilus* and the Buthidae (represented here by *Centruroides*), since they have only eight chelal carinae, hence this character is inapplicable to these taxa. However, the vestigial or obsolete condition of the ventromedian carina is hypothesised to be plesiomorphic in most Scorpionoidea, on the basis of its occurrence in numerous chactoid taxa and the relatively basal Bothriuridae. The distinct condition is hypothesised to be apomorphic, and independently derived, in the Diplocentrinae and the Scorpioninae.

29. Chela, ventrointernal carina: more strongly developed than internomedian carina, which may be obsolete (0); equally or less strongly developed than

internomedian carina (1); inapplicable (-). The ventrointernal carina of the pedipalp chela is more strongly developed than the internomedian carina in *Chaerilus*, hence this condition is hypothesised to be plesiomorphic. Among the Scorpionoidea, the hypothesised plesiomorphic condition occurs in the following taxa: *Heteroscorpion*, the Hemiscorpiinae, *Nebo*, and *Urodacus*. Equal or reduced development of the ventrointernal carina, relative to the internomedian carina, occurs in all other scorpionoid genera. This character is scored inapplicable to *Centruroides*, in which the position of the ventrointernal carina cannot be reliably determined.

30. Chela, ventrointernal carina: equally or more strongly developed than internomedian carina, which may be obsolete (0); less strongly developed than internomedian carina, often obsolete (1); inapplicable (-). The ventrointernal carina of the pedipalp chela is more strongly developed than the internomedian carina in *Chaerilus*, hence this condition is hypothesised to be plesiomorphic. Reduced development of the ventrointernal carina, relative to the internomedian carina, is hypothesised to be synapomorphic for the genera of Ischnuridae. This character is scored inapplicable to *Centruroides*, in which the position of the ventrointernal carina cannot be reliably determined.

31. Chela (male), secondary sexual structure: absent (0); hook-like apophysis (1); semicircular, rimmed depression (2); unknown (?) (additive). This character is an amalgamation of Stockwell's (1989) characters 43 and 44, in which the apomorphic states were treated as separate characters. The adult males of all bothriurid genera, except *Lisposoma* and *Thestylus*, exhibit secondary sexual structures on the internal face of each chela, near the base of the fixed finger (Kraepelin, 1908b; Werner, 1934; San Martín, 1965a; Cekalovic, 1973a; Maury and San Martín, 1973; Maury, 1975; Stockwell, 1989; Acosta, 1990). The genera *Bothriurus*, *Brachistosternus*, *Centromachetes*, *Cercophonius*, *Orobothriurus*, *Phoniocercus*, *Tehuanka*, and *Urophonius* exhibit a hook-like apophysis, whereas *Timogenes* and *Vachonia* exhibit a rimmed depression. The absence of a secondary sexual structure is hypothesised to be plesiomorphic in *Lisposoma* and *Thestylus*, based on outgroup comparison with *Chaerilus*, the bothriids, and the chactoids, whereas the hook-like apophysis is hypothesised to be apomorphic for the remaining bothriurid genera. The

rimmed depression is hypothesised to be further derived from the hook-like apophysis, such that the rim of the depression is homologous with the apophysis (Stockwell, 1989) and synapomorphic for *Timogenes* and *Vachonia*. The character states for *Chiromachetes* are unknown, since adult males are unknown in this genus (Pocock, 1899; Lourenço, 1997). The length of this character did not change in the analyses as a result of unordering.

32. Chela (male), hook-like secondary sexual structure with granular ridge at base of fixed finger: present (0); absent (1); unknown (?); inapplicable (-). Among male bothriurids with a hook-like secondary sexual structure on the chela, the genera *Cercophonius*, *Phoniocercus*, and *Urophonius* exhibit a granular ridge at the base of the fixed finger, providing a potential synapomorphy, which is absent in the genera *Bothriurus*, *Brachistosternus*, *Centromachetes*, *Orobothriurus*, and *Tehuanka* (Cekalovic, 1973a; Maury, 1975; Acosta, 1990). This character is inapplicable to the scorpionoid genera, including bothriurids, without a hook-like secondary sexual structure on the male chela. The character states are unknown for the ischnurid genus *Chiromachetes*, in which adult males are unknown (Pocock, 1899; Lourenço, 1997).

33. Chela fingers, number of rows of primary denticles: single (0); double, often fused at the base (1); multiple (2). This character is a modified version of Stockwell's (1989) character 45. Most scorpionoid genera exhibit a single row of primary denticles, flanked on either side by supernumerary rows, which is hypothesised to be plesiomorphic, based on outgroup comparison with *Chaerilus* and *Centruroides*. The Hemiscorpiinae and Ischnuridae (except the genera *Cheloctonus* and *Palaeocheloctonus*) exhibit a double row of denticles, which are often fused at the base (Kraepelin, 1894; Werner, 1934; Lourenço, 1985, 1989, 1996a). This distinctive condition, which was not distinguished from "multiple rows" by Stockwell (1989:95–96), is hypothesised to be synapomorphic for these taxa, with the two exceptions being reversals. *Heteroscorpion*, *Urodacus*, and three genera of Bothriuridae (*Cercophonius*, *Centromachetes*, and *Urophonius*) exhibit multiple rows (Kraepelin, 1894; Werner, 1934; Koch, 1977; Stockwell, 1989; Acosta, 1990; Lourenço, 1985, 1989, 1996a). The condition in *Heteroscorpion* and *Urodacus* is hypothesised to be synapomorphic and independently derived from the condition in the bothriurids. Stockwell

(1989:95) states of the diplocentrid genus, *Didymocentrus*, that “the granules appear as multiple primary rows.” No such distinction from the remaining diplocentrid genera could be found in the present investigation.

34. Chela fingers, dentate margin: entire (0); markedly scalloped (1). The dentate margin of the fingers is entire in most Recent scorpions, including *Chaerilus* and the Buthidae (represented here by *Centruroides*), hence it is hypothesised to be plesiomorphic. A markedly scalloped dentate margin occurs in the Nebinae (Francke, 1980) and Scorpioninae for which it is hypothesised to be synapomorphic. However, the occurrence of an entire margin in the Diplocentrinae is hypothesised to be a reversal.

35. Chela (male), lobe of movable finger: absent or at most weakly developed, close to base movable finger and lacking an obvious notch in fixed finger (0); well-developed, almost midway along movable finger (if dentate margin markedly scalloped, first lobe disproportionately developed), with a distinct notch in fixed finger, lobe rounded dorsally and lacking a sharp conical tooth (1); well-developed, almost midway along movable finger, with a distinct notch in fixed finger, lobe unevenly pointed dorsally, due to the presence of a sharp conical tooth (2); unknown (?) (additive). The presence in the adult male of a well-developed lobe, almost midway along the movable finger of the pedipalp chela, and a distinct notch in the fixed finger (Newlands, 1980; Newlands and Prendini, 1997), is hypothesised to be synapomorphic for the genera of Ischnuridae. A homologous structure occurs in the scorpionid genera *Heterometrus* and *Pandinus*, in which the dentate margins of the chelal fingers are markedly scalloped, and is hypothesised to be synapomorphic for these genera, but independently derived from the condition in the Ischnuridae. Among the Ischnuridae, the dorsally rounded lobe, lacking a sharp conical tooth, is hypothesised to be relatively plesiomorphic and the unevenly pointed lobe with a sharp conical tooth derived from it and potentially synapomorphic for *Opisthacanthus* (*Opisthacanthus*) (Lourenço, 1979b, 1980, 1981a,b, 1981d, 1983b, 1985, 1987; Armas and Marcano Fondeur, 1992), represented here by *O. elatus*, and the African species of *Iomachus*, represented here by *I. politus*. This character is coded as unknown for the ischnurid genus *Chiromachetes*, in which adult males are unknown (Pocock, 1899; Lourenço, 1997).

The length of this character did not change in the analyses as a result of unordering.

36. Chela (male, also applicable in females with well-developed lobe on movable finger), lobe of fixed finger, projecting downwards: absent (0); present (1); unknown (?). A downward-projecting lobe on the fixed finger of the pedipalp chela in adult males, and adult females with a well-developed lobe on the movable finger, is hypothesised to be apomorphic and occurs in the following ischnurid taxa: *Chiromachetes fergusonii*, *Chiromachus*, *Liocheles*, some species of *Hadogenes*, represented here by *H. tityrus*, and most species of *Opisthacanthus* (*Opisthacanthus*), represented here by *O. elatus* (*O. lecomtei* is an exception). This character is coded as unknown in *Iomachus laeviceps*, in which an adult male was not available for examination (the adult female of this species does not exhibit a well-developed lobe on the movable finger and, hence, could not be scored instead).

37. Chela (female), lobe of movable finger: absent or at most weakly developed, close to base of movable finger, without an obvious notch in fixed finger (0); well-developed, almost midway along movable finger, with distinct notch in fixed finger (1); polymorphic (*). The presence in the adult female of a well-developed lobe, almost midway along the movable finger of the pedipalp chela, and a distinct notch in the fixed finger (Lamoral, 1979; Newlands, 1980; Newlands and Prendini, 1997) occurs in the following ischnurid taxa: *Chiromachetes fergusonii*, *Chiromachus*, *Palaeocheletoonus*, the Malagasy species of *Opisthacanthus* (*Nepabellus*), represented here by *O. madagascariensis*, and most species of *Hadogenes*, represented here by *H. troglodytes* (the lobe is absent in female *H. tityrus*). This character is polymorphic in some of the African species of *Opisthacanthus* (*Nepabellus*), represented here by *O. validus*. It is hypothesised to be synapomorphic for *Chiromachetes* and *Chiromachus*, but independently derived in *Palaeocheletoonus*, *Opisthacanthus* (*Nepabellus*), and *Hadogenes*.

38. Chela (female), sharp conical tooth at base of movable finger and corresponding notch at base of fixed finger: absent (0); present (1). The presence of a sharp conical tooth at the base of the movable finger of the pedipalp chela of the female and a corresponding notch at the base of the fixed finger occurs in *Opisthacanthus* (*Opisthacanthus*) (Lourenço, 1979b, 1980, 1981a,b, 1981d, 1983b, 1985, 1987; Armas and Marcano

Fondeur, 1992), represented here by *O. elatus*, and the African species of *Iomachus*, represented here by *I. politus*, for which it is potentially synapomorphic.

Trichobothria (τ)

Although the utility of trichobothria was recognised early in the history of scorpion systematics (e.g., Kraepelin, 1891, 1894; Birula, 1917a,b), it was not until the work of Vachon (1972, 1974) that the importance of trichobothrial patterns was fully appreciated. Vachon (1974) provided a survey of scorpion trichobothrial patterns and his system of trichobothrial nomenclature, cf. Stahnke's (1970, 1974), remains in widespread use (Sissom, 1990). Francke and Soleglad (1981:238) criticised both Stahnke's (1970) and Vachon's (1974) trichobothrial terminology on the grounds that "there is no evidence of trichobothrial migration [whereas] evidence of trichobothrial gain or loss is widespread." As Francke and Soleglad correctly pointed out, trichobothria are mechanoreceptors, each innervated by a single bipolar neuron, hence any mechanism proposed to account for trichobothrial migration must also explain the migration of their respective neurons. Thus it would seem that the hypothesis of trichobothrial migration reflects "the shortcomings of the terminologies developed by Vachon and Stahnke" (Francke and Soleglad, 1981:238). However, Francke and Soleglad appear to have taken Vachon's usage of the term "migration" too literally. The trichobothrial patterns proposed by Vachon (and Stahnke) must necessarily be interpreted with respect to the morphology of the pedipalp, i.e., the positions, and hence terminology, of individual trichobothria cannot be determined without reference to landmarks such as carinae and other trichobothria. In contrast to the migration of trichobothria, there is abundant evidence for plasticity in the shape of the pedipalps and, hence, in the relative positions of pedipalp carinae (see above). Accordingly, the apparent "migration" of a trichobothrium from one pedipalp surface to another may be nothing more than an interpretation of change in the position of a trichobothrium relative to the carina, which delimits the two surfaces, such that the trichobothrium is now situated on one surface, rather than the other. Any other change in the shape of the pedipalp may similarly be interpreted as a trichobothrial "migration." For example, as noted by Francke and Soleglad (1981:238): "Comparing

the patterns of *Iurus* and *Calchas* . . . the trichobothria on the finger are rather equidistant on both genera, but on *Calchas* they cover most of the finger while on *Iurus* they cover the distal one-half to two-thirds of the finger only . . . allometric growth could account for the differences observed." The "migration" interpretation, albeit inaccurate, presents no difficulty (other than semantics) for the use of Vachon's terminology, since trichobothria were necessarily named according to the position, e.g., dorsal terminal (*dt*), in which they were most commonly observed. Nor does it present any difficulty for homology assessment, which is based on Francke and Soleglad's (1981:238) premise "that trichobothria occupying similar positions are homologous," with the caveat that "similar positions" may appear to be different when modifications to pedipalp shape are manifest as differences in the relative positions of landmarks. It is these apparent differences in position among homologous trichobothria that provide the phylogenetic information described as characters such as those below.

39. Femur, number $e \tau$: one (0); two (1); four (2). This is Stockwell's character 49, modified by the inclusion of a third autapomorphic state for *Chaerilus* and scoring *Vachonia* for the second apomorphic state. Four trichobothria occur on the external surface of the femur in *Chaerilus*, whereas most Buthidae (including *Centruroides*) have only two e trichobothria (Vachon, 1974; Stockwell, 1989; Sissom, 1990). Stockwell (1989) considered the presence of two or more e trichobothria on the femur to be synapomorphic for *Chaerilus* and the Buthidae, since only a single trichobothrium occurs in most other Recent scorpion genera, including all Scorpionioidea (Vachon, 1974), with the exception of the monotypic bothriurid genus *Vachonia*, in which there are two e trichobothria (Maury, 1973a). However, the disposition of this character is unknown in the fossil taxa. The occurrence of two trichobothria in *Vachonia* is hypothesised to be autapomorphic and independently derived from the condition in the Buthidae.

40. Femur, position τi : internal (0); dorsal (1). In most scorpions, trichobothrium i occurs on the internal surface of the pedipalp femur. However, in the scorpionid genus *Scorpio*, trichobothrium i occurs on the dorsal surface (Vachon, 1974). This condition is hypothesised to be autapomorphic for *Scorpio*.

41. Patella, position τd_2 : dorsal (0); internal (1). Stockwell's character 51. The plesiomorphic location

for trichobothrium d_2 is on the dorsal surface of the patella, as in *Chaerilus*, the Buthidae (in which there are five trichobothria on the dorsal surface), and most other genera of Recent scorpions. However, in the Scorpioninae and Diplocentrinae, d_2 occurs on the internal surface of the patella (Vachon, 1974; Francke, 1977a,b, 1980; Stockwell, 1989), a condition that is hypothesised to be independently derived in these taxa.

42. Patella, $v \tau$ absent (0); three prolaterals (1); three or more retrolaterals (2) (additive). This is a modified version of Stockwell's (1989) character 52, in which the different states of *Chaerilus* and the Buthidae were not distinguished. Ventral trichobothria are completely absent from the patella of all buthids, but there are three prolateral v trichobothria in *Chaerilus* and three or more retrolateral v trichobothria in all other Recent genera (Vachon, 1974; Stockwell, 1989). The fossil scorpion *Palaeopisthacanthus* lacks v trichobothria (Kjellesvig-Waering, 1986), so this condition is considered plesiomorphic. Stockwell (1989:100) considered the character states found in *Chaerilus* and the other non-buthid genera to be independently derived from the plesiomorphic condition, in which case the condition in *Chaerilus* would be autapomorphic. Alternatively, the presence of three or more v trichobothria could be synapomorphic for *Chaerilus* and the other non-buthid genera and the presence of three or more retrolateral v trichobothria further derived from the prolateral condition and synapomorphic for the non-buthid genera except *Chaerilus*. These alternative hypotheses were not tested by Stockwell (1989), who scored the prolateral condition of *Chaerilus* as plesiomorphic absence. Irrespective of which hypothesis is postulated, the presence of three or more retrolateral v trichobothria constitutes a synapomorphy for all remaining Recent scorpion taxa (represented here by the Scorpionoidea). This character was rendered uninformative when unordered.

43. Patella, number $v \tau$ absent (0); single row of 3 (1); single row of 4–20 (2); two or more rows, with more than 30 (3). Ventral trichobothria are completely absent from the patella of all buthids (Vachon, 1974; Stockwell, 1989; Sissom, 1990). The orthobothriotaxic number of v trichobothria for non-buthids is 3 (Vachon, 1974; Stockwell, 1989; Sissom, 1990), which is hypothesised to be plesiomorphic based on outgroup comparison with *Chaerilus*. In the Bothriuridae, *Brachistosternus* (*Brachistosternus*), *Vachonia*, and some species of

Timogenes (represented here by *T. mapuche*) exhibit neobothriotaxic patellae (Maury, 1973a,b, 1982; Maury and San Martín, 1973; Vachon, 1974). The neobothriotaxic patellae of *Timogenes* and *Vachonia* are hypothesised to be synapomorphic. The scorpionid genera *Urodacus* and *Pandinus*, and some species of *Opisthophthalmus* (e.g., *O. holmi*), exhibit neobothriotaxic patellae (Vachon, 1965, 1974; Koch, 1977; Lamoral, 1979). *Hadogenes*, *Heteroscorpion*, and one species of *Liocheles* are also neobothriotaxic (Werner, 1934; Vachon, 1974; Lamoral, 1979; Newlands, 1980; Newlands and Cantrell, 1985; Lourenço, 1985, 1989, 1996a; Francke and Lourenço, 1991). Lourenço (1985, 1989) postulated that the neobothriotaxic patella was synapomorphic for *Heteroscorpion* and *Hadogenes*, but Stockwell (1989:101) rejected this hypothesis. In the present analysis, the neobothriotaxic patella is hypothesised to be synapomorphic for *Heteroscorpion* and *Urodacus*, but independently derived in *Hadogenes*. *Pandinus* (Kraepelin, 1894; Werner, 1934; Vachon, 1974) and *Vachonia* (Maury, 1973a) exhibit very high v trichobothrial counts, with the trichobothria arranged in two or more uneven rows, a condition that is hypothesised to be independently derived in these taxa.

44. Patella, position distal $v \tau$ ventral (0); external (1). Stockwell's character 53. The distal trichobothrium of the v series occurs on the external surface of the patella in the bothriurid genus *Lisposoma*, such that only two trichobothria are visible on the ventral surface (Vachon, 1974; Lamoral, 1979; Stockwell, 1989). Although this condition also occurs in certain chactoid taxa, e.g., Iuridae, Vaejovinae, Syntropinae, Superstitionidae, and *Troglotayosicus* (Stockwell, 1989), among the Scorpionoidea it is hypothesised to be autapomorphic for *Lisposoma*.

45. Patella, number $e \tau$ 7 (0); 13, rarely 12 (1); 14 or more (2) (additive). This character is a modified version of Stockwell's (1989) character 60. The orthobothriotaxic and neobothriotaxic conditions of type C trichobothriotaxy are treated as separate states. The basic number of e trichobothria in *Chaerilus* and the Buthidae is 7, whereas the orthobothriotaxic number for the remaining Recent scorpion genera is 13 (Vachon, 1974; Stockwell, 1989; Sissom, 1990). The occurrence of 13 e trichobothria on the patella (type C orthobothriotaxy) is considered plesiomorphic in the remaining genera (represented here by the scorpionoids), since it occurs

in some or all of the genera of the Bothriuridae, Diplocentridae, Ischnuridae, Iuridae, Scorpionidae, Syntropinae, Superstitionidae, and Vaejovinae (Vachon, 1974; Stockwell, 1989). In the Bothriuridae, *Brachistosternus* (*Ministernus*), *Vachonia*, and some species of *Timogenes* (represented here by *T. mapuche*) exhibit neobothriotaxitic patellae (Maury, 1973a,b, 1982; Maury and San Martín, 1973). The neobothriotaxitic condition of *Brachistosternus* (*Ministernus*), in which the number of *e* trichobothria is reduced to 12 (Maury, 1973b; Vachon, 1974), is considered autapomorphic and derived from the orthobothriotaxitic condition. Consequently, *Brachistosternus* (*Ministernus*) is scored for the orthobothriotaxitic condition. The neobothriotaxitic patellae of *Timogenes* and *Vachonia* are hypothesised to be synapomorphic. The scorpionid genera *Habibiella*, *Urodacus*, and *Opisthophthalmus* also exhibit neobothriotaxitic patellae, as do three of the five subgenera of *Pandinus*: *Pandinus* (*Pandinus*), *Pandinus* (*Pandinops*), and *Pandinus* (*Pandinopsis*). *Heteroscorpion*, the ischnurid genus *Hadogenes*, and two species of *Opisthacanthus* (*Opisthacanthus*) are also neobothriotaxitic (Vachon, 1965, 1974; Koch, 1977; Lamoral, 1979; Newlands, 1980; Newlands and Cantrell, 1985; Lourenço, 1979b, 1980, 1981b, 1983b, 1985, 1987, 1989, 1991, 1996a). The neobothriotaxitic patella of *Heteroscorpion* is hypothesised to be synapomorphic with that of *Urodacus*. The length of this character did not change in the analyses as a result of unordering.

46. Chela, number *i* τ : one (0); two (1); three or more (2) (additive). Includes Stockwell's (1989) character 69. Two *i* trichobothria are found in *Chaerilus* and all scorpionoid taxa except certain *Hadogeres*, e.g., *H. zuluanus* Lawrence 1937 (Newlands, 1980); and three of the five subgenera of *Pandinus* (Vachon, 1974), represented here by *P. cavimanus* and *P. imperator*, for which the occurrence of three or more *i* trichobothria is hypothesised to be synapomorphic: *Pandinus* (*Pandinus*), *Pandinus* (*Pandinoides*), and *Pandinus* (*Pandinops*). The disposition of this character is unknown in the fossil taxa, presenting difficulties for determining the polarity of its states. The presence of a single *i* trichobothrium in the Buthidae (Vachon, 1974; Stockwell, 1989) may be plesiomorphic and the presence of two or more *i* trichobothria synapomorphic for *Chaerilus* and the remaining Recent genera (represented here by the scorpionoids). Alternatively, the single *i* trichobothrium may be autapomorphic for the buthids, with two or more *i* trichobothria being plesiomorphic. Nevertheless, an ordered

transformation series can be postulated for the presence of more than two *i* trichobothria in *Pandinus*, which is hypothesised to be derived from the condition with two *i* trichobothria. The length of this character did not change in the analyses as a result of unordering.

47. Chela, position τ *it*: basal or midfinger (0); distal (1); inapplicable (-). Stockwell's (1989) character 70. The hypothesised plesiomorphic location for trichobothrium *it* is on the palm of the chela, near the base of the fixed finger, as in most scorpionoids and other non-buthid genera, except the Hemiscorpiinae, in which it is located near midfinger, together with trichobothrium *ib* (see below). However, in the diplocentrid genus *Nebo*, *it* is located distally on the fixed finger (Vachon, 1965, 1974; Francke, 1977a, 1980; Stockwell, 1989; Sissom, 1990), a condition that is hypothesised to be autapomorphic for this genus. This character is inapplicable to the Buthidae (represented by *Centruroides* in this analysis), which have only one *i* trichobothrium.

48. Chela, position τ *ib* and *it*: basal (0); midfinger (1); inapplicable (-). Stockwell's (1989) character 72. The hypothesised plesiomorphic location for the *i* trichobothria is on the palm of the chela, near the base of the fixed finger, as in most scorpionoids and other non-buthid genera, including *Chaerilus*. In *Nebo*, the *ib* trichobothrium is situated in this position, hence the plesiomorphic state is also assigned to this taxon. However, in the Hemiscorpiinae (*Habibiella* and *Hemiscorpius*), the *i* trichobothria are located near midfinger (Vachon, 1965, 1974; Stockwell, 1989), a condition that is hypothesised to be synapomorphic for these genera. This character is inapplicable to the Buthidae (represented by *Centruroides* in this analysis), which have only one *i* trichobothrium.

49. Chela, number *V* τ : 1 (0); 2 (1); 4 (2); 5 (3); 6 or more (4). This is a modified version of Stockwell's (1989) character 75, in which variation in the number of *V* trichobothria below 4 or above 5 was not considered. *Chaerilus* and the Buthidae have 1 and 2 *V* trichobothria, respectively, whereas all other Recent scorpion genera have at least 4 *V* trichobothria (Vachon, 1974; Stockwell, 1989; Sissom, 1990). Among these remaining genera, the presence of 4 *V* trichobothria on the chela (type C orthobothriotaxy) is hypothesised to be plesiomorphic, since it occurs in some or all of the genera

of the Bothriuridae, Chactinae, Diplocentridae, Euscorpidae, Ischnuridae, Iuridae, Scorpionidae, Scorpipiidae, Syntropinae, Superstitionidae, and Vaejovinae (Vachon, 1974; Stockwell, 1989; Sissom, 1990). Among the Bothriuridae, the plesiomorphic number occurs only in *Lisposoma* and *Thestylus*, whereas 5 *V* trichobothria occur in *Bothriurus*, *Centromachetes*, *Cercophonius*, *Orobthriurus*, *Phoniocercus*, *Tehuanka*, *Urophonius*, *Brachistosternus* (*Brachistosternus*), and *Brachistosternus* (*Leptosternus*) (Maury, 1973a,b; Koch, 1977; Stockwell, 1989; Acosta, 1990; Sissom, 1990). *Brachistosternus* (*Ministernus*), *Timogenes*, and *Vachonia* exhibit 11, 6 to 10, and more than 25 *V* trichobothria, respectively (Maury, 1973a,b, 1982; Maury and San Martín, 1973; Vachon, 1974; Stockwell, 1989; Sissom, 1990). The occurrence of 5 or more *V* trichobothria is hypothesised to be synapomorphic for the bothriurid genera except *Lisposoma* and *Thestylus*, whereas the occurrence of 6 or more is hypothesised to be synapomorphic for *Timogenes* and *Vachonia* and independently derived in *Brachistosternus* (*Ministernus*). Among the remaining Scorpionoidea, more than 6 *V* trichobothria occur in *Hadogenes*, *Heteroscorpion*, *Urodacus*, some species of *Opisththalmus* (represented here by *O. holmi*), and all species of *Pandinus* except *P. (Pandinopsis) dictator* (Vachon, 1965, 1967, 1974; Koch, 1977; Lamoral, 1979; Newlands, 1980; Newlands and Cantrell, 1985; Lourenço, 1985, 1989, 1996a; Lourenço and Cloudsley-Thompson, 1996). Lourenço (1985, 1989) postulated that the neobothriotaxic pattern on the pedipalp chela was synapomorphic for *Heteroscorpion* and *Hadogenes*, but Stockwell (1989:107) rejected this hypothesis. In the present analysis, the neobothriotaxic chela of *Heteroscorpion* is hypothesised to be synapomorphic with *Urodacus*, but independently derived in *Hadogenes*. The neobothriotaxic chela is also hypothesised to be synapomorphic for the species of *Pandinus*, except *P. dictator*, but independently derived within *Opisththalmus*.

50. Chela, distance between τV_2 and V_3 : normal (0); widely separated (1); inapplicable (-). Stockwell's (1989) character 79. In the bothriurid genera *Lisposoma* and *Thestylus*; the scorpionid genera *Heterometrus*, *Opisththalmus*, *Pandinus*, and *Scorpio*; and all diplocentrids trichobothrium V_3 is located nearly equidistant between V_2 and V_4 . This condition is found in most other non-buthid genera and is hypothesised to be plesiomorphic. The Hemiscorpiinae and Ischnuridae share a derived state of this character, in which V_3

is very much closer to V_4 than to V_2 , resulting in the segregation of V_1 and V_2 distally from V_3 and V_4 basally (Stockwell, 1989). Due to the presence of many accessory *V* trichobothria, this character cannot be evaluated in the taxa with neobothriotaxic chelae, such as *Hadogenes*, *Heteroscorpion*, and *Urodacus*; the bothriurid genera except *Lisposoma* and *Thestylus*; most species of *Pandinus*; and some species of *Opisththalmus* (e.g., *O. holmi*), in which it is therefore inapplicable.

51. Chela, position τDb : external surface (0); dorsal surface (1); inapplicable (-). In most Recent scorpion genera, including most Scorpionoidea, trichobothrium *Db* is located on the external surface of the pedipalp chela. However, in the Hemiscorpiinae and Scorpioninae, *Db* occurs on the dorsal surface of the chela (Vachon, 1965, 1974), which is hypothesised to be independently derived in these taxa. This character is inapplicable to *Chaerilus* and the Buthidae (represented here by *Centruroides*), in which the *Db* trichobothrium is absent.

52. Chela, position τDt : manus, at proximal end (0); manus, mid-length or slightly less than mid-length (1); manus, distal half, near base of fixed finger (2); proximal end of fixed finger (3); inapplicable (-) (additive). This character is an amalgamation of Stockwell's (1989) characters 84 and 85, with the addition of an extra apomorphic state to distinguish between distal positions of trichobothrium *Dt* on the manus and fixed finger. In most Recent scorpion genera, trichobothrium *Dt* is located proximally on the manus of the pedipalp chela, a condition that is hypothesised to be plesiomorphic (Stockwell, 1989). Among the Scorpionoidea, the plesiomorphic condition occurs in the Bothriuridae, *Heteroscorpion*, *Urodacus*, and *Opisthacanthus* (*Opisthacanthus*), represented here by *O. elatus*. However, the proximal location of *Dt* in *Opisthacanthus* (*Opisthacanthus*) is hypothesised to be a reversal. Trichobothrium *Dt* is located relatively distally among the remaining scorpionoids, allowing the inference of an ordered transformation series from the proximal end of the manus to the fixed finger: *Dt* is located medially on the manus in the Ischnuridae, except *Opisthacanthus* (*Opisthacanthus*); in the distal half of the manus, near the base of the fixed finger, in the Scorpioninae; and at the proximal end of the fixed finger in the Hemiscorpiinae and Diplocentridae. The latter two states were

not distinguished by Stockwell (1989:111). This character is inapplicable to *Chaerilus* and the Buthidae (represented here by *Centruroides*), in which the *Dt* trichobothrium is absent. The length of this character decreased in all analyses as a result of unordering.

53. Chela, external surface with accessory τ : absent (0); 10–15 (1); more than 20 (2). The presence of accessory trichobothria on the external surface of the pedipalp chela has been reported in only two genera of Recent scorpions, both of which occur within the Scorpionoidea: the ischnurid genus *Hadogenes* and the scorpionid genus *Urodacus* (Vachon, 1974; Koch, 1977; Lammoral, 1979; Newlands, 1980; Newlands and Cantrell, 1985; Lourenço, 1985, 1989). A marked difference in the number of accessory trichobothria in these two genera (species of *Hadogenes* commonly have more than 30, in comparison with species of *Urodacus*, which seldom have more than 10) suggests that these accessory trichobothria evolved independently in the two genera. Accordingly, two apomorphic states have been provided for this character, which are hypothesised to be autapomorphic in each case.

54. Chela, position τ *Eb*₃: in line with *Eb*₁–*Eb*₂ axis (0); distal to *Eb*₁–*Eb*₂ axis (1). In most Recent scorpion genera, including most Scorpionoidea, trichobothrium *Eb*₃ is located proximal to the *Eb*₁–*Eb*₂ axis. However, in the ischnurid genus *Liocheles*, *Eb*₃ is distinctly distal to the *Eb*₁–*Eb*₂ axis, and may be located almost halfway between *Eb*₁–*Eb*₂ and the *Et* series in some species (e.g., *L. karschii* and *L. waigiensis*). Within the Scorpionoidea, the distal position of trichobothrium *Eb*₃ is hypothesised to be autapomorphic for *Liocheles*, but has evolved independently in the chactoid family Scorpipidae (Vachon, 1980b; Stockwell, 1989:111, character 88; Lourenço, 1998a).

55. Chela, position τ *Est*: distal (0); midpalm (1); inapplicable (–). Stockwell's (1989) character 86, with the entries for *Urodacus* corrected. Among most Recent scorpion genera, including most Scorpionoidea, trichobothrium *Est* is located relatively distally, very near the *Et* series, a condition that is hypothesised to be plesiomorphic. However, in the Ischnuridae, *Est* is located medially, about halfway between the *Eb* and the *Et* series, a condition that is hypothesised to be synapomorphic for the genera of Ischnuridae (Stockwell, 1989). The position of *Est* cannot be ascertained in *Hadogenes* and *Urodacus*, due to the presence of numerous accessory trichobothria on the external surface of the

chela, and is therefore inapplicable to these taxa. Stockwell (1989:274) scored *Urodacus* for the plesiomorphic condition.

56. Chela, position τ *Et*₂: external surface (0); ventral surface (1). Stockwell's (1989) character 87. In most Recent scorpion genera, including most Scorpionoidea, trichobothrium *Et*₂ is located externally near the movable finger condyle, a condition that is hypothesised to be plesiomorphic. However, in all bothriurid genera, *Et*₂ is located ventrally (Vachon, 1974; Stockwell, 1989; Sissom, 1990). The occurrence of the apomorphic state of this character in *Lisposoma* was first recognised by Vachon (1974). It was subsequently used by Francke (1982a), in combination with several other characters, as justification for the transfer of this genus from the Scorpionidae to the Bothriuridae. This condition is hypothesised to be synapomorphic for the genera of Bothriuridae.

57. Chela, number *d* τ : two (0); four (1). As indicated by Vachon (1974), only two *d* trichobothria occur on the fixed finger of *Chaerilus* and the Buthidae (represented here by *Centruroides*), whereas four *d* trichobothria occur on the fixed finger of all other Recent scorpion genera (represented here by the Scorpionoidea). The disposition of this character is unknown in the fossil orthosterns, hence the polarity of its states cannot be established.

58. Chela, position τ *db*: fixed finger (0); manus (1). In most Recent scorpion genera, including most Scorpionoidea, trichobothrium *db* is located on the fixed finger of the pedipalp chela. However, in the Bothriuridae, including *Lisposoma*, *db* is located on the manus (Vachon, 1974), a condition that is hypothesised to be synapomorphic for the genera of Bothriuridae.

59. Chela, position τ *db*: dorsal (0); internal (1). The dorsal location of trichobothrium *db* is hypothesised to be plesiomorphic in the Bothriuridae, *Heteroscorpion*, and *Urodacus*, on the basis of its occurrence in *Chaerilus* and the Buthidae (represented here by *Centruroides*). The internal location of trichobothrium *db* is hypothesised to be synapomorphic for the remaining scorpionoid taxa, except the ischnurids *Hadogenes* and *Liocheles* and the African species of *Iomachus* (represented here by *I. politus*), in which *db* is also located dorsally. The dorsal location of trichobothrium *db* is hypothesised to be a reversal in these taxa and may have evolved independently in *Hadogenes*.

60. Chela, position τ *dsb*: below *db*–*dst* axis (0); in

line with *db-dst* axis (1); inapplicable (-). The location of trichobothrium *dsb* below the *db-dst* axis is hypothesised to be plesiomorphic in the Bothriuridae, on the basis of its occurrence in many chactoid taxa (Vachon, 1974). Accordingly, the location of *dsb* approximately in line with the *db-dst* axis is hypothesised to be synapomorphic for the remaining genera of Scorpionoidea. This character is inapplicable to *Chaerilus* and the Buthidae (represented here by *Centruroides*), in which only two trichobothria are present in the *d* series.

61. Chela, position of τ *eb*: proximal region of fixed finger (0); manus, behind point of articulation between fixed and movable fingers (1); inapplicable (-). Trichobothrium *eb* is located in the proximal region of the pedipalpal fixed finger in all scorpionoid genera except the Ischnuridae, in which it is located on the manus, behind the point of articulation between the fixed and the movable fingers (Vachon, 1974), a condition that is hypothesised to be synapomorphic for the genera of Ischnuridae. The disposition of this character cannot be evaluated for the Buthidae (represented here by *Centruroides*) and *Chaerilus*, which have type A and type B trichobothrial patterns, respectively, and is therefore inapplicable to these taxa.

62. Chela, position of τ *esb*: manus, behind point of articulation between fixed and movable fingers and below *eb-est-et* axis (0); midway along fixed finger, in line with *eb-est-et* axis (1); inapplicable (-). The location of trichobothrium *esb* on the manus, behind the point of articulation between the fixed and the movable fingers and below the *eb-est-et* axis, is hypothesised to be plesiomorphic in the Bothriuridae, on the basis of its occurrence in many chactoid taxa (Vachon, 1974). Accordingly, the location of *esb* midway along the fixed finger, in line with the *eb-est-et* axis, is hypothesised to be synapomorphic for the remaining scorpionoid genera, except the Ischnuridae, in which a reversal to the plesiomorphic condition is hypothesised. The disposition of this character cannot be evaluated for the Buthidae (represented here by *Centruroides*) and *Chaerilus*, which have type A and type B trichobothrial patterns, respectively, and is therefore inapplicable to these taxa.

Legs

63. Retrolateral pedal spurs: present (0); absent (1). Stockwell's (1989) character 90. Lamoral (1980) considered the presence of retrolateral pedal spurs to be

plesiomorphic in Recent scorpions, on the basis of its occurrence in *Chaerilus*, Buthidae, Chactidae, Iuridae, and Vaejovidae, whereas the absence of retrolateral pedal spurs was hypothesised to be synapomorphic for the genera of Scorpionoidea. However, Stockwell (1989) noted that retrolateral pedal spurs are absent in the three most basal bothriurid genera, *Lisposoma*, *Thestylus*, and *Phoniocercus*, whereas they are present in eight of the nine remaining bothriurid genera. This suggests that the absence of retrolateral pedal spurs is ancestral in the Bothriuridae, with these remaining genera sharing a reversal to the plesiomorphic condition. *Vachonia* also displays the absence of pedal spurs, but this is presumably independently evolved, given the relatively derived position of this genus within the Bothriuridae.

64. Prolateral pedal spurs: present (0); absent (1). The absence of prolateral pedal spurs is autapomorphic for the monotypic diplocentrid genus *Oiclus* (Francke, 1978; Sissom, 1990) and uninformative in this analysis.*

65. Telotarsi, laterodistal lobes: truncated, base of median dorsal lobe flush (0); rounded, notches at base of median dorsal lobe (1); secondarily truncated, notches at base of median dorsal lobe (2) (additive). This is a modified version of Stockwell's character 92. Truncated laterodistal lobes occur in most Recent scorpions, including the scorpionoid taxa *Heteroscorpion*, the Hemiscorpiinae, and the Ischnuridae, whereas rounded laterodistal lobes occur in the scorpionoid taxa *Urodacus*, the Scorpioninae, and *Nebo* (Kraepelin, 1894; Werner, 1934; Lawrence, 1955; Lamoral, 1980; Lourenço, 1985, 1989; Stockwell, 1989; Sissom, 1990) for which they are potentially synapomorphic. Stockwell (1989:117; see also Stockwell, 1988; Sissom and Walker, 1992) noted that the laterodistal lobes are also truncated in the Diplocentrinae and scored them for the plesiomorphic state. However, the presence of distinct notches at the base of the median dorsal lobe in the Diplocentrinae suggests that they are homologous with rounded laterodistal lobes, from which they are hypothesised to be derived in the present analysis. A third state, termed "secondarily truncated," is thus provided for this condition. The length of this character did not change in the analyses as a result of unordering.

66. Telotarsi, laterally flattened: absent (0); present (1). The presence of laterally flattened telotarsi is hypothesised to be autapomorphic for the bothriurid genus *Brachistosternus* (Maury, 1973a).

67. Telotarsi I, numerous pores ventrally and prolaterally: absent (0); present (1). The presence of conspicuous pores on the ventral and prolateral surfaces of telotarsi I is hypothesised to be autapomorphic for the diplocentrid genus *Tarsoporosus* (Francke, 1978; Sissom, 1990).

68. Telotarsi, well-developed ventromedian row of setae: spiniform (0); setiform (1); absent (2). Lamoral (1980) erroneously hypothesised that the presence of a ventromedian row of spiniform setae on the telotarsi was apomorphic for the Chactoidea, but absent in the Scorpionoidea. Stockwell (1989) rejected this character, noting that ventromedian setae were absent in chactoid taxa such as the Typlochactinae (Francke, 1982b) and some Chactinae (González-Sponga, 1977), yet present in scorpionoid genera such as *Habibiella*, *Hemiscorpius*, *Cheloctonus*, *Hadogenes*, *Iomachus*, *Opisthacanthus* (Lourenço, 1985, 1989), and *Diplocentrus*. In the present analysis, the presence of a complete or partial ventromedian row of spiniform setae on the telotarsi is hypothesised to be plesiomorphic in Recent scorpions, based on its occurrence in *Chaerilus* and the buthids (represented here by *Centruroides*) and occurs among the scorpionoid taxa Diplocentridae, Heteroscorpionidae, Hemiscorpiinae, and the ischnurid genera *Cheloctonus*, *Hadogenes*, *Iomachus*, *Opisthacanthus*, and *Palaeocheloctonus* (Sreenivasa-Reddy, 1968a,b,c,d; Lourenço, 1985, 1989, 1996a; Sissom, 1990). The occurrence of a setiform ventromedian row, which is presumably derived from the spiniform condition, is considered synapomorphic for the genera of Bothriuridae (Kraepelin, 1894; Werner, 1934), including *Lisposoma*. The absence of a ventromedian row of setae is hypothesised to be synapomorphic for the ischnurid genera *Chiromachetes*, *Chiromachus*, and *Liocheles* (Lourenço, 1985, 1989). The absence of a ventromedian row in *Urodacus* and the Scorpioninae (Koch, 1977; Lourenço, 1985, 1989) is also potentially independently derived from the condition in the ischnurid genera. The occurrence of the plesiomorphic condition in the Diplocentridae is hypothesised to be a reversal.

69. Telotarsi I–IV, ventrosubmedian setae distribution: setiform on I–IV (0); setiform on I or I–II, spiniform on III–IV (1); spiniform (or secondarily setiform) on I–IV (2) (additive). This is a modified version of Stockwell's (1989) character 93. An extra state has been added to distinguish bothriurids in which spiniform

setae occur on all telotarsi from those in which spiniform setae are present only on telotarsi III–IV. Two ventrosubmedian rows of setae occur on the telotarsi of most Recent scorpions. In *Chaerilus*, the Buthidae (represented here by *Centruroides*), and most chactoid genera, these ventrosubmedian rows are setiform (hair-like), a condition which is therefore hypothesised to be plesiomorphic (Stockwell, 1989). However, in most genera of the scorpionoid families Bothriuridae, Diplocentridae, Ischnuridae, and Scorpionidae, the ventrosubmedian setae are spiniform, with large limbed sockets, a condition that is hypothesised to be synapomorphic for the genera of Scorpionoidea. In one bothriurid genus, *Brachistosternus*, the ventrosubmedian rows are entirely setiform, a condition that Francke (1982a) considered plesiomorphic among bothriurids. However, the occurrence of spiniform setae in the bothriurid genera *Lisposoma* and *Thestylus*, which are relatively basal to *Brachistosternus* on the grounds of other characters, suggests that the presence of setiform setae in *Brachistosternus* is autapomorphic and derived from the spiniform condition (Stockwell, 1989). This hypothesis is supported by the occurrence of several bothriurid genera in which the ventrosubmedian setae are spiniform on telotarsi III–IV, but setiform on telotarsi I or I–II: *Bothriurus*, *Cercophonius*, *Tehuanka*, *Timogenes*, *Urophonius*, and *Vachonia* (Werner, 1934; Cekalovic, 1973a; Koch, 1977; Maury, 1973a, 1982; Acosta, 1990). Accordingly, an ordered transformation series is postulated for this character, in which the condition with both setiform and spiniform setae is intermediate between the entirely setiform and the entirely spiniform conditions. The length of this character decreased in all analyses as a result of unordering.

70. Telotarsi, ventrosubmedian setae type: stout spiniform (0); slender spiniform (1); few secondarily setiform (2); numerous secondarily setiform (3); inapplicable (–). This is a modification of Stockwell's (1989) character 94. Several additional states are recognised here, including an autapomorphic state for the ischnurid genus *Chiromachus*. Among the scorpionoid genera, only the bothriurid genus *Brachistosternus* possesses truly setiform (hair-like) setae in the ventrosubmedian rows of the telotarsi. However, several other scorpionoid genera display setae that may be described as secondarily setiform (Stockwell, 1989), since they are longer and more slender than typical

spiniform setae, but nevertheless have limbed sockets. Secondarily setiform setae appear to have evolved on several occasions in the Scorpionoidea: in the bothriurid genus *Phoniocercus* (Kraepelin, 1894; Werner, 1934; Acosta, 1990) and the ischnurid genera *Chiromachus*, *Iomachus*, and *Liocheles* (Kraepelin, 1894; Werner, 1934; Sreenivasa-Reddy, 1968a,b,c,d; Lourenço, 1985, 1989; Stockwell, 1989; Sissom, 1990). The secondarily setiform setae of *Phoniocercus*, *Iomachus*, and *Liocheles* are similar in structure and number, hence they are scored for the same state. The occurrence of such setae is hypothesised to be synapomorphic for *Iomachus* and *Liocheles*, but independently derived in *Phoniocercus*. Lourenço (1985, 1989) and Stockwell (1989) considered the secondarily setiform setae of *Chiromachus* to be synapomorphic with those in *Iomachus* and *Liocheles*. However, the setae of *Chiromachus* are structurally different and considerably more numerous than those in the latter genera and it is questionable whether they are homologous. Accordingly, an autapomorphic state is provided for the secondarily setiform setae of *Chiromachus* in the present analysis. In addition to these secondarily setiform setae, a condition almost intermediate between the latter and the truly spiniform setae, referred to here as “slender spiniform setae,” occurs uniquely in the Hemiscorpiinae (Sissom, 1990), for which it is hypothesised to be autapomorphic. This character is inapplicable to *Chaerilus*, the Buthidae (represented here by *Centruroides*), and *Brachistosternus*, in which truly setiform setae occur on all telotarsi.

71. Telotarsi IV, prolateral row of ventrosubmedian spiniform setae: present (0); absent (1); inapplicable (-). Absence of the prolateral row of ventrosubmedian spiniform setae on telotarsi IV occurs in many species of *Opisththalmus* (Purcell, 1899; Kraepelin, 1894, 1896; Lawrence, 1955; Lamoral, 1979) and is considered apomorphic. This character is inapplicable to the outgroups and the bothriurid genus *Brachistosternus*, in which ventrosubmedian spiniform setae are absent altogether from the telotarsi.

72. Basitarsi I–II, retrolateral row of macrochaete setae: absent (0); spiniform (1); setiform, sand comb (2); unknown (?) (additive). The absence of a retrolateral row of macrochaete setae on basitarsi I–II is hypothesised to be plesiomorphic in Recent scorpions, based

on its occurrence in *Chaerilus*, most buthids (e.g., *Centruroides*), and most chactoids. Among the Scorpionoidea, a distinct retrolateral row of macrochaete setae occurs in the bothriurid genera *Bothriurus*, *Brachistosternus*, *Centromachetes*, *Orobothriurus*, *Timogenes*, and *Vachonia* (the disposition of this character is unknown in *Tehuanka*) and in the scorpionid genera *Heterometrus*, *Opisththalmus*, *Pandinus*, *Scorpio*, and *Urodacus*. The presence of a retrolateral row is hypothesised to be independently derived within the Bothriuridae, the Scorpioninae, and the Urodacinae. The occurrence of spiniform macrochaete setae in the retrolateral row is hypothesised to be plesiomorphic within the bothriurids, based on its occurrence in *Bothriurus*, *Centromachetes*, and *Orobothriurus*, and the setiform (“sand comb”) condition of the psammophilous genera *Brachistosternus*, *Timogenes*, and *Vachonia* to be derived from it. Among the scorpionids, the apomorphic setiform condition is hypothesised to be independently derived from the spiniform condition in the psammophilous species of *Opisththalmus* (represented here by *O. capensis* and *O. holmi*) and *Urodacus* (*U. yaschenko*). The length of this character did not change in the analyses as a result of unordering.

73. Basitarsi I–II, reduction in the number of macrochaete setae in the retrolateral row from three or more to two: absent (0); present (1); inapplicable (-); unknown (?). The number of macrochaete setae in the retrolateral row of basitarsi I–II is reduced from three or more to two in the scorpionid genera *Heterometrus* and *Pandinus*, for which this condition is hypothesised to be synapomorphic. This character is inapplicable for the taxa in which a retrolateral row of macrochaete setae is absent from basitarsi I–II. The disposition of this character is unknown in the bothriurid genus *Tehuanka*.

74. Stridulatory surface on opposing surfaces of coxae of pedipalps and first walking legs: absent (0); partially developed (1); fully developed (2). This is a modified version of Stockwell’s character 95. The presence of an area of stridulatory setae on the opposing surfaces of the coxae of the pedipalps and first pair of walking legs has generally been regarded as synapomorphic for the scorpionid genera *Heterometrus* and *Pandinus* (Pocock, 1896a,b; Werner, 1934; Dumortier, 1964; Couzijn, 1981; Stockwell, 1989; Acosta and

Maury, 1990). Constantinou and Cloudsley-Thompson's (1984) SEM study revealed the presence of a partially developed stridulatory surface in the scorpionid genus *Scorpio*, which is probably homologous given its occurrence on opposing surfaces of the coxae of the pedipalps and first pair of walking legs.

75. Stridulatory surface on opposing surfaces of coxae of pedipalps and first walking legs: rasp on pedipalpal coxa, scraper on coxa of first walking leg (0); scraper on pedipalpal coxa, rasp on coxa of first walking leg (1); inapplicable (-). The "rasp" and "scraper" components of the stridulatory surface are situated on the coxae of the pedipalps and first pair of walking legs, respectively, in *Pandinus* and *Scorpio*, whereas in *Heterometrus*, their positions are reversed (Pocock, 1896a,b; Werner, 1934; Constantinou and Cloudsley-Thompson, 1984; Acosta and Maury, 1990). This character is inapplicable to all genera except *Heterometrus*, *Pandinus*, and *Scorpio*, in which the stridulatory surface is present.

76. Maxillary lobes, shape of first pair: rounded-truncate anteriorly (0); tapering anteriorly (1). This character is a re-interpretation of Stockwell's (1989) character 96. According to Stockwell (1989:119) the first and second pairs of maxillary lobes of most Recent scorpion genera are roughly equal in length and free at the tips, whereas those of the Ischnuridae and Scorpioninae are apomorphic in that the first pair is longer and encircles the second pair. In the present investigation, the first pair of maxillary lobes was found to be distinctly elongated and anteriorly tapered in the Ischnuridae. However, in the Scorpioninae, the maxillary lobes were found to be no different from those of the other scorpionoids, roughly equal to the second pair in length, and rounded-truncate anteriorly. Hence, this character has been redefined and the anteriorly tapering maxillary lobes are hypothesised to be synapomorphic only for the genera of Ischnuridae.

Reproductive Anatomy

77. Embryonic development: apoikogenic (0); katoikogenic (1). Stockwell's (1989) character 101. Laurie (1896a,b) classified the type of ovariuterine development in scorpion embryos into two groups. In scorpions with apoikogenic development, embryos develop within the lumen of the ovariuterus, whereas in scorpions with katoikogenic development, embryos develop

in diverticula of the ovariuterus and obtain nutrition through specialised connections with digestive caeca. Although there are other differences that heighten the distinction between the two types (Pavlovsky, 1924b, 1925; Werner, 1934; Francke, 1982c; Warburg and Rosenberg, 1990) and could be used as additional characters, only a single character is employed here, in accordance with Stockwell (1989). Katoikogenic development occurs only in the families Diplocentridae, Heteroscorpionidae, Ischnuridae, and Scorpionidae (Pflugfelder, 1930; Vachon, 1953; Rosin and Shulov, 1963; Subburam and Reddy, 1981; Francke, 1982c; Warburg and Rosenberg, 1990) for which it is hypothesised to be synapomorphic. Apoikogenic development occurs in all other Recent families (Laurie, 1890; Matthiessen, 1970; Francke, 1982c; Warburg and Rosenberg, 1990) and is hypothesised to be symplesiomorphic.

78. Ovariuterine follicles: sessile (0); stalked (1). Stockwell's (1989) character 103. The oocytes resting along the ovariuterus may be described as sessile (resting directly on the external surface of the ovariuterus) or stalked (attached to the ovariuterus by a narrow stalk of tissue). The sessile condition is hypothesised to be plesiomorphic, based on its occurrence in *Chaerilus* and the Buthids (represented here by *Centruroides*). Within the scorpionoids, the sessile condition occurs in the bothriurids (including *Lisposoma*), whereas the stalked condition occurs in the remaining taxa (Laurie, 1896a,b; Francke, 1982c; Stockwell, 1989), for which it is hypothesised to be synapomorphic.

79. Testis: straight (0); coiled (1); unknown (?). Stockwell's (1989) character 104. In most Recent scorpions, the male testis is a simple, uncoiled net of tubules that fits comfortably within the mesosomal lumen, where it is obscured by the more conspicuous digestive glands. This condition is hypothesised to be plesiomorphic, based on outgroup comparison with *Chaerilus* and the Buthids (represented here by *Centruroides*). Among the scorpionoids, the net-like testis of the bothriurid genera *Bothriurus*, *Brachistosternus*, *Centromachetes*, *Cercophonius*, *Orobothriurus*, *Phoniocercus*, *Timogenes*, and *Urophonius* is highly coiled and approximately equal in volume to the digestive gland tissue in the mesosoma, a condition that is hypothesised to be synapomorphic for these genera. The bothriurid genera *Lisposoma* and *Thestylus* exhibit the plesiomorphic condition, whereas the disposition of the testis is unknown in the bothriurid genera *Tehuánkea* and *Vachonia*. This character is

also unknown in the ischnurid genus *Chiromachetes*, in which adult males are unknown.

80. Genital opercula (female): separated (0); loosely joined (1); fused (2). This character is an amalgamation of Stockwell's (1989) characters 105 and 107, in which the apomorphic states were treated as separate characters. The genital opercula of female Buthidae (represented here by *Centruroides*) and *Chaerilus* are completely separated, a condition which is hypothesised to be plesiomorphic. The genital opercula of female Scorpionioidea, excluding most genera of Bothriuridae, are fused together along the midline (Lamoral, 1980; Stockwell, 1989). In some cases, the fusion is complete but in most, at least a faint suture indicates the separation of the two plates. This condition is hypothesised to be synapomorphic for the Scorpionioidea. Among the Bothriuridae, all genera except for *Lisposoma* exhibit loosely joined genital opercula, which are hypothesised to be synapomorphic and derived from the condition of fused genital opercula. The ischnurid genus *Hadogenes* also exhibits loosely joined genital opercula similar to those of the bothriurids (Stockwell, 1989), but this is hypothesised to be independently derived from the fused condition.

81. Genital opercula (male): separated (0); loosely joined (1); unknown (?). Stockwell's (1989) character 109. In most Recent scorpions, the genital opercula of males are completely separated. However, in all bothriurid genera, except *Lisposoma*, the genital opercula are loosely joined together along the anterior one-fifth to one-fourth of their length, a condition which is hypothesised to be synapomorphic within the bothriurids (Stockwell, 1989). The state of this character is unknown in the ischnurid genus *Chiromachetes*, in which adult males are unknown (Pocock, 1899; Lourenço, 1997).

Hemispermatochore and Paraxial Organ

The following characters are scored unknown (?) for the ischnurid genus *Chiromachetes*, in which adult males are unknown (Pocock, 1899; Lourenço, 1997).

82. Hemispermatochore: flagelliform (0); fusiform (1); lamelliform (2); unknown (?) (additive). This is an amalgamation of Stockwell's (1989) characters 110 and 111. The three kinds of hemispermatochore are treated

as separate states of a single character. Scorpion hemispermatochore have been classified as either "flagelliform" or "lamelliform" (Francke, 1979), although Lamoral (1979, 1980) employed the terms "rod-like" and "fusiform." Francke's terminology, adopted by Stockwell (1989), is employed here. The flagelliform type is characterised by a long, slender trunk, a simple sperm duct and a long, filamentous projection at the distal end, called the flagellum. Lamelliform hemispermatochore are variable with respect to the shape of the trunk, but are generally shorter and broader. The sperm duct may be simple or highly elaborate, with sclerotised projections and detachable mating plugs. The characteristic feature of the lamelliform hemispermatochore is the long, lamellate structure, projecting from the distal end and referred to as the distal lamina (Lamoral, 1979). Flagelliform hemispermatochore occur only in the Buthidae, whereas lamelliform hemispermatochore occur in the non-buthids, except *Chaerilus* (Francke, 1979; Lamoral, 1979; Stockwell, 1989; Sissom, 1990). A third kind of hemispermatochore, combining features of both the lamelliform and the flagelliform hemispermatochore, was recognised in *Chaerilus* by Stockwell (1989) and referred to as "fusiform." The distal lamina of the fusiform hemispermatochore is poorly developed and scarcely one-fourth the length of the overall structure. There is no network of external carinae and no truncal flexure like those of most lamelliform hemispermatochore, which are triggered by the flexing of the distal lamina against the trunk (Alexander, 1957). According to Stockwell (1989), the most characteristic features of the chaerilid hemispermatochore are the long, narrow trunk, keel-like median lobe, and simple sperm duct, all of which closely resemble the elongated trunk, median lobe, and simple sperm duct of buthid hemispermatochore, triggered by the flexing and compressing of the entire trunk against the foot and substrate (Alexander, 1957). Although Lamoral (1979) considered flagelliform and lamelliform hemispermatochore to be equally derived, Lamoral (1980) subsequently considered the lamelliform hemispermatochore to be synapomorphic for *Chaerilus* and the remaining non-buthid genera, implying that the flagelliform hemispermatochore was plesiomorphic. Contrary to the homologies postulated by Lamoral (1979), Stockwell (1989:128) proposed that

the flagellum of buthid hemispermatophores was homologous with the distal lamina of non-buthid hemispermatophores and postulated a transformation series by means of which both the flagelliform and the lamelliform hemispermatophores could be derived from the fusiform hemispermatophore of *Chaerilus*. In other words, Stockwell proposed that the flagelliform and lamelliform hemispermatophores are mutually apomorphic, relative to the fusiform hemispermatophore. Irrespective of which hypothesis is adopted, the lamelliform hemispermatophore is considered to be derived from the fusiform hemispermatophore and synapomorphic for all Recent scorpions except the buthids and chaerilids. This character is rendered uninformative when treated nonadditively.

83. Hemispermatophore, truncal flexure: absent (0); present (1); unknown (?). Stockwell's (1989) character 114. Stockwell considered the presence of a truncal flexure at the posterior base of the distal lamina to be apomorphic in Recent scorpions (represented here by the Scorpionoidea), based on its absence in *Chaerilus* and the Buthids (represented here by *Centruroides*). However, since the disposition of this character is unknown in the fossil taxa, the polarity of its states cannot be determined.

84. Paraxial organ, internobasal reflection of sperm duct: absent (0); present (1); unknown (?). Stockwell's (1989) character 120. The sperm ducts of the Bothriuridae, Diplocentridae, Ischnuridae, and Scorpionidae are complex, relative to those of other Recent scorpions (Stockwell, 1989). In addition to a distinct "trough," these sperm ducts display an internobasal reflection projecting from the back into the trough that, when everted, forms a pair of guide valves for the delivery of sperm to the female (Alexander, 1957). The presence of an internobasal reflection is hypothesised to be synapomorphic for the Scorpionoidea, based on outgroup comparison with other Recent scorpions.

85. Paraxial organ, internal wall of sperm duct: simple (0); with semilunar shelf (1); unknown (?). Stockwell's (1989) character 121. All bothriurid genera, including *Lisposoma*, display a narrow, crescentic shelf extending along the outside of the internal wall of the sperm duct, a character not found in other Recent scorpion genera and hypothesised to be synapomorphic for the Bothriuridae (Stockwell, 1989).

86. Hemispermatophore, distal lamina: smooth (0); with prominent crest (1); unknown (?). Stockwell's

(1989) character 122. All bothriurid genera, except *Lisposoma*, exhibit a distinct, sclerotised distal crest on the distal lamina (Maury, 1980), which was first hypothesised by Francke (1982a) to be synapomorphic for these genera. The absence of this crest is hypothesised to be plesiomorphic in *Lisposoma* (Lamoral, 1979; Stockwell, 1989), based on outgroup comparison with other Recent scorpions.

87. Hemispermatophore, distal lamina: simple (0); with complex differentiation (1); unknown (?); inapplicable (-). The distal lamina of the hemispermatophore is simple in most scorpionoids, but complexly differentiated in *Palaeocheiloctonus* and the Malagasy species of *Opisthacanthus* (*Nepabellus*) (Lourenço, 1985, 1987, 1996a), represented here by *O. madagascariensis*, a condition that is potentially synapomorphic for these taxa, based on outgroup comparison with the remaining scorpionoids. This character is scored as inapplicable in the outgroups, which do not have a lamelliform hemispermatophore.

88. Hemispermatophore, lamellar hook and median lobe: separate (0); fused (1); unknown (?). Stockwell's (1989) character 123. The lamellar hook, characteristic of the hemispermatophores of most Recent scorpions, is absent from the hemispermatophore of diplocentrids, and there is a lobe between the base of the lamella and sperm duct opening that Stockwell (1989:134) suggested could be the fused homologues of the lamellar hook and median lobe. This condition is considered synapomorphic for the Diplocentridae.

89. Hemispermatophore, position of lamellar hook: basal (0); distal (1); unknown (?); inapplicable (-). The lamellar hook is located basally on the distal lamina of the hemispermatophore of most scorpionoids, except for the bothriurid genus *Lisposoma* (Lamoral, 1979) and the ischnurid taxa *Iomachus*, *Liocheles*, and *Opisthacanthus* (*Opisthacanthus*) (Lourenço, 1983b, 1985, 1987, 1989), in which it is located distally. The distal location is hypothesised to be autapomorphic for *Lisposoma* and independently derived in the ischnurid taxa, for which it is potentially synapomorphic. This character is inapplicable to the Diplocentridae, which do not have a lamellar hook.

90. Hemispermatophore, lamellar hook: single (0); double (1); unknown (?); inapplicable (-). A single lamellar hook occurs in the hemispermatophore of most scorpionoids and is hypothesised to be plesiomorphic, based on outgroup comparison with other

non-buthids. The occurrence of a doubled hook is hypothesised to be autapomorphic for the ischnurid genus *Hadogenes* (Sissom, 1990; Newlands and Prendini, 1997). This character is scored as inapplicable in the Diplocentridae, which do not have a lamellar hook.

91. Hemispermatothore, spines in capsular region: absent (0); present (1); unknown (?). The presence of spines in the capsular region of the hemispermatothore is hypothesised to be autapomorphic for the bothriurid genus *Brachistosternus* (San Martín, 1969; Maury, 1973a, 1975, 1980; Sissom, 1990).

92. Hemispermatothore, sclerotised mating plug: absent (0); present (1); unknown (?). Stockwell's (1989) character 117. Modification of the internobasal reflection into a sclerotised mating plug is hypothesised to be autapomorphic for the scorpionid genus *Urodacus* (Stockwell, 1989).

Mesosoma

93. Pretergites III to VI with stridulatory granules: absent (0); present (1). Acosta and Maury (1990) reported a mesosomal stridulatory apparatus in the bothriurid genus *Timogenes*, consisting of groups of granules on the pretergites III to VI, which are rubbed by the distal edge of the previous tergite as the scorpion curves the body in a defensive posture. The stridulatory apparatus is hypothesised to be autapomorphic for *Timogenes*.

Metasoma

94. Metasomal segments I–IV, dorsoventrally compressed: absent (0); present (1). Dorsoventral compression of metasomal segments I–IV is hypothesised to be autapomorphic for the diplocentrid genus *Tarsoporosus* (Francke, 1978; Sissom, 1990).

95. Metasomal segments I–IV, carinae: paired ventrosubmedian carinae (0); single ventromedian carina (1). Stockwell's character 132. Most Recent scorpions, including *Chaerilus* and the Buthidae (represented here by *Centruroides*), exhibit the hypothesised plesiomorphic state of this character, viz. a pair of ventrosubmedian carinae on metasomal segments I–IV. Fusion of this pair to form a single ventromedian carina, which occurs in four scorpionoid genera, *Habibiella*, *Hemiscorpius*, *Heteroscorpion*, and *Urodacus* (Kraepelin, 1894, 1905; Birula, 1917b; Werner, 1934; Lourenço, 1985,

1989; Stockwell, 1989), is potentially synapomorphic. Stockwell (1989:137) erroneously stated that a single ventromedian carina occurs in the ischnurid genus *Hadogenes*. The metasomal segments of all members of this genus are strongly compressed laterally (Newlands and Cantrell, 1985; Newlands and Prendini, 1997), such that the ventrosubmedian carinae are very close together. Nonetheless, they are distinctly paired. Lourenço (1989:163) argued against the use of this character for delimiting the subfamilies of Scorpionidae recognised at the time (Hemiscorpiinae, Heteroscorpioninae, Ischnurinae, Scorpioninae, and Urodacinae) on the grounds that it had been found to vary among species of the buthid genus *Tityus* C. L. Koch 1836, e.g., *Tityus discrepans* (Karsch 1897) and *Tityus gasci* Lourenço 1981 (Lourenço, 1981e). However, there is no precedent for assuming that a character which is interspecifically variable in one higher taxon will be variable in all others. No evidence of interspecific variation in this character was found within the scorpionoid genera investigated in the present study.

96. Metasomal segments I–IV, carinae: more strongly developed on III–IV than I–II (0); more strongly developed on I–II than III–IV (1); inapplicable (–). There is a tendency for the metasomal carinae to become more prominent towards the distal end of the metasoma in most Recent scorpions, including *Chaerilus* and the Buthidae (represented here by *Centruroides*), a condition that is therefore considered plesiomorphic. This tendency is reversed in several taxa, in which it is hypothesised to be independently derived. First, the bothriurid genera *Bothriurus*, *Centromachetes*, *Cercophonius*, *Orobothriurus*, *Thestylus*, and *Urophonius* exhibit the reverse condition, which is potentially synapomorphic, based on the occurrence of the alternative condition in *Lisposoma* (*Phonicercus* exhibits a reversal to the plesiomorphic condition). However, this character cannot be evaluated for the bothriurids in which metasomal carinae are completely absent (*Brachistosternus*, *Tehuanka*, *Timogenes*, and *Vachonia*) and is therefore inapplicable to these taxa. Second, the reverse tendency is hypothesised to be synapomorphic for the Diplocentridae. Finally, the reverse tendency is potentially synapomorphic for the scorpionid genus *Scorpio* and a single species of *Opisththalmus* (*O. boehmi*), which has been previously placed in *Scorpio* (Kraepelin, 1899;

Werner, 1934). The remaining species of *Opisththalmus* (represented here by *O. capensis* and *O. holmi*) display a reversal to the plesiomorphic condition.

97. Metasomal segment I, ventrosubmedian carinae with circular configuration: absent (0); present (1). The circular configuration of the ventrosubmedian carinae of metasomal segment I is autapomorphic for the bothriurid genus *Thestylus* (Kraepelin, 1894) and uninformative in this analysis.*

98. Metasomal segment V, ventrolateral carinae: continuous from proximal to distal edges (0); discontinuous, interrupted in distal region (1). The occurrence of discontinuous ventrolateral carinae on metasomal segment V in the bothriurid genera *Timogenes* and *Vachonia* (Abalos, 1954; San Martín, 1965a; Maury and San Martín, 1973; Maury, 1976, 1982) is hypothesised to be synapomorphic.

99. Metasomal segment V, ventromedian carina distal portion: straight (0); bifurcating (1); breaking up into numerous granules (2); inapplicable (-). A distinct bifurcation of the ventromedian carina of metasomal segment V is evident in the bothriurid genera *Cercophonius* and *Urophonius* (Acosta, 1990) and the scorpionid genus *Urodacus* (Koch, 1977; Lourenço, 1985, 1989). This is hypothesised to be synapomorphic for *Cercophonius* and *Urophonius* and independently derived in *Urodacus*. In the scorpionid genus *Scorpio* (Lourenço, 1985, 1989) and a single species of *Opisththalmus* (*O. boehmi*), which has been previously placed in *Scorpio* (Kraepelin, 1899), the ventromedian carina of metasomal segment V breaks up distally into numerous granules, a condition that is potentially synapomorphic for these taxa. The absence of this condition in the remaining species of *Opisththalmus* (represented here by *O. capensis* and *O. holmi*) is hypothesised to be a reversal. This character is inapplicable to the bothriurid genera in which it could not be evaluated due to obsolescence of the ventromedian carina of metasomal segment V (*Lisposoma*, *Phoniocercus*, *Thestylus*, *Timogenes*, and *Vachonia*).

100. Metasomal segment V, transverse carina: absent (0); bothriurid type I, discontinuous and merging proximally with ventrolateral carinae (1); bothriurid type II, continuous, not merging proximally with ventrolateral carinae (2) (additive). This is a modification of Stockwell's (1989) character 134. A ventral transverse carina

occurs in two groups of Recent scorpions, the Diplocentrinae and some genera of Bothriuridae. It is hypothesised to be apomorphic and independently derived in the two groups (Stockwell, 1989). Stockwell (1989:138) used the mere presence of a transverse carina as a character, despite the fact that the transverse carinae of bothriurids and diplocentrines are not structurally homologous. Furthermore, the existence of additional states within each of these groups, representing clear transformation series, warrants their treatment as two separate characters, an approach that is followed in this analysis. The transverse carina of bothriurids is hypothesised to be synapomorphic for the genera *Bothriurus*, *Timogenes*, and *Vachonia* and one species of *Orobothriurus*, *O. crassimanus* (Abalos, 1954; San Martín, 1965a,b; Maury and San Martín, 1973; Maury, 1976, 1982; Sissom, 1990). The continuous transverse carina, not merging proximally with the ventrolateral carinae, is hypothesised to be synapomorphic for *Timogenes* and *Vachonia* and derived from the discontinuous transverse carina, merging proximally with the ventrolateral carinae, of *Bothriurus* and *O. crassimanus*. The length of this character did not change in the analyses as a result of unordering.

101. Metasomal segment V, transverse carina: absent (0); diplocentrid type, partially developed (1); diplocentrid type, fully developed (2) (additive). This is a modification of Stockwell's (1989) character 134. The diplocentrid genera *Bioculus*, *Cazierius*, *Didymocentrus*, *Diplocentrus*, *Oiclus*, and *Tarsoporosus* exhibit a fully developed transverse carina, which is hypothesised to be synapomorphic (Francke, 1977a,b, 1978; Stockwell, 1989; Sissom, 1990). Stockwell (1989:138) commented on the presence of "a loose field of tubercles that could possibly be homologous" in the genus *Heteronebo* (illustrated by Francke, 1978), but nonetheless scored *Heteronebo* for the plesiomorphic condition. Examination of numerous specimens of *Heteronebo* by W. D. Sissom (pers. comm.) and myself has revealed a distinctly discernible, although not fully developed transverse carina in certain species, e.g., *H. dominicus* Armas 1981. Accordingly, a separate state is assigned for this condition in *Heteronebo*, hypothesised to be intermediate between plesiomorphic absence and the presence of a fully developed transverse carina. The length of this character decreased in the analysis with equal weights as a result of unordering.

102. Metasomal segment II, ventral surface with numerous spiniform granules: absent (0); present (1). The ventral surface of metasomal segment II is covered with numerous spiniform granules in the ischnurid genus *Hadogenes* and some species of *Liocheles* (Kraepelin, 1894; Newlands and Prendini, 1997), represented here by *L. australasiae*. The presence of spiniform granules is hypothesised to be apomorphic, but may be independently derived in *Hadogenes* and *Liocheles*.

103. Metasomal segment V (male), dorsal surface with paired androvestigia (glands): absent (0); present (1). A pair of glands, termed androvestigia by Cekalovic (1973b), occurs on the dorsal surface of metasomal segment V in males of the bothriurid genus *Brachistosternus* (Cekalovic, 1973b) and four species of *Timogenes* (Maury, 1982), represented in this analysis by *T. dorbignyi* and *T. mapuche*. These glands are potentially synapomorphic for *Brachistosternus* and *Timogenes*.

Telson

104. Vesicle (male), dorsal surface with androvestigia (glands): absent (0); single (1); paired (2). A single, elliptical gland occurs on the dorsal surface of the vesicle in males of the bothriurid genera *Bothriurus*, *Orobothriurus*, and *Urophonius* (Kraepelin, 1908b; Werner, 1934; San Martín, 1965b; San Martín and Gambardella, 1974), providing a potential synapomorphy for these genera. In addition, a pair of glands occurs on the dorsal surface of the vesicle in males of two species of *Timogenes* (Maury, 1982), represented in this analysis by *T. mapuche*. These paired glands may be derived from the single gland condition, but their absence from three species of *Timogenes* suggests that they were independently derived.

105. Aculeus: long, shallowly curved (0); very short, sharply curved (1). The aculeus of most Recent scorpions, including *Chaerilus* and the Buthidae (represented here by *Centruroides*), is fairly long in comparison with the vesicle and shallowly curved. This condition is hypothesised to be plesiomorphic. The very short, sharply curved aculeus of the Hemiscorpiinae and Ischnuridae is hypothesised to be synapomorphic for these taxa and independently derived from the very short, sharply curved aculeus of the Diplocentridae.

106. Subaculear tubercle: absent (0); distinct (1). Stockwell's (1989) character 135. A subaculear tubercle

is absent from the vesicle of all fossil and many non-buthid scorpions, including *Chaerilus*, hence this condition is hypothesised to be plesiomorphic. The presence of a subaculear tubercle in all genera of Diplocentridae has been used as a diagnostic character since Pocock (1893) created the family and is considered synapomorphic (Stockwell, 1989).

107. Vesicle (male), laterally compressed: absent (0); present (1). A laterally compressed vesicle occurs in adult male Heteroscorpionidae, Hemiscorpiinae, and Ischnuridae (Pavlovsky, 1924a; Werner, 1934), for which it is hypothesised to be synapomorphic.

108. Vesicle (female), laterally compressed: absent (0); present (1). A laterally compressed vesicle occurs in adult female Heteroscorpionidae and Ischnuridae, for which it is hypothesised to be synapomorphic. The absence of lateral compression in adult female Hemiscorpiinae (Pavlovsky, 1924a; Werner, 1934) is hypothesised to be a reversal.

109. Vesicle (male), elongated with pair of distal lobes: absent (0); present (1); unknown (?). Elongation of the vesicle, and the presence of a pair of distal lobes, occurs only in adult male Hemiscorpiinae (Kraepelin, 1894, 1908b; Pavlovsky, 1924a; Werner, 1934; Lourenço, 1985, 1989) for which it is hypothesised to be synapomorphic. However, at least one species of *Urodacus*, *U. megamastigus* Koch 1977 (according to E. S. Volschenk, pers. comm., there are others undescribed), exhibits an elongated vesicle (distal lobes are absent) in the adult male. The state of this character is unknown in the ischnurid genus *Chiromachetes*, in which adult males are unknown (Pocock, 1899; Lourenço, 1997). Note that the use of characters representing telson shape has been argued against by Lourenço (1989:164) on the grounds that telson shape is highly variable within genera, particularly in the Buthidae. Aside from the fact that there is no precedent for assuming that a character which is interspecifically variable in one higher taxon will be variable in all others, no evidence for interspecific variation in the characters of telson shape (107–109) was found within the scorpionoid genera examined in this study.

110. Vesicle, anterodorsal lateral lobes (*sensu* San Martín and Gambardella, 1974): present (0); absent (1). The presence of anterodorsal lateral lobes is hypothesised to be plesiomorphic in the Bothriuridae, based on outgroup comparison with *Chaerilus* and the Buthidae (represented here by *Centruroides*). The absence of lobes

is hypothesised to be synapomorphic for *Heteroscorpion*, the Ischnuridae, and the Scorpionidae (including *Urodacus* and the Hemiscorpiinae), whereas the presence of lobes in the Diplocentridae is hypothesised to be a reversal.

111. Vesicle, ventral surface: with two or more longitudinal granular carinae extending towards aculeus (0); with transverse row of granules at proximal edge, remainder smooth (1); without granules (2). Longitudinal granular carinae occur on the vesicles of most Recent scorpions, including *Chaerilus* and the Buthidae (represented here by *Centruroides*), although in some taxa these carinae may be manifest as nothing more than weak granulation on the vesicle surface. The presence of granular carinae or granulation is considered homologous and hypothesised to be plesiomorphic (Lamoral, 1978). The absence thereof is hypothesised to be synapomorphic for most species of Ischnuridae, exceptions being some species of *Hadogenes*, represented here by *H. troglodytes*, and some of the African species of *Opisthacanthus* (*Nepabellus*), represented here by *O. validus*. Although the presence of only two longitudinal carinae in the latter (Lawrence, 1955; Lourenço, 1981c, 1982, 1983c, 1985, 1987) could represent a state intermediate between the plesiomorphic state and the derived absence of granulation, the occurrence of two or more carinae is considered homologous in the present analysis. A third state, the presence of a smooth vesicle, with a transverse row of granules at the proximal edge (interpreted as the remaining proximal granules of each longitudinal row), occurs in three diplocentrid genera, *Bioculus*, *Didymocentrus*, and *Diplocentrus*, for which it is potentially synapomorphic, the remaining diplocentrid genera displaying the hypothesised plesiomorphic condition. The general applicability of this state is currently uncertain. For example, several species of *Diplocentrus* (other than those included as exemplars in this analysis) exhibit limited granulation in the basal third of the vesicle in addition to the transverse row (W. D. Sissom, pers. comm.).

112. Vesicle, ventral surface with semicircular carina: absent (0); present (1). A semicircular carina on the ventral surface of the vesicle is hypothesised to be autapomorphic for the bothriurid genus *Timogenes* (Maury and San Martín, 1973).

113. Venom glands: complex (0); simple (1). Stockwell's character 137. Differences in the epithelial lining of the venom glands were first noted by Pavlovsky

(1913, 1924a), who recognised type I or simple, unfolded glands and type II or complex, folded glands. Pavlovsky's characters were adopted by subsequent authors (Birula, 1917b; Werner, 1934; Francke and Solglad, 1981; Lourenço, 1985, 1989, 1991; Stockwell, 1989). Complex glands, which occur in the scorpionoid taxa Bothriuridae, Diplocentridae, Scorpioninae, and *Urodacus*, are derived from simple ones during ontogeny (Pavlovsky, 1924a) and are therefore hypothesised to be synapomorphic. This is concordant with outgroup comparison, since simple glands occur in *Chaerilus*. However, the occurrence of simple glands in *Heteroscorpion*, the Hemiscorpiinae, and the Ischnuridae is hypothesised to be a reversal, based on outgroup comparison with the Bothriuridae (Stockwell, 1989). This contrasts with the opinion of Lourenço (1985, 1991), who considered the simple glands of the Ischnuridae to be plesiomorphic. Stockwell (1989:140) considered Lourenço's (1985, 1989, 1991) four grades of venom glands to be arbitrary delimitations of a continuum. "Simple" and "complex" are defined here in accordance with Stockwell's treatment and are synonymous, respectively, with Lourenço's "smooth" and "prelobed" vs "semilobed" and "lobed."

114. Venom pigment: opalescent (0); reddish (1). The venom of all scorpionoids is opalescent, except for the Diplocentridae, in which the venom has a reddish pigment (Sissom, 1990). The reddish pigment is hypothesised to be synapomorphic for the genera of Diplocentridae.

Behaviour

115. Mesosomal percussion: absent (0); present (1). Rosin and Shulov (1961) reported mesosomal percussion in the scorpionid genus *Scorpio*. It is hypothesised to be autapomorphic for this genus.

APPENDIX 4

Distribution of Unambiguous Synapomorphies on Trees Obtained in the Analyses with Equal Weights (EW),

Successive Weights (SW), and Implied Weights (IW) with Six Values for the Concavity Constant (k)

Different character optimisations, resulting from topological differences among the trees located in these analyses, are listed after the relevant clades or terminal taxa, followed in parentheses by abbreviations for the analyses in which they were obtained (clades or terminals without such a listing were supported by the same synapomorphies in all analyses). Analyses with multistates ordered and unordered are indicated, respectively, by subscripts "O" and "U". Synapomorphies supporting clades in the strict consensus tree are presented for those analyses in which more than one MPT was obtained. Unnamed clades are referred to by listing the subtended terminal families, subfamilies, genera, or species. Character numbers refer to Appendix 3. Character transformations are denoted by listing the ancestral and derived states separated by a ">". Unambiguous synapomorphies for the preferred hypothesis of relationships among the families of Scorpionoidea are optimised on the cladogram in Fig. 7.

Bioculus: 8:0>1, 111:0>1 (EW_O, SW_O, IW_O: $k = 3-6$); 20:0>1, 23:0>1, 27:2>1 (IW_O: $k = 1$); 8:0>1 (IW_O: $k = 2$); 8:0>1, 111:0>1 (EW_U, IW_U: $k = 1-6$).

(*Bioculus comondae* + *Oiclus*): 1:1>2 (SW_U).

(*Bioculus* + *Cazierius* + *Oiclus*): 23:0>1 (EW_{O/U}, SW_U, IW_U: $k = 2-6$); 20:0>1, 23:0>1 (SW_O, IW_O: $k = 2-6$, IW_U: $k = 1$).

Bothriuridae: 10:0>1, 23:0>1, 26:0>1, 27:1>3, 56:0>1, 58:0>1, 68:0>1, 85:0>1 (EW_O, SW_O, IW_O: $k = 1-2, 4-6$); 10:0>1, 20:0>1, 21:0>1, 23:0>1, 26:0>1, 27:1>3, 29:0>1, 56:0>1, 58:0>1, 68:0>1, 85:0>1 (IW_O: $k = 3$); 10:0>1, 23:0>1, 26:0>1, 56:0>1, 58:0>1, 68:0>1, 85:0>1 (EW_U, SW_U, IW_U: $k = 1-6$).

(*Bothriurus* + *Timogenes* + *Vachonia*): 10:1>0, 69:2>1 (EW_O, SW_{O/U}, IW_{O/U}: $k = 1-6$).

(*Brachistosternus* + *Centromachetes* + *Orobothriurus* + *Bothriurus* + *Timogenes* + *Vachonia*): 15:0>1.

Brachistosternus: 66:0>1, 69:1>0, 72:1>2, 91:0>1, 103:0>1 (EW_O, SW_O, IW_O: $k = 1-6$); 66:0>1, 91:0>1, 103:0>1 (EW_U, SW_U, IW_U: $k = 1-6$).

(*Cazierius* + *Oiclus* + *Diplocentrus* + *Didymocentrus* + *Bioculus*): 21:0>1 (IW_O: $k = 1-2$).

(*Cazierius* + *Oiclus*): 23:0>1 (IW_O: $k = 1$).

(*Centromachetes* + *Orobothriurus* + *Bothriurus* + *Timogenes* + *Vachonia*): 69:1>2.

Centromachetes: 33:0>2.

(*Cercophonius* + *Urophonius* + *Tehuanka* + *Brachistosternus* + *Centromachetes* + *Orobothriurus* + *Bothriurus* + *Timogenes* + *Vachonia*): 63:1>0, 69:2>1 (EW_O, SW_O, IW_O: $k = 1-6$); 63:1>0 (EW_U, SW_U, IW_U: $k = 1-6$).

(*Cercophonius* + *Urophonius*): 33:0>2, 99:0>1.

Cheloctonus: 33:1>0.

(*Cheloctonus* + *Hadogenes* + *Opisthacanthus madagascariensis* + *Palaeocheloctonus* + *Chiromachetes* + *Chiromachus* + *Opisthacanthus elatus* + *Iomachus* + *Liocheles*): 111:0>2 (EW_{O/U}).

Chiromachus: 70:0>3.

(*Chiromachetes* + *Chiromachus* + *Opisthacanthus elatus* + *Iomachus* + *Liocheles*): 36:0>1 (EW_{O/U}, SW_{O/U}, IW_{O/U}: $k = 2-6$).

(*Chiromachetes fergusonii* + *Chiromachus* + *Opisthacanthus madagascariensis* + *Palaeocheloctonus*): 37:0>1 (IW_O: $k = 1$).

(*Chiromachetes fergusonii* + *Chiromachus*): 37:0>1 (EW_{O/U}, SW_{O/U}, IW_O: $k = 2-6$, IW_U: $k = 1-6$); 36:0>1, 68:0>2 (IW_O: $k = 1$).

(*Chiromachetes tirupati* + *Chiromachetes fergusonii* + *Chiromachus*): 68:0>2 (EW_{O/U}, SW_{O/U}, IW_{O/U}: $k = 2-6$).

Didymocentrus: 24:0>1, 27:2>3, 28:1>0 (EW_{O/U}, SW_O, IW_O: $k = 1-6$, IW_U: $k = 2-6$); 8:0>1, 24:0>1, 27:1>3 (IW_U: $k = 1$); 8:0>1, 24:0>1, 27:1>3, 111:0>1 (SW_U).

(Diplocentrinae + Scorpioninae + Hemiscorpiinae + Ischnuridae): 52:0>12, 59:0>1 (EW_{O/U}, SW_{O/U}).

(Diplocentrinae + Scorpioninae + Urodacinae + Heteroscorpionidae + Hemiscorpiinae + Ischnuridae): 3:0>2, 4:0>1, 7:0>1, 77:0>1, 78:0>1, 110:0>1 (EW_O, SW_{O/U}, IW_O: $k = 3$); 3:0>2, 65:0>1, 77:0>1, 78:0>1 (IW_O: $k = 1-2$, IW_U: $k = 1-6$); 3:0>2, 4:0>1, 7:0>1, 77:0>1, 78:0>1 (EW_U, IW_O: $k = 4-6$).

(Diplocentrinae + Scorpioninae + Urodacinae): 65:0>1 (IW_O: $k = 3$).

(Diplocentrinae + Scorpioninae): 16:0>1, 65:0>1 (EW_{O/U}); 65:0>1 (SW_{O/U}); 16:0>1, 52:0>2, 59:0>1 (IW_O: $k = 3-6$).

Diplocentrinae: 52:2>3, 88:0>1, 106:0>1, 110:1>0, 114:0>1 (EW_O, SW_O); 52:0, 2>3, 88:0>1, 105:0>1, 106:0>1, 114:0>1 (IW_O: $k = 1-2, 4-6$, IW_U: $k = 1-6$); 52:2>3, 88:0>1, 105:0>1, 106:0>1, 110:1>0, 114:0>1 (IW_O: $k = 3$); 88:0>1, 106:0>1, 110:1>0, 114:0>1 (SW_U).

Diplocentrinae: 4:1>0, 7:1>0, 65:1>2, 96:0>1, 101:0>2 (EW_O, SW_U); 4:1>0, 7:1>0, 65:1>2, 96:0>1, 101:0>1 (SW_O, IW_O: $k = 3-6$); 15:0>1, 28:0>1, 41:0>1, 65:1>2, 96:0>1, 101:0>1 (IW_O: $k = 1-2$, IW_U: $k = 2-6$);

4:1>0, 7:1>0, 65:1>2, 101:0>1 (EW_U); 15:0>1, 41:0>1, 65:1>2, 96:0>1, 101:0>1 (IW_U: k = 1).

Diplocentrus: 27:1>2 (IW_U: k = 1).

(*Diplocentrus* + *Didymocentrus*): 27:1>2, 111:0>1 (EW_{O/U}, SW_{O/U}, IW_O: k = 3-6, IW_U: k = 1-6); 27:1>2 (IW_O: k = 2).

(*Diplocentrus* + *Didymocentrus* + *Bioculus*): 27:1>2, 111:0>1 (IW_O: k = 1).

(*Diplocentrus* + *Didymocentrus* + *Heteronebo* + *Tarsoporus*): 20:1>0 (EW_U, IW_U: k = 2-6).

(*Diplocentrus* + *Heteronebo* + *Tarsoporus* + *Cazierius* + *Oiclus* + *Bioculus*): 28:0>1 (EW_U, SW_U).

(*Diplocentrus gertschi* + *Didymocentrus* + *Bioculus*): 8:0>1 (IW_O: k = 1).

(*Diplocentrus gertschi* + *Didymocentrus*): 8:0>1 (EW_O, SW_O, IW_O: k = 2-6).

Habiella: 45:1>2 (EW_{O/U}, SW_{O/U}, IW_O: k = 3-4).

(*Hadogenes* + *Opisthacanthus madagascariensis* + *Palaeocheloctonus* + *Chiromachetes* + *Chiromachus* + *Opisthacanthus elatus* + *Iomachus* + *Liocheles*): 16:0>1, 18:0>1 (EW_{O/U}).

(*Hadogenes* + *Opisthacanthus validus* + *Cheloctonus*): 3:2>1 (SW_{O/U}, IW_{O/U}: k = 1-6).

Hadogenes: 23:0>1, 25:0>1, 43:1>2, 45:1>2, 49:2>4, 53:0>2, 59:1>0, 80:2>1, 90:0>1, 102:0>1 (EW_{O/U}, SW_{O/U}, IW_O: k = 3-4, IW_U: k = 2-6); 23:0>1, 25:0>1, 43:1>2, 49:2>4, 53:0>2, 59:1>0, 80:2>1, 90:0>1, 102:0>1 (IW_O: k = 1-2, 5-6, IW_U: k = 1).

(*Hemiscorpiinae* + *Ischnuridae*): 1:2>1, 2:0>1, 11:1>0, 33:2>1, 43:2>1, 49:4>2, 52:0>1, 59:0>1, 105:0>1 (IW_O: k = 1-2, 6); 2:0>1, 11:1>0, 52:0>1, 59:0>1, 105:0>1 (IW_O: k = 3-5); 2:0>1, 8:0>1, 11:1>0, 33:0>1, 50:0>1, 107:0>1, 113:0>1 (EW_{O/U}, SW_O); 2:0>1, 8:0>1, 11:1>0, 33:0>1, 50:0>1, 107:0>1, 113:0>1 (SW_U); 2:0>1, 11:1>0, 33:2>1, 105:0>1 (IW_U: k = 1-6).

Hemiscorpiinae: 18:0>1, 48:0>1, 51:0>1, 52:12>3, 70:0>1, 95:0>1, 109:0>1 (EW_O); 18:0>1, 48:0>1, 51:0>1, 70:0>1, 95:0>1, 109:0>1 (EW_U); 48:0>1, 51:0>1, 52:12>3, 70:0>1, 95:0>1, 109:0>1 (SW_O); 48:0>1, 51:0>1, 70:0>1, 95:0>1, 109:0>1 (SW_U); 48:0>1, 51:0>1, 52:1, 2>3, 70:0>1, 108:1>0, 109:0>1 (IW_O: k = 1-2, 6); 48:0>1, 51:0>1, 52:1>3, 70:0>1, 109:0>1 (IW_O: k = 3-5); 48:0>1, 51:0>1, 70:0>1, 109:0>1 (IW_U: k = 1-6).

Heterometrus: 75:0>1.

(*Heterometrus* + *Pandinus*): 23:0>1, 35:0>1, 73:0>1, 74:0>2.

Heteronebo: 16:1>0, 101:2>1 (EW_{O/U}, SW_U, IW_U: k = 1-6); 16:1>0 (SW_O, IW_O: k = 3-6).

(*Heteronebo* + *Tarsoporus*): 21:1>0 (EW_{O/U}, SW_U, IW_U: k = 1-6).

Heteroscorpion: 8:0>1, 18:0>1, 107:0>1, 108:0>1, 113:0>1 (EW_{O/U}, SW_{O/U}); 43:1>2, 45:1>2, 49:2>4 (IW_O: k = 3).

(*Heteroscorpionidae* + *Hemiscorpiinae* + *Ischnuridae*): 8:0>1, 18:0>1, 65:1>0, 107:0>1, 108:0>1, 113:0>1 (IW_O: k = 1-2); 8:0>1, 18:0>1, 107:0>1, 113:0>1 (IW_O: k = 3-5); 8:0>1, 18:0>1, 107:0>1, 108:0>1, 113:0>1 (IW_O: k = 6); 8:0>1, 18:0>1, 65:1>0, 107:0>1, 113:0>1 (IW_U: k = 1-6).

(*Heteroscorpionidae* + *Urodacinae*): 33:0>2, 43:1>2, 45:1>2, 49:2>4, 95:0>1 (EW_{O/U}, SW_{O/U}).

(*Iomachus laeviceps* + *Iomachus politus* + *Liocheles*): 9:1>3, 70:0>2.

(*Iomachus politus* + *Liocheles*): 59:1>0.

Ischnuridae: 3:2>1, 30:0>1, 35:0>1, 55:0>1, 61:0>1, 62:1>0, 76:0>1, 108:0>1 (EW_O); 3:2>1, 30:0>1, 35:0>1, 52:3>1, 55:0>1, 61:0>1, 62:1>0, 76:0>1, 108:0>1 (EW_U); 30:0>1, 35:0>1, 55:0>1, 61:0>1, 62:1>0, 76:0>1, 108:0>1 (SW_O); 30:0>1, 35:0>1, 52:3>1, 55:0>1, 61:0>1, 62:1>0, 76:0>1, 108:0>1 (SW_U); 20:0>1, 21:0>1, 29:0>1, 30:0>1, 35:0>1, 55:0>1, 61:0>1, 62:1>0, 76:0>1, 95:1>0 (IW_O: k = 1-2, 6); 20:0>1, 21:0>1, 29:0>1, 30:0>1, 35:0>1, 55:0>1, 61:0>1, 62:1>0, 76:0>1 (IW_O: k = 3-5); 20:0>1, 21:0>1, 29:0>1, 30:0>1, 35:0>1, 55:0>1, 61:0>1, 62:1>0, 76:0>1 (IW_U: k = 1); 16:0>1, 20:0>1, 21:0>1, 29:0>1, 30:0>1, 35:0>1, 55:0>1, 61:0>1, 62:1>0, 76:0>1, 95:1>0, 111:0>2 (IW_U: k = 2-6).

Liocheles: 54:0>1, 68:0>2.

Lisposoma: 44:0>1, 89:0>1.

Nebo: 47:0>1 (EW_{O/U}, SW_{O/U}, IW_O: k = 3-6); 34:0>1, 47:0>1 (IW_O: k = 1-2, IW_U: k = 1-6).

Oiclus: 64:0>1 (EW_O, SW_{O/U}, IW_O: k = 2-6, IW_U: k = 1); 1:1>2, 64:0>1 (EW_U, IW_O: k = 1, IW_U: k = 2-6).

(*Opisthacanthus elatus* + *Iomachus* + *Liocheles*): 89:0>1 (EW_{O/U}, SW_{O/U}, IW_O: k = 1-6, IW_U: k = 2-6).

(*Opisthacanthus madagascariensis* + *Palaeocheloctonus* + *Chiromachetes* + *Chiromachus* + *Opisthacanthus elatus* + *Iomachus* + *Liocheles*): 3:1>2 (EW_{O/U}).

(*Opisthacanthus madagascariensis* + *Palaeocheloctonus*): 37:0>1, 87:0>1 (EW_{O/U}, SW_{O/U}, IW_{O/U}: k = 2-6); 87:0>1 (IW_{O/U}: k = 1).

(*Opisthacanthus validus* + *Cheloctonus*): 18:1>0 (SW_O/

U , IW_O : $k = 1-6$, IW_U : $k = 1$); 16:1>0, 18:1>0 (IW_U : $k = 2-6$).

Opisthophthalmus: 13:0>1, 45:1>2, 71:0>1 ($EW_{O/U}$, $SW_{O/U}$, IW_O : $k = 3-6$); 13:0>1, 71:0>1 (IW_O : $k = 1-2$, IW_U : $k = 1-6$).

(*Opisthophthalmus capensis* + *Opisthophthalmus holmi*): 6:0>1, 72:1>2.

(*Orobothriurus* + *Bothriurus* + *Timogenes* + *Vachonia*): 5:0>1, 104:0>1 (EW_O , $SW_{O/U}$, $IW_{O/U}$: $k = 1-6$).

(*Orobothriurus crassimanus* + *Bothriurus* + *Timogenes* + *Vachonia*): 100:0>1 (EW_O , $SW_{O/U}$, $IW_{O/U}$: $k = 1-6$).

Palaeocheloctonus: 33:1>0.

Pandinus: 43:1>3, 45:1>2 ($EW_{O/U}$, $SW_{O/U}$, IW_O : $k = 3-6$); 43:1>3 (IW_O : $k = 1-2$, IW_U : $k = 1-6$).

(*Pandinus imperator* + *Pandinus cavimanus*): 46:1>2, 49:2>4.

Phoniocercus: 70:0>2.

(*Phoniocercus* + *Cercophonius* + *Urophonius* + *Tehuauke* + *Brachistosternus* + *Centromachetes* + *Orobothriurus* + *Bothriurus* + *Timogenes* + *Vachonia*): 31:0>1, 49:2>3, 79:0>1.

Scorpio: 40:0>1, 74:0>1, 115:0>1.

(*Scorpio* + *Opisthophthalmus*): 3:2>1.

(Scorpioninae + Urodacinae + Heteroscorpionidae + Hemiscorpiinae + Ischnuridae): 110:0>1 (IW_O : $k = 1-2$, IW_U : $k = 1-6$).

Scorpioninae: 22:0>1, 51:0>1, 68:0>2, 72:0>1 (EW_O , SW_O , IW_O : $k = 6$); 22:0>1, 51:0>1, 52:3>2, 68:0>2, 72:0>1 (EW_U); 22:0>1, 28:0>1, 51:0>1, 52:3>2, 68:0>2 (SW_U); 15:0>1, 22:0>1, 28:0>1, 34:0>1, 41:0>1, 51:0>1 (IW_O : $k = 1-2$); 22:0>1, 51:0>1 (IW_O : $k = 3-5$); 15:0>1, 22:0>1, 28:0>1, 34:0>1, 51:0>1, 52:0>2 (IW_U : $k = 1-6$).

Scorpionoidea: 11:0>1, 63:0>1, 69:0>2, 80:0>2, 84:0>1.

Tarsoporosus: 67:0>1, 94:0>1.

(*Tarsoporosus* + *Cazierius* + *Oiclus* + *Diplocentrus* + *Didymocentrus* + *Bioculus*): 101:1>2 (SW_O , IW_O : $k = 1-6$).

(*Tarsoporosus* + *Heteronebo* + *Diplocentrus* + *Didymocentrus*): 20:1>0 (EW_O).

(*Tehuauke* + *Brachistosternus* + *Centromachetes* + *Orobothriurus* + *Bothriurus* + *Timogenes* + *Vachonia*): 32:0>1.

Thestylus: 97:0>1.

(*Thestylus* + *Phoniocercus* + *Cercophonius* + *Urophonius* + *Tehuauke* + *Brachistosternus* + *Centromachetes* + *Orobothriurus* + *Bothriurus* + *Timogenes* + *Vachonia*): 9:1>2, 16:0>1, 80:2>1, 81:0>1, 86:0>1 ($EW_{O/U}$, $SW_{O/$

U , IW_O : $k = 3-6$); 9:1>2, 80:2>1, 81:0>1, 86:0>1 (IW_O : $k = 1-2$, IW_U : $k = 1-6$).

Timogenes: 93:0>1, 103:0>1, 112:0>1.

(*Timogenes* + *Vachonia*): 31:1>2, 49:3>4, 72:1>2, 98:0>1, 100:1>2, 104:1>0 (EW_O , $SW_{O/U}$, $IW_{O/U}$: $k = 1-6$); 31:1>2, 49:3>4, 98:0>1, 100:0, 1>2 (EW_U).

Urodacus: 53:0>1, 65:0>1, 68:0>2, 72:0>1, 92:0>1, 99:0>1 (EW_O , SW_O); 53:0>1, 65:0>1, 68:0>2, 92:0>1, 99:0>1 (EW_U , SW_U); 53:0>1, 92:0>1, 99:0>1 (IW_O : $k = 1-2$, 4-5, IW_U : $k = 1-6$); 43:1>2, 45:1>2, 49:2>4, 53:0>1, 92:0>1, 99:0>1 (IW_O : $k = 3$); 53:0>1, 68:0>2, 72:0>1, 92:0>1, 99:0>1 (IW_O : $k = 6$).

(Urodacinae + Heteroscorpionidae + Hemiscorpiinae + Ischnuridae): 33:0>2, 95:0>1 (IW_O : $k = 1-2$); 33:0>2, 43:1>2, 45:1>2, 49:2>4, 95:0>1 (IW_O : $k = 6$); 21:1>0, 33:0>2, 95:0>1 (IW_U : $k = 1$); 20:1>0, 21:1>0, 33:0>2, 95:0>1 (IW_U : $k = 2-6$).

Urophonius: 104:0>1.

Vachonia: 1:1>2, 39:0>1, 43:1>3, 63:0>1.

ACKNOWLEDGMENTS

This research was supported by a Prestigious Scholarship from the Foundation for Research Development, Pretoria; the S.A. College Croll and Myer Levinson (EMDIN) Funds of the University of Cape Town; two Grants in Support of Research from the Theodore Roosevelt Memorial Fund of the American Museum of Natural History; a Collections Study Grant from the American Museum of Natural History; and an Ernst Mayr Grant from the Museum of Comparative Zoology, Harvard University. The California Academy of Sciences provided additional support. These ideas were presented at the XIVth International Congress of Arachnology and 22nd Annual Meeting of the American Arachnological Society, Chicago, 1998 (attendance supported by the American Arachnological Society), and at the Inaugural Conference of the South African Society for Systematic Biology, Stellenbosch, 1999. This work would not have been possible without the assistance, hospitality, and discussion provided by the following: Elizabeth Bonwich, Neil Caithness, James Carpenter, Rob DeSalle, Gonzalo Giribet, Daniel Janies, Norman Platnick, and Ward Wheeler (AMNH); Jonathan Coddington and Scott Larcher (USNM); Marymegan Daly, Sue Hottenrott, Diana Lipscomb, and Kai Raab, George Washington University; Charles Griswold, David Kavanaugh, and Darrell Ubick (CAS); Ardis Johnston and Laura Leiben-sperger (MCZ); W. David Sissom, West Texas A&M University; and Rudy Jocque (MRAC). The following assisted with the loan of specimens from their institutions or private collections: Ben Brugge (ZMA); Jonathan Coddington (USNM); Margie Cochrane (SAM); Julio Ferrer (NRS); Martin Filmer (TM); Eryn Griffin (SMN); Charles Griswold (CAS); Michelle Hamer (NM); Paul Hillyard (BMNH); Rudy Jocque (MRAC); Manfred Moritz, Shahin Nawai, and Jason

Dunlop (ZMB); and Norman Platnick (AMNH). W. David Sissom provided access to his extensive private collection of diplocentrids during my visit and personally discussed many of the characters used in the analysis. Timothy Crowe assisted with the financial and logistical organisation of my trips to the U.S.A. James Carpenter, Jonathan Coddington, Timothy Crowe, Victor Fet, Gonzalo Giribet, Charles Griswold, H. Peter Linder, Jyrki Muona, Norman Platnick, W. David Sissom, and Ward Wheeler provided constructive comments on various drafts of the manuscript that have greatly improved its quality. Elizabeth Scott provided long-distance encouragement throughout the progress of this project.

Note added in proof. While this paper was in press, the monotypic ischnurid genus *Hormiops* Fage 1933 was reinstated by W. R. Lourenço and L. Monod (1999, "Confirmation de la validité du genre *Hormiops* Fage, 1933 avec redescription d'*Hormiops davidovi* Fage, 1933 (Scorpiones, Ischnuridae)." *Zoosystema* **21**, 337–344). Lourenço (1989, p. 170) had previously synonymised *Hormiops* with *Liocheles*. Lourenço and Monod (1999, p. 337) now propose the following characters for separating *Hormiops* from *Liocheles*: "presence of two [pairs of] lateral eyes, a trichobothrium *db* of chela on the external surface, and an hemispermatophore very simple, with reduced hooks."

Among the Ischnuridae, *H. davidovi* is autapomorphic for the presence of two, as opposed to three, pairs of lateral ocelli. However, as discussed in Appendix 3 (character 1), the apomorphic condition of two pairs occurs in many other scorpion genera and is known to vary interspecifically in at least two of these: *Bioculus* and *Opisthophthalmus*. Therefore, this character is unsuited to providing generic status for *H. davidovi*. The external (dorsal) position of trichobothrium *db* is synapomorphic for the species of *Liocheles* (Appendix 3, character 59) and thus cannot be used to separate *Hormiops* either. Finally, the putative differences between the hemispermatophores of *H. davidovi* and *Liocheles karschii* (Keyserling 1885) could not be gauged from Lourenço and Monod's (1999, p. 342) Fig. 4. The differences between these hemispermatophores are no greater than those among the hemispermatophores of different species of *Liocheles* (personal observation). However, examination of Lourenço and Monod's (1999, pp. 339–340) Figs. 1 and 2 reveals a synapomorphy of *H. davidovi* with certain species of *Liocheles*. The ventral surface of metasomal segment II displays spiniform granules similar to those seen in *L. australasiae* and *Liocheles nigripes* (Pocock 1897), as discussed in Appendix 3 (character 102). Therefore, *H. davidovi* may be more closely related to these species than to others in the genus, e.g., *L. karschii* and *L. waigiensis*, in which case the provision of generic status for *H. davidovi* would render *Liocheles* paraphyletic.

On the basis of this evidence, the generic status of *H. davidovi* is unjustifiable. *Hormiops* is hereby returned to synonymy with *Liocheles*, and *Liocheles davidovi* (Fage 1933), *NEW COMBINATION*, is recognised accordingly.

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