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Scorpion higher phylogeny and classification, taxonomic anarchy, and standards for peer review in online publishing

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Abstract

Soleglad and Fet's (2003a) attempt to reconstruct the phylogeny of Recent (including extant) scorpions, the revised classification derived from it, and recent emendations, mostly published in their self-edited online journal, *Euscorpius*, are deficient. Separate analyses of three independent matrices (morphology, 16S rDNA, 18S rDNA) were presented. In the morphological matrix, 52 binary and 10 tristate trichobothrial characters were replaced with one character comprising six ordered states representing trichobothrial "types". The remaining matrix of 105 characters was further reduced to 33 "fundamental" characters (20% of the morphological dataset), the analysis of which appears to be the basis for the revised classification presented. The taxon sample for the morphological analysis included 14 supraspecific terminal taxa representing genera, the monophyly of only 7 (12.5%) of which has been confirmed. A composite terminal, assembled from the fragments of fossils that may not be confamilial let alone monophyletic, was created for the Palaeopisthacanthidae, employed as the primary outgroup for the analysis. Other important outgroup taxa, notably eurypterids, xiphosurans and other arachnids, were omitted entirely. The morphological characters presented contained numerous unjustifiable assumptions of character polarity and phylogenetic relationship. An approach to character coding, deliberately adopted to reduce "homoplasy", biased the analysis towards a preconceived result. Structurally and topographically similar features in different taxa were explicitly assigned separate (often autapomorphic) states according to presumed phylogenetic relationships among the taxa in which they were observed. Putative "reversals" were coded as separate characters or states. Character transformation was forced by ordering, additive coding or Sankoff optimization through allegedly intermediate states for which there is no empirical evidence. Many characters were defined in a manner that demonstrates either a lack of understanding of, or disregard for, established methods and standards of morphological character coding. Some states display overlapping variation whereas others subsume variation that is not structurally or topographically similar. Polymorphic "states" were created for terminals with interspecific variation and unknown "states" for terminals that should have been scored unknown. Many characters were not evaluated for particular terminal taxa, but merely scored inapplicable although the structures and, consequently, the characters in question are present and therefore applicable to them. In view of the significant theoretical and empirical problems with the approach to cladistics taken by Soleglad and Fet, we find no justification for accepting either the results of their analyses or the revised classification derived from them. Pending the outcome of a rigorous phylogenetic analysis, published according to acceptable standards of scholarship in a peer-reviewed journal, we revert to the suprageneric classification of Scorpiones reflected by the most recent peer-reviewed, published treatments and reject all changes to the classification proposed by Soleglad, Fet and colleagues since 2001. We argue that an analysis and revised classification of the kind presented in various papers by these authors could not survive the peer-review process of a mainstream scientific journal. The poor scholarship exemplified by these and other papers published in *Euscorpius* emphasize the importance of quality control associated with the emergent infrastructure of online publishing. A centralized register of taxa may be the only solution for ensuring quality control in the taxonomy of the future.

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> Currently, anyone can publish anything about a group as long as they can find someone to publish it (or, as has several times happened, they can set up their own journal to avoid traditional scrutiny). (Godfray and Knapp, 2004, p. 564)

> [T]echnophilia has permitted taxonomic anarchy. The ease of electronic publishing has encouraged some individuals to name electronically a plethora of dubious new species … The resultant mess will take decades to clear up. (Lee, 2002, p. 788)

> A more transparent system of peer review for Web publication is something that will be needed … to maintain quality. (Scoble, 2004, p. 702)

> Peer review is imperfect, but it is the only known instrument to screen out flawed and fraudulent research. (El-Munshid, 2001, p. 281)

The suprageneric classification of Recent (including extant) scorpions is in a state of flux. In 1980, seven families were recognized and grouped into three superfamilies, Buthoidea C.L. Koch, 1837, Chactoidea Pocock, 1893 and Scorpionoidea Latreille, 1802 (Lamoral, 1980). By 2000, between 16 and 20 families were recognized by different authors, who placed them in 4–6 superfamilies, or none at all (Table 1). Few of these classifications were based on cladistic evidence, most on nothing more than appeals to authority.

Stockwell (1989, 1992) attributed the dysfunctional state of the suprageneric classification of scorpions, where the familial assignment of specimens often required prior identification to genus, to the infrequent application of quantitative phylogenetic methods by contemporary workers. A decade later, Prendini (2000) observed that little had changed. The first quantitative phylogenetic analysis of Recent scorpions, excluding buthids, was undertaken by Stockwell (1989), but never published. Stockwell's (1989) matrix of 89 taxa and 138 morphological characters incorporated all non-buthid genera recognized at the time, a single buthid terminal taxon (a composite of the 50 buthid genera recognized at the time), seven composite fossil scorpion terminals, and composite terminals representing eurypterids, "arachnids" and xiphosurans. Stockwell's (1989) analysis identified four major clades of Recent scorpions, for which he proposed superfamilial status: Buthoidea; Chactoidea; Scorpionoidea; Vaejovoidea Thorell, 1976.

Prendini (2000, 2003a) and Prendini et al. (2003) pointed out fundamental problems with Stockwell's (1989) analysis, including the use of supraspecific terminals rather than exemplar species (Prendini, 2001a) which, given the prevalence of paraphyletic scorpion genera, reduces confidence in Stockwell's (1989) cladistic findings and, consequently, his revised classification. Nevertheless, three subsequent analyses of family level relationships among scorpions ignored these criticisms (Soleglad and Sissom, 2001; Soleglad and Fet, hereafter S&F, 2001, 2003a). The most recent of these (S&F, 2003a), published online in *Euscorpius—Occasional Publications in Scorpiology* (http://www.science.marshall.edu/fet/euscorpius/), edited by the authors, Victor Fet and Michael E. Soleglad, treated all scorpion families and proposed a radical reworking of the suprageneric classification (Table 2). The category of "parvorder" (Sibley and Monroe, 1990; McKenna and Bell, 1997) was introduced and four extant parvorders created within the scorpion infraorder Orthosterni. Six extant superfamilies, two new (Iuroidea and Pseudochactoidea), were recognized and two were synonymized (Bothriuroidea Simon, 1880; Vaejovoidea). Fourteen extant families were recognized, including a new family, Caraboctonidae (formerly Caraboctoninae in Iuridae). One family was synonymized (Troglotayosicidae Lourenço, 1998) and three were downgraded to subfamilies of other families (Diplocentridae Karsch, 1880; Hemiscorpiidae; Heteroscorpionidae Kraepelin, 1905). Subfamilies, tribes and subtribes were established within Chactidae, and various chactoid genera were transferred from one family to another.

Further revisions to the classification, some contradicting S&F's (2003a) earlier actions, were recently implemented by Fet et al. (2004a) and Soleglad et al. (2005). Fet et al. (2004a) resurrected subfamilies Bothriurinae and Lisposominae of Bothriuridae, while Soleglad et al. (2005) downgraded Urodacidae Kraepelin, 1905 to a subfamily of Scorpionidae, proposed Hemiscorpiidae Pocock, 1893 as a senior synonym of Liochelidae Fet and Bechly, 2001, and Hormurinae as a senior synonym of Liochelinae Fet and Bechly, 2001, and transferred Heteroscorpioninae to Hemiscorpiidae. In the latest contribution, Fet et al. (2005) proposed new

Table 1
Numbers of suprageneric taxa recognized in classifications of Recent (extant) scorpions proposed during the past 25 years

Author	Superfamilies	Families	Subfamilies	Tribes	Subtribes
Lamoral (1980)	3	7	–	–	–
Stockwell (1989)	4	13	16	4	–
Sissom (1990)	–	9	17	–	–
Kovařík (1998)	–	13	–	–	–
Fet et al. (2000)	–	16	16	–	–
Lourenço (2000)	6	20	16	–	–
Soleglad and Fet (2003a)	6	14	16	10	2
Soleglad et al. (2005)	6	13	18	10	2

Table 2
The suprageneric classification of Recent (extant) scorpions proposed by Soleglad and Fet (2003a) with emendations by Fet et al. (2004a) and Soleglad et al. (2005)

- Parvorder Pseudochactida Soleglad and Fet, 2003
  - Superfamily Pseudochactoidea Gromov, 1998
    - Family Pseudochactidae Gromov, 1998
- Parvorder Buthida Soleglad and Fet, 2003
  - Superfamily Buthoidea C.L. Koch, 1837
    - Family Buthidae C.L. Koch, 1837
    - Family Microcharmidae Lourenço, 1996
- Parvorder Chaerilida Soleglad and Fet, 2003
  - Superfamily Chaeriloidea Pocock, 1893
    - Family Chaerilidae Pocock, 1893
- Parvorder Iurida Soleglad and Fet, 2003
  - Superfamily Chactoidea Pocock, 1893
    - Family Chactidae Pocock, 1893
      - Subfamily Chactinae Pocock, 1893
        - Tribe Chactini Pocock, 1893
        - Tribe Nullibrotheini Soleglad and Fet, 2003
      - Subfamily Brotheinae Simon, 1879
        - Tribe Brotheini Simon, 1879
          - Subtribe Brotheina Simon, 1879
          - Subtribe Neochactina Soleglad and Fet, 2003
        - Tribe Belisariini Lourenço, 1998
      - Subfamily Uroctoninae Mello-Leitão, 1934
    - Family Euscorpiidae Laurie, 1896
      - Subfamily Euscorpiinae Laurie, 1896
      - Subfamily Megacorminae Kraepelin, 1905
        - Tribe Chactopsini Soleglad and Sissom, 2001
        - Tribe Megacormini Kraepelin, 1905
      - Subfamily Scorpiopinae Kraepelin, 1905
        - Tribe Scorpiopini Kraepelin, 1905
        - Tribe Troglocormini Soleglad and Sissom, 2001
    - Family Superstitioniidae Stahnke, 1940
      - Subfamily Superstitioniinae Stahnke, 1940
      - Subfamily Typhlochactinae Mitchell, 1971
    - Family Vaejovidae Thorell, 1876
      - Superfamily Iuroidea Thorell, 1876
    - Family Caraboctonidae Kraepelin, 1905
      - Subfamily Caraboctoninae Kraepelin, 1905
      - Subfamily Hadrurinae Stahnke, 1974
    - Family Iuridae Thorell, 1876
      - Superfamily Scorpionoidea Latreille, 1802
    - Family Bothriuridae Simon, 1880
      - Subfamily Bothriurinae Simon, 1880
      - Subfamily Lisposominae Lawrence, 1928
    - Family Hemiscorpiidae Pocock, 1893
      - Subfamily Hemiscorpiinae Pocock, 1893
      - Subfamily Heteroscorpioninae Kraepelin, 1905
      - Subfamily Hormurinae Laurie, 1896
    - Family Scorpionidae Latreille, 1802
      - Subfamily Diplocentrinae Karsch, 1880
        - Tribe Diplocentrini Karsch, 1880
        - Tribe Nebini Kraepelin, 1905
      - Subfamily Scorpioninae Latreille, 1802
      - Subfamily Urodacinae Pocock, 1893

suprageneric groupings within Buthidae, based on an analysis of six characters scored for 82 genera, but refrained from naming these groups formally.

Many of the proposed taxonomic changes are controversial. For example, S&F (2003a, 2004) placed the North American *Uroctonus* Thorell 1876, previously considered a basal vaejovid (Stockwell, 1989; Sissom, 1990, 2000a; Lourenço, 2000), in subfamily Uroctoninae of the largely Neotropical Chactidae, along with *Anuroctonus* Pocock, 1893, another North American chactoid, formerly placed in subfamily Hadrurinae (of Vaejovidae, by Stahnke, 1974; of Iuridae, by Stockwell, 1989, 1992; Lourenço, 2000; Sissom and Fet, 2000), or considered *incertae sedis* in Chactoidea (Francke and Soleglad, 1981; Sissom, 1990). In contrast to the findings of S&F (2003a), Stockwell's (1989) unpublished phylogenetic analysis, deemed "important and highly regarded" by Soleglad et al. (2005, p. 5), supported the placements of *Uroctonus* and *Anuroctonus* in the Vaejovidae and Hadrurinae (the latter placed under Caraboctonidae by S&F, 2003a), respectively.

Another controversial example is provided by *Belisarius* Simon, 1879, an eyeless endogean scorpion from the Pyrenees of France and Spain, placed in Chactidae, in an otherwise exclusively Neotropical epigean subfamily Brotheinae, by S&F (2003a). Regardless of disagreements concerning its taxonomic rank (reviewed by Coddington et al., 2004), most previous authors either suggested a possible relationship to, or grouped this genus with, other mostly eyeless endogean and hypogean scorpions, viz., *Troglotayosicus* Lourenço (1981) and/or the Typhlochactinae, all of which are currently placed in Superstitioniidae (Francke, 1982; Stockwell, 1989, 1992; Lourenço, 1998, 2000; Sissom and Cokendolpher, 1998; Fet and Sissom, 2000; Sissom, 2000b; S&F, 2003a). The latter position was also supported in Stockwell's (1989) phylogenetic analysis.

The Neotropical genus *Chactopsis* Kraepelin, 1912, first transferred to Euscorpiidae by Soleglad and Sissom (2001), presents yet another example of a genus with controversial phylogenetic placement. S&F (2003a) continue to regard this genus as a euscorpiid although it was traditionally grouped with the Neotropical chactids (Sissom, 1990; Lourenço, 2000; Sissom, 2000c), a position once again confirmed in Stockwell's (1989) analysis.

Besides removing *Chactopsis* from Chactidae, S&F (2003a, pp. 97–102) extensively revised the remaining Neotropical chactid genera. Three genera were synonymized, a new genus erected, and 48 new combinations proposed, decisions based almost entirely on an analysis of trichobothrial patterns obtained from the literature. Only seven specimens in six genera and species of Neotropical Chactidae were actually examined for this "revision" (*vide* S&F, 2003a, p. 7).

The ranking of various families and subfamilies by these authors is also questionable, particularly in view of the justification provided for doing so (S&F, 2003a, p. 86):

> Our treatment of the entire taxonomic diversity of scorpions compels us to approach the family group ranks with a degree of *balance* and *proportionality*. Thus, while we accept [the] topology of Prendini (2000), we downgrade three of his families

> in Scorpionoidea (Diplocentridae, Hemiscorpiidae, and Heteroscorpionidae) to subfamily rank (under, respectively, Scorpionidae, Liochelidae, and Urodacidae). At the same time, in an opposite move, we elevate Caraboctoninae to the family rank in Iuroidea. These taxonomic acts, in our opinion, are justified by the required *proportionality* of cladistically defined family level distinctions. While family group ranks are somewhat arbitrary, the taxonomic *balance* within superfamilies Iuroidea, Chactoidea, and Scorpionoidea is best achieved by assigning family level only to primary clades (two in Iuroidea, four in Chactoidea, and four in Scorpionoidea). From our viewpoint, retaining Hemiscorpiidae, Heteroscorpionidae, or even a traditional Diplocentridae as families would create an unnecessary emphasis on family *diversity* of Scorpionoidea—in fact, subfamilies in Chactoidea (i.e., Chactinae and Brotheinae) present deeper evolutionary *differences* than, say, those between Scorpioninae and Diplocentrinae. [italics added]

The issue, however, is not balance, proportionality, diversity or divergence, but monophyly, and the fact remains that the monophyly of many of the groups, redefined as families by S&F (2003a) and Soleglad et al. (2005), remains uncertain in spite of previous analyses. For example, Prendini (2000, 2003a) obtained two alternative placements for *Urodacus* Peters, 1861 and *Heteroscorpion* Birula, 1903, one in which they were monophyletic and another in which they were not. This finding was discussed at length by Soleglad and Sissom (2001, p. 72), S&F (2003a, pp. 115–117) and, recently, Soleglad et al. (2005), who attempted to re-examine the matter in a flawed reanalysis of Prendini's (2000) data that retrieved yet another hypothesis for the relative positions of these genera. Given the uncertainty, a prudent strategy to retain stability in the current classification would be to continue recognizing the well-supported families Heteroscorpionidae and Urodacidae as separate monophyletic units (in the absence of evidence to the contrary), rather than incorporating them into other families, and regardless of whether Scorpionoidea might then contain greater familial diversity than Chactoidea, until more data accumulate and their phylogenetic positions are more robustly supported.

Many systematists agree that stability is an important attribute of any taxonomic classification (Kluge, 1989; Kluge and Wolf, 1993; Knapp et al., 2004) or, at least, that predictivity is maximized for classifications that are stable to the addition of new data, thus equating stability with repeatability, an attribute desired throughout the sciences (Nixon and Carpenter, 1996). Changes to a classification should attempt to bring stability. Stability cannot be promoted at the expense of scientific discovery, however. Classifications must change to reflect new hypotheses of relationship (Nelson, 1972, 1973; Gaffney, 1979; Dominguez and Wheeler, 1997). New hypotheses, in turn, must be supported by rigorous, unbiased analyses of all the available evidence in order to be accepted by the scientific community. The stability of S&F's (2003a) classification and recent emendations (e.g., Fet et al., 2004a,b, 2005; S&F, 2004; Soleglad et al., 2005) therefore depends on the rigor of their phylogenetic analyses. Regrettably, the analyses presented by these authors cannot be termed rigorous or unbiased because they fail to meet the most basic standards in systematics, as we will demonstrate. In view of the significant theoretical and empirical problems with S&F's approach to cladistics, we find no justification for accepting either the results of their analyses or the revised classification derived from them. We further submit that an analysis and revised classification of the kind presented in various papers by these authors could not survive the peer-review process of a mainstream scientific journal. The poor scholarship exemplified by S&F (2003a), Fet et al. (2005), Soleglad et al. (2005), and other papers published in their self-edited online journal, *Euscorpius*, emphasize the importance of quality control associated with the emergent infrastructure of online publishing that have recently been raised by others (Hansen et al., 2000; El-Munshid, 2001; Siemens et al., 2001; Kling et al., 2002; Lee, 2002; Godfray and Knapp, 2004; Knapp et al., 2004; Scoble, 2004).

Morphological and molecular data analyzed separately

S&F (2003a) presented separate analyses of three independent datasets: a morphological dataset (discussed further below), a dataset of 55 partial 16S rDNA sequences, and a dataset of 7 partial 18S rDNA sequences (S&F, 2003a, pp. 148–154, appendix B). The choice of separate analyses by these authors is understandable, given the paucity of their molecular datasets (see below), yet inadvisable. The many advantages of simultaneous analysis compared with separate analysis have been thoroughly discussed (Crowe, 1988; Kluge, 1989, 1998; Eernisse and Kluge, 1993; Kluge and Wolf, 1993; Chippindale and Wiens, 1994; Nixon and Carpenter, 1996; Edgecombe et al., 1999, 2000; Giribet et al., 1999; Wiens, 2004) and shall not be elaborated here. The arguments of Nixon and Carpenter (1996) concerning explanatory power, character independence and the emergence of secondary signals are considered sufficient justification for this approach. Besides the obvious advantage of a phylogenetic hypothesis based on all available evidence, the information provided by independent data sets can assist in resolving relationships at different levels in the tree, the common signal between them can be amplified, thus reducing noise, and characters included in the combined matrix can be reinterpreted during the analysis, thereby supporting clades that were not present in the partitioned data sets. Insofar as S&F's (2003a) phylogenetic hypothesis, and the classification derived from it are not based on a simultaneous analysis of the morphological, 16S rDNA and 18S rDNA data available, they lack explanatory power, i.e., fail to accomplish the goal of phylogenetic analysis, which is to account for all available evidence (Farris, 1983, 1986; Farris and Kluge, 1985, 1986). These criticisms apply equally to the analyses by S&F (2001) and Fet et al. (2003, 2005).

Poor taxon sampling

S&F (2003a, pp. 65, 80, 116) followed Soleglad and Sissom (2001, p. 72) in criticizing the taxon sampling strategy of Prendini (2000) as part of their rejection of the exemplar approach (also discussed further below). However, the taxon sample for the molecular analyses presented by these authors scarcely meets their own specifications:

> … that any demonstrated monophyly can be convincing only if the designated groups are well represented. (S&F, 2003a, p. 65)

In the 16S rDNA dataset, for example, the 80 genera and more than 680 extant species of Buthidae were represented by only 17 (21%) genera and 23 (3%) species, the 10 genera and *c.* 155 species of Vaejovidae (including *Uroctonus*) by only 4 (40%) genera and 16 (10%) species, the 11 genera and more than 60 species of "Euscorpiidae" by only 8 (13%) species, all in a single genus, and the *c.* 20 species of Chaerilidae by a single species (counts obtained on 8 August 2005 from the *Synopsis of Described Scorpions of the World*, http://insects.tamu.edu/research/collection/hallan/acari/Scorpiones1.htm, and *The Scorpion Files*, http://www.ub.ntnu.no/scorpion-files/). The entire 16S rDNA dataset presented by S&F (2003a) comprised 27 genera and 55 species, just 16% and 4% of the total generic (165) and species (*c.* 1500) diversity of Scorpiones, whereas the 18S rDNA dataset comprised seven genera and species, a mere 4% and 0.5%, respectively. Neither of the molecular datasets presented by S&F (2003a) contained any Chactidae (other than *Anuroctonus*, the placement in Chactidae of which remains to be rigorously tested), Old World Iuridae, Superstitioniidae, Bothriuridae or any other Scorpionoidea, despite the fact that sequences for at least some of these taxa were available in GenBank at the time of the study (e.g., Prendini et al., 2003). Many of the taxa omitted are pivotal to resolving the internal phylogeny of scorpions and testing the monophyly of families and subfamilies proposed by S&F (2003a). Similar criticisms apply to the analysis of buthid phylogeny by Fet et al. (2003), also published in *Euscorpius*, which was based on 400–450 base-pairs of 16S rDNA from 17 buthid species (Coddington et al., 2004).

Morphological data partitioned and discarded

Related to the issue of separate versus simultaneous analysis is S&F's (2003a) treatment of their morphological data. Two morphological matrices, each scored for the same 60 terminal taxa, were presented. The first matrix (reproduced here as Table 3 and Appendix 1) contains 62 trichobothrial "existence" characters, each specifying the absence, presence and relative size ("petite" or full size) of the so-called fundamental trichobothria on the pedipalps of scorpions. In the second matrix (reproduced here as Table 4 and Appendix 2), these 62 characters (52 binary and 10 tristate) were converted into a single character, with six ordered states, defining trichobothrial "types" (character 1), to which 104 additional morphological characters were added. In total, S&F (2003a) presented 167 morphological characters, the 63rd of which replaces the preceding 62. No justification was provided for the decision not to analyze the 62 trichobothrial "existence" characters simultaneously with the other 104 characters but, instead, to replace them with a single ordered character that does not exactly portray real observations. However, a clue as to why this was done is provided in a discussion on character weighting by Soleglad et al. (2005, p. 5):

> The temptation to assign *a priori* weights is understandable … For example, no scorpiologist would consider the relative evolutionary significance of the presence or absence of cheliceral serrulae to be equivalent, for example, to fundamental orthobothriotaxic patterns. Surely the latter is a *much more important* evolutionary event and any systematist would certainly want it to have more influence on the branching process. [italics added]

These authors claim to have prior knowledge about the relative evolutionary importance of characters and decided which characters to exclude from, or weight differentially in their analyses based on a perceived "numerical imbalance":

> Selective *a priori* weighting can be applied also if the systematist believes there is a numerical imbalance across the character set. (Soleglad et al., 2005, p. 5)

Such decisions cannot be justified in the accepted paradigm of phylogenetic analysis, however, which demands that all evidence bearing on a hypothesis be included and weighted equally in an analysis, at least *a priori* (Farris, 1983, 1986; Farris and Kluge, 1985, 1986). Discarding characters ignores potentially informative data (Kearney and Clark, 2003; Malia et al., 2003), whereas weighting characters *a priori* increases the background knowledge of a phylogenetic hypothesis. The end result of both procedures is a reduction in empirical content (Kluge, 1989, 1997; Siebert, 1992; Brower, 1999, 2000; Frost et al., 2001).

Table 3
Orthobothriotaxy character matrix of Soleglad and Fet (2003a, p. 68, table 4): 62 trichobothria "existence" characters (listed in Appendix 1). Character states, weighted using Sankoff optimization, are scored 0 (trichobothrium absent) ↔ 1 (trichobothrium present, petite in size) ↔ 2 (trichobothrium present, full size), i.e., two steps are required to transform from state 0 to state 2 and vice versa

	1 10 20 30 40 50 60
Palaeopisthacanthidae	00000000202222002200002222002000020000000002000000000220020020
Archaeobuthus	00200200222222002200002000202200220000002022000002200222220020
Pseudochactas	22200200202222002200002000202220022000200022200000222222222220
Chaerilus	22200200222222202200002000222200022000202022202222200020222222
Centruroides	02200200212222102200102200202222122000202022200002211212222200
Isometrus	02200200212222102200102200202222122000202022200002211212222200
Tityus	02200200212222102200102200202222122000202022200002211212222200
Microtityus	02200200212222102200102200202222122000202022200002211212222200
Mesobuthus	02200200212222102200102200202222122000202022200002211212222200
Androctonus	02200200212222102200102200202222122000202022200002211212222200
Karasbergia	02200200212222102200102200202222022000202022200002211202222200
Orthochirus	02200200212222102200102200202222122000202022200002211202222200
Microbuthus	02200200212222002200002200202222122000202022200002211202222200
Liobuthus	02200200212222102200102200202222122000202022200002211212222200
Grosphus	02200200212222102200102200202222122000202022200002211212222200
Lychas	02200200212222102200102200202222122000202022200002211212222200
Uroplectes	02200200212222102200102200202222122000202022200002211212222200
Microcharmus	02200200212222102200102200202222122000202022200002211212222200
Iurus	22222222212222211222122122202200021222212222122222000200002000
Calchas	22222222212222211222122122202200021222212222122222000200002000
Hadruroides	22222222222222212222122222202200022222212222222222000200002000
Hadrurus	22222222222222212222122222202200022222212222222222000200002000
Bothriurus	22222222222222212222122222202200022222212222222222000200002000
Brachistosternus	22222222222222212222122222202200022222212222222222000200002000
Cercophonius	22222222222222212222122222202200022222212222222222000200002000
Phoniocercus	22222222222222212222122222202200022222212222222222000200002000
Centromachetes	22222222222222212222122222202200022222212222222222000200002000
Hadogenes	22222222222222212222122222202200022222212222222222000200002000
Liocheles	22222222222222212222122222202200022222212222222222000200002000
Hemiscorpius	22222222222222212222122222202200022222212222222222000200002000
Scorpio	22222222222222212222122222202200022222212222222222000200002000
Diplocentrus	22222222222222212222122222202200022222212222222222000200002000
Urodacus	22222222222222212222122222202200022222212222222222000200002000
Euscorpius	22222222222222212222122222202200022222212222222222000200002000
Megacormus	22222222222222212222122222202200022222212222222222000200002000
Chactopsis	22222222222222212222122222202200022222212222222222000200002000
Scorpiops	22222222222222212222122222202200022222212222222222000200002000
Troglocormus	22222222222222212222122222202200022222212222222222000200002000
Belisarius	22222222222222212222122222202200022222212222222222000200002000
Brotheas	22222222222222212222122222202200022222212222222222000200002000
Neochactas	22222222222222212222122222202200022222212222222222000200002000
Chactas	22222222222222212222122222202200022222212222222222000200002000
Teuthraustes	22222222222222212222122222202200022222212222222222000200002000
Nullibrotheas	22222222222222212222122222202200022222212222222222000200002000
Anuroctonus	22222222222222212222122222202200022222212222222222000200002000
Uroctonus	22222222222222212222122222202200022222212222222222000200002000
Superstitionia	22222222222222212222122222202200022222212222222222000200002000
Troglotayosicus	22222222222222212222122222202200022222212222222222000200002000
Typhlochactas	22222222222222212222122222202200022222212222222222000200002000
Alacran	22222222222222212222122222202200022222212222222222000200002000
Vaejovis nitidulus	22222222222222212222122222202200022222212222222222000200002000
Vaejovis eusthenura	22222222222222212222122222202200022222212222222222000200002000
Vaejovis punctipalpi	22222222222222212222122222202200022222212222222222000200002000
Smeringurus	22222222222222212222122222202200022222212222222222000200002000
Paruroctonus	22222222222222212222122222202200022222212222222222000200002000
Vejovoidus	22222222222222212222122222202200022222212222222222000200002000
Paravaejovis	22222222222222212222122222202200022222212222222222000200002000
Pseudouroctonus	22222222222222212222122222202200022222212222222222000200002000
Serradigitus	22222222222222212222122222202200022222212222222222000200002000
Syntropis	22222222222222212222122222202200022222212222222222000200002000

Table 4
Main character matrix of Soleglad and Fet (2003a, p. 66, table 3). Character states are scored 0–9, a–d, ? (unknown) or – (inapplicable). Refer to Appendix 2 for character descriptions. Ordered six-state character 1 replaces the 62 existence characters representing orthobothriotaxy (Table 3, Appendix 1)

	1 10 20 30 40 50 60 70 80 90 100
Palaeopisthacanthidae	00------------------------------------0000-00-0----0----0-0??-00-----0000-?-----??00000-00???00---??0----
Archaeobuthus	1000----------------------------------1???-3?-0----0----?-200-00-----????-?-----????0??-?????01---??0----
Pseudochactas	2100----------------------------------1200-00-0----0----1-000-00-----000?-?-----0010011-1000-00---0?1----
Chaerilus	412---------0---------0---------------1000-10-0----0----2-200-01-----1001-0-----0011011-2000-10---1000---
Centruroides	3221-------------------------00-------1101-01-0----1----2-200-021----0012-0------011021-2100-01---112----
Isometrus	3110-------------------------00-------1101-01-0----0----2-200-020----0012-0------011021-2100-01---112----
Tityus	3221-------------------------00-------1101-01-0----0----2-200-021----0012-0------011021-2100-01---112----
Microtityus	3221-------------------------00-------1101-01-0----0----2-200-020----0012-0------011021-2100-01---112----
Mesobuthus	3110-------------------------00-------1101-01-0----0----2-000-020----0012-0------011021-2000-01---112----
Androctonus	3110-------------------------00-------1101-01-0----0----2-000-020----0012-0------011021-2000-01---112----
Karasbergia	322--------------------------00-------1101-02-0----0----2-000-020----0012-0------0110??-2000-???--112----
Orthochirus	311--------------------------00-------1101-01-0----0----2-000-020----0012-0------011021-2000-01---112----
Microbuthus	311--------------------------00-------1101-01-0----0----2-000-020----0012-0------011021-2000-01---112----
Liobuthus	3000-------------------------11-------1101-01-0----0----2-200-020----0012-0------011021-2000-01---112----
Grosphus	3221-------------------------00-------1101-01-0----0----2-000-020----0012-0------011021-2000-01---112----
Lychas	3110-------------------------00-------1101-01-0----0----2-000-020----0012-0------011021-2100-01---112----
Uroplectes	3221-------------------------00-------1101-01-0----0----2-000-020----0012-0------011021-2100-01---112----
Microcharmus	3221-------------------------00-------1101-01-0----0----2-100-020----0012-0------011021-2000-01---111----
Iurus	5---0-010-40110000----110------00000---002-0200-000--0--3-200-1--0-0000030000---??11011-2000-2000-1041---
Calchas	5---0-010-40110000----110------00000---002-0200-000--0--3-000-1--0-0000030000---0011011-2000-2000-0030---
Hadruroides	5---0-000000101110----101------00001---012-0200-000--0--3-200-1--0-0000230000---1011012-2010-2000-1031---
Hadrurus	5---0-000000101110----101------11111---012-0200-000--0--3-200-1--0-0000230000---3011012-2010-2000-1041---
Bothriurus	5---0-001232000110----001------20000--4003002010030-00--4-220-1--1-0000031120---?211011-201202000-1051---
Brachistosternus	5---0-001230000110----001------20000--4023002010030-00--4-220-1--1-0000031120---?211011-201202000-1061---
Cercophonius	5---0-001230000110----001------20000--4023002010030-10--4-220-1--1-0000031120---?211011-201202000-1051---
Phoniocercus	5---0-001232000110----001------20000--4023002010000-00--4-210-1--1-0000031120---?211011-201202000-1051---
Centromachetes	5---0-001232000110----001------20000--4023002010030-10--4-220-1--1-0000031120---?211011-201202000-1051---
Hadogenes	5---0-0?000?20011?----001------44044--5003002010030-10--4-210-1--021001030120---?111031-201112001-0061---
Liocheles	5---0-000000200111----001------00000--5003002010030-10--4-210-1--021001030120---?111031-201112001-0051---
Hemiscorpius	5---0-000000000111----001------00000--5003002010030-10--4-210-1--031000030120---?111111-201112001-0061---
Scorpio	5---0-000000000111----001------00000--4003002010030-00--4-211-1--020000030120---2111011-201102000-1061---
Diplocentrus	5---0-000000000111----001------00000--4003002010030-20--4-211-1--020000030120---2111011-221102000-1061---
Urodacus	5---0-0?000?20011?----001------33033--4003002010030-10--4-211-1--020000030120---?111211-201102000-1053---
Euscorpius	5---0010012100011001000010000--a00aa--2033002010110--0-05020001--0000000300110001411341020103200011082000
Megacormus	5---0010012100011001000010000--000aa--3033102010111--0-05020011--0000000300110001411311020103200011082030
Chactopsis	5---00100151?21110?1300010000--000aa--2033102010111--0-05020011--00000003?0?????4110110201032000001082030
Scorpiops	5---0000012100011001200010020--000bb--3033202010112--0-05020001--0100000300101101411011020113200011085042
Troglocormus	5---0010012100011001200010020--000bb--3033202110112--0-05020001--0100000300101101411011020113200011082002
Belisarius	5---1101012100011031000010001--00000---033002010000--00051200-1--0-0000030010110?51101102010220000107202?
Brotheas	5---1101012100011051110010001--00088---033002010000--00051200-1--0-000003001011015110110201022000010a2001
Neochactas	5---1101012100011041000010001--00088---033002010000--00051200-1--0-00000300101101511011020102200001072001
Chactas	5---1101012100011021000010010--0007700-033002010020--0105020001--0-00000300101101511011020102200001072001
Teuthraustes	5---1101012100011021000010010--0007700-033002010020--0115020001--0-00000300101??151101102010220000107200 1
Nullibrotheas	5---1101012100011021000010010--0007711-033402010000--0005020001--0-00000300101101511013020112200001072000
Anuroctonus	5---1101012100011001000010001--90099---033302010000--0005020001--0-00000300000001511011020112200021094000
Uroctonus	5---1101012100011001000010001--00000---033302010000--0205020001--0-00000300100001511011020112200021094000
Superstitionia	5---0001011100011010--1011100--00000---033002011000--1-052200-1--0500000300100001411051120102200001082000
Troglotayosicus	5---1101011100011010--1011100--00000---03302201?000--1-054200-1--05?00003?0??0????110?10201??20000107201?
Typhlochactas	5---0100011100011010--0211100--00000---043002011000--0-053230-1--040100030010020141105102010220000108201?
Alacran	5---0100016133011010--0010100--0d00d---033022011000--0-053230-1--04010003001002 0?4110510201??20000108201?
Vaejovis nitidulus	5---0-00000000011000--101010---0000c---033002010000--0-05020001--0-000003001000113110111201142010-10a1100
Vaejovis eusthenura	5---0-00000000011000--101010---00000---033002010000--0-05020021--0-000003001000111110111201042010-10a1100
Vaejovis punctipalpi	5---0-00000000011000--101010---00000---033002010000--0-05020021--0-000003001000111110111201042010-10a1100
Smeringurus	5---0-00000000011000--101010---00000---033502210000--0-05020001--0-000003001000113110110201042010-10a1100
Paruroctonus	5---0-00000000011000--101010---00000---033502210000--0-05020001--0-000003001000113110110201042010-10a1100
Vejovoidus	5---0-00000000011000--101010---00000---033002210000--0-050200?1--0-000003001000113115141201042010-10a1100
Paravaejovis	5---1-00000000011000--101010---c0000---033002010000--0-05020001--0-00000300100011?110111201042010-1091100
Pseudouroctonus	5---0-00000000011000--101010---00000---033602210000--0-05020021--0-000003001000113110111201152010-10a1100
Serradigitus	5---0-00000000011000--101010---00000---033002010000--0-05020001--0-000003001000111110111201042010-10a1100
Syntropis	5---0-00000000011000--101010---00000---033002010000--0-05020021--0-00000300100011111461120 1??2010-10a1100

Besides partitioning their morphological data into two matrices, S&F (2003a) performed an analysis of a reduced dataset comprising 33 (20%) of their morphological characters (Appendix 2):

> … fundamental characters, which, in our opinion, provide the most precise, clear delineation of upper-level divisions in Recent scorpions. (S&F, 2003a, p. 69)

The original cladograms retrieved by S&F's (2003a) morphological analyses were not provided for scrutiny but we assume that their classification is based largely on the analysis of these "fundamental" characters, representing only one fifth of their morphological dataset. S&F's (2003a, p. 71) showcase fig. 114, presenting the phylogeny of Recent scorpions to the level of family, is derived from their "fundamental" character analysis and so, presumably, are figs 115 and 116 (S&F, 2003a, pp. 78, 81), respectively portraying the phylogeny of the buthoid and chactoid branches of their tree. Setting aside the question of how S&F (2003a) decided which characters are "fundamental", this action, tantamount to the long discredited method of clique or compatibility analysis (LeQuesne, 1969; Estabrook et al., 1976a,b; Meacham and Estabrook, 1985), again reduces the explanatory power of their analysis and classification. Besides the philosophical objection to throwing away or ignoring data, the tree constructed from the subsample of "fundamental" characters may be globally unparsimonious because characters excluded from the analysis *a priori* can fit the tree only with extra steps *a posteriori* (Farris and Kluge, 1979; Siebert, 1992; Schuh, 2000).

Supraspecific taxa versus species as terminals

In the abstract of their paper, S&F (2003a, p. 1) state:

> We conducted a comprehensive, cladistic morphological analysis of 90 extant genera (over 150 species) of scorpions belonging to all recognized families.

In reality, their matrices comprise 60 terminals, representing only 56 extant scorpion genera, assembled from observations of 75 species, respectively 34% and 5% of the total generic and species diversity of extant Scorpiones (Table 5). One genus (*Vaejovis* C.L. Koch, 1836) was represented by three terminals, for the eusthenura, nitidulus and punctipalpi species groups. A further 37 genera and 78 species were allegedly examined, but were not scored for the phylogenetic analysis (S&F, 2003a, pp. 6–9, 67).

Soleglad (*vide* S&F, 2001, 2003a; Soleglad and Sissom, 2001; Fet et al., 2005; Soleglad et al., 2005) continues to reject exemplar species in favor of supraspecific terminal taxa, despite widespread condemnation thereof in the mainstream systematics literature (Yeates, 1995; Kron and Judd, 1997; Bininda-Emonds et al., 1998; Griswold et al., 1998; Wiens, 1998a; Prendini, 2001a, 2003a; Simmons, 2001; Giribet, 2002; Malia et al., 2003; Prendini et al., 2003; Kaila, 2004). According to Soleglad and Sissom (2001, p. 72):

> … the exemplar approach employed in [Prendini's (2000)] analysis probably did not provide enough taxa to ascertain in detail the patterns and extent of neobothriotaxic conditions … (less than 20% of scorpionoid species were actually evaluated).

This statement amounts to a criticism of taxon sampling, not a criticism of the use of exemplars *per se*, but the argument is simplistic. It is not the quantity of exemplar species that matters, so much as the extent to which they encompass the character diversity within the group they represent. It is well known that the derived character states of some species reduce their utility as representatives of the groundplans of higher taxa (Donoghue et al., 1989; Lecointre et al., 1993; Doyle et al., 1994; Adachi and Hasegawa, 1995). This, in turn, is the reason exemplars are not selected randomly but rather according to specific criteria, some of which are concerned with representing higher taxa in a manner that will provide the strongest test of monophyly (Yeates, 1995; Griswold et al., 1998; Prendini, 2000, 2001a). This particular issue also seems to concern S&F (2003a, pp. 65, 80, 116):

> It is important to note here that ample taxa representation from all major scorpion groups is necessary in order to convincingly show monophyly of groups of interest. Using a token ("exemplar") species here or there does not meet this requirement. (S&F, 2003a, p. 80)

Further, it is erroneous to equate the use of exemplars with the inclusion of two or three species per genus or higher taxon, as suggested by Soleglad and Sissom (2001), S&F (2003a) and, more recently, Soleglad et al. (2005, p. 28):

> There is a tendency in Prendini's (2000, 2003a, 2003b) analytic methodology to approach cladistic analysis in a somewhat rote, cook-book manner—the choice of two or three species per genus regardless of the genus size or complexity (adherence to the "exemplar method") …

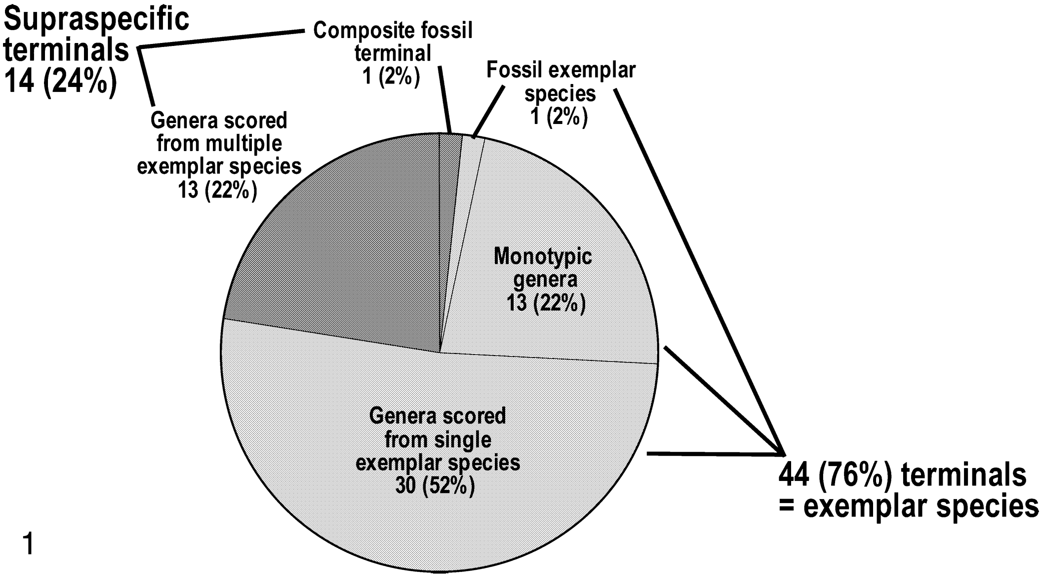
Prendini (2001a, p. 297) explicitly recommended a *minimum* sample of two exemplars to test monophyly, and added that more than two is desirable for representing diverse groups, in which interspecific variation is prevalent. Nevertheless, a sample of two morphologically diverse exemplar species is more defensible philosophically than a supraspecific terminal constructed from observations of 20 species (indeed, the more taxonomically inclusive a supraspecific terminal, the less defensible it becomes), for reasons expounded elsewhere (Prendini, 2000, 2001a, 2003a; Prendini et al., 2003).

Table 5
Terminal taxa (boldface) used in morphological character matrices by Soleglad and Fet (2003a), and the exemplar species on which their observations were based, determined from the "Material examined" section (pp. 6–9)

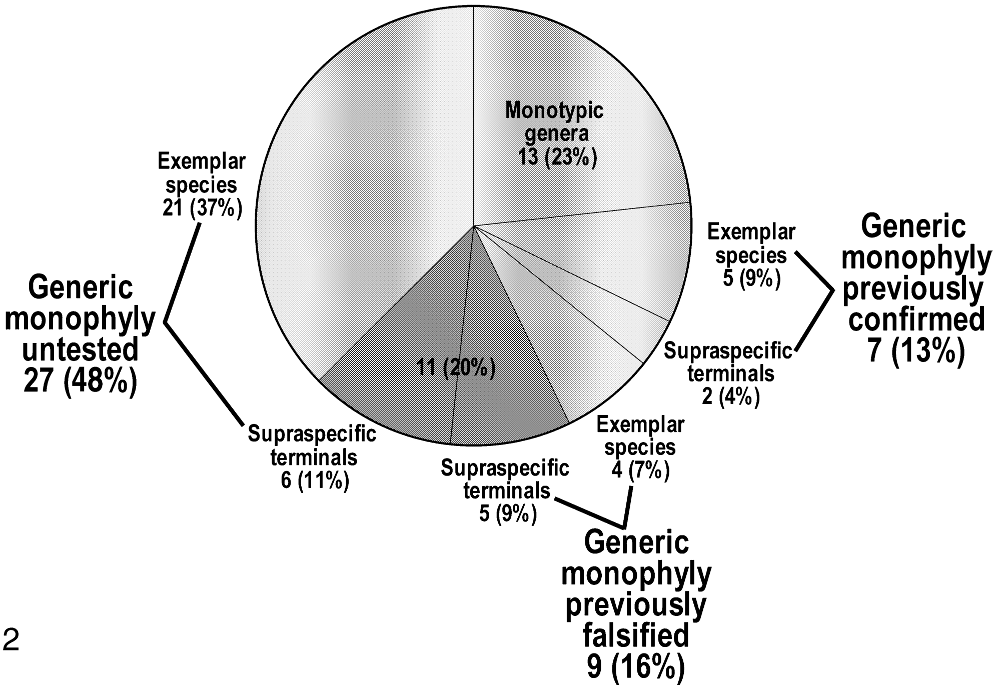
Palaeopisthacanthidae Kjellesvig-Waering, 1986: Composite of *Palaeopisthacanthus schucherti* Petrunkevitch, 1913, *P. vogelandurdeni* Jeram, 1994, *Compsoscorpius elegans* Petrunkevitch, 1949, *Cryptoscorpius americanus* Jeram, 1994; ***Archaeobuthus* Lourenço, 2001[1]:** *A. estephani* Lourenço, 2001; ***Pseudochactas* Gromov, 1998[1]:** *P. ovchinnikovi* Gromov, 1998; ***Chaerilus* Simon, 1877:** *C. variegatus* Simon, 1877[3], *C. celebensis* Pocock, 1894, *C. petrzelkai* Kovařík, 2000 [*C. tichyi* Kovařík, 2000, *C. tryznai* Kovařík, 2000 examined but not scored]; ***Centruroides* Marx, 1890[2]:** *C. exilicauda* (Wood, 1863) [*C. anchorellus* Armas, 1976, *C. hentzi* (Banks, 1910) examined but not scored]; ***Isometrus* Ehrenberg, 1828[2]:** *I. maculatus* (DeGeer, 1778) [*Isometrus* sp., probably *I. melanodactylus* (L. Koch, 1867), examined but not scored]; ***Tityus* C.L. Koch, 1836[2]:** *T. nematochirus* Mello-Leitão, 1940; ***Microtityus* Kjellesvig-Waering, 1966[2]:** *M. jaumei* Armas, 1974; ***Mesobuthus* Vachon, 1950:** *M. caucasicus* (Nordmann, 1840)[3], *M. eupeus* (C.L. Koch, 1839); ***Androctonus* Ehrenberg, 1828[2]:** *A. bicolor* Ehrenberg, 1828; ***Karasbergia* Hewitt, 1913[1]:** *K. methueni* Hewitt, 1913; ***Orthochirus* Karsch, 1891[2]:** *O. scrobiculosus* (Grube, 1873); ***Microbuthus* Kraepelin, 1898[2]:** *Microbuthus* sp. [based on locality data, probably *M. pusillus* Kraepelin, 1898]; ***Liobuthus* Birula, 1898[1]:** *L. kessleri* Birula, 1898; ***Grosphus* Simon, 1880:** *G. hirtus* Kraepelin, 1901[3], *G. bistriatus* Kraepelin, 1900; ***Lychas* C.L. Koch, 1845:** *Lychas* spp. [based on locality data, probably *L. mucronatus* (Fabricius, 1798), *L. perfidus* (Keyserling, 1885), and *L. scutilus* C.L. Koch, 1845]; ***Uroplectes* Peters, 1861[2]:** *U. vittatus* (Thorell, 1876); ***Microcharmus* Lourenço, 1995[2]:** *M. hauseri* Lourenço, 1996; ***Iurus* Thorell, 1876[1]:** *I. dufoureius* (Brullé, 1832); ***Calchas* Birula, 1899[1]:** *C. nordmanni* Birula, 1899; ***Hadruroides* Pocock, 1893:** *H. maculatus* (Thorell, 1876)[3], *H. charcasus* (Karsch, 1879); ***Hadrurus* Thorell, 1876:** *H. obscurus* Williams, 1970[3], *H. aztecus* Pocock, 1902, *H. hirsutus* (Wood, 1863) [*H. arizonensis* Ewing, 1928, *H. concolor* Stahnke, 1969, *H. pinteri* Stahnke, 1969 examined but not scored]; ***Bothriurus* Peters, 1861:** *B. burmeisteri* Kraepelin, 1894[3], *B. araguayae* Vellard, 1934; ***Brachistosternus* Pocock, 1893[2]**: *B. ehrenbergii* (Gervais, 1841); ***Cercophonius* Peters, 1861[2]:** *C. squama* (Gervais, 1843), *Cercophonius* sp. [based on locality data, probably also *C. squama*]; ***Phoniocercus* Pocock, 1893[2]:** *P. pictus* Pocock, 1893 [*P. sanmartini* Cekalovic, 1973 examined but not scored]; ***Centromachetes* Lönnberg, 1897[2]:** *C. pocockii* (Kraepelin, 1894); ***Hadogenes* Kraepelin, 1894[2]:** *H. troglodytes* (Peters, 1861) [misidentification, based on locality data; probably *H. gunningi* Purcell, 1899]; ***Liocheles* Sundevall, 1833:** *Liocheles* spp. [potentially *L. karschii* (Keyserling, 1885) and *L. penta* Francke & Lourenço, 1991][3], *L. australasiae* (Fabricius, 1775); ***Hemiscorpius* Peters, 1861[2]:** *H. maindroni* (Kraepelin, 1900); ***Scorpio* Linnaeus, 1758:** *S. maurus* Linnaeus, 1758; ***Diplocentrus* Peters, 1861[2]:** *D. ochoterenai* Hoffmann, 1931 [*D. whitei* (Gervais, 1844) examined but not scored]; ***Urodacus* Peters, 1861[2]:** *U. manicatus* (Thorell, 1876); ***Euscorpius* Thorell, 1876:** *E. italicus* (Herbst, 1800)[3], *E. tergestinus* (C.L. Koch, 1837), *E. mingrelicus* (Kessler, 1874) [*E. flavicaudis* (DeGeer, 1778), *E. gamma* (Caporiacco, 1950), *E. naupliensis* (C.L. Koch, 1837) examined but not scored]; ***Megacormus* Karsch, 1881[2]:** *M. gertschi* Díaz Nájera, 1966 [*M. granosus* (Gervais, 1843) examined but not scored]; ***Chactopsis* Kraepelin, 1912[2]:** *C. insignis* Kraepelin, 1912; ***Scorpiops* Peters, 1861[2]:** *S. tibetanus* Hirst, 1911; ***Troglocormus* Francke, 1981[2]:** *T. willis* Francke, 1981; ***Belisarius* Simon, 1879[1]:** *B. xambeui* Simon, 1879; ***Brotheas* C.L. Koch, 1837[2]:** *B. granulatus* Simon, 1877; ***Neochactas* Soleglad and Fet, 2003[2]:** *N. delicatus* (Karsch, 1879); ***Chactas* Gervais, 1844[2]:** *Chactas* sp. [based on locality data, probably *C. exsul* (Werner, 1939)]; ***Teuthraustes* Simon, 1878[2]:** *T. oculatus* Pocock, 1900; ***Nullibrotheas* Williams, 1974[1]:** *N. allenii* (Wood, 1863); ***Anuroctonus* Pocock, 1893:** *A. phaiodactylus* (Wood, 1863)[3], *Anuroctonus* sp.; ***Uroctonus* Thorell, 1876[2]:** *U. mordax mordax* Thorell, 1876, *U. mordax pluridens* Hjelle, 1972 [treated as *U. mordax*]; ***Superstitionia* Stahnke, 1940[1]:** *S. donensis* Stahnke, 1940; ***Troglotayosicus* Lourenço, 1981[1]:** *T. vachoni* Lourenço, 1981 [not examined]; ***Typhlochactas* Mitchell, 1971[2]:** Composite of all six species and, apparently, also *Sotanochactas elliotti* (Mitchell, 1971) *vide* Soleglad and Fet (2003a, p. 141) [none examined]; ***Alacran* Francke, 1982[1]:** *A. tartarus* Francke, 1982; ***Vaejovis nitidulus* C.L. Koch, 1843[2]:** *V. nitidulus* [*V. nigrescens* Pocock, 1898, *V. solegladi* Sissom, 1991 examined but not scored]; ***V. eusthenura* (Wood, 1863)[2]:** *V. eusthenura* [*V. gravicaudus* Williams, 1970, *V. punctatus* Karsch, 1879, *V. puritanus* Gertsch, 1958, *V. spinigerus* (Wood, 1863), *V. viscainensis* Williams, 1970, *V. vittatus* Williams, 1970, *V. waeringi* Williams, 1970 examined but not scored]; ***V. punctipalpi* (Wood, 1863)[2]:** *V. punctipalpi* [*V. bruneus* Williams, 1970, *V. cazieri* Williams, 1968, *V. hirsuticauda* Banks, 1910 examined but not scored]; ***Smeringurus* Haradon, 1983:** *S. aridus* (Soleglad, 1972), *S. grandis* (Williams, 1970), *S. mesaensis* (Stahnke, 1957); ***Paruroctonus* Werner, 1934[2]:** *P. silvestrii* (Borelli, 1909) [*P. arnaudi* Williams, 1972, *P. boreus* (Girard, 1854), *P. gracilior* (Hoffmann, 1931), *P. luteolus* (Gertsch and Soleglad, 1966), *P. stahnkei* (Gertsch and Soleglad, 1966) examined but not scored]; ***Vejovoidus* Stahnke, 1974[1]:** *V. longiunguis* (Williams, 1969); ***Paravaejovis* Williams, 1980[1]:** *P. pumilis* (Williams, 1970); ***Pseudouroctonus* Stahnke, 1974[2]:** *P. reddelli* (Gertsch and Soleglad, 1972) [*P. andreas* (Gertsch and Soleglad, 1972), *P. angelenus* (Gertsch and Soleglad, 1972), *P. apacheanus* (Gertsch and Soleglad, 1972), *P. minimus castaneus* (Gertsch and Soleglad, 1972) examined but not scored]; ***Serradigitus* Stahnke, 1974[2]:** *S. subtilimanus* (Soleglad, 1972) [*S. calidus* (Soleglad, 1974), *S. gertschi gertschi* (Williams, 1968), *S. joshuaensis* (Soleglad, 1972), *S. minutis* (Williams, 1970), *S. wupatkiensis* (Stahnke, 1940) examined but not scored]; ***Syntropis* Kraepelin, 1900[1]:** *S. macrura* Kraepelin, 1900.

[1] Monotypic genera. [2] Terminals based on observations from a single species. [3] Species from which most characters were scored in terminals based on observations from more than one species, according to the "Taxa Set" section (pp. 65, 67).

Although S&F (2003a) rejected the exemplar approach, 44 (76%) of the terminal taxa in their sample are, in fact, exemplar species (Fig. 1): 13 (22%) of the extant genera represented in their analysis are monotypic and 30 (52%) of the "genera" that are not monotypic were based on scores from a single species (Table 5). No criteria were provided for the selection of these exemplar species, however. As such, we doubt that S&F (2003a) have met their commitment to "convincingly demonstrate" monophyly by adequate taxon representation, an opinion further supported by the observation that 14 (24%) of the taxa in their analysis are supraspecific terminals, amalgamations of observations scored from more than one exemplar species (Table 5, Fig. 1). One of these (*Typhlochactas*) is an explicit composite of all species in the genus and its putative sister genus, *Sotanochactas* Francke, 1986, based entirely on observations from the literature; no specimens of either genus were examined (S&F, 2003a, p. 67). The problems with using such composite terminals have been elaborated by several authors (Nixon and Carpenter, 1993; Yeates, 1995; Kron and Judd, 1997; Griswold et al., 1998; Wiens, 1998a, 2000; Prendini, 2001a, 2003a; Simmons, 2001; Giribet, 2002; Prendini



1



2

Figures 1, 2. Taxonomic sampling in Soleglad and Fet's (2003a) analysis. Refer to Table 5 for list of taxa. 1. The relative proportions of exemplar species and supraspecific terminal taxa in the analysis. 2. The relative proportions of genera, the monophyly of which has been confirmed, falsified or is presently untested.

et al., 2003; Kaila, 2004) and include: loss of information resulting from the conversion of characters pertaining to multiple exemplar species into single supraspecific terminals; low potential for repeatability of this process, e.g., it is unclear from S&F's (2003a) methodological discussion how decisions regarding character polarity were made, and interspecific variation accommodated, *a priori*; the fact that the monophyly of genera (or higher taxa) was assumed, rather than tested in the analysis; the implications this could have for resolving (rather than assuming) the ancestral states of the supraspecific taxa (genera) in the course of a global analysis.

S&F (2003a) stress the importance of monophyly in taxon sampling but make no attempt to test the monophyly of their supraspecific terminal taxa or to consider the implications of not doing so. Of the 43 extant genera in their matrix that actually contain more than one species (Fet et al., 2000), the monophyly of only 7 (12.5%) has been confirmed cladistically (Fig. 2): *Brachistosternus*, *Centromachetes*, *Hadogenes*, *Liocheles*, *Phoniocercus*, *Scorpio*, *Urodacus* (Prendini, 2000). Monophyly of the remaining 36 (64% of the genera included in the study by S&F, 2003a) has either been falsified (Prendini, 2000) or is presently untested, but about half of all scorpion genera may not be monophyletic (Prendini, 2000). A prudent approach would therefore be to claim ignorance, rather than making assumptions about the monophyly of the terminal taxa, and score a defensible set of carefully selected exemplar species as representatives for the genera in which they are currently placed. These points are clearly lost on S&F, however, who continue to flog a dead horse in their latest discussion on the "use of generic names as terminal tokens" (Fet et al., 2005, p. 19):

> We need to stress here that the use of generic names as terminal taxa in the cladograms presented in this analysis, and analyses in previous publications for that matter (e.g., Soleglad and Fet, 2003[a], etc.) does not necessarily imply monophyly of these genera. This should be particularly clear when … the actual species set used for the cladistic analysis of that genus is *specifically stated*, and in many cases only one or two species were considered. It is clear that monophyly for a given genus can *only* be demonstrated if and only if a competent detailed species-level cladistic analysis is conducted which includes all species defined under that genus and select individuals from all immediate putative sister genera are included as outgroups; as for example, recently presented in Prendini's [2004] impressive analysis of genus *Pseudolychas* which included all three species. Therefore, we emphasize here that the use of no less than 82 generic names in our cladograms in this paper certainly does not state or even imply that they are monophyletic.

Obviously, the set of species studied for a cladistic analysis is irrelevant if, as in S&F (2003a), Fet et al. (2005), etc., each and every one of those species is not scored in the resultant matrix. Disclaiming the assumption of monophyly for the supraspecific terminals used in an analysis is also irrelevant if, as in S&F (2003a), Fet et al. (2005), etc., the monophyly of those terminals, created from observations of several species, is not tested.

Composite fossil outgroup

Besides the 58 terminals representing extant scorpions, the analysis by S&F (2003a) included a single fossil exemplar species, *Archaeobuthus estephani*, and a composite terminal, purported to represent the extinct family Palaeopisthacanthidae, and serving as the primary outgroup. This composite terminal, first devised by S&F (2001), is an amalgamation of states observed by paleontologists in four fossil scorpion species from the Upper Carboniferous of England and the USA (Kansas and Illinois) (Petrunkevitch, 1913, 1949, 1953; Kjellesvig-Waering, 1986; Jeram, 1994, 1998; Fet, 2000). According to S&F (2003a, p. 65):

> The outgroup used in this analysis is the Carboniferous orthostern genus *Palaeopisthacanthus*. The definition of this genus has been expanded to incorporate information extracted from all species comprising its family Palaeopisthacanthidae … So, from the cladistic viewpoint, our concept of the genus "Palaeopisthacanthus" can be considered a composite of all the species in its family. This approach was necessary to maximize available information for hypothesized polarity argumentation.

The fossil scorpions in question are fragmentary, visible in only a single dimension, and consequently unscorable for particular carinae, trichobothria and so forth, but the authors considered the mere presence of a structure (e.g., a trichobothrium) in any of the four species to be evidence of its presence in the entire family (S&F, 2001; Fig. 3; Table 6), regardless of the fact that nobody has thus far demonstrated empirically that these fossils are confamilial, let alone monophyletic. Indeed, according to Jeram's (1994) analysis, *Palaeopisthacanthus* is paraphyletic with respect to Recent scorpions, a finding mentioned by Fet (2000). Palaeopisthacanthidae would therefore also be paraphyletic.

The rationale underlying S&F's (2001, 2003a) decision to combine observations from several fossils into a single composite terminal is, presumably, to reduce the number of missing entries, widely considered to render some taxa unstable, leading to multiple equally parsimonious trees, poorly resolved consensus trees, inflated measures of tree and nodal support, and generally ambiguous results (Nixon and Davis, 1991; Platnick et al., 1991; Novacek, 1992; Maddison, 1993; Wilkinson and Benton, 1995; Wilkinson, 1995a,b, 2003; Wiens, 1998b, 2003a,b; Makovicky, 2000; Norell and Wheeler, 2003; but see Kearney, 2002; Kearney and Clark, 2003). However, S&F's (2001, 2003a) use of a hypothetical outgroup, again repeated by S&F (2004, p. 107), is inadvisable for many of the same reasons as their use of supraspecific terminal taxa (Nixon and Carpenter, 1993; Bryant, 1997; Bininda-Emonds et al., 1998; Wiens, 1998a, 2000; Prendini, 2001a; Malia et al., 2003). This practice artificially dictates the outcome of the study by forcing the ingroup to be monophyletic and the polarities to be known *a priori*, while leaving both untested, and is likely to produce results different from those obtained in analyses where real outgroup taxa are included (Nixon and Carpenter, 1993; Prendini, 2001a; Kaila, 2004).

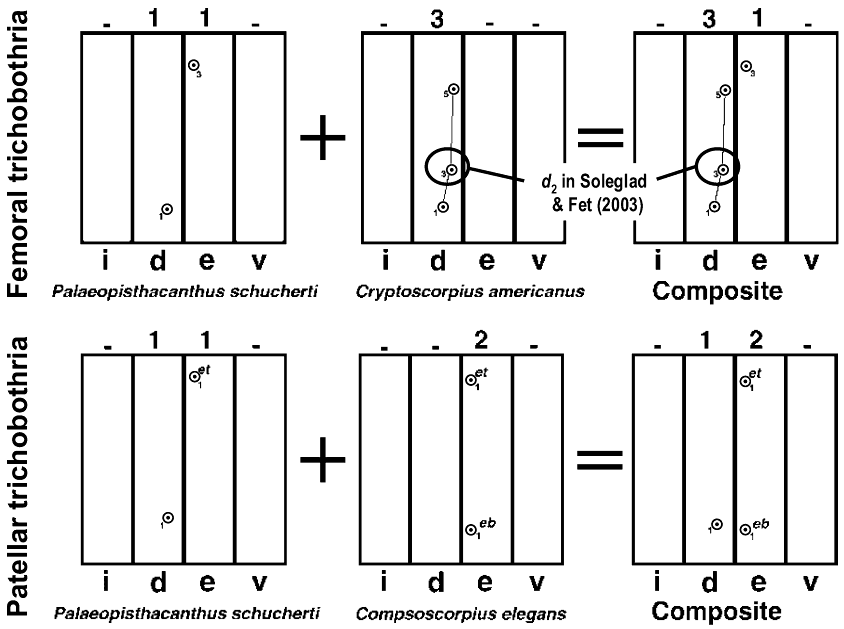


Fig. 3. Soleglad and Fet's (2001, 2003a) "method" for creating composite terminals, illustrated using their example of coding trichobothria on the femur and patella of the terminal representing the extinct family Palaeopisthacanthidae Kjellesvig-Waering, 1986, from observations in three fossil scorpion species, *Compsoscorpius elegans* Petrunkevitch, 1949, *Cryptoscorpius americanus* Jeram, 1994, and *Palaeopisthacanthus schucherti* Petrunkevitch, 1913 (modified from fig. 1 of Soleglad and Fet, 2001, p. 7). Note the discrepancy in coding one trichobothrium on the dorsal surface of the femur between the matrices presented by Soleglad and Fet (2001) and Soleglad and Fet (2003a). Refer to Table 6 for actual coding.

Table 6
Soleglad and Fet's (2001, 2003a) "method" for creating composite terminals, illustrated using their example of coding trichobothria on the pedipalps (femur, patella, chela manus and fixed finger) of the terminal representing the extinct family Palaeopisthacanthidae Kjellesvig-Waering, 1986, from observations in four fossil scorpion species, *Compsoscorpius elegans* Petrunkevitch, 1949, *Cryptoscorpius americanus* Jeram, 1994, and *Palaeopisthacanthus schucherti* Petrunkevitch, 1913, and *P. vogelandurdeni* Jeram, 1994 (modified from table 1 of Soleglad and Fet, 2001, p. 5)

Segment	Surface	Seta	*C. elegans*	*C. americanus*	*P. schucherti*	*P. vogelandurdeni*	Composite (S&F, 2001)	Composite (S&F, 2003a)
Femur	Dorsal	d_1	?[1]	X	X		1	1
		d_2	?[1]				0	1
		d_3	?[1]	X			1	0
		d_5	?[1]	X			1	1
		e_3	?[1]		X		1	1
Patella	Dorsal	d_1			X		1	1
	External	eb_1	X				1	1
		et_1	X		X		1	1
Finger	External	eb	X	X	X	X	1	1
		est	X	X	X		1	1
		et	X		X		1	1
Manus	External	Eb_1	?[2]		X		1	1
		Eb_2	?[2]		X		1	1
		Est	?[2]	X	X		1	1
		Et_1	X	X	X	X	1	1
	Ventral	V_1	X	X	X		1	1
		V_2	X	X	X		1	1
		V_3	?[2]	X	X		1	1
		V_4	?[2]	X	X		1	1

"X" denotes trichobothria reported and/or illustrated by Jeram (1994). [1] Three trichobothria reported by Jeram (1994), but not individually identified. [2] Eight trichobothria reported by Jeram (1994), but only six illustrated. Note the discrepancy in coding one trichobothrium on the dorsal surface of the femur between the matrices presented by Soleglad and Fet (2001) and Soleglad and Fet (2003a).

Other concerns with the approach taken by S&F (2001, 2003a) are the operational problems of scoring a composite terminal, which beset all supraspecific terminals (Prendini, 2001a). For example, it is noteworthy (Table 6) that character 55 (pedipalp femoral trichobothrium d_2) was scored 0 (absent) in the palaeopisthacanthid composite by S&F (2001), but 1 (present) by S&F (2003a), whereas character 56 (pedipalp femoral trichobothrium d_3) was scored 1 by S&F (2001), but 0 by S&F (2003a). Were these characters in fact polymorphic in Palaeopisthacanthidae, they should have been scored as such, i.e., [01]. That is the case with character 56 which, according to S&F's (2001, p. 5) Table 2, is present in *Cryptoscorpius* but absent in the other palaeopisthacanthids. However, character 55, scored present in Palaeopisthacanthidae in S&F's (2003a) matrix, is absent in all four. We presume this is an error, based on the similar trichobothrial designations in S&F's (2001, p. 7) fig. 1 and S&F's (2003a, p. 34) fig. 64.

The *Typhlochactas* composite, incorporating *Sotanochactas*, provides a similar example. S&F (2003a) scored state 0 of character 14 (chelal finger trichobothria *ib* and *it* situated close together) in the composite, although these trichobothria are close together in *Typhlochactas*, and separated (states 1–3; Appendix 2) in *Sotanochactas* (Francke, 1982, p. 7, figs 13, 16, 19, 22 and 25).

A more pragmatic approach than making arbitary decisions regarding which states to score in a composite terminal would be to score each fossil or extant species individually and let parsimony determine the ancestral condition (or "groundplan") of the Palaeopisthacanthidae or (*Sotanochactas* + *Typhlochactas*) if, in fact, either are monophyletic. Malia et al. (2003) reached a similar conclusion in their analysis of the effects of composite taxa in supermatrices. These authors argued that taxa should be kept separate in phylogenetic analyses because, although missing data may lead to a loss of resolution in the phylogeny, the alternative of combining taxa and possibly obtaining misleading results is a far more serious problem. Missing data simply represent the unknown and should not be viewed as an impediment to considering all available evidence in a phylogenetic analysis (Kearney, 2002; Kearney and Clark, 2003). As such, we question whether scoring the absence of trichobothria in a fossil is justifiable. Absence might be nothing more than an artifact of preservation, given the difficulty with which trichobothria are generally observed in fossils, especially those preserved in rock (Jeram, 1994; Lourenço and Weitschat, 1996, 2000, 2001; De Carvalho and Lourenço 2001; Lourenço, 2001, 2003). In our view, trichobothria should be treated as "presence-only data" in fossils, their absence being scored "unknown" (?), rather than definitively absent (0) as in S&F (2001, 2003a).

Arachnid and chelicerate outgroups omitted

Soleglad et al. (2005, p. 28) recently criticized the choice of outgroups for Prendini's (2000) analysis of scorpionoid relationships. Their own analyses contradict their criticism, however, as illustrated, for example, by S&F's (2003a) approach to rooting their morphological phylogeny of scorpions.

The phylogenetic position of scorpions within the Chelicerata is controversial (for reviews of the topic, see Sissom, 1990; Dunlop and Braddy, 2001; Coddington et al., 2004). At least three main hypotheses have been proposed in the literature: scorpions are basal arachnids, sister to the remaining Arachnida, Lipoctena (Boudreaux, 1979; Weygoldt and Paulus, 1979; Weygoldt, 1998); scorpions are derived arachnids, forming the Dromopoda clade with Opiliones, Pseudoscorpiones and Solifugae (Shultz, 1990, 2000; Wheeler et al., 1993; Wheeler and Hayashi, 1998; Giribet et al., 2002); scorpions are the sister group of the extinct eurypterids, perhaps with horseshoe crabs (Xiphosura) as the sister group of both, rendering Arachnida paraphyletic (Bergström, 1979; Starobogatov, 1990; Dunlop and Selden, 1998; Dunlop, 1998; Jeram, 1998; Braddy et al., 1999; Dunlop and Webster, 1999; Dunlop and Braddy, 2001). Much of the controversy arises because paleontologists consider some fossil scorpions to have been aquatic (Kjellesvig-Waering, 1986; Dunlop and Selden, 1998; Dunlop, 1998; Jeram, 1998; Dunlop and Webster, 1999), implying either that terrestrial scorpions invaded land independently, or returned to the seas secondarily. If the former, similar arachnid innovations for terrestrial life may be convergent rather than homologous (Jeram, 1998; Dunlop and Selden, 1998; Dunlop and Webster, 1999). Conclusions remain tentative and ambiguous, however, because of the paucity of informative characters and the poor or incomplete preservation of existing fossils (Coddington et al., 2004).

S&F (2003a) rooted their phylogeny on the composite fossil terminal Palaeopisthacanthidae, discussed above. Other arachnid orders and other Chelicerata, extinct and extant, were omitted entirely. Given the controversy surrounding the phylogenetic position of scorpions and the implications that their placement might have on the polarity of characters affecting the basal relationships and major lineages within Scorpiones, the omission of taxa such as eurypterids, xiphosurans and other arachnids is conspicuous, the more so as morphological characters and DNA sequences for the 16S rDNA and 18S rDNA gene loci have been published for most of the outgroup taxa in question (e.g., Shultz, 1990; Wheeler et al., 1993; Wheeler and Hayashi, 1998; Giribet et al., 2002).

Also on the subject of outgroups and rooting, it is noteworthy that the separate molecular analyses by S&F (2003a, pp. 148–154, appendix B), and the separate molecular and morphological analyses in two contributions on buthid phylogeny by Fet et al. (2003, 2005), were all rooted on *Pseudochactas*, the phylogenetic position of which remains to be verified unambiguously (Coddington et al., 2004; Prendini et al., in press). Both phylogenetic analyses which have thus far attempted to determine its position are incongruent. S&F (2001) placed it as the sister group of Buthidae, whereas S&F (2003a) placed it as the sister group of all other extant scorpions. Despite the uncertainty, the use of *Pseudochactas* as primary outgroup for other analyses was justified on the basis of a morphological analysis, rooted on a composite fossil scorpion, from which crucial outgroup arachnids and chelicerates were omitted.

Primary homology assigned on preconceived notions of relationship

Homology is the basis of phylogenetic analysis (Patterson, 1982; Schuh, 2000). Recognition that every homology statement involves an initial proposition of homology and subsequent testing of that hypothesis through congruence (Patterson, 1982; Rieppel, 1988) led De Pinna (1991) to propose the concepts of primary and secondary homology, and Brower and Schawaroch (1996) to identify the two stages involved in the formulation of a primary homology hypothesis: comparative morphological or molecular study of organismal variation to define characters, which are then partitioned into character states and scored in terminal taxa to create a data matrix. Any structure that is topographically, compositionally and (presumably) ontogenetically similar constitutes a primary homology statement, or character, and should be coded as one column in a data matrix, structures that appear "the same but different" among terminal taxa representing the character states (Patterson, 1982; Rieppel, 1988; Platnick, 1989; De Pinna, 1991; Brower and Schawaroch, 1996; Hawkins et al., 1997; Schuh, 2000). Although the data matrix, and hence the procedure of primary homology assessment, is the prime determinant of cladistic analysis, it remains contentious and sometimes subjective because different workers perceive and define characters in different ways (Archie, 1985; Pimentel and Riggins, 1987; Bryant, 1989; Pogue and Mickevich, 1990; De Pinna, 1991; Stevens, 1991; Lipscomb, 1992; Maddison, 1993; Pleijel, 1995; Wilkinson, 1995c; Hawkins et al., 1997; Hawkins, 2000; Strong and Lipscomb, 1999; Wiens, 2001, 2004; Scotland et al., 2003). As the link between observation and explanation, primary homology assessment must reflect the evidential significance of the observations, and alternative methods for character coding should be judged on their ability, or inability, to achieve this goal (Strong and Lipscomb, 1999). In practice, this means that character coding should result in states that are homologous, independent and non-redundant (Pimentel and Riggins, 1987).

S&F (2003a), Fet et al. (2004a) and Soleglad et al. (2005), criticized the manner in which Prendini (2000, 2003a) coded various characters, and suggested that their own approach was superior. However, setting aside differences in the interpretation of structures (discussed below), it is clear that these authors fail to grasp either the concept or methods of primary homology assessment, as we will demonstrate.

By way of example, we cite S&F's (2003a, p. 115) objections to Prendini's (2000, 2003a) approach to coding trichobothria, first raised by Soleglad and Sissom (2001) and recently elaborated by Soleglad et al. (2005, pp. 7–15). Prendini (2000, 2003a) used multistate characters to portray the numbers of trichobothria observed on various surfaces of the pedipalp segments. This approach was employed so as to represent trichobothrial variation with the fewest *a priori* assumptions about the homology of individual trichobothria (which, as discussed further below, may be difficult, if not impossible, to determine in many cases):

> Based on the many *important* characters, which the genus *Heteroscorpion* uniquely shares with the family Liochelidae, and likewise, does not share with the genus *Urodacus*, we decided to investigate Prendini's (2000) original cladistic analysis which combined these two taxa as sister elements [one of two alternative hypotheses proposed by Prendini, the second of which did not group these genera as sister taxa]. This questioning of the clade "*Urodacus* + *Heteroscorpion*" was precipitated, in part, by the somewhat "high-level" approach to neobothriotaxy taken by Prendini (2000), which was discussed in detail by Soleglad and Sissom (2001: 71–72). They pointed out that Prendini considered almost all neobothriotaxic conditions found within the superfamily as single derivations within the pedipalp segment surfaces. This approach, in the opinion of Soleglad and Sissom (2001), predictively created severe homoplasy (i.e., the *simplistic model* did not convey *true* evolutionary lines for this complicated set of derivations). [italics added]

Soleglad and Sissom (2001; pp. 71, 72) had previously stated:

> We believe [Prendini's] *conservative assumption-free* approach was excessive in this case and *better* results would have been obtained, i.e., hypotheses that best reflect the *true* evolution, if separate characters and/or states had been used to *model* neobothriotaxy [italics added]

S&F (2003a) and, more recently, Soleglad et al. (2005), sought to implement their approach and assigned separate states to Prendini's (2000) neobothriotaxy characters (characters 32–38, Appendix 2), to the metasomal ventromedian carina (character 85), and to other characters with which they disagreed:

> We implement a high-level *modeling scheme* in our approach to neobothriotaxy, *based primarily on putative family designations.* (S&F, 2003a, p. 138) [italics added]

> … as with neobothriotaxy, we question Prendini's character 95, where he assigns three disparate genera groups that exhibit a single ventral median carina on metasomal segments I–IV to the same state, *Heteroscorpion*, *Urodacus*, and *Hemiscorpius* + *Habibiella.* We assign each *group* its own state thus removing this assumption of homologous derivation (which also uncouples *Heterometrus* [*sic*, this should, presumably, read "*Heteroscorpion*"] from Hemiscorpiinae as well). (S&F, 2003a, p. 116) [italics added]

Far from removing assumptions, however, these authors achieved precisely the opposite. These actions pervaded their analyses with *a priori* assumptions about phylogenetic relationship and character transformation, none of which were tested. There are numerous cases in which these authors explicitly scored terminals on the basis of their presumed phylogenetic relationship, rather than, and often in spite of, unambiguous evidence of similarity in structure and position (primary homology *sensu* De Pinna, 1991). One of many examples of this practice is provided by character 60 (Appendix 2):

> We see variability in the number of pedal spurs in genera *Sotanochactas* and *Typhlochactas*, from no spurs to both present. Due to *Alacran*'s apparent close taxonomic position to *Typhlochactas*, we assign the same state to this genus (only the prolateral pedal spur is present in *Alacran*). (S&F, 2003a, p. 141)

Another example is provided by character 85 (Appendix 2), in which six states accommodate two structurally different conditions of the carinae on the ventral surface of metasomal segments I–IV: paired (0); single (Hemiscorpiinae) (1); single (Urodacidae) (2); single (Euscorpiidae) (3); single (Vaejovidae, *Syntropis*) (4); single (Vaejovidae, *Vejovoidus*) (5). The single ventromedian carina is structurally and topographically similar in all scorpions in which it has been observed. However, in the view of S&F (2003a, p. 144):

> We considered the condition of a single ventral median carina on metasomal segments I–IV to be localized to individual scorpion groups. Therefore, we assign a separate state to each scorpion group where it occurs.

Three states were also provided to accommodate two alternative positions of the em_1–em_2 and esb_1 trichobothria (character 28, Appendix 2): em_1–em_2 and esb_1 near midsegment (Vaejovidae, Brotheinae, Uroctoninae, Superstitioniidae) (0); em_1–em_2 and esb_1 proximal (1/3 distance from proximal edge) (Chactinae) (1); em_1–em_2 and esb_1 proximal (1/3 distance from proximal edge) (Scorpiopinae) (2). According to S&F (2003a, p. 138):

> We consider the similar trichobothrial positions as exhibited in chactid subfamily Chactinae and the euscorpiid subfamily Scorpiopinae as independent derivations (a hypothesis).

The structural and topographical similarity of the carinae assigned states 1–5 of character 85 and the setae assigned states 1 and 2 of character 28 in each case satisfies the criteria of primary homology and requires that they be assigned the same state, hypotheses to be tested at the next step of (secondary) homology assessment by congruence with other characters (Patterson, 1982; Rieppel, 1988; De Pinna, 1991; Brower and Schawaroch, 1996), but which cannot be tested if they are assigned different states at the outset.

S&F (2003a) provided six states to accommodate the presence and relative development of the lateral carinae on metasomal segment V (character 86, Appendix 2): present, complete (Palaeopisthacanthidae) (0); partially present (most Recent scorpions) (1); absent (most Buthoidea) (2); absent (Scorpionoidea) (3); absent (Euscorpiidae) (4); absent (Superstitioniidae) (5); absent (Vaejovidae) (6). According to S&F (2003a, p. 144):

> The lateral carinae of metasomal segment V are … absent in most buthoids … and a few scattered genera throughout the scorpionoids and chactoids. Consequently, we assign separate states to these losses, not considering them homologous to that of the *major* loss seen in the buthoids. [italics added]

Similar examples are provided by character 105, with five states of pectinal fulcra development, three of which score the absence of fulcra separately in Superstitioniidae, *Belisarius*, and Euscorpiidae, respectively (Appendix 2) and character 6 of Fet et al. (2005), discussed further below. Setting aside the well-known problems with coding "absence" as a character state (Pimentel and Riggins, 1987; Meier, 1994; Strong and Lipscomb, 1999), it would appear that S&F (2003a) recognize different kinds of "absence", some of which are more important than others!

Perhaps the most absurd example is character 102, with six partially ordered states representing the number of lateral ocelli, varying from 0 to 5 in extant scorpions: 2 (relatively primitive) (Chaerilidae) (0); 3 (Iuroidea, Scorpionoidea, Vaejovidae) (1); 0–2 (Euscorpiidae, Chactidae, Superstitioniidae) (2); 2 (Urodacidae) (3); 3–4 (Uroctoninae) (4); 3 (Scorpiopini) (5); Pseudochactidae and Buthoidea (–). This coding scheme was supported by an elaborate argumentation (S&F, 2003a, p. 146):

> This character is partially ordered as (0 (1 ((2 (4, 5)) (3))). This ordering suggests the following derivation: we consider the two eyes found in the chaerilids as "relatively primitive"; from this state we have three eyes as found in the iuroids, scorpionoids, and vaejovids … Family Urodacidae looses [*sic*] an eye, a derivation from the three eye state; similarly, none to two lateral eyes exhibited in families Euscorpiidae, Chactidae, and Superstitioniidae are also derived from a three-eye state. Finally, the three to four eyes found in the chactid subfamily Uroctoninae is a derivation from a two-eye state. For completeness here, we see primitive genus *Pseudochactas* with

Table 7
Selected problems with the morphological characters presented by Soleglad and Fet (2003a), and examples of the characters affected

Problem	Characters affected (percentage of total): Appendix: Character
Similar stuctures in different taxa assigned separate states based on putative phylogenetic relationship	38 (23%): Appendix 2: 10–15, 21, 22, 24, 28, 32–36, 39, 41–44, 46–48, 50, 55, 60, 62, 67, 72, 82, 85, 86, 87, 93, 101, 102, 104, 105
Similar stuctures in different taxa assigned separate characters based on putative phylogenetic relationship	2 (1%): Appendix 2: 97, 98
Forced "reversal"	6 (4%): Appendix 2: 37, 38, 41, 47, 48, 60
Trichobothrial transformation forced through intermediate state, petite, i.e., 0 ↔ 1 ↔ 2	10 (6%): Appendix 1: 10, 15, 17, 24, 33, 35, 45, 52, 53, 55
Trichobothrial transformation forced through intermediate state not observed, i.e., 0 ↔ 2	30 (18%): Appendix 1: 1, 2, 4, 5, 7, 8, 19, 20, 22, 25, 26, 32, 36–39, 41, 42, 46–51, 56–61
Other forced transformation (additive binary or ordered multistate)	16 (10%): Appendix 2: 1, 10, 19–21, 27, 41–43, 47, 48, 57, 58, 60, 82, 102
Redundancy and lack of independence	25 (15%): Appendix 1: 10, 17, 24, 35, 45; Appendix 2: 11, 14, 15, 17, 20–22, 25, 29, 36–38, 42, 43, 49, 52, 57, 58, 66, 67
Trichobothrial homology across basic pattern types	73 (44%): Appendix 1: 1–62; Appendix 2: 1–4, 23–29
States concepts, not observations	14 (8%): Appendix 2: 1, 32–38, 63–68
Other characters subsuming non-homologous variation	14 (8%): Appendix 2: 13, 19, 27, 28, 31, 36, 60, 63–65, 93, 97, 99, 101
States overlap	15 (9%): Appendix 2: 12, 22, 32–36, 39, 55, 72, 86, 98, 101, 102, 105
States subsume non-homologous variation	34 (20%): Appendix 2: 5, 8, 10–13, 15, 18, 26, 42, 45–48, 50, 54–59, 61, 62, 68, 73, 85, 86, 89, 90, 97, 98, 102, 104, 105
Polymorphic "state"	6 (4%): Appendix 2: 41, 45, 60, 102, 104, 105
Unknown "state"	2 (1%): Appendix 2: 57, 73
Scored inapplicable in taxa to which applicable	56 (34%): Appendix 2: 4–8, 10–14, 16–21, 24–36, 39, 49, 51–53, 55, 56, 62, 67, 74, 76–82, 88, 89, 93, 97, 100, 102–105
Errors, interpretations, misrepresentations, and guesswork in scoring of certain taxa	28 (17%): Appendix 2: 4, 8, 10–14, 16, 18, 23, 24, 26–28, 30, 42, 43, 47, 48, 53, 60, 61, 68, 82, 85, 92, 95, 96, 99
Total (affected by at least one problem)	158 (95%)

> one lateral eye, and the buthoids usually with three to five eyes, clearly a derivation for this family.

Curiously, *Pseudochactas* and the buthoids were scored inapplicable for character 102, implying that they lack eyes (discussed further below).

In all, S&F (2003a, pp. 136–137) applied their "general hypothesis" that similar character derivations in allegedly disparate groups evolved independently, and should thus be assigned separate states—a procedure adopted from the unpublished PhD dissertation of Stockwell (1989)—to 38 (23%) of the characters in their matrix (Table 7). In a revealing discussion on their "understanding" of homology, Soleglad et al. (2005, p. 6) recently attempted to defend this unconventional method of coding, citing examples of this practice from Stockwell (1989), previously rejected by Prendini (2000), as a putative justification:

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

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

Fet et al. (2005) reiterated this position, in defence of character 6, in which the absence of tibial spurs on legs III–IV or IV was scored as no fewer than five separate states: spur present or sometimes vestigial (*Pseudochactas*, *Charmus* and *Uroplectes* groups, and most genera of *Buthus*, *Ananteris*, and *Isometrus* groups) (0); spur absent (*Archaeobuthus*) (1); spur absent (*Buthus* group: *Lanzatus*, *Liobuthus*, *Pectinibuthus*, *Plesiobuthus*, *Sabinebuthus*, *Vachoniolus*) (2); spur absent (*Ananteris* group: *Akentrobuthus*) (3); spur absent (*Isometrus* group: *Isometrus*, *Afroisometrus*) (4); spur absent (*Tityus* group) (5). According to Fet et al. (2005, pp. 20–21):

> This somewhat irregular character, from a cladistic perspective, is included because we believe it is phylogenetically significant for the New World *Tityus* group, for reasons discussed elsewhere. Other occurrences, *modeled* as separate state derivations, are *considered less important phylogenetically*, many possibly the byproduct of specialized microhabitat adaptation. As suggested recently in Soleglad et al. (2005), the use of separate state values for similar looking derivations is a weaker assumption than assuming all such character changes occurred as a single derivation, and we adopt this approach here. Not only is it a weaker assumption, but equally as important, we do not *believe* these 19 occurrences of tibial spur losses are the product of a single evolutionary event and therefore, *model* these character states in accordance with the results based on the other characters. The presumed primitive state, tibial spurs being present, is based on their presence in many fossils, as well as in the most primitive Recent scorpion *Pseudochactas*. [italics added]

These excerpts reveal that S&F mistakenly regard the test of congruence (secondary homology) as an assumption. They reveal, furthermore, that S&F either do not understand the need for, or are unconcerned with testing hypotheses of homology (e.g., whether the single ventromedian carina might be synapomorphic for *Heteroscorpion* and *Urodacus*) or monophyly (e.g., whether *Heteroscorpion* and *Urodacus* might be monophyletic) for they apparently already know the true phylogenetic relationships among their study taxa (this prior knowledge, indeed, is part of their assumption-set). S&F's approach of "modelling" characters, deliberately adopted to "reduce homoplasy" (or "lessen the assumption level") by assigning separate (often autapomorphic) states to structurally and topographically similar features observed in different taxa, regardless of whether that process is iterative or not, contradicts the very foundation of cladistics, Hennig's (1966) Auxiliary Principle: homology must be assumed until proven otherwise (i.e., through a test of congruence with other characters). S&F's approach has many severely negative effects. Information is lost during the conversion of potential synapomorphies into autapomorphies, homology is not tested, monophyly is forced on predetermined groups rather than tested, and relationships among the terminals are constrained across the entire tree, in turn preventing internal groupings from being tested adequately, and ultimately biasing the entire analysis towards a preconceived result. Such an analysis cannot be considered a rigorous test of all the available evidence. It defeats the object of phylogenetics and is tantamount to an appeal to authority.

Forced character transformations

Additional untested assumptions were built into S&F's (2003a) analysis by forcing character polarity. Among the more obvious examples are six forced "reversals" (4% of the characters in the matrix), coded as separate states or characters (Table 7), e.g., partially ordered character 60 (Appendix 2), coding the number of pedal spurs: 2, both retrolateral and prolateral present (0); 1, prolateral present (Scorpionoidea) (1); 2 spurs (secondary development, Bothriuridae) (2); 0–2, variable in genus (Typhlochactinae) (3). According to S&F (2003a, p. 141):

> The primitive state is two pedal spurs. The lost [*sic*] of the retrolateral spur is constant in Scorpionoidea, and the fact that two pedal spurs are found in many bothriurids is considered a secondary development from a single spur condition (i.e., a "reversal").

Similarly, ordered character 41 (Appendix 2) "models" the subdistal denticles on the dorsal edge of the cheliceral movable finger as follows: 1 subdistal denticle (0); 2 subdistal denticles (Caraboctonidae) (1); 2 subdistal denticles (Bothriuridae, reversal) (2); 2 subdistal denticles (Chactoidea) (3); 1–2 subdistal denticles, variable in genus (Superstitioniidae) (4).

Notwithstanding that S&F's (2003a) character 60 fails the criteria of primary homology and should have been coded as two separate characters, i.e., pro- and retrolateral pedal spurs (Table 7), the manner in which characters 41 and 60 were coded prevented the possibility of testing whether two pedal spurs and two subdistal denticles are, indeed, apomorphic reversals in the Bothriuridae (cf. the coding of these same structures, in characters 10, 63 and 64, by Prendini, 2000, pp. 48, 59).

Reversals were also forced by S&F (2003a) using additive coding, through various dependent characters, denoted "primary" and "secondary". Characters 47 and 48 (Appendix 2), "modelling" the alignment of the median denticle (MD) row of the pedipalp chelal finger, provide an example. Primary character 47 comprises two states: oblique, primitive (0); non-oblique (1). The second state then becomes the first state of secondary character 48, whereas the first state becomes inapplicable: non-oblique (state 1 from character 47) (0); oblique (Superstitioniidae) (1); primitive oblique (–). As with so many of their characters, S&F (2003a, p. 140) justified this coding on the basis of preconceived notions of phylogenetic relationship and character polarity:

> The oblique alignment, a primitive condition, is exhibited in the palaeopisthacanthids, archaeobuthids and all primitive Recent scorpions … We consider the oblique condition of the MD row exhibited in the superstitioniids to be a secondary derivation from a non-oblique condition.

Such forced reversals inevitably lead to contradictory coding of taxa in the matrix. For example, in character 47, *Alacran*, *Superstitionia* and *Typhlochactas* were scored for non-oblique rows (state 1) whereas, in character 48, the same taxa were scored for oblique rows (state 1). *Troglotayosicus*, the holotype and only known specimen of which was not examined by S&F (2003a), and the chelal finger dentition of which was described ambiguously by Lourenço (1981), was scored state 1 for non-oblique rows in character 47, but unknown (?) in character 48.

In a similar manner, additive characters 42 and 43 "model" the ventral edge of the cheliceral movable finger. Partially ordered primary character 42 comprises four states: crenulated to small denticles (Palaeopisthacanthidae, Pseudochactidae, Chaerilidae) (0); two large denticles (Buthoidea) (1); one very large rounded denticle (Iuroidea) (2); smooth (other) (3). State 3 is then further subdivided in secondary character 43, whereas the others become inapplicable: smooth (from state 3 in character 42) (0); crenulate (Megacorminae) (1); crenulate (Scorpiopinae) (2); crenulate (Uroctoninae) (3); crenulate (Nullibrotheini) (4); crenulate (*Paruroctonus* and related genera) (5); crenulate (*Pseudouroctonus* and related genera) (6). Table 7 lists 56 (34%) examples in which character transformations were forced by S&F (2003a) using additive coding, ordering or Sankoff optimization (Sankoff and Rousseau, 1975).

Many have argued against using ordered or additive characters on the grounds that they incorporate hypotheses about character transformation that should be tested, rather than assumed, by cladistic analysis (Hauser and Presch, 1991; Hauser, 1992; Wilkinson, 1992; Slowinski, 1993; Hormiga, 1994; Griswold et al., 1998). Unordered or nonadditive analysis has been defended by invoking the principle of indifference, which asserts that if there is no apparent reason for considering one event to be more probable than its alternatives, then all should be considered equiprobable (Wilkinson, 1992). Unordered analysis does not, however, avoid premises of transformation—it merely provides a questionable alternative theory of transformation (Mickevich, 1982). Allowing a state to transform directly into any other often amounts to nothing more than the "common equals primitive" criterion (Platnick, 1989). The most commonly occurring states will tend to be placed toward the base of the tree, with all other states being independently derived from them. Potential synapomorphies may consequently be lost in favor of autapomorphies (Schuh, 2000). Some consider such denial of nested similarity to be epistemologically equivalent to the omission of evidence and, hence, invalid for cladistic analysis (Pimentel and Riggins, 1987; Lipscomb, 1992; Prendini, 2000). Regardless of whether or not this position is accepted, however, it is clear that considerations of character state transformation are secondary to the definition of character states (which can, of course, be easily unordered during the analysis). The initial definition of character states should be devoid of such assumptions. Structural, topographical, and (if possible) ontogenetic identity in different taxa imply that they should be assigned the same state and conjectures of primary homology which do not conform to these criteria, such as those outlined in the examples from S&F (2003a) above, simply do not exist (De Pinna, 1991).

Sankoff optimization of trichobothria and the "existence" of intermediate states

Among the many questionable examples of forced transformation in the matrix of S&F (2003a), 62 characters "modelling" the "existence" of fundamental trichobothria in scorpions (orthobothriotaxy *sensu* Vachon, 1974), first proposed by S&F (2001), warrant additional scrutiny. S&F (2001, 2003a) recognized three states for these characters: trichobothrium absent (0); trichobothrium present, "petite" in size (1); trichobothrium present, full size (2). S&F (2001; appendix A) presented quantitative data to distinguish the "petite" condition from the normal or "full size" condition, along with a Sankoff stepmatrix (Sankoff and Rousseau, 1975), specifying the transformation costs between these states:

	Absent	Petite	Full
Absent	0	1	2
Petite	1	0	1
Full	2	1	0

This stepmatrix is identical to using an ordered multistate character provided the state weight changes are incremental by one: 0 (absence) ↔ 1 (petite) ↔ 2 (full size). The petite condition is interpreted as an intermediate state in the transformation from no trichobothrium to a trichobothrium of full size, an assumption explicitly stated by S&F (2001, p. 3):

> We suggest here that a petite trichobothrium is a trichobothrium that is either evolving to a full trichobothrium or, is in the process of being lost. We assign a cost (i.e., a cladistic "weight") of "one" for the state transitions of "*absent* ↔ *petite*" or "*petite* ↔ *full*" and a cost of "two" for the transition "*absent* ↔ *full*", therefore modeling the intermediate state of a petite trichobothrium.

No empirical evidence exists, however, to suggest that a petite trichobothrium is a trichobothrium in the process of being lost or gained. The petite trichobothrium might be a different kind of sensory seta altogether. Regardless of this important detail, 10 (6%) of the characters in S&F's (2003a, p. 68) Table 4 (Appendix 1) force this transformation to proceed through the allegedly intermediate state, i.e., 0 ↔ 1 ↔ 2, whereas 30 (18%) of their characters force the transformation to proceed through an intermediate state that has not been observed, i.e., 0 ↔ 2 (Table 7). If absence includes losses, there is certainly no evidence that the loss of a full size trichobothrium should be weighted twice the loss of a petite trichobothrium. Merely weighting all other characters in the data matrix by 2, as Soleglad et al. (2005, p. 5) recently claimed to have done in their previous analysis (this was not the case, however, for the trichobothrial "existence" characters were not analysed simultaneously with the remaining morphological characters, as we have shown above), is an inappropriate solution to a problem which should not be there in the first place:

> Soleglad and Fet (2003[a]), in their analysis that combined the entire set of orthobothriotaxic trichobothria with other morphological characters, also weighted all other characters by 2 to equalize the characters in the data matrix (i.e., statements on the trichobothria existence were implemented with a Sankoff character, which assigned a full trichobothrium the weight of 2).

Redundancy and lack of character independence

Aside from forcing character transformations, many of S&F's (2003a) characters fail to meet the criteria of independence and non-redundancy, i.e., homoplasy in one implies homoplasy in the other (Felsenstein, 1982; Farris, 1983; Riggins and Farris, 1983; Wilkinson, 1992; Hawkins et al., 1997; Strong and Lipscomb, 1999; Hawkins, 2000). One example is provided by additive characters 20 and 21 "modelling" the relative positions of chelal trichobothria in the *et–eb* series. Primary character 20 comprises two states: *esb* closest to finger edge with respect to *eb* (0); *eb* closest to finger edge with respect to *esb* (next to membrane) (Chactidae, Euscorpiidae) (1). State 1 then becomes state 0 of secondary character 21, with four states: no change, *eb* closest to finger edge (0); *esb* and *eb* in straight line, *eb* most proximal (Brotheina) (1); *esb* and *eb* in straight line, *eb* most proximal (Scorpiopinae) (2); *esb* and *eb* in straight line, *eb* most proximal (*Chactopsis*) (3). Knowledge that a particular taxon exhibits state 0 of S&F's (2003a) character 21 implies that the same taxon also exhibits state 1 of character 20. Coding state 1 of character 20 and state 0 of character 21 in the same taxon thus introduces redundancy into the analysis (Pimentel and Riggins, 1987; Strong and Lipscomb, 1999).

When characters are not independent, the evidential significance of the underlying variation is overweighted (Pimentel and Riggins, 1987; Meier, 1994; Wilkinson, 1995c; Strong and Lipscomb, 1999). Should redundant states 0 and 1 of characters 21 and 20 be synapomorphic in the taxa in question, they will be weighted twice relative to other states in other taxa, suggesting twice the evidence for that particular grouping than actually exists. Should the redundant states be homoplastic, the additional weighting might cause the taxa to be united by this "non-homology".

Redundancy and lack of independence are also evident in characters 47 and 48 (discussed above) and characters 45 and 46, portraying the number of denticles on the fixed finger of the chelicera: character 45 (primary): 4–5, major protuberances (Palaeopisthacanthidae, Pseudochactidae, Chaerilidae) (0); 0–2 (2), major protuberances (Buthoidea) (1); absent (2); character 46 (secondary): none (state 2 of character 45) (0); present, Euscorpiidae (*Troglocormus*) (1); present, Vaejovidae (*Paruroctonus*, related genera and some *Pseudouroctonus*) (2); non-Iurida (–). The absence of denticles receives a double score in states 2 and 0, respectively, thereby doubling the support for a grouping of any taxa in which denticles are absent. The structural and topographical identity of the denticle row in characters 47 and 48, and at least some of the cheliceral protuberances in characters 45 and 46, satisfies the criteria of primary homology and requires that each be scored as part of the same character.

At least 25 (15%) of the characters in S&F's (2003a) data matrix are characterized by redundancy or a lack of independence (Table 7). When redundancy is widespread in a matrix, the resultant analysis may suffer from a "homoplasy bias" causing "pseudoparsimonious" cladograms and character optimizations that are an absurd and inaccurate representation of the observations (Meier, 1994; Strong and Lipscomb, 1999). When characters are not independent, there is no meaning in their agreement; that agreement is simply an expression of their mutual dependence (Goloboff, 1995; Hawkins et al., 1997).

Pitfalls in primary homology assessment of trichobothria

No discussion on primary homology assessment in scorpions would be complete without addressing the challenges of determining trichobothrial homology, a subject that remains contentious (Lamoral, 1979; Francke and Soleglad, 1981; Francke, 1982; Stockwell, 1989; Sissom, 1990; Prendini, 2000). Until recently, three basic trichobothrial patterns were recognized among Recent scorpions due, principally, to the work of Vachon (1972, 1974). An alternative system of trichobothrial nomenclature, proposed by Stahnke (1970, 1974), is not widely accepted. The Type A pattern, restricted to Buthidae, is characterized by 11 femoral, 13 patellar, and 15 chelal trichobothria (Table 8). The Type B pattern, restricted to Chaerilidae, contains nine femoral, 14 patellar and 14 chelal trichobothria. Some variation of the basic, orthobothriotaxic Type C pattern, in which there are three femoral, 19 patellar and 26 chelal trichobothria, occurs in all remaining scorpions, except the Pseudochactidae, extinct Archaeobuthidae, and extinct Palaeopisthacanthidae, for which the Type D, Type F1, and Type P patterns, respectively, were recently proposed by S&F (2001). In the Type D pattern, there are 12 femoral, 10 patellar and 13 chelal trichobothria (Prendini et al., in press), in Type F1, there are 8 femoral, 8 patellar and 11 chelal trichobothria and, in Type P, there are 4 femoral, 3 patellar and 11 chelal trichobothria (Table 8). The Type F1 and Type P patterns cannot be considered comprehensive, however. The low numbers of trichobothria may simply reflect the difficulties of identifying trichobothria in fossils, especially those preserved in rock (e.g., see Jeram, 1994; Lourenço and Weitschat, 1996, 2000, 2001; De Carvalho & Lourenço 2001; Lourenço 2001, 2003).

In addition to considerable differences among these patterns, much variation exists within the Type C and, to a lesser extent, Type A patterns (Vachon,

Table 8
The six basic (orthobothriotaxic) trichobothrial patterns on the pedipalps (femur, patella, chela manus and fixed finger) of scorpions, proposed to date for the Buthidae C.L. Koch, 1837 (*sensu lato*, i.e., including Microcharmidae Lourenço, 1996), Chaerilidae Pocock, 1893, Pseudochactidae Gromov, 1998; Archaeobuthidae Lourenço, 2001, Palaeopisthacanthidae Kjellesvig-Waering, 1986, and the remaining families (Vachon, 1974; Sissom, 1990; Gromov, 1998; Soleglad and Fet, 2001). Trichobothrial designations and putative homologies follow Soleglad and Fet (2001, 2003a). Petite trichobothria (*sensu* Vachon, 1974) are denoted by square brackets

Type (Family)	Segment	Internal surface	Dorsal surface	External surface	Ventral surface	No.
A (Buthidae s.l.)	Femur	4 (i_1, i_2, [i_3], [i_4])	5 (d_1, [d_2], d_3–d_5)	2 (e_1, e_2)		11
	Patella	1 (i_1)	5 (d_1–d_4, [d_5])	7 (eb_1, eb_2, esb_1, em_1, *est*, et_1, et_2)		13
	Manus			6 (Eb_1, Eb_2, [Eb_3], *Est*, Et_1, [Et_4])	2 (V_1, V_2)	8
	Finger	1 (*it*)	2 (*db*, *dt*)	4 (*eb*, [*esb*], *est*, *et*)		7
	Total					39
B (Chaerilidae)	Femur	1 (i_1)	4 (d_1, d_3–d_5)	4 (e_1–e_4)		9
	Patella	2 (i_1, i_2)	2 (d_1, d_2)	7 (eb_1, eb_2, esb_1, em_1, *est*, et_1, et_2)	3 (v_1–v_3)	14
	Manus			5 (Eb_1–Eb_3, *Est*, Et_1)	1 (V_1)	6
	Finger	2 (ib_1, *it*)	2 (*db*, *dt*)	4 (*eb*, *esb*, *est*, *et*)		8
	Total					37
C (other families)	Femur	1 (i_1)	1 (d_1)	1 (e_1)		3
	Patella	1 (i_1)	2 (d_1, d_2)	13 (eb_1–eb_5, esb_1, [esb_2], em_1, em_2, *est*, et_1–et_3)	3 (v_1–v_3)	19
	Manus		2 (*Db*, *Dt*)	10 (Eb_1–Eb_3, [*Esb*], *Est*, Et_1– Et_3, [Et_4], Et_5)	4 (V_1–V_4)	16
	Finger	2 (ib_1, *it*)	4 (*db*, *dsb*, *dst*, *dt*)	4 (*eb*, *esb*, *est*, *et*)		10
	Total					48
D (Pseudochactidae)	Femur	4 (i_1, i_2, [i_3], i_4)	5 ([d_1], [d_2], d_3, [d_4], d_5)	3 (e_1–e_3)		12
	Patella	1 (i_1)	3 (d_1–d_3)	6 (eb_1, eb_2, esb_1, [*est*], et_1, et_2)		10
	Manus			4 (Eb_1, Eb_2, *Est*, Et_1)	1 (V_1)	5
	Finger	3 ([ib_2][1], ib_1, *it*)	2 (*db*, *dt*)	3 (*eb*, *est*, *et*)		8
	Total					35
F1 (Archaeobuthidae)	Femur	2 (i_1, i_2)	5 (d_1–d_5)	1 (e_3)		8
	Patella	1 (i_1)	3 (d_1, d_2, d_5)	4 (eb_1, em_1, *est*, et_1)		8
	Manus			4 (Eb_1, Eb_2, *Est*, Et_1)	1 (V_1)	5
	Finger		2 (*db*, *dt*)	4 (*eb*, *esb*, *est*, *et*)		6
	Total					27
P (Palaeopisthacanthidae)	Femur		3 (d_1, d_2[2], d_5)	1 (e_3)		4
	Patella		1 (d_1)	2 (et_1, eb_1)		3
	Manus			4 (Eb_1, Eb_2, *Est*, Et_1)	4 (V_1–V_4)	8
	Finger			3 (*eb*, *est*, *et*)		3
	Total					18

[1] Additional petite trichobothrium, not observed by Gromov (1998) or Soleglad and Fet (2001, 2003a), described by Prendini et al. (in press).
[2] Designated d_3 by Soleglad and Fet (2001) and d_2 by Soleglad and Fet (2003a).

1974; Stockwell, 1989; Sissom, 1990; Prendini, 2000; Soleglad and Sissom, 2001; S&F, 2003a; Fet et al., 2005). First, the number of trichobothria deviates from the "fundamental" number in many genera. Patterns containing more or fewer than the basic number are termed neobothriotaxic (Vachon, 1974). Patterns with fewer trichobothria are rare outside Buthidae, and usually involve only one or a few trichobothria. However, additive patterns are common among non-buthids and frequently used as phylogenetic characters (Stockwell, 1989; Prendini, 2000; S&F, 2001, 2003a; Soleglad and Sissom, 2001). In some of these additive patterns, there may be so many accessory trichobothria that most of the "fundamental" trichobothria are impossible to identify (Lamoral, 1979; Newlands and Cantrell, 1985; Sissom, 1990; Soleglad and Sissom, 2001; Lourenço and Goodman, 2002). Second, the positions of putatively homologous trichobothria are not fixed, although they do occur in generally predictable limits called "territories" (Vachon, 1974; Lamoral, 1979; Sissom, 1990). In some cases, the variability in position is so drastic that Vachon (1974) and Stahnke (1974) postulated some form of trichobothrial "migration" to account for it.

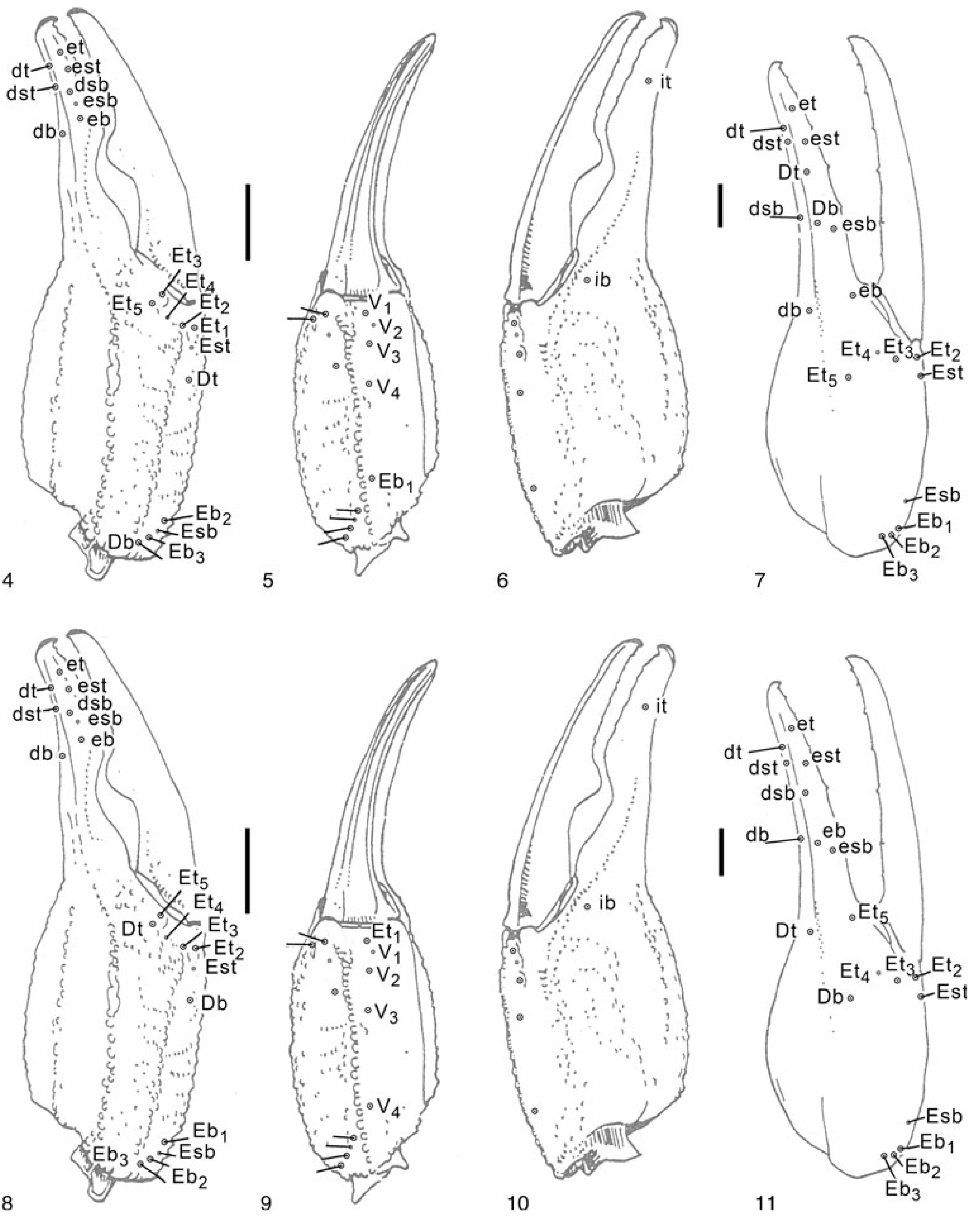
Francke and Soleglad (1981, p. 238) and Francke (1982; pp. 59–60) criticized the trichobothrial terminologies developed by Stahnke (1970, 1974) and Vachon (1972, 1974) on the grounds that there is no evidence of trichobothrial migration, whereas there is abundant evidence of trichobothrial loss or gain. These authors pointed out that 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, a scenario that seems implausible unless they are developmentally connected.

Prendini (2000) responded that the "migration" interpretation, albeit inaccurate, presents no difficulty (besides semantics), for using the terminology proposed by Vachon (or Stahnke), which must necessarily be interpreted with respect to the morphology of the pedipalp—the positions, terminology, and, ultimately, homology of individual trichobothria cannot be determined without reference to landmarks such as carinae and other trichobothria (notably the petite trichobothria which are readily identified due to their smaller size). 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. The apparent "migration" of a trichobothrium from one pedipalp surface to another may thus be nothing more than an interpretation of change in the position of a trichobothrium, relative to a carina which delimits the two surfaces, such that the trichobothrium is now situated on one surface, rather than the other (Prendini, 2000), or allometric change in the length of a segment, such that trichobothria are situated relatively closer or farther apart (Francke, 1982). The premise that trichobothria occupying similar positions are homologous can therefore be accepted 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 (Prendini, 2000, p. 54). Significant differences in the relative positions of landmarks may, indeed, cause significant differences in the interpretation of trichobothrial homology, as the following examples illustrate.

According to Vachon (1974) and Francke and Soleglad (1981), *Calchas* and *Iurus* share three trichobothrial derivations: *Dt* is situated just proximal and adjacent to *Est* (Fig. 4); the four ventral trichobothria are compressed into the distal third of the chela palm (Fig. 5); *it*, but not *ib*, is located near the tip of the fixed finger (Fig. 6). Stockwell (1989) provided what he regarded as a more parsimonious interpretation. Based on the position of Et_4, a landmark petite trichobothrium, Stockwell (1989, p. 113) proposed a distribution for the *Et* series "more like that of other scorpions", in which Et_1 (labeled V_1 by Vachon, 1974) occupies a putatively plesiomorphic position on the ventral surface of the chela, rather than on the external surface. This interpretation changes the positions of the *V*, *Eb*, and *D* trichobothria, such that the *V* and *Eb* series conform to putatively plesiomorphic patterns (Figs 8 and 9), and *Db* and *Dt* are located near the *Et* series (Fig. 8) with *Db* just proximal to *Est* (labeled *Dt* by Vachon, 1974), and *Dt* just dorsal of Et_5. In Stockwell's (1989) reinterpretation, the positions of the *i* and *D* series trichobothria are still considered synapomorphic for *Iurus* and *Calchas* (Figs 8 and 10). Although S&F (2003a) did not state so explicitly, it is clear from their coding (e.g., of characters 8 and 16) and diagnosis for the Iuridae that they retained the original coding scheme of Vachon (1974) and Francke and Soleglad (1981) for *Calchas* and *Iurus*.

Stockwell (1989) also proposed a change to the trichobothrial scheme originally suggested by Vachon (1974) for *Caraboctonus* and adopted by Francke and Soleglad (1980, 1981) for *Hadruroides*. According to Vachon (1974) and Francke and Soleglad (1980, 1981) the *Db* and *Dt* trichobothria are situated near the middle of the fixed finger (Fig. 7) but, in Stockwell's (1989) more parsimonious interpretation, these trichobothria are situated farther back on the distal aspect of the chela palm (Fig. 11). S&F (2003a, p. 35) accepted Stockwell's (1989) reinterpretation in this particular case:

> Although distally situated, [the] relative distance and positions [of *Db* and *Dt*] are comparable to other configurations normally found on the proximal aspect of the palm; in addition, *Db* and *Dt* straddle the digital carina, also typical of Type C pattern scorpions therefore this new interpretation is a more intuitive designation. Finally, under this new interpretation, the pattern of the *db–dsb–dst–dt* series is now consistent with other Type C pattern scorpions, another reason to accept this new



Figures 4–11. Pitfalls in the primary homology assessment of trichobothria in scorpions, illustrated by alternative designations for the trichobothria on the pedipalp chela of iurid scorpions. 4–6, 8–10. *Iurus dufoureius* (Brullé, 1832) (modified from figs 170–174 of Stockwell, 1989, p. 363). 7, 11. *Caraboctonus keyserlingi* Pocock, 1893 (modified from figs 175 and 176 of Stockwell, 1989, p. 365). 4, 7, 8, 11. Dorsoexternal aspect. 5, 9. Ventral aspect. 6, 10. Ventrointernal aspect. Scale bars = 1 mm. 4–6. Vachon's (1974) interpretation, adopted by Francke and Soleglad (1981) and Soleglad and Fet (2003a). 7. Vachon's (1974) interpretation, adopted by Francke and Soleglad (1980, 1981). 8–10. Stockwell's (1989) interpretation. 11. Stockwell's (1989) interpretation, adopted by Soleglad and Fet (2003a), and accepted here.

> interpretation … Stockwell's interpretation of trichobothria *esb* and *eb* could also be reversed, but we accept these designations for overall completeness with his change.

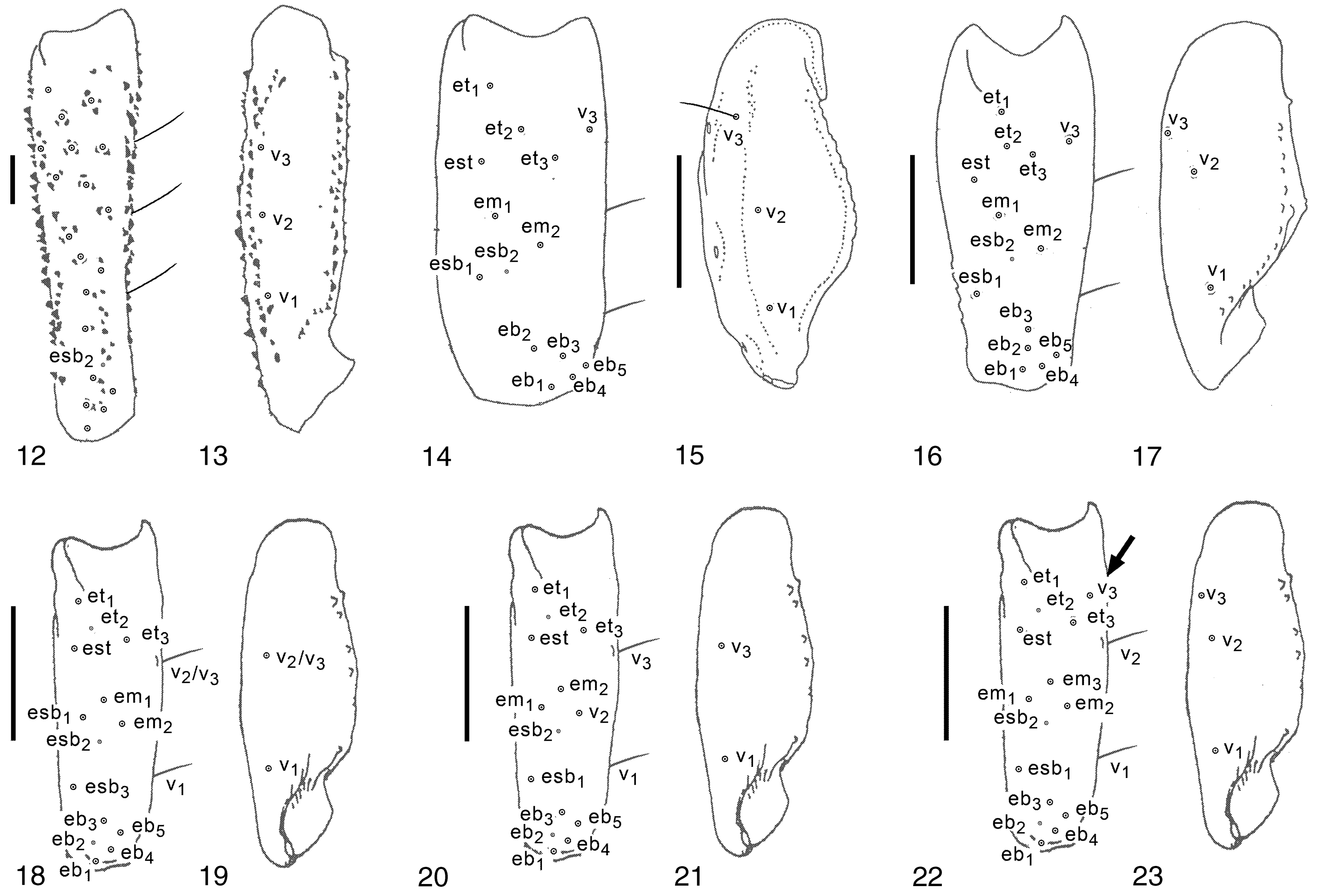
According to S&F (2003a, p. 35), the new interpretation "establishes common patterns" within the genera assigned to their newly erected superfamily Iuroidea and family Caraboctonidae: *db–dt* and *eb–et* occupy the distal half to two thirds of the finger in most Iuroidea, whereas Et_5 occurs on the chelal fixed finger in all Caraboctonidae. It is both inconsistent and unclear as to why S&F (2003a) adopted Stockwell's (1989) revised interpretation of the trichobothria in the genera they assigned to Caraboctonidae, but not his revised interpretation of the trichobothria in *Calchas* and *Iurus*, especially considering that all of these genera were formerly grouped in the same family, Iuridae.

Two alternative interpretations have been proposed to account for the patellar trichobothrial patterns of *Sotanochactas* and *Typhlochactas*, currently placed in subfamily Typhlochactinae of Superstitioniidae (Mitchell, 1968, 1971; Vachon, 1974; Mitchell and Peck, 1977; Sissom, 1988; Stockwell, 1989; Sissom and Cokendolpher, 1998; S&F, 2003a; Table 9). Both genera share an apomorphic pattern in which there are two trichobothria on the ventral surface of the patella, and 14 on its external surface. The possible sister taxon, *Alacran*, exhibits the putatively plesiomorphic condition of three ventral trichobothria (Fig. 13), but also 20 or 21 external trichobothria, obscuring the pattern among the 13 "fundamental" external trichobothria (Fig. 12). In contrast, the other superstitioniid genera, *Superstitionia* and *Troglotayosicus*, exhibit 13 external trichobothria, and three ventral trichobothria, the third, v_3, situated externally according to most authors (Figs 14–17; Table 9). In Stockwell's (1989) interpretation, adopted from Mitchell (1968, 1971), either the second or third ventral trichobothrium has been lost in *Sotanochactas* and *Typhlochactas*. An additional trichobothrium, situated proximally, dorsal to the *eb* series, and labeled *sb* by Mitchell (1968, pp. 761, 767, and 1971, pp. 141, 142)

Table 9
Alternative interpretations of trichobothrial homology on the external and ventral surfaces of the pedipalp patella in superstitioniid scorpions proposed by past authors, except Francke (1982, 1986) who largely rejected the notion that homology assessment is possible with trichobothria, and a reinterpretation proposed here

Taxon	*Typ.*	*Sot.*, *Typ.*	*Sup.*	*Sot.*, *Typ.*	*T. syl.* (dextral)	*T. syl.* (sinstral)	*Tro.*	*Sot.*, *Typ.*	*Sot.*, *Typ.*	*T. syl.* (dextral)	*T. syl.* (sinstral)	*Sot.*, *Typ.*
Author(s)	M68	M71	V74 S&F03 here	V74 S88 S&C98 S&F03	M&P77	M&P77	L81 S&F03 here	S89A favored	S89B	here	here	here
External surface	t	di	et_1	et_1	et_1	et_1	et_1	et_1	et_1	et_1	et_1	et_1
	[st_2]	[sdi_2]	[et_2]	[et_2]	[et_2]	[et_2]	[et_2]	[et_2]	[et_2]	[et_2]	[et_2]	[et_2]
			v_3		et_3	et_3	v_3			v_3		
	st_1	sdi_3	et_3	et_3	**sn**		et_3	et_3	et_3	et_3	et_3	et_3
	st_3	sdi_1	est	est	est	est	est	est	est	est	est	est
	m_2	m_2	em_1	em_2	em_2	em_2	em_1	em_1	em_1	**em_3**	**em_3**	**em_3**
	m_4	m_1		em_1	em_1	em_1		esb_1	esb_1	em_1	em_1	em_1
	m_1	m_4	em_2	v_2	v_2	v_2	em_2	em_2	em_2	em_2	em_2	em_2
	[m_3]	[m_3]	[esb_2]	[esb_2]	[esb_2]	[esb_2]	[esb_2]	[esb_2]	[esb_2]	[esb_2]	[esb_2]	[esb_2]
	sb	**sb**	esb_1	esb_1	esb_1	esb_1	esb_1	**esb_3**	**esb_3**	esb_1	esb_1	esb_1
	b_3	b_3	eb_3	eb_3	eb_3	eb_3	eb_3	eb_3	eb_3	eb_3	eb_3	eb_3
	[b_5]	[b_2]	[eb_2]	[eb_2]	[eb_2]	[eb_2]	[eb_2]	[eb_2]	[eb_2]	[eb_2]	[eb_2]	[eb_2]
	b_1	b_4	eb_5	eb_5	eb_5	eb_5	eb_5	eb_5	eb_5	eb_5	eb_5	eb_5
	b_2	b_5	eb_4	eb_4	eb_4	eb_4	eb_4	eb_4	eb_4	eb_4	eb_4	eb_4
	b_4	b_1	eb_1	eb_1	eb_1	eb_1	eb_1	eb_1	eb_1	eb_1	eb_1	eb_1
Ventral surface	v_2	v_1	v_2	v_3	v_3	v_3	v_2	v_3	v_2	v_2	v_2	v_2
	v_1	v_2	v_1	v_1	v_1	v_1	v_1	v_1	v_1	v_1	v_1	v_1

Taxa as follows: *Sot.* = *Sotanochactas* Francke, 1986; *Sup.* = *Superstitionia* Stahnke, 1940; *Tro.* = *Troglotayosicus* Lourenço, 1981; *Typ.* = *Typhlochactas* Mitchell, 1971; *T. syl.* = *Typhlochactas sylvestris* Mitchell and Peck, 1977 (dextral and sinstral pedipalps of holotype). Homology interpretations, in order of appearance, as follows: M68 = Mitchell (1968, pp. 760, 761, 767, 768) figs 17–19 and 36–38; M71 = Mitchell (1971, pp. 140–143) figs 15–26; V74 = Vachon (1974, pp. 930–932) figs 167, 182, 183; M&P77 = Mitchell and Peck (1977, pp. 162, 163) figs 11–13; L81 = Lourenço (1981, pp. 654, 655) figs 50, 51; S88 = Sissom (1988, pp. 368, 369) figs 6–8; S89 = Stockwell (1989, p. 343) figs 108, 114, 115; S&C98 = Sissom and Cokendolpher (1998, p. 288) figs 5–7; S&F03 = Soleglad and Fet (2003a, p. 40) fig. 80. Each row in the table represents a trichobothrium in a topographically similar position on the patella among the different taxa. Trichobothria are listed in approximate order of appearance from distal to proximal end of patella. Landmark petite trichobothria (*sensu* Vachon, 1974) are denoted by square brackets. Trichobothria hypothesized to be accessory (supernumary *sensu* Mitchell and Peck, 1977) by different authors are indicated in boldface. All trichobothria are recorded on both pedipalps of all the taxa, with the exception of *T. sylvestris*, in which the dextral and sinstral trichobothria differ. Note that although the terminology of Mitchell (1968, 1971) predates the widely accepted nomenclature of Vachon (1972, 1974), the interpretations remain unambiguous. Stockwell (1989) did not, explicitly, provide a hypothesis of trichobothrial homology for the patella of *Superstitionia* and *Troglotayosicus*. S89A and S89B denote two alternative hypotheses of Stockwell (1989).



Figures 12–23. Pitfalls in the primary homology assessment of trichobothria in scorpions, illustrated by alternative codings for the trichobothria on the pedipalp patella of superstitioniid scorpions. 12, 13. *Alacran tartarus* Francke, 1982 (modified from figs 7 and 8 of Francke, 1982, p. 58). 14, 15. *Superstitionia donensis* Stahnke, 1940 (modified from fig. 182 of Vachon, 1974, p. 932 and fig. 108 of Stockwell, 1989, p. 343). 16, 17. *Troglotayosicus vachoni* Lourenço, 1981 (modified from figs 50 and 51 of Lourenço, 1981, p. 655). 18–23. *Typhlochactas reddelli* Mitchell, 1968 (modified from figs 114 and 115 of Stockwell, 1989, p. 363). 12, 14, 16, 18, 20, 22. External aspect. 13, 15, 17, 19, 21, 23. Ventral aspect. Scale bars = 1 mm. 18, 19. Mitchell's (1968, 1971) interpretation of the trichobothria of *Sotanochactas* Francke, 1986 and *Typhlochactas* Mitchell, 1971, adopted by Stockwell (1989): v_2 (Stockwell's favored interpretation, S89A) or v_3 (S89B) has been lost and an accessory, esb_3 (Mitchell's *sb*), gained. 20, 21. Vachon's (1974) interpretation, adopted by Mitchell and Peck (1977), Sissom (1988), Sissom and Cokendolpher (1998), and Soleglad and Fet (2003a): v_2 has "migrated" or been "displaced" to the external surface. 22, 23. Reinterpretation proposed here: v_3 has been lost from the external surface, although it is observed on the dextral pedipalp of the holotype of *Typhlochactas sylvestris* Mitchell and Peck, 1977 (arrow), and an accessory trichobothrium, em_3, gained. Refer to Table 9 for more details.

and esb_3 by Stockwell (1989, p. 343), has appeared on the external surface (Figs 18 and 19; Table 9). Stockwell's (1989, p. 103) statement that this is an *eb* trichobothrium conflicts with his fig. 115 but makes no difference to the interpretation. In this scenario, loss of one of the ventral trichobothria serves as a potential synapomorphy for (*Sotanochactas* + *Typhlochactas*), whereas the additional esb_3 trichobothrium serves as a potential synapomorphy for (*Alacran* (*Sotanochactas* + *Typhlochactas*)). Stockwell (1989) favored loss of the second ventral trichobothrium (v_2) in *Sotanochactas* and *Typhlochactas* (S89A in Table 9) rather than the alternative (S89B)—loss of the third ventral trichobothrium from a presumably external position (implying that the distal ventral trichobothrium is actually v_2)—due to the apparently close phylogenetic relationship (based on other characters) between these genera and *Alacran*, in which v_3 is situated ventrally. Either scenario implies two events: the loss of a ventral trichobothrium and the gain of an external.

An alternative interpretation, first proposed by Vachon (1974) and subsequently adopted by Mitchell and Peck (1977), Sissom (1988), Sissom and Cokendolpher (1998), and S&F (2003a), is that Stockwell's (1989) accessory esb_3 trichobothrium, i.e., Mitchell's (1968, 1971) *sb*, is actually esb_1, his esb_1 and em_1 are, respectively, em_1 and em_2 (esb_2 is petite and therefore unambiguously identifable), and his em_2 is v_2, "displaced" to the external surface, with the distal ventral trichobothrium, v_3, remaining on the ventral surface (Figs 20 and 21). This interpretation, albeit more parsimonious than either of Stockwell's (1989) alternatives, is also unprecedented: in all scorpions surveyed to date, distal ventral trichobothria are always "displaced" first.

A third interpretation, proposed here, is supported by Mitchell and Peck's (1977, pp. 162, 163, fig. 12) observation, in the holotype of *T. sylvestris*, of an accessory trichobothrium, labeled *sn*, on the external surface of the dextral pedipalp patella (Fig. 22; Table 9). Based on positional similarity with other superstitioniids, we reinterpret this *sn* trichobothrium to be et_3, and Mitchell and Peck's (1977) et_3 instead to be v_3 in its external position, as observed in *Superstitionia* and *Troglotayosicus*, but usually unexpressed (i.e., absent) in *Typhlochactas* and *Sotanochactas*. Yet another, fourth interpretation is that the *sn* trichobothrium is v_3, in which case et_3 would be consistent with Mitchell and Peck's (1977) interpretation. We consider this alternative unlikely based on the dissimilar positions of the trichobothria in question, relative to those of other *Typhlochactas*, *Sotanochactas*, *Troglotayosicus* and *Superstitionia*. This alternative, or one of the others (Vachon, 1974; Stockwell, 1989) might be supported by Mitchell and Peck's (1977, p. 162) observation that the *sn* trichobothrium is shorter than other trichobothria, suggesting that it is petite, autapomorphic and thus uninformative. However, we have studied the holotype (deposited in the collection of the American Museum of Natural History, New York), and the areola of the trichobothrium in question is not noticeably reduced in size, compared with that of et_1 and et_2 (which is often reduced in typhlochactines). We see no other reason to assume that this trichobothrium, situated on the dextral pedipalp patella of the holotype of *T. sylvestris*, in a similar position to et_3, is not homologous with it. On the basis of these observations, we consider the second ventral trichobothrium to be v_2 (Fig. 23), in accordance with Stockwell's (1989) less favored hypothesis (S89B in Table 9), but in a very similar position to that observed in *Troglotayosicus* (Lourenço, 1981; Fig. 17). We regard the external trichobothria of *Sotanochactas* and *Typhlochactas* as identical to those observed in *Superstitionia* and *Troglotayosicus*, with the addition of one accessory trichobothrium, situated distal to em_1 and em_2, which we label em_3. The designations of em_1 and em_3 could also be reversed without changing the interpretation. This new interpretation of trichobothrial homology achieves the same potential synapomorphies as Stockwell's (1989), but is more consistent, topographically, across the superstitioniid genera (cf. the scheme adopted by S&F, 2003a).

As these examples and others—compare, e.g., the trichobothrial designations for *Pseudochactas* proposed by Gromov (1998) and S&F (2001)—demonstrate, primary homology assessment of trichobothria, even within the basic trichobothrial patterns, is no trivial exercise. Establishing primary homology across the basic patterns (Table 8) is even more difficult. Indeed, prior to the work of S&F (2001, 2003a), it had never seriously been attempted, chiefly because the primary homology of topographical landmarks, e.g., carinae, needed to guide decisions regarding the primary homology of trichobothria, also becomes increasingly difficult to determine across the major lineages of scorpions. Vachon's (1972, 1974) terminology, though establishing a common nomenclature, was probably not intended to reflect homology statements across his three pattern types (S&F, 2001, p. 10), but was, almost certainly, intended to do so within them (Francke, 1982). According to Stockwell (1989, p. 97), the overall trichobothrial patterns cannot be derived from one another, although certain components of each type exhibit character state transformations that extend across the broader patterns (e.g., the three trichobothria on the ventral surface of the patella in *Chaerilus* and the Type C taxa). In our view, the establishment of trichobothrial homologs across all scorpions is a worthy objective but we agree with previous authors (e.g., Lamoral, 1979; Francke and Soleglad, 1981; Sissom, 1990; Prendini, 2000) that assumptions of primary homology should be made with great caution and we do not accept S&F's (2001, 2003a) homology scheme uncritically. There is considerable variability in trichobothrial number and pattern, both intra- and interspecifically, this variability is not well understood for many taxa (Sissom, 1990), and many of the alleged trichobothrial homologs proposed by S&F (2001, 2003a), especially among the 73 (44%) characters that extend across the six basic trichobothrial patterns (Table 7), fail to meet the criterion of topographical similarity.

States as concepts, not observations

Another category of S&F's (2003a) characters or states that fail the criteria of topographical and compositional similarity, and hence the test of primary homology, includes 14 (8%) that portray concepts, not real observations (Table 7). The states of these characters represent higher-level composites of lower-level observations akin to supraspecific terminal taxa based on observations of exemplar species (or individual specimens). Ordered character 1 of Appendix 2, representing the six types of orthobothriotaxy, derived from the 62 "existence" characters (the actual observations) in Table 3 (Appendix 1), is one example: Type P, Palaeopisthacanthidae (0); Type F1, Archaeobuthidae (1); Type D, Pseudochactida (2); Type A, Buthida (3); Type B, Chaerilida (4); Type C, Iurida (5). "Fundamental" character 63, representing sternum "basic type", adopted from S&F's (2003b) online treatise on the scorpion sternum, is another: type 1—posterior depression, outer ridge, single internal process (primitive) (0); type 2—posterior emargination, lateral lobes; two internal processes (parvorder Iurida) (1). At least three characters, pertaining to the posterior depression and/or ridge, the lateral lobes, and internal processes, could potentially be recognized here.

The impression that S&F do not understand the character concept is reinforced by another recent comment, on the coding of these very structures, by Soleglad et al. (2005, p. 5):

> The first example can be rectified to a degree by considering all the trichobothria comprising the orthobothriotaxic patterns, thus a "single character" is transformed into many characters; this approach was utilized by Soleglad and Fet (2001) in their study of the evolution of orthobothriotaxy. The quantification of fundamental sternum types by Soleglad and Fet (2003a) is another example where a "single character" was broken down into several substructures (i.e., its basic type, existence of compression within a type, important morphometric ratios, etc.).

Besides the fact that S&F (2003a) coded the trichobothria and sternum in exactly the opposite manner to that described in the quotation, the definition of "character" used by these authors is grossly at odds with that accepted by the systematics community (Patterson, 1982; Rieppel, 1988; Platnick, 1989; De Pinna, 1991; Brower and Schawaroch, 1996; Hawkins et al., 1997; Schuh, 2000).

Characters 32–36, presenting patterns of neobothriotaxy (accessory trichobothria) on the pedipalps are beset with the same problem. These characters do not portray the accessory trichobothria in question, but instead group "patterns" of accessory trichobothria observed in taxa of presumed phylogenetic affinity, as shown in character 32 (Appendix 2) portraying neobothriotaxy on the chela ventral surface: absent (0); present (Iuroidea) (1); present (Bothriuridae) (2); present (Urodacidae) (3); present (Liochelidae) (4); present (Scorpionidae) (5); present (Hemiscorpiinae) (6); present type Ch1 (Chactinae) (7); present type Ch2 (Brotheinae) (8); present type Ch3 (Uroctoninae) (9); present type Eu1 (Euscorpiinae, Megacorminae) (a); present type Eu2 (Scorpiopinae) (b); present (Vaejovidae) (c); present type Su1 (Superstitioniidae) (d); Type D, A, and B patterns (–). S&F's (2003a, p. 138) justification for this approach follows the trend throughout their papers in which observed variation is apportioned among taxa according to their presumed phylogenetic relationships:

> We divide this modeling into two types, Type A (the buthoids) and Type C (the iuroids, scorpionoids, and chactoids). We suspect that subtractive neobothriotaxy found in some buthid genera may imply a primitive state of these genera. On the other hand, additive neobothriotaxy in the buthids is clearly derived and is therefore considered autapomorphic to the genera involved. For the substantial additive neobothriotaxy found in Type C scorpions we make no interfamilial assumptions as to common derivations of neobothriotaxy. We believe that neobothriotaxic conditions must be studied in great detail in closely related groups in order to establish potential connections across major familial groups.

These authors claim to make no interfamilial assumptions but are content to assign the same or different trichobothrial "types" to taxa that may or may not be related phylogenetically, in so doing, either forcing them to be monophyletic or preventing their monophyly from being tested and ignoring their own advice regarding the coding of trichobothria:

> We do not believe that the gross coding at a surface level accurately depicts the important phylogenetic data presented by trichobothria … We should strongly emphasize here, however, that homology arguments at the individual accessory trichobothrium level would be yet a further refinement, and certainly a major improvement … In theory, every trichobothrium is a separate character and needs to be considered as such. (Soleglad and Sissom, 2001, p. 73)

> Our approach to trichobothria analysis is to model the various fundamental trichobothrial systems as proposed by Vachon (1972, 1974), Gromov (1998), Jeram (1994) and Lourenço (2001) by establishing consistent homologies across all the patterns and using cladistic analysis to evaluate these hypothesized homologies—which means accepting homologies that are the most efficient with respect to trichobothrium gains or losses (i.e., the most parsimonious). This approach is more

> comprehensive than the gross "number approach" discussed above since individual trichobothrium derivation is considered. (S&F, 2001, p. 3)

Given the superiority of coding individual trichobothria (setting aside the significant challenges to doing so, especially across the basic patterns, as discussed above) and analysing their distributions parsimoniously, S&F's (2003a) decisions to substitute such characters with others that, by their own admission, do not represent homologous variation, are incomprehensible.

States that overlap or subsume non-homologous variation

Besides the problems already mentioned, many of S&F's (2003a) characters demonstrate either a lack of understanding of, or disregard for, established methods and standards for morphological character coding in systematics. Fifteen (9%) of their characters contain states with grossly overlapping variation (Table 7), despite well-known methods for coding continuous variation, one cited by Soleglad et al. (2005, p. 5), which stipulate that gaps in the variation must be evident in order to code states discretely or that quantitative data should be analyzed as such if, indeed, they should be included at all (Pimentel and Riggins, 1987; Cranston and Humphries, 1988; Felsenstein, 1988; Chappill, 1989; Stevens, 1991; Thiele, 1993; Gift and Stevens, 1997; Rae, 1998; Swiderski et al., 1998; Schuh, 2000; Wiens, 2001; Goloboff et al., 2004).

Overlapping variation is evident in characters 55 and 72 (Appendix 2). Character 55 represents the number of denticle groups in the median denticle row of the pedipalp chelal movable finger: 5–6 (*Anuroctonus*, Brotheinae) (0); 7–9 (Chactini) (1); 7–8 (*Uroctonus*) (2). Character 72 represents the proportions (anterior lengths) of leg coxae II and IV: IV_L/II_L = 1.3–2.0 (0); IV_L/II_L = 2.2–2.9 (Buthoidea) (1); IV_L/II_L = 2.3–2.6 (Caraboctonidae) (2). State 2 of both characters falls entirely within the range of state 1 and should be merged with the latter. Character 67, which "models significant proportional differences" (S&F, 2003a, p. 142) in the sternum, demonstrates the same problem: length ≤ width (Euscorpiidae) (0); length > width (Euscorpiidae: Scorpiopinae) (1); length ≤ width (Scorpionoidea: non-bothriurids) (2); length > width (Hemiscorpiinae) (3); length ≥ width (Typhlochactinae) (4); length < width (Superstitioniinae) (5).

In contrast to such characters with overlapping states, the states in 34 (20%) of S&F's (2003a) characters encompass variation that is not structurally or topographically identical and would be more appropriately accommodated in separate states or perhaps separate characters (Table 7). This is observed in states 2 and 4 of character 102, portraying the number of lateral ocelli (discussed further above): 0–2 (Euscorpiidae, Chactidae, Superstitioniidae) (2); 3–4 (Uroctoninae) (4). This character represents an example of quantitative variation that should have been analyzed as such (Thiele, 1993; Wiens, 2001; Goloboff et al., 2004). Additional states should have been created to represent the conditions for which corresponding states were not already provided (0 and 4 ocelli), and the other conditions scored for the states that already were.

Three states were provided to accommodate two conditions of the tarsal ventrodistal spinule (*VDS*) pairs (character 62, Appendix 2): 1 pair (or one spinule) (Vaejovidae, Euscorpiidae, Chactidae) (0); 2 + pairs (Euscorpiidae) (1); 2 + pairs (Vaejovidae) (2). According to S&F (2003a, p. 142):

> We consider the differences in *VDS* pair numbers exhibited in the chactoid families Vaejovidae and Euscorpiidae to be independently derived, thus they are assigned different states.

States 1 and 2 are in fact oversimplifications of a more complex pattern (*vide* McWest, 2000; Soleglad and Sissom, 2001; Fet et al., 2004b) probably requiring multiple additional states scored in multiple exemplars. Interestingly, this same criticism was levelled at Prendini's (2000) character portraying the number of rows of denticles on the pedipalp chela fingers, adopted from Stockwell (1989), although S&F (2003a) cited this as a weakness of the exemplar approach:

> We also question this somewhat simplistic modeling of this complex structure … this character requires some serious reanalysis involving many species in several genera, something not possible with the token species set used in the "exemplar method" … (S&F, 2003a, p. 116)

> This characterization (adopted, in part, from Prendini (2000)) is somewhat superficial. Clearly, a detailed analysis of all scorpionoid genera needs to be conducted, where multiple species per genus are considered. Issues involving two rows, more than two rows, multiple rows only present basely, etc., need to be carefully quantified. This analysis proved to be quite difficult in the family Euscorpiidae (Soleglad and Sissom, 2001), which was not resolved to any satisfaction until several species with simple patterns were investigated. This, in turn, allowed the determination of homologies in species with more complex patterns. (S&F, 2003a, p. 141)

Soleglad et al. (2005, p. 19) reinvestigated this particular character, among others, in more detail by studying additional species of *Heteroscorpion* and *Urodacus* that were not represented in Prendini's (2000) original sample, but did not score these additional species in their reanalysis. Soleglad et al. (2005, p. 20, figs 45–49) presented evidence of different dentition in the distal third of the finger, among four species of *Urodacus* and two species of *Heteroscorpion*, but then proceeded to assign the same state to Prendini's (2000) original four exemplar species in the two genera:

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

Character 101 in S&F's (2003a) matrix, which portrays stigma shape "partitioned by superfamily and/or upper clades", provides an example of a character in which some states overlap and others subsume non-homologous variation: circular, small (Palaeopisthacanthidae, Archaeobuthidae, Chaerilidae) (0); oval, small (Pseudochactidae, *Microcharmus*) (1); slit-like, small to long (most Buthoidea) (2); oval (Iuroidea) (3); slit-like (Iuroidea) (4); oval (Scorpionoidea) (5); slit-like (Scorpionoidea) (6); circular, small (*Troglotayosicus*, Chactinae, most Brotheinae) (7); oval, small (Superstitioniidae, Euscorpiidae) (8); oval, medium to long (Uroctoninae, *Paravaejovis*) (9); slit-like, medium to long (Vaejovidae, *Brotheas*) (a). S&F's (2003a, p. 146) desire to reduce homoplasy again guided their coding of this character:

> All major Recent scorpion groups exhibit small circular to oval stigmata as well as more elongated slit-like stigmata. Within these groups we see numerous derivations spanning these shapes … It is clear from the diversity exhibited in the shape of the stigma across all major groups that these derivations happened independently and are therefore assigned separate states.

The distinctions between "circular", "oval" and "slit-like", and between "small", "small to long" and "medium to long" are tenuous at best (Table 7). It is precisely such vague and arbitrary character and character state definitions that have recently led some to question the rigor, objectivity and, ultimately, the relevance of morphological phylogenetics in an age of genomics (see discussions in Wiens, 2001, 2004; Scotland et al., 2003; Jenner, 2004).

Polymorphic "states", unknown "states" and inapplicable "states"

Further evidence of substandard character coding by S&F (2003a) is provided by six characters in which polymorphic "states" were created for terminals with interspecific variation (Table 7). For example, in character 104, pectinal fulcra development was scored as follows: present (Vaejovidae, most Chactidae) (0); absent (most Superstitioniidae) (1); absent (*Belisarius*) (2); absent (Euscorpiidae) (3); variable within the genus (Euscorpiidae) (4). Pectinal fulcra are present in some euscorpiids, but absent in others (Soleglad and Sissom, 2001; S&F, 2003a). The presence of these structures is thus polymorphic at the family level in Euscorpiidae, although it is not at the species level. At a minimum, the euscorpiids in question should have been scored polymorphic, e.g., * or [03] (Rice et al., 1997; Wiens, 1998a; Simmons, 2001), not provided with an autapomorphic "state", which would artificially force them to be monophyletic. A superior strategy, however, would be to include the exemplar species displaying the variation and score the actual observations in those (Yeates, 1995; Prendini, 2001a).

A similar example is provided by character 60, portraying the number of pedal spurs (discussed further above). S&F (2003a, p. 141) observed:

> We see variability in the number of pedal spurs in genera *Sotanochactas* and *Typhlochactas*, from no spurs to both present.

Instead of portraying the polymorphism in the subfamily appropriately (as discussed below, the number of pedal spurs was misrepresented in these taxa), an autapomorphic "state" was again provided: 0–2, variable in genus (Typhlochactinae). In order to assign an appropriate polymorphism score, an additional state would be required to reflect the absence of both pedal spurs, at which point it would be prudent to score the actual observations in exemplar species, an option unavailable to S&F (2003a) because of their use of a composite terminal representing Typhlochactinae.

Such examples suggest that S&F (2003a) are unaware of more than 20 years of literature on strategies for coding and analyzing polymorphic data (Mickevich and Mitter, 1981; Archie, 1985; Pimentel and Riggins, 1987; Nixon and Davis, 1991; Platnick et al., 1991; Mabee and Humphries, 1993; Thiele, 1993; Wiens, 1995, 1998a, 1998c, 1999, 2000, 2001; Nixon and Carpenter, 1996; Kron and Judd, 1997; Rice et al., 1997; Wiens and Servedio, 1997, 1998; Swiderski et al., 1998; Kornet and Turner, 1999; Prendini, 2001a; Simmons, 2001; Smith and Gutberlet, 2001).

It is also worth noting characters 57 and 73, in which an unknown, putatively plesiomorphic condition was assigned state 0 in each case! Character 57 (Appendix 2) portrays the leg tarsal armature as follows: primitive state, unknown (Palaeopisthacanthidae) (0); dual median spinule rows (Pseudochactida) (1); numerous irregularly positioned setae (Buthoidea, Chaerilidae) (2); ventrally positioned spinule clusters (Iuroidea) (3); large paired laterally positioned socketed spinoid setae (Scorpionoidea) (4); small laterally positioned socketed setae and/or ventrally positioned spinules (Chactoidea) (5). Character 73 (Appendix 2) presents hemispermatophore shape: primitive form (UNKNOWN) (0); fusiform (Chaerilidae) (1); flagelliform (Buthoidea) (2); lamelliform (Scorpionoidea and Chactoidea) (3). As a comment to the latter, S&F (2003a, p. 143) asserted:

> The primitive form of the hemispermatophore is unknown. We assign a "null state" as primitive.

It seems almost too obvious to mention that most contemporary systematists would assign a question mark when a condition is unknown, and a dash (–) when a condition is inapplicable, rather than inventing an autapomorphic "state". The precedent for this practice was set by Fet et al. (2001; pp. 157, 158), who assigned state "0 = inapplicable" to four characters (5, 6, 18 and 19, reproduced here in Appendix 3) in a matrix of 19 for a phylogenetic analysis of the hirsutus group of *Hadrurus*.

Characters omitted, scored unknown or inapplicable in taxa in which known or applicable

Remarkably, many characters in the matrix of S&F (2003a) were not even evaluated for particular terminal taxa, but merely scored inapplicable (–) regardless of whether the structures, and consequently the characters, in question were present and therefore applicable to them. For example, although all scorpions have a pedipalp patella, the non-Iurida were scored inapplicable for the presence or absence of a "vaulted projection" on its internal surface (character 97). All scorpions have pectines, but non-chactoids were scored inapplicable for the number of pectinal teeth (character 103). In another example, *Pseudochactas* and Buthoidea were scored inapplicable for the number of lateral ocelli on the carapace (character 102) although these taxa possess lateral ocelli, a fact of which S&F (2003a, p. 146) were certainly aware:

> … we see primitive genus *Pseudochactas* with one lateral eye, and the buthoids usually with three to five eyes.

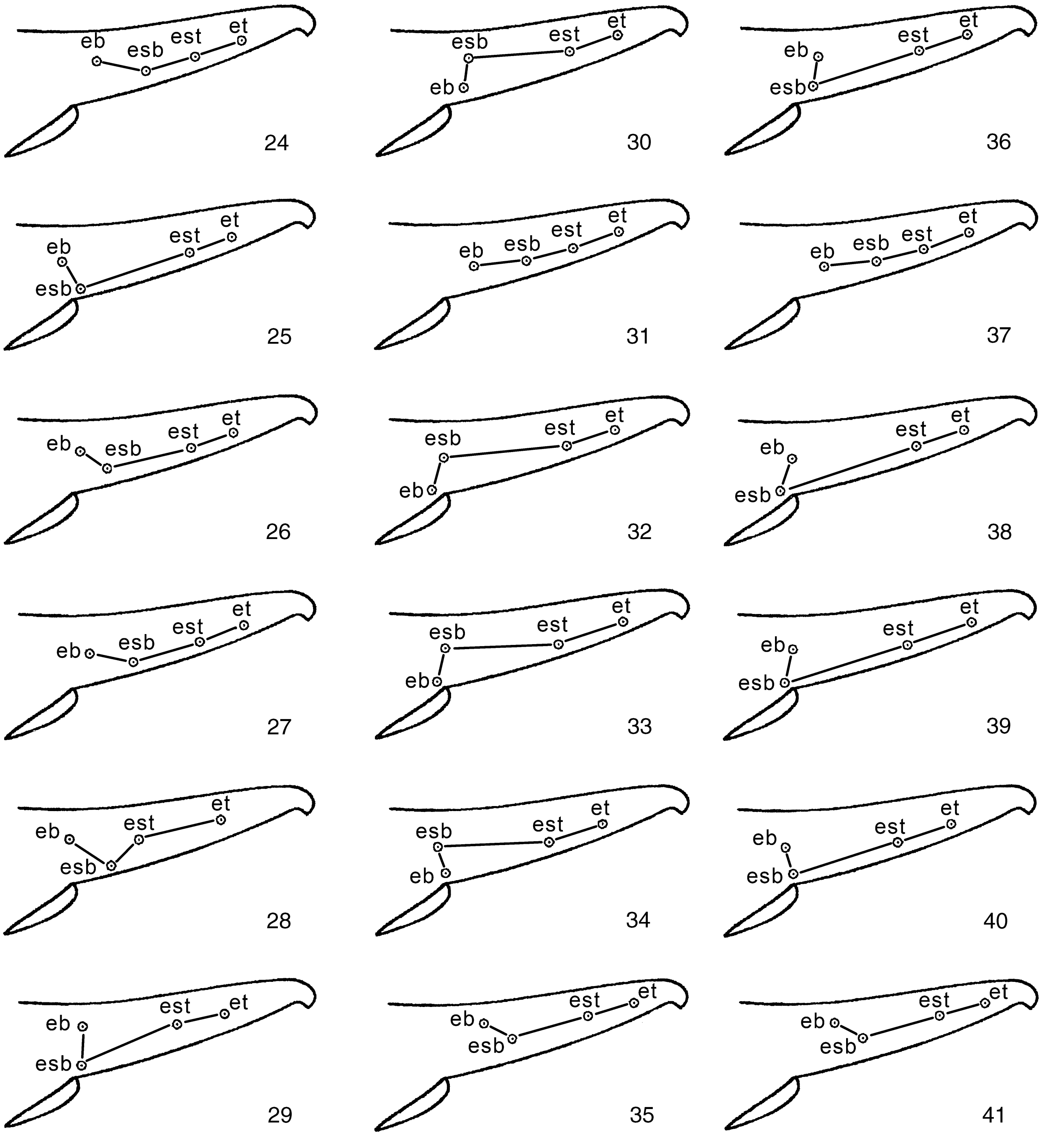
Similarly, several characters were scored unknown (?) in particular taxa, although the condition in these taxa has been documented by others. For example, *Chactopsis* was scored unknown (?) for characters 13 (position of chelal trichobothria *db–dt* and *eb–et*) and 19 (position of chelal trichobothria *Db* and *Dt*) although, according to Vachon (1974, p. 933, fig. 190), González-Sponga (1996, pp. 112–116, figs 245, 249, 253, 257 and 261), Stockwell (1989, character 73) and others, these trichobothria are situated distally on the fixed finger in this genus, a hypothesis that reiterates the problems associated with primary homology assessment of trichobothria (discussed above). *Vejovoidus* was scored unknown (?) for the number of ventrodistal spinule pairs on the telotarsi (character 62; Appendix 2), although Stockwell (1989) scored one or two pairs for the genus (state 0 of his character 100).

These are but six of 56 (34%) characters in S&F's (2003a) matrix that were scored in only a subset of the taxa in which they are known or applicable (Table 7). Indeed, of the 2071 cells scored inapplicable in the original matrix—93 cells were scored unknown (?)—798 (39%) are applicable to the taxa in question (8% of all cells in the matrix). Yet further examples are provided in recent works by Fet et al. (2004a) and Soleglad et al. (2005). Apparently, these authors do not understand the meaning of "inapplicable" (an observation supported by their coding of inapplicables in the analysis by Fet et al., 2001), although it has been elaborated in numerous works, including basic texts on cladistics (Platnick et al., 1991; Lipscomb, 1992, 1998; Maddison, 1993; Lee and Bryant, 1999; Strong and Lipscomb, 1999; Schuh, 2000). Notwithstanding the poor scholarship, treatment of data in this manner casts further doubt on the results of S&F (2003a), Fet et al. (2004a) and Soleglad et al. (2005), given that inapplicable entries (–), treated the same as missing entries (?) by existing phylogenetic algorithms, have insidious effects on phylogenetic analyses (Nixon and Davis, 1991; Platnick et al., 1991; Novacek, 1992; Maddison, 1993; Wilkinson and Benton, 1995; Wilkinson, 1995a,b, 2003; Wiens, 1998b, 2003a,b; Makovicky, 2000; Norell and Wheeler, 2003).

On the subject of scholarship, it is noteworthy that at least 124 (potentially 131) characters bearing on the relationships of extant Scorpiones, from prior analyses by Lamoral (1980), Stockwell (1989), Prendini (2000), Soleglad and Sissom (2001), and a further 34 bearing on the relationships of fossil Scorpiones, from prior analyses by Stockwell (1989) and Jeram (1994, 1998), were omitted from the analysis by S&F (2003a). Some of these characters would challenge the controversial placements of particular taxa (e.g., *Anuroctonus*) in S&F's (2003a) analysis and should have been included to test these alternative hypotheses. No justification was provided for their omission. Some of Prendini's (2000) characters were likewise omitted by Soleglad et al. (2005, p. 23).

Errors, interpretations, misrepresentations and guesswork

Fet et al. (2004a) and Soleglad et al. (2005) recently accused Prendini (2000, 2003a,b) of ignoring and misrepresenting evidence. For example, these authors claimed that Prendini (2000, 2003a,b) mistakenly cited the absence of certain pedipalpal and metasomal carinae



Figures 24–41. Pitfalls in the primary homology assessment of trichobothria in scorpions, illustrated by alternative codings for the trichobothria on the external surface of the fixed finger (*eb–et* series) of the pedipalp chela of chactoid scorpions (stylised diagrams, modified from fig. 79 of Soleglad and Fet, 2003a, p. 39). 24. *Serradigitus* sp., *Syntropis macrura* Kraepelin, 1900 and *Vaejovis* sp. 25. *Pseudouroctonus angelenus* (Gertsch and Soleglad, 1972) and *P. bogerti* (Gertsch and Soleglad, 1972). 26. *Pseudouroctonus andreas* (Gertsch and Soleglad, 1972) and *Uroctonites huachuca* (Gertsch and Soleglad, 1972). 27. *Paruroctonus* sp., *Smeringurus* sp. and *Vejovoidus longiunguis* (Williams, 1969). 28. *Paravaejovis pumilis* (Williams, 1970). 29. *Superstitionia donensis* Stahnke, 1940. 30, 36. *Euscorpius* sp., *Megacormus* sp. and *Plesiochactas* sp. 31, 37. *Alloscorpiops* sp., *Dasyscorpiops grandjeani* Vachon, 1974, *Euscorpiops* sp., *Neoscorpiops* sp., *Parascorpiops montanus* Banks, 1928, *Scorpiops* sp. and *Troglocormus* sp. 32, 38. *Anuroctonus phaiodactylus* (Wood, 1863) and *Uroctonus mordax* Thorell, 1876. 33, 39. *Chactas* sp., *Nullibrotheas allenii* (Wood, 1863), *Teuthraustes* sp., *Vachoniochactas* sp. 34, 40. *Belisarius xambeui* Simon, 1879 and "*Neochactas*" sp. 35, 41. *Brotheas* sp., *Broteochactas* sp., *Hadrurochactas* sp. 24–29. Vachon's (1974) interpretation, adopted by Stockwell (1989) and Soleglad and Fet (2003a), and accepted here. 30–35. Vachon's (1974) interpretation, adopted by Soleglad and Fet (2003a). 36–41. Stockwell's (1989) interpretation, accepted here.

in the two species of *Lisposoma* Lawrence, 1928 and in other bothriurid scorpions, as evidence for the distinctiveness of a new bothriurid genus, *Brandbergia* Prendini, 2003:

> In Prendini's (2000, 2003a) general cladistic modeling of the pedipalp chelal carina, he states that the digital (*D1*) and ventroexternal (*V1*) carinae are *obsolete* in all bothriurids except for the species *Brandbergia haringtoni*. Both carinae in *B. haringtoni* are indeed present and granular, especially *V1* … The question arises whether these carinae are really *absent* in the other bothriurids. The answer to this question is no … (Fet et al., 2004a, p. 198) [italics added]

> Prendini (2003a), in his depiction of these carinae in *L. elegans* and *L. josehermana*, as contrasted to *B. haringtoni*, has either ignored the development of carinae in *L. josehermana*, or misrepresented it in part. (Fet et al., 2004a, pp. 200, 202)

In response to these allegations, it must first be stated that Prendini's (2000, pp. 50, 51, 65; 2003a, pp. 170, 172) depiction was grossly misrepresented by Fet et al. (2004a). The carinae in question were described as "obsolete", not "absent", and some authors, including Lamoral (1979), whose work was cited and misquoted by Fet et al. (2004a, pp. 197, 198), recognize a qualitative difference between these terms. For example, in his diagnosis of *Lisposoma*, Lamoral (1979, p. 661) stated:

> Pedipalp chela … without *distinct* finger [digital] or accessory keels [carinae] … [italics added]

The chelal carinae of *L. josehermana* Lamoral (1979) were described as follows:

> … although no keels are visible on [chela] handback, their normal position is indicated by longitudinal lightly infuscated bands. (Lamoral, 1979, p. 665)

In contrast to the depiction by Fet et al. (2004a), it is clear that the observations of Lamoral (1979) are congruent with those of Prendini (2000, 2003a): the carinae of *Lisposoma* (and most other bothriurids) are obsolete or indistinct, not absent *per se*. That said, it must also be accepted that different workers inevitably disagree in the interpretation and coding of particular structures even in the same taxa, often a function of the quality and quantity of material at their disposal for examination, the methods of study and analysis (e.g., the indices used to codify similarity), and so forth. Such discrepancies do not, in themselves, disqualify or nullify the impact of a work. Allegations that data have been misrepresented are another matter, however. Such accusations should not be made lightly, particularly when they are, in fact, more appropriately directed at the work of the accusers, as we have demonstrated repeatedly in this paper. Additional examples from S&F (2003a), among others listed in Table 7 (some of which may, perhaps, be legitimate errors on the part of those authors), shall serve to further illustrate the point.

Some of the most conspicuous examples come from the trichobothria. For example, *Anuroctonus*, *Belisarius*, *Nullibrotheas*, *Superstitionia*, *Troglotayosicus*, *Uroctonus*, and four Neotropical chactid genera (*Brotheas*, *Chactas*, "*Neochactas*" and *Teuthraustes*) were scored state 1 of character 8 (trichobothrium Eb_1 situated on the chelal ventral surface or on the ventroexternal carina) but it is a matter of interpretation, as seen in S&F's (2003a, pp. 42–51) illustrations, especially figs 81, 86 and 87, whether some, if not all, of these taxa should have been scored state 0 (Eb_1 situated on external surface). Furthermore, it is difficult to determine the identity of Eb_1 unambiguously in *Anuroctonus* on account of the large number of accessory trichobothria in this genus (Vachon, 1974; Sissom, 1990; S&F, 2003a).

Although the *db–dt* and *eb–et* trichobothria of *Alacran*, *Chactopsis*, *Iurus* and *Sotanochactas* are situated on the distal half of the chelal fixed finger in all these taxa (Vachon, 1974; pp. 933, 939, figs 190 and 216; Francke, 1982, p. 56, figs 9 and 10; Francke, 1986, p. 7, fig. 12; Stockwell, 1989, p. 363, figs 170 and 173; González-Sponga, 1996, pp. 112–116, figs 245, 249, 253, 257 and 261; S&F, 2003a, p. 39, fig. 79), only *Iurus* and *Alacran* were scored for this condition, in separate states 1 and 3, respectively, of character 13. *Chactopsis* was scored unknown (?), whereas *Sotanochactas*, incorporated into a composite terminal with *Typhlochactas* (S&F, 2003a, p. 67), was scored state 0 (*db–dt* and *eb–et* evenly spread out on finger). *Calchas* and *Hadrurus* were scored state 1 (*db–dt* and *eb–et* on distal half of finger), although their trichobothria are spread out across the finger, as seen in Vachon's (1974, p. 939) fig. 212 and Stockwell's (1989, p. 351) fig. 144. *Urodacus* was scored state 2 of character 13 (*db–dt* and *eb–et* on proximal half of fixed finger), but could have been scored state 0, as seen in Vachon's (1974, p. 24) fig. 131 and Prendini's (2000, p. 37) fig. 8H.

Diplocentrus, *Hemiscorpius*, *Liocheles* and *Scorpio* were all assigned state 1 of character 18 (chelal trichobothria V_2 and V_3 separated, distance between V_2 and V_3 much greater than distances between V_1 and V_2 and V_3 and V_4). However, the distance between V_2 and V_3 is only slightly greater than the distances between V_1 and V_2 or V_3 and V_4 in *Diplocentrus* and *Scorpio* compared with *Hemiscorpius* and *Liocheles*, as illustrated in Vachon's (1974, p. 917) figs 71 and 72, Stockwell's (1989, pp. 354–359) figs 156, 157 and 161, and Prendini's (2000, p. 37) figs 8B, E). Furthermore, *Anuroctonus*, *Euscorpius*, *Hadrurus*, *Paravaejovis*, and five bothriurid genera (*Bothriurus*, *Brachistosternus*, *Centromachetes*, *Cercophonius* and *Phoniocercus*) were each scored state 0 of this character (V_2 and V_3 evenly spaced). These taxa display more than four trichobothria on the ventral surface of the chela (Vachon, 1974; Stockwell, 1989; Sissom, 1990; Prendini, 2000; Soleglad and Sissom, 2001; S&F, 2003a; *Euscorpius* is interspecifically polymorphic in this regard) and the identity of their individual trichobothria cannot therefore be determined unambiguously.

Soleglad et al. (2005, pp. 14, 15) recently attempted to justify this coding with a "method" that amounts to guessing which trichobothria are homologous in neobothriotaxic genera and species by comparing them with putatively related genera and species that present lower numbers of trichobothria, an approach that inevitably introduces subjectivity and preconceived bias:

> We believe, using orthobothriotaxic genera as a reference within these three scorpionoid families, that we distinguish, *with some certainty*, the V_1–V_4 series from the accessory trichobothria occurring on that surface. For example, for the bothriurids, we agree with Vachon's (1974: Figs 203, 205–206) designations of V_1–V_4 for genera *Centromachetes*, *Thestylus*, and *Timogenes*, which match favorably in relative spacing of these trichobothria. The same spacing is observed in genera *Brachistosternus*, *Bothriurus*, and *Lisposoma* (Fet et al., 2004a: Figs 5–8). Using *Lisposoma* and *Thestylus* as a basis for orthobothriotaxy, we can see that Vachon's designations of V_1–V_4 *are very likely to be correct* for other bothriurid genera. This same approach can be used in the family Scorpionidae. Again referring to Vachon (1974: Figs 68, 71, 74) for diplocentrine genera *Oiclus*, *Diplocentrus*, and *Nebo*; Lamoral (1979: Figs 362, 384, 396, 404) for four species of genus *Opistophthalmus*; Kovařík (2004a: Fig. 2) for genus *Heterometrus*; and our Fig. 24 for genus *Scorpio*, we see that the spacing between these three trichobothria, as quantified by our ratio, are similarly spaced and the trichobothria V_2 and V_3 are spaced farther than that seen in the bothriurids [substantiating our criticism above]. In family Hemiscorpiidae, we see the most exaggerated spacing as indicated by the ratio. This is illustrated by Vachon (1974: Figs 111, 120, 123) for *Hemiscorpius*, *Liocheles*, and *Iomachus*, and in our Figs 19–23, for *Opisthacanthus* and *Heteroscorpion*. [italics added]

Characters 20 and 21, portraying the relative positions of trichobothria in the *eb*–*et* series of the fixed finger of the chela, might be construed as a misrepresentation *sensu* Fet et al. (2004a). According to S&F (2003a, p. 39), and illustrated in their fig. 79 (reproduced here as Figs 24–29) and figs 118–125, *esb* is closer to the finger edge than *eb* in the Vaejovidae and Superstitioniidae, which were therefore scored state 0 of character 20. In contrast, *eb* is allegedly closer to the finger edge than *esb* in *Anuroctonus*, *Chactopsis*, *Nullibrotheas*, *Scorpiops*, *Uroctonus*, four Neotropical chactid genera (*Brotheas*, *Chactas*, "*Neochactas*" and *Teuthraustes*), and three euscorpiid genera (*Euscorpius*, *Megacormus* and *Troglocormus*), as seen in Figs 30–35. This interpretation, actually adopted from Vachon (1974), was rejected by Stockwell (1989), who reversed Vachon's (1974) designations of *eb* and *esb* among the taxa in question, achieving a homology assessment that is more consistent, topographically, across the chactoid genera (Figs 36–41). Stockwell's (1989) interpretation was not discussed by S&F (2003a), but we agree with it and consequently reject S&F's (2003a) characters 20 and 21. This putative synapomorphy represents the primary justification for S&F's (2003a, pp. 99–102, figs 118–125) new chactid genus, *Neochactas*, and their monogeneric subtribe Neochactina. S&F (2003a) provide no evidence, by way of a cladistic analysis of species relationships among the Neotropical chactids, to demonstrate that the remaining diagnostic characters of *Neochactas* (i.e., the "more basal" positions of the *Db*–*Dt* and Et_3–Et_5 trichobothria) are synapomorphic for these taxa. Once again, these authors failed to heed their own advice (Fet et al., 2005, p. 19):

> It is clear that monophyly for a given genus can *only* be demonstrated if and only if a competent detailed species-level cladistic analysis is conducted which includes all species defined under that genus and select individuals from all immediate putative sister genera are included as outgroups …

Another example that might be construed as a misrepresentation *sensu* Fet et al. (2004a) is provided by S&F's (2003a) treatment of the very similar trichobothrial patterns on the pedipalp patella of *Anuroctonus* and *Hadrurus*, perpetuated in more recent papers by Fet et al. (2004b) and S&F (2004). As illustrated, for example, by Vachon (1974, p. 926, figs 143 and 146), Stockwell (1989, p. 343, fig. 110), Sissom (1990, p. 72, fig. 3.6) and S&F (2003a, p. 43, fig. 82), both genera exhibit many accessory trichobothria on the ventral surface, the most distal trichobothria being situated on the external surface, which exhibits additional accessory trichobothria. Consequently, the identity of the individual trichobothria on these surfaces cannot be determined unambiguously in these taxa. Despite this problem, and despite the similarity in number and disposition of the trichobothria in the two genera, *Anuroctonus* was scored state 0 of character 23 (trichobothrium v_3 situated on external surface) by S&F (2003a), whereas *Hadrurus* was scored state 1 (v_3 situated on ventral surface). In addition, both *Anuroctonus* and *Hadrurus* were scored state 0 of character 24 (trichobothrium v_2 situated on ventral surface of patella).

Other examples are provided by characters 26, 28 and 29 "modelling" trichobothria on the external surface of the pedipalp patella (esb_1–esb_2 alignment, em_1–em_2 and esb_1 alignment, and comparative distance of em_1–em_2 and esb_1–esb_2, respectively), each of which were scored in *Anuroctonus*, *Chactopsis*, *Nullibrotheas*, *Scorpiops*, two superstitioniid genera (*Alacran* and *Typhlochactas*) and the abovementioned Neotropical chactid and euscorpiid genera. All these genera display more than 13 trichobothria on the external surface of the patella (Vachon, 1974; Stockwell, 1989; Sissom, 1990; González-Sponga, 1996; Soleglad and Sissom, 2001; S&F, 2003a) rendering it difficult, if not impossible, to identify individual trichobothria in many of the series, despite the best efforts to define "territories" (e.g., Vachon, 1974; Soleglad and Sissom, 2001; S&F, 2003a).

We question many of the putative homologies proposed in these characters. For example, although "landmark" petite trichobothrium esb_2 is usually obvious because it is smaller in size, the identity of trichobothrium esb_1 cannot be determined unambiguously in *Anuroctonus*, *Chactopsis*, *Euscorpius* and *Megacormus*. Each of these genera displays more than two trichobothria in the *esb* and/or *eb* series of the patella (*vide* Vachon, 1974; pp. 926, 932, figs 143, 146, 177 and 181; Sissom, 1990, p. 72, fig. 3.6; González-Sponga, 1996, pp. 112–116, figs 246, 250, 254, 258 and 262; Soleglad and Sissom, 2001, p. 50, figs 106 and 107; S&F, 2003a, p. 43, fig. 82), although *Euscorpius* is interspecifically polymorphic in this regard (Vachon, 1974, p. 932, figs 178 and 179; Soleglad and Sissom, 2001, pp. 50, 51, figs 109–111). Trichobothrium esb_2 is not petite in *Chactopsis* either (Vachon, 1974; González-Sponga, 1996; Soleglad and Sissom, 2001). As such, characters 26, 28 and 29 cannot be scored unambiguously in these taxa. Similarly, the identity of em_1 and, especially, em_2 cannot be determined unambiguously in *Anuroctonus*, *Chactopsis*, *Nullibrotheas*, *Scorpiops*, the four Neotropical chactid genera, the three euscorpiid genera and the two superstitioniid genera. All these taxa display accessory trichobothria in the *em* series and, with the exception of *Typhlochactas*, also in the *est* series (Vachon, 1974; Stockwell, 1989; Sissom, 1990; González-Sponga, 1996; Soleglad and Sissom, 2001; S&F, 2003a; Table 9). Therefore, characters 28 and 29 cannot be scored unambiguously in these taxa either.

Anuroctonus, *Chactopsis*, *Nullibrotheas*, *Scorpiops*, the four Neotropical chactid genera and three euscorpiid genera were also scored state 0 of character 27 (patellar trichobothrium v_3 situated proximal or equal to midpoint, proximal of *est* and et_3, distance between v_3 and v_2 < distance between v_2 and v_1). In addition to the numerous accessory trichobothria on the external surface of the patella, these taxa exhibit accessory trichobothria on the ventral surface (Vachon, 1974; Stockwell, 1989; Sissom, 1990; González-Sponga, 1996; Soleglad and Sissom, 2001; S&F, 2003a) rendering it not only impossible to identify et_3 and, in some cases, *est*, but also v_1, v_2 and v_3. Scoring this character in these particular taxa is guesswork and would best be achieved by scoring them unknown (?) or inapplicable (–). This approach was taken by Stockwell (1989), Prendini (2000, 2003a) and even S&F (2003a, character 18) when coding the disposition of particular trichobothria in taxa with major neobothriotaxy (e.g., *Hadogenes* and *Urodacus*), but was criticized by Soleglad et al. (2005, pp. 14, 15), who would now prefer to guess the identity of the trichobothria in question:

> In Prendini's (2000) character 55, the location of the chelal *Est* trichobothrium, we see that inapplicable codes are assigned to genera *Urodacus* and *Hadogenes*. By referencing two *Urodacus* species with minimal neobothriotaxy, *U. manicatus* (Fig. 13) and *U. mckenziei*, we can *with reasonable certainty* determine the position of trichobothrium *Est*, which in our opinion, is located on the distal aspect of the palm … We also think it reasonable to believe that the position of *Est* in other species of *Urodacus* that exhibit massive neobothriotaxy, e.g., *U. yaschenkoi* (Fig. 18), *U. hoplurus* (Fig. 17) and *U. elongatus* (Fig. 16), would be consistent with other species. Consequently we have changed the data matrix accordingly. [italics added]

Typhlochactas was scored state 1 of character 27 (v_3 situated distal of midpoint, distal or equal to *est* and et_3, distance between v_3 and $v_2 \geq$ distance between v_2 and v_1), but, as discussed above, it is more plausible to assume that the trichobothrium regarded as v_3 by S&F (2003a) is, in fact, v_2.

Errors and misinterpretations affect other characters, besides trichobothria, in S&F's (2003a) data matrix (Table 7). For example, *Vejovoidus* was scored state 0 of character 43 (cheliceral movable finger, ventral edge smooth, i.e., not crenulate and without small denticles), although the ventral edge is crenulate in this genus (Stockwell, 1989, characters 34–36).

The fossil palaeopisthacanthid composite was scored state 0 of character 47 (chelal finger median denticle row with oblique alignment of primary subrows) although, according to Stockwell (1989, character 46), the primary subrows are straight in Palaeopisthacanthidae, Jeram's (1994) discussion, on which S&F's (2001, 2003a) coding of the composite was based, provides no indication to the contrary, and S&F (2003a) did not examine the fossils in question.

As noted previously, the typhlochactine genera *Alacran* and *Typhlochactas* were scored state 3 of character 60 (0–2 pedal spurs). However, as noted by Francke (1982, p. 61) retrolateral pedal spurs are absent in these genera (and also in *Sotanochactas*), some of which have prolateral pedal spurs whereas others do not.

Hadogenes was scored state 1 of character 82 (sclerites of female genital operculum fused), but should have been scored state 2 (sclerites loosely connected), as indicated in S&F's (2003a, p. 144) character description (Appendix 2), and following Stockwell (1989, character 108) and Prendini (2000, character 80).

Archaeobuthus was scored state 1 of character 95 (patella, dorsomedian carina present), although the presence of this state is unknown in the fossil taxon, as indicated in S&F's (2003a, p. 145) character description (Appendix 2).

Pseudouroctonus and all other vaejovid genera included in S&F's (2003a) matrix, besides *Uroctonus*, were scored state 1 of character 96 ("dorsal patellar spur carina" present). According to Stockwell (1989, character 42), this carina is absent in *Pseudouroctonus* and several other vaejovid genera that were excluded from S&F's (2003a) matrix, e.g., *Uroctonites*. An examination of material in the collection of the American Museum of Natural History confirmed the presence of this carina in *P. andreas*, *P. angelenus* and *P. reddelli*, but not in *P. apacheanus* and three species of *Uroctonites*, the patellar carinal development of which was not obviously different from that observed in *Uroctonus*.

Chaerilus, the Chactidae, Euscorpiidae and Vaejovidae were all scored state 1 of character 99 (venom gland epithelial walls folded). It is well known that these taxa exhibit simple, unfolded glands, i.e., state 0 (Pavlovsky, 1913; Birula 1917a,b; Sissom, 1990; Prendini, 2000; S&F, 2003a, pp. 58–59).

Although *Uroctonus* displays only three pairs of lateral ocelli like most vaejovids (Gertsch and Soleglad, 1972, p. 556, fig. 19; S&F, 2004, p. 85), it was scored state 4 of character 102 (three or four pairs of lateral ocelli), and not states 3 or 5, both of which score three pairs (Appendix 2). This coding forced *Uroctonus* to group with *Anuroctonus*, which has four pairs, an uncommon state in scorpions that is probably autapomorphic (Hjelle, 1972; Williams, 1980, 1986; Stockwell, 1989) and thus uninformative:

> Both genera [*Uroctonus* and *Anuroctonus*] have more than two lateral eyes on each side of the carapace, which is considered a derivation for Uroctoninae from the typical two eyes found in most chactids … Interestingly … *Anuroctonus* has a small *fourth* eye, situated above eyes 2 and 3. (S&F, 2004, p. 85)

Further examples abound. Collectively, we have identified 28 (17%) of S&F's (2003a) characters in which there are errors, misinterpretations or misrepresentations (Table 7), and we do not consider this list exhaustive. Similar problems pepper other recent contributions by these authors (Fet et al., 2001, 2004a,b, 2005; Soleglad and Sissom, 2001; S&F, 2004, 2005; Soleglad et al., 2005) but will be addressed in more detail elsewhere.

Biogeographical "characters"

In concluding the discussion on problems with the characters employed by Soleglad, Fet and colleagues, it is worth noting their repeated use of biogeographical "characters" in cladistic analysis. For example, in their analysis of the relationships between one species and two subspecies of *Anuroctonus*, S&F (2004, p. 107) included one character in a list of nine (table IX, character 9), portraying the geographical ranges of these taxa: zero outgroup (0); parapatric (*A. p. pococki*, *A. p. bajae*) (1); allopatric (*A. phaiodactylus*) (2). The precedent had already been set by Fet et al. (2001, pp. 145, 146, 158), who presented four "biogeographical-based characters" (reproduced here as Appendix 3) in a matrix of 19 for a phylogenetic analysis of the hirsutus group of *Hadrurus*. Characters portraying the geographical distributions of taxa, if appropriately coded, may validly be used *post hoc* to investigate the historical biogeography of a group of organisms, for example by optimization on a cladogram derived from an analysis of characters portraying heritable variation (for a recent example of this practice, see Bertelli and Giannini, 2005). However, such characters would never be considered for inclusion in the analysis *a priori*. We fail to see how parapatry or allopatry could be viewed as potential synapomorphies of any particular taxon.

Peer review, online publishing and taxonomic anarchy

We agree with others that changes to a taxonomic classification are required to reflect new hypotheses of relationship (Nelson, 1972, 1973; Gaffney, 1979; Dominguez and Wheeler, 1997), but that such changes should also increase its predictivity and stability (Kluge, 1989; Kluge and Wolf, 1993; Nixon and Carpenter, 1996; Knapp et al., 2004). In our view, this is only possible if the new hypotheses are supported by a rigorous and unbiased analysis of all the available evidence.

It follows from this argument that the stability of S&F's (2003a) classification, recent updates and emendations (Fet et al., 2004a,b, 2005; S&F, 2004; Soleglad et al., 2005) depend on the rigor of their phylogenetic analyses. As we have demonstrated, these analyses fail to meet the most basic standards in systematics and cannot be termed rigorous or unbiased. S&F's bizarre brand of cladistics, exemplified by their "existence approach" to trichobothrial homology, in which the directionality of trichobothrial states is forced by Sankoff optimization (S&F, 2001), their "fundamental character" analyses, in which "important" characters are isolated and analyzed separately from less important characters (S&F, 2003a; Fet et al., 2005), their failure to analyze different sources of evidence simultaneously (Fet et al., 2003, 2005; S&F, 2003a), their continued use of hypothetical outgroups (S&F, 2001, 2004) and supraspecific terminal taxa (S&F, 2001, 2003a; Fet et al., 2005), and, most importantly, their approach to "modelling" characters by assigning homology on the basis of preconceived notions of phylogenetic relationship and character transformation (S&F, 2003a; Fet et al., 2004a, 2005; Soleglad et al., 2005), is nothing more than an elaborate scheme designed to achieve and legitimize a desired result. In this respect, S&F's "methods", such as they can be considered so, are reminiscent of the long-discredited clique or compatibility analysis (LeQuesne, 1969; Estabrook et al., 1976a,b; Meacham and Estabrook, 1985).

Soleglad et al. (2005, p. 28) described Prendini (2000, 2003a,b) as approaching cladistic analysis in a "rote, cook-book manner". This portrayal is as ironic as it is inappropriate, given the depauperate knowledge of cladistic theory and the lack of understanding of, or flagrant disregard for, established methods and standards of cladistic practice apparent in works by Soleglad, Fet and colleagues. We have identified one or more of the problems outlined above in 158 (95%) of the characters in S&F's (2003a) data matrix alone (Table 7). Similar problems pervade other recent contributions by these authors (Fet et al., 2001, 2004a,b, 2005; Soleglad and Sissom, 2001; S&F, 2004, 2005; Soleglad et al., 2005). In view of the significant theoretical and empirical problems with the approach to cladistics taken by these authors, we find no justification for accepting either the results of their analyses or the revised classification derived from them. Pending the outcome of a rigorous phylogenetic analysis, published according to acceptable standards of scholarship in a peer-reviewed journal, we revert to the suprageneric classification of Scorpiones reflected by the most recent peer-reviewed, published treatments (Fet et al., 2000; Prendini, 2000, 2001b, 2003a; Prendini et al., 2003; Table 10). We reject all changes and additions to the classification proposed on the basis of analyses by Soleglad, Fet and colleagues after Fet et al. (2000). In our opinion, this classification (Table 10), albeit imperfect, is preferable to the alternative derived from a biased and methodologically deficient analysis.

We further submit that an analysis and revised classification of the kind published by these authors in their self-edited online journal, *Euscorpius*, could not survive the peer-review process of a mainstream scientific journal, and hence that *Euscorpius* is not peer reviewed or, if it is, that the standards for acceptance of papers are unacceptably low. We say this in spite of the editors' opinion to the contrary, as proclaimed in this excerpt on "Reviewing and Acceptance" from the *Euscorpius* website, with its disclaimer of editorial responsibility for evaluating content:

> *Euscorpius* is a peer-reviewed publication. … The authors are encouraged to submit a list of potential reviewers with their email addresses, or indicate non-desired reviewers to avoid a conflict of interests, a standard practice in grant applications. … We strongly believe that the authors are solely responsible for accuracy and content since their reputation will be based, in part, as in all publications, on the totality of quality of the papers they author. *Euscorpius* editors are not responsible for evaluating authors' opinions, theories or hypotheses; however, *Euscorpius* reserves the right to decline manuscripts which do not comply with professional standards.

We follow others in regarding peer review as the cornerstone, if not the "gold standard", of academic publishing because it provides the expert evaluation of manuscripts needed both to weed out flawed and fraudulent research, and to improve good research through constructive criticism, in so doing, ensuring high standards in the published literature (Roberts, 1999; El-Munshid, 2001; Siemens et al., 2001; Arms, 2002; Kling et al., 2002; Kaplan, 2005). Peer review is imperfect and varies greatly in its effectiveness in establishing the accuracy and value of research (Horrobin, 1990; Enserink, 2001; Jefferson et al., 2002; Lawrence, 2003). Nevertheless, it remains the benchmark by which all other approaches to quality are measured (Harnad, 1999; Roberts, 1999; El-Munshid, 2001; Arms, 2002; Mooney, 2004). One essential requirement for effective peer review is independence between author and reviewer. Independence is not achieved by serving as the editor of your own papers.

We have already demonstrated major flaws in several papers by the authors in question, the five largest and most significant of which appeared in *Euscorpius* (S&F, 2001; Fet et al., 2003, 2005; S&F, 2003a; Soleglad et al., 2005). We are confident that most, if not all, these problems would have been detected and corrected if the manuscripts in question were subjected to critical review by independent peers (as we have, in essence, done here). We do not think these are isolated incidents, judging by our observations that one of the editors was also the first author on 36% (13) of the papers and 61% (440) of the pages of *Euscorpius* published to date (36 papers in 30 issues, 718 pages in total), and both of the editors were sole authors on 17% (6) of the papers and 45% (325) of the pages published to date. We believe these and several other papers published in *Euscorpius* provide examples of the "unscrupulous taxonomic practices" recently mentioned by Lee (2002, p. 788), and emphasize the importance of quality control associated with the emergent infrastructure of online publishing.

Despite obvious benefits in cost, speed, convenience, dissemination and storage space (Odlyzko, 1997; Valauskas, 1997; Butler, 1999; Kling and McKim, 1999, 2000; Siemens et al., 2001; Tenopir and King, 2001; Godfray, 2002a; Kling et al., 2002; Scoble, 2004; Wheeler et al., 2004), the advent of electronic publishing has placed a strain on the peer-review process. The number of scholarly resources available on the internet is increasing daily, and many of these resources are disseminated outside the processes traditionally provided by scholarly journals and academic presses. Such resources include new genres of scholarly publication such as online electronic archives, databases and websites, as well as traditional genres, such as articles and reviews that are provided online by individual scholars (Kling and McKim, 1999, 2000; Kling et al., 2002; for examples from systematics, see Bisby et al., 2002; Gewin, 2002; Godfray, 2002a; Knapp et al., 2002; Scoble, 2004). Insofar as peer review is essential for maintaining the integrity of science, the scholarly community urgently needs a means of providing peer review to assess and document the quality of such

Table 10

The suprageneric classification of Recent (extant) scorpions accepted here. This classification reflects the most recent peer-reviewed, published treatments (Fet et al., 2000; Prendini, 2000, 2001b, 2003a; Prendini et al., 2003). All changes and additions to the classification proposed on the basis of analyses by Soleglad, Fet and colleagues after Fet et al. (2000) are rejected for reasons discussed in the present paper, with the exception of Fet and Bechly's (2001) revised name for Ischnuridae Simon, 1879, a junior homonym of Ischnurinae Fraser, 1957 (Insecta, Odonata), approved by the ICZN (2003). Superfamilial categories (including Soleglad and Fet's "parvorders") are abolished, and no claims made about the monophyly of families, subfamilies and genera, other than those tested by Prendini (2000, 2001c, 2003a,c, 2004) and Prendini et al. (2003), pending a rigorous phylogenetic revision, published according to acceptable standards of scholarship in a peer-reviewed journal. These decisions necessitate the following new synonymies (superfamilial categories, although not regulated by the ICZN, are synonymized for completeness): Parvorder Buthida Soleglad and Fet, 2003 = Order Scorpiones C.L. Koch, 1850, **syn. n.**; Parvorder Chaerilida Soleglad and Fet, 2003 = Order Scorpiones C.L. Koch, 1850, **syn. n.**; Parvorder Iurida Soleglad and Fet, 2003 = Order Scorpiones C.L. Koch, 1850, **syn. n.**; Parvorder Pseudochactida Soleglad and Fet, 2003 = Order Scorpiones C.L. Koch, 1850, **syn. n.**; Superfamily Bothriuroidea Simon, 1880 = Order Scorpiones C.L. Koch, 1850, **syn. n.**; Superfamily Buthoidea C.L. Koch, 1837 = Order Scorpiones C.L. Koch, 1850, **syn. n.**; Superfamily Chactoidea Pocock, 1893 = Order Scorpiones C.L. Koch, 1850, **syn. n.**; Superfamily Chaeriloidea Pocock, 1893 = Order Scorpiones C.L. Koch, 1850, **syn. n.**; Superfamily Iuroidea Thorell, 1876 = Order Scorpiones C.L. Koch, 1850, **syn. n.**; Superfamily Pseudochactoidea Gromov, 1998 = Order Scorpiones C.L. Koch, 1850, **syn. n.**; Superfamily Scorpionoidea Latreille, 1802 = Order Scorpiones C.L. Koch, 1850, **syn. n.**; Superfamily Vaejovoidea Thorell, 1876 = Order Scorpiones C.L. Koch, 1850, **syn. n.**; Family Caraboctonidae Kraepelin, 1905 = Family Iuridae Thorell, 1876, **syn. n.**; Subfamily Bothriurinae Simon, 1880 = Family Bothriuridae Simon, 1880, **syn. n.**; Subfamily Brotheinae Simon, 1879 = Family Chactidae Pocock, 1893, **syn. n.**; Subfamily Chactinae Pocock, 1893 = Family Chactidae Pocock, 1893, **syn. n.**; Subfamily Euscorpiidae Laurie, 1896 = Family Euscorpiidae Laurie, 1896, **syn. n.**; Subfamily Hemiscorpiinae Pocock, 1893 = Family Hemiscorpiidae Pocock, 1893, **syn. n.**; Subfamily Hormurinae Laurie, 1896 = Family Liochelidae Fet and Bechly, 2001 (1879), **syn. n.**; Subfamily Lisposominae Lawrence, 1928 = Family Bothriuridae Simon, 1880, **syn. n.**; Subfamily Megacorminae Kraepelin, 1905 = Family Euscorpiidae Laurie, 1896, **syn. n.**; Subfamily Scorpioninae Latreille, 1802 = Family Scorpionidae Latreille, 1802, **syn. n.**; Subfamily Scorpiopinae Kraepelin, 1905 = Family Scorpiopidae Kraepelin, 1905, **syn. n.**; Subfamily Uroctoninae Mello-Leitão, 1934 = Family Vaejovidae Thorell, 1876, **syn. n.**; Tribe Brotheini Simon, 1879 = Family Chactidae Pocock, 1893, **syn. n.**; Tribe Chactini Pocock, 1893 = Family Chactidae Pocock, 1893, **syn. n.**; Tribe Chactopsini Soleglad and Sissom, 2001 = Family Chactidae Pocock, 1893, **syn. n.**; Tribe Diplocentrini Karsch, 1880 = Subfamily Diplocentrinae Karsch, 1880, **syn. n.**; Tribe Megacormini Kraepelin, 1905 = Family Euscorpiidae Laurie, 1896, **syn. n.**; Tribe Nullibrotheini Soleglad and Fet, 2003 = Family Chactidae Pocock, 1893, **syn. n.**; Tribe Scorpiopini Kraepelin, 1905 = Family Scorpiopidae Kraepelin, 1905, **syn. n.**; Tribe Troglocormini Soleglad and Sissom, 2001 = Family Euscorpiidae Laurie, 1896, **syn. n.**; Subtribe Brotheina Simon, 1879 = Family Chactidae Pocock, 1893, **syn. n.**; Subtribe Neochactina Soleglad and Fet, 2003 = Family Chactidae Pocock, 1893, **syn. n.**; *Franckeus* Soleglad and Fet, 2005 = *Vaejovis* C.L. Koch, 1836, **syn. n.**; *Hoffmannihadrurus* Fet and Soleglad, 2004 = *Hadrurus* Thorell, 1876, **syn. n.**; *Neochactas* Soleglad and Fet, 2003 = *Broteochactas* Pocock, 1893, **syn. n.**

Family Bothriuridae Simon, 1880

    Bothriurus Peters, 1861; *Brachistosternus* Pocock, 1893; *Brandbergia* Prendini, 2003; *Brazilobothriurus* Lourenço and Monod, 2000; *Centromachetes* Lönnberg, 1897; *Cercophonius* Peters, 1861; *Lisposoma* Lawrence, 1928; *Orobothriurus* Maury, 1975; *Pachakutej* Ochoa, 2004; *Phoniocercus* Pocock, 1893; *Tehuankea* Cekalovic, 1973; *Thestylus* Simon, 1880; *Timogenes* Simon, 1880; *Urophonius* Pocock, 1893; *Vachonia* Abalos, 1954

Family Buthidae C.L. Koch, 1837

    Afroisometrus Kovařík, 1997; *Akentrobuthus* Lamoral, 1976; *Alayotityus* Armas, 1973; *Ananteris* Thorell, 1891; *Androctonus* Ehrenberg, 1828; *Anomalobuthus* Kraepelin, 1900; *Apistobuthus* Finnegan, 1932; *Australobuthus* Locket, 1990; *Babycurus* Karsch, 1886; *Baloorthochirus* Kovařík, 1996; *Birulatus* Vachon, 1974; *Buthacus* Birula, 1908; *Butheoloides* Hirst, 1925; *Butheolus* Simon, 1882; *Buthiscus* Birula, 1905; *Buthoscorpio* Werner, 1936; *Buthus* Leach, 1815; *Centruroides* Marx, 1890; *Charmus* Karsch, 1879; *Cicileus* Vachon, 1948; *Compsobuthus* Vachon, 1949; *Congobuthus* Lourenço, 1999; *Darchenia* Vachon, 1977; *Egyptobuthus* Lourenço, 1999; *Grosphus* Simon, 1880; *Hemibuthus* Pocock, 1900; *Hemilychas* Hirst, 1911; *Himalayotityobuthus* Lourenço, 1997; *Hottentotta* Birula, 1908; *Iranobuthus* Kovařík, 1997; *Isometroides* Keyserling, 1885; *Isometrus* Ehrenberg, 1828; *Karasbergia* Hewitt, 1913; *Kraepelinia* Vachon, 1974; *Lanzatus* Kovařík, 2001; *Leiurus* Ehrenberg, 1828; *Liobuthus* Birula, 1898; *Lissothus* Vachon, 1948; *Lychas* C.L. Koch, 1845; *Lychasioides* Vachon, 1974; *Mesobuthus* Vachon, 1950; *Mesotityus* González-Sponga, 1981; *Microananteris* Lourenço, 2003; *Microbuthus* Kraepelin, 1898; *Microtityus* Kjellesvig-Waering, 1966; *Neobuthus* Hirst, 1911; *Neogrosphus* Lourenço, 1995; *Odontobuthus* Vachon, 1950; *Odonturus* Karsch, 1879; *Orthochirus* Karsch, 1861; *Orthochiroides* Kovarik, 1998; *Parabuthus* Pocock, 1890; *Paraorthochirus* Lourenço and Vachon, 1997; *Pectinibuthus* Fet, 1984; *Plesiobuthus* Pocock, 1900; *Polisius* Fet, Capes and Sissom, 2001; *Psammobuthus* Birula, 1911; *Pseudolissothus* Lourenço, 2001; *Pseudolychas* Kraepelin, 1911; *Pseudouroplectes* Lourenço, 1995; *Razianus* Farzanpay, 1987; *Rhopalurus* Thorell, 1876; *Sabinebuthus* Lourenço, 2001; *Sassanidothus* Farzanpay, 1987; *Simonoides* Vachon and Farzanpay, 1987; *Somalibuthus* Kovařík, 1998; *Somalicharmus* Kovařík, 1998; *Thaicharmus* Kovařík, 1995; *Tityobuthus* Pocock, 1893; *Tityopsis* Armas, 1974; *Tityus* C.L. Koch, 1836; *Troglorhopalurus* Lourenço, Baptista and Giupponi, 2004; *Troglotityobuthus* Lourenço, 2000; *Uroplectes* Peters, 1861; *Uroplectoides* Lourenço, 1998; *Vachoniolus* Levy, Amitai and Shulov, 1973; *Vachonus* Tikader and Bastawade, 1983; *Zabius* Thorell, 1893

Family Chactidae Pocock, 1893

    Auyantepuia González-Sponga, 1978; *Brotheas* C.L. Koch, 1837; *Broteochactas* Pocock, 1893; *Cayooca* González-Sponga, 1981; *Chactas* Gervais, 1844; *Chactopsis* Kraepelin, 1912; *Guyanochactas* Lourenço, 1998; *Hadrurochactas* Pocock, 1893; *Nullibrotheas* Williams, 1974; *Teuthraustes* Simon, 1878; *Vachoniochactas* González-Sponga, 1978

Family Chaerilidae Pocock, 1893

    Chaerilus Simon, 1877

Family Diplocentridae Karsch, 1880, **new rank**

  Subfamily Diplocentrinae Karsch, 1880

    Bioculus Stahnke, 1968; *Cazierius* Francke, 1978; *Didymocentrus* Kraepelin, 1905; *Diplocentrus* Peters, 1861; *Heteronebo* Pocock, 1899; *Oiclus* Simon, 1880; *Tarsoporosus* Francke, 1978

  Subfamily Nebinae Kraepelin, 1905, **new rank**

    Nebo Simon, 1878

Table 10
Continued

Family Euscorpiidae Laurie, 1896
Euscorpius Thorell, 1876; *Megacormus* Karsch, 1881; *Plesiochactas* Pocock, 1900; *Troglocormus* Francke, 1981
Family Hemiscorpiidae Pocock, 1893
Habibiella Vachon, 1974; *Hemiscorpius* Peters, 1861
Family Heteroscorpionidae Kraepelin, 1905, **new rank**
Heteroscorpion Birula, 1903
Family Iuridae Thorell, 1876
Subfamily Caraboctoninae Kraepelin, 1905
Caraboctonus Pocock, 1893; *Hadruroides* Pocock, 1893
Subfamily Hadrurinae Stahnke, 1974
Anuroctonus Pocock, 1893; *Hadrurus* Thorell, 1876
Subfamily Iurinae Thorell, 1876, **new rank**
Calchas Birula, 1899; *Iurus* Thorell, 1876
Family Liochelidae Fet and Bechly, 2001 (1879), **new rank**
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 Microcharmidae Lourenço, 1996
Ankaranocharmus Lourenço, 2004; *Microcharmus* Lourenço, 1995; *Neoprotobuthus* Lourenço, 2000
Family Pseudochactidae Gromov, 1998
Pseudochactas Gromov, 1998
Family Scorpionidae Latreille, 1802
Heterometrus Ehrenberg, 1828; *Opistophthalmus* C.L. Koch, 1837; *Pandinus* Thorell, 1876; *Scorpio* Linnaeus, 1758
Family Scorpiopidae Kraepelin, 1905, **new rank**
Alloscorpiops Vachon, 1980; *Dasyscorpiops* Vachon, 1974; *Euscorpiops* Vachon, 1980; *Neoscorpiops* Vachon, 1980; *Parascorpiops* Banks, 1928; *Scorpiops* Peters, 1861
Family Superstitioniidae Stahnke, 1940
Subfamily Superstitioniinae Stahnke, 1940
Superstitionia Stahnke, 1940
Subfamily Typhlochactinae Mitchell, 1971
Alacran Francke, 1982; *Sotanochactas* Francke, 1986; *Typhlochactas* Mitchell, 1971
Family Troglotayosicidae Lourenço, 1998, **new rank**
Subfamily Belisariinae Lourenço, 1998, **new rank**
Belisarius Simon, 1879
Subfamily Troglotayosicinae Lourenço, 1998, **new rank**
Troglotayosicus Lourenço, 1981
Family Urodacidae Pocock, 1893, **new rank**
Urodacus Peters, 1861
Family Vaejovidae Thorell, 1876
Paravaejovis Williams, 1980; *Paruroctonus* Werner, 1934; *Pseudouroctonus* Stahnke, 1974; *Serradigitus* Stahnke, 1974; *Smeringurus* Haradon, 1983; *Syntropis* Kraepelin, 1900; *Uroctonites* Williams and Savary, 1991; *Uroctonus* Thorell, 1876; *Vaejovis* C.L. Koch, 1836; *Vejovoidus* Stahnke, 1974

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currently unreviewed online resources (Roberts, 1999; El-Munshid, 2001; Siemens et al., 2001; for some ideas, see Butler, 1999; Hansen et al., 2000; Arms, 2002; Kling et al., 2002). Nowhere is this more apparent than in taxonomy, where the ease of electronic publishing has the potential to exacerbate an already existing problem (unreviewed, self-edited "journals"), creating anarchy that will take decades to rectify (Lee, 2002; Godfray and Knapp, 2004; Knapp et al., 2004; Scoble, 2004). There are examples of online taxonomic publications that satisfy the criteria of rigorous peer-review, e.g., *ZooTaxa* (http://www.mapress.com/zootaxa/), but they are outnumbered by publications that appear to have been created to avoid traditional scrutiny (Lee, 2002; Godfray and Knapp, 2004). Recent proposals for a "unitary" taxonomy, or at least for a centralized register of taxa, moderated by international review panels akin to the system used for evaluating grant proposals (for further discussion, see Godfray, 2002a,b; Knapp et al., 2002, 2004; Lee, 2002; Godfray and Knapp 2004; Scoble, 2004; Dayrat, 2005), may be the only solution for ensuring quality control in the taxonomy of the future. Such proposals should be considered seriously by the ICZN.

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Appendix 1

Orthobothriotaxy character list of Soleglad and Fet (2003a, p. 68, table 4): 62 trichobothria "existence" characters (character matrix in Table 3). Character states, weighted using Sankoff optimization, are scored 0 (trichobothrium absent) ↔ 1 (trichobothrium present, petite in size) ↔ 2 (trichobothrium present, full size), i.e., two steps are required to transform from state 0 to state 2 and vice versa.

1. Chela, internal surface, *ib*: absent (0); present, full size (2).

2. Chela, internal surface, *it*: absent (0); present, full size (2).

3. Chela, dorsal surface, *db*: absent (0); present, full size (2).

4. Chela, dorsal surface, *dsb*: absent (0); present, full size (2).

5. Chela, dorsal surface, *dst*: absent (0); present, full size (2).

6. Chela, dorsal surface, *dt*: absent (0); present, full size (2).

7. Chela, dorsal surface, *Db*: absent (0); present, full size (2).

8. Chela, dorsal surface, *Dt*: absent (0); present, full size (2).

9. Chela, external surface, *eb*: absent (0); present, full size (2).

10. Chela, external surface, *esb*: absent (0); present, petite (1); present, full size (2).

11. Chela, external surface, *est*: absent (0); present, full size (2).

12. Chela, external surface, *et*: absent (0); present, full size (2).

13. Chela, external surface, Eb_1: absent (0); present, full size (2).

14. Chela, external surface, Eb_2: absent (0); present, full size (2).

15. Chela, external surface, Eb_3: absent (0); present, petite (1); present, full size (2).

16. Chela, external surface, *Esb*: absent (0); present, petite (1).

17. Chela, external surface, *Est*: absent (0); present, petite (1); present, full size (2).

18. Chela, external surface, Et_1: absent (0); present, full size (2).

19. Chela, external surface, Et_2: absent (0); present, full size (2).

20. Chela, external surface, Et_3: absent (0); present, full size (2).

21. Chela, external surface, Et_4: absent (0); present, petite (1).

22. Chela, external surface, Et_5: absent (0); present, full size (2).

23. Chela, ventral surface, V_1: absent (0); present, full size (2).

24. Chela, ventral surface, V_2: absent (0); present, petite (1); present, full size (2).

25. Chela, ventral surface, V_3: absent (0); present, full size (2).

26. Chela, ventral surface, V_4: absent (0); present, full size (2).

27. Patella, internal surface, i_1: absent (0); present, full size (2).

28. Patella, internal surface, i_2: absent (0); present, full size (2).

29. Patella, dorsal surface, d_1: absent (0); present, full size (2).

30. Patella, dorsal surface, d_2: absent (0); present, full size (2).

31. Patella, dorsal surface, *d_3*: absent (0); present, full size (2).

32. Patella, dorsal surface, *d_4*: absent (0); present, full size (2).

33. Patella, dorsal surface, *d_5*: absent (0); present, petite (1); present, full size (2).

34. Patella, external surface, *eb_1*: absent (0); present, full size (2).

35. Patella, external surface, *eb_2*: absent (0); present, petite (1); present, full size (2).

36. Patella, external surface, *eb_3*: absent (0); present, full size (2).

37. Patella, external surface, *eb_4*: absent (0); present, full size (2).

38. Patella, external surface, *eb_5*: absent (0); present, full size (2).

39. Patella, external surface, *esb_1*: absent (0); present, full size (2).

40. Patella, external surface, *esb_2*: absent (0); present, petite (1).

41. Patella, external surface, *em_1*: absent (0); present, full size (2).

42. Patella, external surface, *em_2*: absent (0); present, full size (2).

43. Patella, external surface, *est*: absent (0); present, full size (2).

44. Patella, external surface, *et_1*: absent (0); present, full size (2).

45. Patella, external surface, *et_2*: absent (0); present, petite (1); present, full size (2).

46. Patella, external surface, *et_3*: absent (0); present, full size (2).

47. Patella, ventral surface, *v_1*: absent (0); present, full size (2).

48. Patella, ventral surface, *v_2*: absent (0); present, full size (2).

49. Patella, ventral surface, *v_3*: absent (0); present, full size (2).

50. Femur, internal surface, *i_1*: absent (0); present, full size (2).

51. Femur, internal surface, *i_2*: absent (0); present, full size (2).

52. Femur, internal surface, *i_3*: absent (0); present, petite (1); present, full size (2).

53. Femur, internal surface, *i_4*: absent (0); present, petite (1); present, full size (2).

54. Femur, dorsal surface, *d_1*: absent (0); present, full size (2).

55. Femur, dorsal surface, *d_2*: absent (0); present, petite (1); present, full size (2).

56. Femur, dorsal surface, *d_3*: absent (0); present, full size (2).

57. Femur, dorsal surface, *d_4*: absent (0); present, full size (2).

58. Femur, dorsal surface, *d_5*: absent (0); present, full size (2).

59. Femur, external surface, *e_1*: absent (0); present, full size (2).

60. Femur, external surface, *e_2*: absent (0); present, full size (2).

61. Femur, external surface, *e_3*: absent (0); present, full size (2).

62. Femur, external surface, *e_4*: absent (0); present, full size (2).

Appendix 2

Main character list of Soleglad and Fet (2003a, pp. 135–147, appendix A). Character states are scored 0–9, a–d, ? (unknown) or – (inapplicable). Refer to Table 4 for character matrix. Ordered six-state character 1 replaces the 62 "existence" characters representing orthobothriotaxy (Table 3, Appendix 1). Ordered characters are denoted by ORD, partially ordered characters by PART-ORD. ^{F}Denotes characters deemed "fundamental" by Soleglad and Fet (2003a).

Trichobothria, orthobothriotaxy, existence

1.^{F} Major trichobothrial patterns: Type P, Palaeopisthacanthidae (0); Type F1, Archaeobuthidae (1); Type D, Pseudochactida (2); Type A, Buthida (3); Type B, Chaerilida (4); Type C, Iurida (5). [ORD: 0, 1, 2, 3, 4, 5]

Trichobothria, orthobothriotaxy, positional

2.^{F} Femur, Types P, F1, A, B and D, subpattern: $d_1 \rightarrow d_3$ parallel to dorsoexternal carina (rarely beta) (0); points toward dorsoexternal carina (typically beta) (1); points away from dorsoexternal carina (alpha) (2); Type C pattern (–).

3.^{F} Femur, Types P, F1, A, B and D, subpattern: $d_3 \rightarrow d_4$ parallel to dorsoexternal carina (rarely beta) (0); points away from dorsoexternal carina (typically beta) (1); points toward dorsoexternal carina (alpha) (2); Type C pattern (–).

4.^{F} Femur, Types P, F1, A, B and D, placement of *d_2*: on dorsal surface (usually beta) (0); on internal surface (usually alpha) (1); Type C pattern (–).

5. Femur, Type C, *d* and *i* alignment: *d* is proximal to *i* (0); *d* is equal or definitely distal to *i* (1); Type D, A and B patterns (–).

6. Femur, Type C, *d* position: mid- to semi-mid segment (Euscorpiidae) (0); next to dorsoexternal carina (1); Type D, A and B patterns, Vaejovidae (–).

7. Chela, Type C, palm, *V_4* position: ventral surface (0); external surface (Euscorpiinae, Megacorminae) (1); Type D, A and B patterns (–).

8. Chela, Type C, palm, *Eb_1* position: external surface (0); ventral surface or on ventroexternal (V1) carina (1); Type D, A and B patterns (–).

9.$^{\mathrm{F}}$ Chela, Type C, palm, Et_2 position: external surface (0); ventral surface (1); Type D, A and B patterns (–).

10.$^{\mathrm{F}}$ Chela, Type C, palm, *ib* position: on fixed finger, midfinger to finger base (0); at extreme base of fixed finger or on palm (Chactoidea) (1); at extreme base of fixed finger or on palm (Scorpionoidea) (2); Type D, A and B patterns (–).

11. Chela, Type C, palm, *it* position: on fixed finger, midfinger to finger base (Vaejovidae) (0); at extreme base of fixed finger (Superstitioniidae) (1); on palm, next to articular membrane (Euscorpiidae, Chactidae) (2); at extreme base of fixed finger or on palm (Scorpionoidea) (3); on distal aspect of finger (Iuridae) (4); on distal aspect of finger (*Chactopsis*) (5); on distal aspect of finger (*Alacran*) (6); Type D, A and B patterns (–).

12.$^{\mathrm{F}}$ Chela, Type C, palm, V_1–V_4 orientation: in straight line, extending across entire palm (0); angled internally (V_2) or in straight line, not extending across entire palm (Chactoidea) (1); angled towards internal aspect (Scorpionoidea) (2); Type D, A and B patterns (–).

13.$^{\mathrm{F}}$ Chela, Type C, fixed finger, *db–dt* and *eb–et* position: evenly spread out on finger (0); on distal half of finger (Iuroidea) (1); on proximal half of finger (Scorpionoidea) (2); on distal half of finger (Chactoidea) (3); Type D and A patterns (–).

14. Chela, Type C, fixed finger, *ib/it* relative orientation: together (0); separated (Iuridae) (1); separated (Euscorpiidae) (2); separated (Superstitioniidae) (3); Type D, A and B patterns (–).

15. Chela, Type C, palm, Et_5 position: on palm (0); well on fixed finger (Caraboctonidae) (1); Type D, A and B patterns (–).

16. Chela, Type C, palm, Et_1 position: external surface (Iuridae) (0); ventral surface (1); Type D, A and B patterns (–).

17.$^{\mathrm{F}}$ Chela, Type C, additional chelal petite trichobothria, *esb*, *Est* and V_2: present (Iuridae) (0); not present (1); Type D, A and B patterns (–).

18. Chela, Type C, palm, V_2 and V_3: evenly spaced (0); greatly separated, distance between V_2 and V_3 much greater than distances between V_1 and V_2 and V_3 and V_4 (1); Type D, A and B patterns (–).

19. Chela, Type C, position of trichobothria *Db/Dt*: *Db/Dt* basal, proximal of palm midpoint (Vaejovidae, Euscorpiidae, and Uroctoninae) (0); *Db* basal, *Dt* base of fixed finger (Superstitoniidae) (1); *Db* basal, *Dt* palm midpoint (Chactinae) (2); *Db/Dt* very basal (*Belisarius*) (3); *Db* proximal to distal of base, *Dt* past midpointfinger base (*Neochactas*) (4); *Db* distal to base, *Dt* well past midpoint (*Brotheas*) (5); non-chactoids (–). [PART-ORD]

20. Chela, Type C, trichobothria positions *et–eb* series of finger (primary): *esb* closest to finger edge with respect to *eb* (Vaejovidae, Superstitioniidae) (0); *eb* closest to finger edge with respect to *esb* (next to membrane) (Chactidae, Euscorpiidae) (1); non-chactoids (–).

21. Chela, Type C, finger *eb–et* series (secondary): no change, *eb* closest to finger edge (see above) (0); *esb* and *eb* in straight line, *eb* most proximal (Brotheina) (1); *esb* and *eb* in straight line, *eb* most proximal (Scorpiopinae) (2); *esb* and *eb* in straight line, *eb* most proximal (*Chactopsis*) (3); non-chactids and noneuscorpiids (–).

22. Chela, Type C, Et_1–Et_5 series, position of Et_3–Et_5 (secondary): Et_5 on midpalm (all Chactidae other than Brotheina) (0); Et_5 on fixed finger (Brotheina) (1); non-chactids (–).

23.$^{\mathrm{F}}$ Patella, Type B/C, ventral, V_3 position: on ventral surface (0); on external surface (1); Type D and A patterns (–).

24.$^{\mathrm{F}}$ Patella, Type B/C, ventral, V_2 position: on ventral surface (0); on external surface (Iuridae) (1); on external surface (Typhlochactini) (2); Type D and A patterns (–).

25. Patella, Type B/C, additional patellar petite trichobothria, et_2 and eb_2: present (Iuridae) (0); no, other Type C (1); non-Type C (–).

26. Patella, Type B/C, alignment of patellar external trichobothria series esb_1–esb_2: esb_1–esb_2 slant downwards (0); esb_1–esb_2 either parallel to the patella width, or slant upwards (Superstitioniidae) (1); non-chactoids (–).

27. Patella, Type B/C, vertical position of patellar v_3 trichobothrium: proximal or equal to midpoint, proximal of *est* and et_3, distance between v_3 and v_2 < distance between v_2 and v_1 (Chactidae, Euscorpiidae) (0); distal of midpoint, distal or equal to *est* and et_3, distance between v_3 and v_2 ≥ distance between v_2 and v_1 (Vaejovidae, Superstitioniidae) (1); non-chactoids (–). [ORD]

28. Patella, Type B/C, em_1–em_2 and esb_1 vertical alignment: em_1–em_2 and esb_1 near midsegment (Vaejovidae, Brotheinae, Uroctoninae, Superstitioniidae) (0); em_1–em_2 and esb_1 proximal (1/3 distance from proximal edge) (Chactinae) (1); em_1–em_2 and esb_1 proximal (1/3 distance from proximal edge) (Scorpiopinae) (2); non-chactoids (–).

29. Patella, Type B/C, comparative distance em_1–em_2 and esb_1–esb_2: distance between esb_1 and esb_2 ≤ distance between em_1 and em_2 (Chactinae, Euscorpiidae) (0); distance between esb_1 and esb_2 > > > distance between em_1 and em_2 (Brotheinae, Uroctoninae) (1); non-chactoids, Vaejovidae (–).

Trichobothria, neobothriotaxy

30. Type A, found on patella: absent (0); present (*Liobuthus*) (1); non-Type A pattern (–).

31. Type A, found on femur: absent (0); present (*Liobuthus*) (1); non-Type A pattern (–).

32. Type C, found on chelal ventral surface: absent (0); present (Iuroidea) (1); present (Bothriuridae) (2); present

(Urodacidae) (3); present (Liochelidae) (4); present (Scorpionidae) (5); present (Hemiscorpiinae) (6); present type Ch1 (Chactinae) (7); present type Ch2 (Brotheinae) (8); present type Ch3 (Uroctoninae) (9); present type Eu1 (Euscorpiinae, Megacorminae) (a); present type Eu2 (Scorpiopinae) (b); present (Vaejovidae) (c); present type Su1 (Superstitioniidae) (d); Type D, A and B patterns (–).

33. Type C, found on chelal external surface: absent (0); present (Iuroidea) (1); present (Bothriuridae (2); present (Urodacidae) (3); present (Liochelidae) (4); present (Scorpionidae) (5); present (Hemiscorpiinae) (6); present type Ch1 (Chactinae) (7); present type Ch2 (Brotheinae) (8); present type Ch3 (Uroctoninae) (9); present type Eu1 (Euscorpiinae, Megacorminae) (a); present type Eu2 (Scorpiopinae) (b); present (Vaejovidae) (c); present type Su1 (Superstitioniidae (d); type D, A and B patterns (–).

34. Type C, found on chelal internal surface: absent (0); present (Iuroidea) (1); present (Bothriuridae) (2); present (Urodacidae) (3); present (Liochelidae) (4); present (Scorpionidae) (5); present (Hemiscorpiinae) (6); present type Ch1 (Chactinae) (7); present type Ch2 (Broteinae) (8); present type Ch3 (Uroctoninae) (9); present type Eu1 (Euscorpiinae, Megacorminae) (a); present type Eu2 (Scorpiopinae) (b); present (Vaejovidae) (c); present type Su1 (Superstitioniidae) (d); type D, A and B patterns (–).

35. Type C, found on patella ventral surface: absent (0); present (Iuroidea) (1); present (Bothriuridae) (2); present (Urodacidae) (3); present (Liochelidae) (4); present (Scorpionidae) (5); present (Hemiscorpiinae) (6); present type Ch1 (Chactinae) (7); present type Ch2 (Brotheinae) (8); present type Ch3 (Uroctoninae) (9); present type Eu1 (Euscorpiinae, Megacorminae) (a); present type Eu2 (Scorpiopinae) (b); present (Vaejovidae) (c); present type Su1 (Superstitioniidae) (d); type D, A and B pattern (–).

36. Type C, found on patellar external surface: absent (0); present (Iuroidea) (1); present (Bothriuridae (2); present (Urodacidae) (3); present (Liochelidae) (4); present (Scorpionidae) (5); present (Hemiscorpiinae) (6); present type Ch1 (Chactinae) (7); present type Ch2 (Brotheinae) (8); present type Ch3 (Uroctoninae) (9); present type Eu1 (Euscorpiinae, Megacorminae) (a); present type Eu2 (Scorpiopinae) (b); present (Vaejovidae) (c); present type Su1 (Superstitioniidae) (d); type D, A and B patterns (–).

37. Type C, number of accessory trichobothria in est series (Ch1 neobothriotaxy): 2 accessory (Chactini) (0); 3 accessory (Nullibrotheini) (1); non-Chactinae (–).

38. Type C, number of accessory trichobothria in patellar ventral series (Ch1 neobothriotaxy): 3 accessory (Chactini) (0); 4 accessory (Nullibrotheini) (1); non-Chactinae (–).

Chelicerae

39. Movable finger, distal denticle alignment: ventral extends considerably beyond dorsal (0); ventral dorsal approximately equal (1); ventral > dorsal (Euscorpiidae) (2); ventral == dorsal (Euscorpiidae) (3); ventral ≫ dorsal (Scorpionoidea) (4); ventral == dorsal (Scorpionoidea: Liochelidae and Hemiscorpiinae) (5).

40.^{F} Movable finger, dorsal edge, basal denticle: 1 basal denticle (0); 2 basal denticles (Buthidae) (1); absent (Pseudochactidae) (2).

41.^{F} Movable finger, dorsal edge, subdistal denticles: 1 subdistal denticle (0); 2 subdistal denticles (Caraboctonidae) (1); 2 subdistal denticles (Bothriuridae, reversal) (2); 2 subdistal denticles (Chactoidea) (3); 1–2 subdistal denticles, variable in genus (Superstitioniidae) (4). [PART-ORD]

42.^{F} Movable finger, ventral edge (primary): crenulated to small denticles (Palaeopisthacanthidae, Pseudochactidae, Chaerilidae) (0); two large denticles (Buthoidea) (1); one very LARGE rounded denticle (Iuroidea) (2); smooth (other) (3). [PART-ORD]

43. Movable finger, ventral edge (secondary) (only state = 3 of 42 is applicable): smooth (from state 3 in 42) (0); crenulate (Megacorminae) (1); crenulate (Scorpiopinae) (2); crenulate (Uroctoninae) (3); crenulate (Nullibrotheini) (4); crenulate (*Paruroctonus* and related genera) (5); crenulate (*Pseudouroctonus* and related genera) (6); non-chactoids (–).

44. Fixed finger, median and basal denticles: median and basal denticles on a "trunk" (0); median and basal denticles separate, not on a "trunk" (Chaerilidae) (1); median and basal denticles separate, not on a "trunk" (Superstitioniidae) (2); median and basal denticles fused as a single denticle (*Archaeobuthus*) (3).

45.^{F} Fixed finger, denticles on ventral surface (primary): 4–5, major protuberances (Palaeopisthacanthidae, Pseudochactidae, Chaerilidae) (0); 0–2 (2), major protuberances (Buthoidea) (1); absent (2).

46. Fixed finger, denticles on ventral surface (secondary): none (state 2 of 45) (0); present, Euscorpiidae (*Troglocormus*) (1); present, Vaejovidae (*Paruroctonus*, related genera and some *Pseudouroctonus*) (2); non-Iurida (–).

Pedipalp chelal finger dentition

47.^{F} Fundamental chelal finger median denticle (MD) row alignment (primary): oblique, primitive (0); non-oblique (1).

48.^{F} Fundamental chelal finger median denticle (MD) row alignment (secondary): non-oblique (state 1 from 47) (0); oblique (Superstitioniidae) (1); primitive oblique (–).

49.^{F} Inner accessory denticles (IAD): absent (0); present (Euscorpiidae) (1); type D, A and B patterns (–).

50. Outer denticle (OD) removed from MD row: no (0); yes, conspicuous (Euscorpiidae) (1); yes (Chactini) (2); yes (Scorpionoidea) (3); type D, A, and B patterns (–).

51. Outer accessory denticles (OAD): absent (Euscorpiinae) (0); present, irregular (Megacorminae) (1); present, alternating (Scorpioninae) (2); Type D, A, and B patterns (–).

52. Accessory denticles, miscellaneous: no (0); accessory, outside median groups (*Centruroides*) (1); type C pattern (–).

53. "Multiple rows": no (0); yes (1); minimal (*Diplocentrus*) (2); non-scorpionoids (–).

54. Internal denticle (ID) development: normal, larger than median row denticles (0); significantly larger than median denticles (Superstitioniinae) (1); Type D, A, and B patterns (–).

55. Movable finger, number of denticle groups in median denticle (MD) row: 5–6 (*Anuroctonus*, Brotheinae) (0); 7–9 (Chactini) (1); 7–8 (*Uroctonus*) (2); non-chactid (–).

56. Fixed finger, basal outer denticle (OD): normal size (0); highly enlarged (*Teuthraustes*) (1); non-chactoid (–).

Leg spination

57.^{F} Tarsal armature (primary): primitive state, unknown (Palaeopisthacanthidae) (0); dual median spinule rows (Pseudochactidae) (1); numerous irregularly positioned setae (Buthoidea, Chaerilidae) (2); ventrally positioned spinule clusters (Iuroidea) (3); large paired laterally positioned socketed spinoid setae (Scorpionoidea) (4); small laterally positioned socketed setae and/or ventrally positioned spinules (Chactoidea) (5).

58. Tarsal armature (secondary): spinules, no modification (Uroctoninae, Chactinae, Vaejovidae) (0); stout setae (usually as two ventral lateral rows) (Brotheinae) (1); elongated clusters of spinules (*Superstitionia*) (2); setal pairs flanking ventral surface, ventral spinules absent or minimal (Typhlochactinae) (3); thin seta-like spines (Scorpionoidea: some Liochelidae) (4); elongated clusters of setae/spinules (*Troglotayosicus*) (5); non-chactoids and non-scorpionoids (–).

59. Tibial spurs, legs III–IV: present, legs III–IV (0); present, leg IV (*Microcharmus*) (1); absent (2).

60.^{F} Pedal spurs: two, both retrolateral and prolateral present (0); one, prolateral present (Scorpionoidea) (1); two spurs (secondary development, most Bothriuridae) (2); 0–2, variable in genus (Typhlochactinae) (3). [PART-ORD]

61. Tarsus distal termination: "squared off", epitarsus (= tarsomere III) exposed (most scorpions) (0); "rounded", surrounding epitarsus (Scorpionidae) (1).

62. Tarsus ventral distal spinule (VDS) pairs: 1 pair (or one spinule) (Vaejovidae, Euscorpiidae, Chactidae) (0); 2+ pairs (Euscorpiidae) (1); 2+ pairs (Vaejovidae) (2); non-chactoids (–).

Sternum

63.^{F} Basic type: type 1—posterior depression, outer ridge, single internal process (primitive) (0); type 2—posterior emargination, lateral lobes, two internal processes (parvorder Iurida) (1).

64.^{F} Type 1: no horizontal compression or concave region, minimal outer ridge (Palaeopisthacanthidae, Pseudochactidae) (0); minor compression, minimal outer ridge, concave region marginal (Chaerilidae) (1); horizontal compression, outer ridge and concave region well-developed (Buthoidea) (2); sternum type 2 (–).

65. Type 1, with horizontal compression: small-medium depression, short concave area, outer ridge proximal (0); maximum depression, well developed concave area and outer ridge (1); type 1 sternum scorpions without compression and type 2 sternum (–).

66.^{F} Type 2: no vertical compression (0); vertical compression (Bothriuridae) (1); type 1 sterna scorpions (–).

67. Length/posterior width: length ≤ width (Euscorpiidae) (0); length > width (Euscorpiidae: Scorpiopinae) (1); length ≤ width (Scorpionoidea: non-bothriurids) (2); length > width (Hemiscorpiinae) (3); length ≥ width (Typhlochactinae) (4); length < width (Superstitioniinae) (5); other group (–).

68. Posterior width and anterior width proportions: definitely anterior width wider than posterior (Liochelidae) (0); equal or posterior wider (1).

69. Apex/lateral lobes: apex pointed, depressed; lateral lobes convexed (0); apex rounded, minimal depression; lateral lobes flat (Typhlochactinae) (1); sternum type 1 (–).

Maxillary lobes

70. Maxillary lobes II: non-spatulate (0); spatulate (Chaerilidae) (1). [UNINFORM]

71. Maxillary lobes I: rounded, terminating flush with lobes II (0); evenly narrowed, terminating beyond lobes II (liochelines) (1).

Coxae

72. Leg coxae II and IV proportions: IV/II (anterior lengths): IV_L/II_L = 1.3–2.0 (0); IV_L/II_L = 2.2–2.9 (Buthoidea) (1); IV_L/II_L = 2.3–2.6 (Caraboctonidae) (2).

Hemispermatophore

73.^{F} Hemispermatophore, general shape: primitive form (UNKNOWN) (0); fusiform (Chaerilidae) (1); flagelliform (Buthoidea) (2); lamelliform (Scorpionoidea and Chactoidea) (3).

74.^{F} Hemispermatophore, lamina terminus: without "crest" (0); with "crest" (Bothriuridae) (1); non-lamelliform (–).

75.^{F} Paraxial organ with internobasal reflection of sperm duct: absent (0); present and complex (Scorpionoidea) (1).

76. Hemispermatophore, capsule: capsule absent (Iuroidea) (0); capsule present, at least weakly (1); capsule present, significant development (Scorpionoidea) (2); non-lamelliform (–).

77. Hemispermatophore, ental channel: absent (0); present (*Euscorpius* and *Megacormus*) (1).

78. Hemispermatophore, truncal flexure: present (0); not present (Scorpiopinae, Brotheinae, Chactinae) (1); non-chactoids (–).

79. Hemispermatophore, lamina terminus: thin to medium blade-like, modest to medium tapering (Euscorpiinae, Megacorminae, Uroctoninae, Superstitioniidae, Vaejovidae) (0); tenuous, thin, highly tapered (Scorpiopinae, Brotheinae, Chactinae) (1); spatulate, wider than base (Typhlochactinae) (2); non-chactoids (–).

80. Hemispermatophore, laminar "hook" on lamina base: absent (Euscorpiidae, Chactidae, Superstitioniidae) (0); present (Vaejovidae) (1); non-chactoids (–).

Genital operculum

81. Genital papillae of male: visible entire length of genital operculum (Pseudochactidae, Chaerilidae, *Calchas*) (0); conspicuously visible at posterior edge of genital operculum (Chactoidea) (1); under genital operculum, do not extend posteriorly or modestly visible (2); absent (*Hadrurus*) (3).

82. Sclerites of the genital operculum of female: separated for most of length (Pseudochactidae (Buthoidea, Chaerilidae, Iuroidea) (0); generally fused (Scorpionoidea, and some Vaejovidae) (1); loosely connected (Bothriuridae, *Hadogenes*) (2); separated at the posterior 20–25% of their length (*Vaejovis nitidulus*, *Paruroctonus* and *Pseudouroctonus*) (3); loosely connected (Superstitioniidae, Euscorpiidae) (4); separated for most of length (Chactidae) (5). [PART-ORD: (0 (1 (2, 3 (4 (5)))))]

Metasoma

83. Dorsal lateral carinae, segment V: present (Palaeopisthacanthidae) (0); absent (Recent scorpions) (1). [UNINFORM]

84.^{F} Ventral median carina, segment V: distinctly paired (Palaeopisthacanthidae and Pseudochactidae) (0); single (1).

85. Ventral median carinae, segments I–IV: paired (0); single (Hemiscorpiinae) (1); single (Urodacidae) (2); single (Euscorpiidae) (3); single (Vaejovidae, *Syntropis*) (4); single (Vaejovidae, *Vejovoidus*) (5).

86. Lateral carinae, segment V: present and complete (Palaeopisthacanthidae) (0); partially present (most Recent scorpions) (1); absent (most Buthoidea) (2); absent (Scorpionoidea) (3); absent (Euscorpiidae) (4); absent (Superstitioniidae) (5); absent (Vaejovidae) (6).

87. Lateral carinae, segment IV: present, complete (Palaeopisthacanthidae) (0); absent (most Recent scorpions) (1); present, partial (Iuroidea: *Hadrurus* and *Hadruroides*) (2); present, partial (Chactidae) (3); present, partial (Vaejovidae) (4).

88. Metasomal segment IV, dorsal-lateral carina termination: not conspicuous, angles downward to articulation condyle (0); conspicuously flared, straight (most Vaejovidae) (1); non-chactoids (–).

89. Transverse anterior carinae: well developed on all five segments (Palaeopisthacanthidae) (0); developed on at least basal segments I–III (1); absent, or slight remnants (2). [UNINFORM]

Telson

90. Telson, subaculear tooth/tubercle: none (0); tooth (Buthoidea) (1); tubercle (Diplocentrinae) (2).

Pedipalpal ornamentation

91.^{F} Chela: fundamental configuration: "Eight (8) carinae" configuration (D2, V2 absent, I present) (0); "Ten (10) carinae" configuration (9–10 present, usually D2 vestigial and I missing) (1).

92. Chela, V1 carina distal termination: terminates at external condyle completely, or in part, split distally (0); curves inward, trichobothrium Et_1 external to carina (1); entire carina "torqued" inward, trichobothrium Et_2 follows to ventral aspect (some Bothriuridae) (2).

93. Chela, overall orientation: rounded (Scorpionidae, Bothriuridae) (0); flat (Liochelidae) (1); rounded (Chactidae, Superstitioniidae) (2); flat, "hexagon-shaped" (Euscorpiidae) (3); rounded (most Vaejovidae) (4); flat (Vaejovidae, *Pseudouroctonus* and *Uroctonites*) (5); "8-carinae" configuration (–).

94.^{F} Patella, fundamental configuration: 7 carinae (Palaeopisthacanthidae, Pseudochactida, Buthida) (0); 6 carinae (Chaerilida) (1); 5 (Iurida) (2).

95.^{F} Patella, dorsomedian (DMc) carina: absent (non-buthoids) (0); present (Buthoidea and *Archaeobuthus* (?)) (1).

96.^{F} Patella, dorsal patellar spur (DPS), carina development, 5-carinae configuration: absent (Iuroidea, Euscorpiidae, Chactidae, Superstitioniidae, Scorpionoidea) (0); present (Vaejovidae) (1); non-Iurida (–).

97. Patella, internal surface with a vaulted projection: weak to obsolete (0); strong to medium (Liochelidae) (1); non-Iurida (–).

98. Dorsal patellar spur (DPS) and ventral patellar spur (VPS), overall development: weak to obsolete (0); well-developed (Euscorpiidae) (1); developed (Uroctoninae) (2); non-chactoids (–).

Telson

99. Venom gland epithelium walls overall construction: simple (Pseudochactidae, Liochelidae, *Calchas*) (0); folded (1).

Reproductive anatomy

100.^{F} Number of "cells" in ovariuterus: reticulate mesh of 6 cells (0); reticulate mesh of 8 cells (Buthidae) (1).

Sternites

101. Stigma shape, partitioned by superfamily/or upper clades: circular, small (Palaeopisthacanthidae, Archaeobuthidae, Chaerilidae) (0); oval, small (Pseudochactidae and *Microcharmus*) (1); slit-like, small to long (most Buthoidea) (2); oval (Iuroidea) (3); slit-like (Iuroidea) (4); oval (Scorpionoidea) (5); slit-like (Scorpionoidea) (6); circular, small (*Troglotayosicus*, Chactinae, most Brotheinae) (7); oval, small (most Superstitioniidae, Euscorpiidae) (8); oval, medium to long (Uroctoninae and *Paravaejovis*) (9); slit-like, medium to long (Vaejovidae and *Brotheas*) (a).

Carapace

102. Number of lateral eyes on carapace: 2 (relatively primitive) (Chaerilidae) (0); 3 (Iuroidea, Scorpionoidea, Vaejovidae) (1); 0–2 (Euscorpiidae, Chactidae, Superstitioniidae) (2); 2 (Urodacidae) (3); 3–4 (Uroctoninae) (4); 3 (Scorpiopini) (5); Pseudochactidae and Buthoidea (–). [PART-ORD: (0 (1 ((2 (4, 5)) (3)))].

Pectines

103. Relative pectines development (number of teeth): reduced development (Euscorpiidae, Chactidae, Superstitioniidae) (0); well-developed (Vaejovidae) (1); non-chactoids (–).

104. Pectinal fulcra development: present (Vaejovidae, most Chactidae) (0); absent (most Superstitioniidae) (1); absent (*Belisarius*) (2); absent (Euscorpiidae) (3); variable within the genus (Euscorpiidae) (4); non-chactoids (–).

105. Pectinal lamellae development: middle lamellae bead-like, all plates well delineated, fulcra, if present, well-formed (0); single plate, or two, semifused with anterior lamellae, fulcra, if present, quite reduced in size (1); single plate, or two, semifused with anterior lamellae (2); entire genus lacks fulcra (?); non-chactoids (–).

Appendix 3

Six characters from Fet et al. (2001, pp. 157–158, appendix 1). Character states are scored 0–4.

TRICHOBOTHRIA-based characters (0–6)

5. *Est*/palm length RATIO: inapplicable (0); 0.445–0.526 (0.486), *H. arizonensis*; 0.360–0.456 (0.408) (1); *H. spadix* and *H. obscurus* (2).

6. *esb–eb*/*esb–Et*$_{5}$ RATIO: inapplicable (0); 0.369–0.466 (0.417), *H. spadix* (1); 0.275–0.397 (0.336), *H. obscurus* (2).

BIOGEOGRAPHICAL-based characters (16–19)

16. Sympatric/Allopatric/Parapatric Distribution: Sympatric, *H. pinteri* (with *H. concolor* and, to a limited degree, *H. arizonensis*) (0); Allopatric/parapatric (by areas), all other species (1).

17. General allopatric areas, DISJUNCT: Baja area: *H. pinteri*, *H. concolor* and *H. hirsutus* (0); United States area: *H. arizonensis*, *H. spadix* and *H. obscurus* (1).

18. Specific parapatric areas, CONNECTED: inapplicable, *H. pinteri* (0); Baja area, Baja Sur subarea: *H. concolor* (1); Baja area, Cape Region subarea: *H. hirsutus* (2); United States area, CA–AZ subarea: *H. arizonensis* (3); United States area, CA–NV subarea: *H. spadix* and *H. obscurus* (4).

19. Specific parapatric microareas, CONNECTED: inapplicable, "hirsutus" subgroup (0); CA–AZ subarea, California microarea: *H. a. pallidus* (1); CA–AZ subarea, Arizona microarea: *H. a. arizonensis* (2); CA–NV subarea, California microarea: *H. obscurus* (3); CA–NV subarea, Nevada microarea: *H. spadix* (4).