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Assembling the Scorpion Tree of Life: 'High-level Systematics and Phylogeny of the Extant Scorpions (Scorpiones: Orthosterni)' Reanalysed

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Introduction

The suprageneric phylogeny and classification of scorpions is in a state of flux. In 1980, seven families were recognised and grouped into three superfamilies, Buthoidea C.L. Koch, Chactoidea Pocock and Scorpionoidea Latreille, based on a manual cladistic analysis by Lamoral (1980). By 2000, between 16 and 20 families were recognised by different authors, who placed them in 4 to 6 superfamilies, or none at all (Fig. 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 familial assignment of specimens often required prior identification to genus, to the infrequent application of quantitative phylogenetic methods by contemporary workers, who defend taxonomic proposals on the basis of authority, rather than evidence. A decade later, Prendini (2000) observed that little had changed and this remains mostly true today. Authoritarianism continues to prevail in scorpion systematics, although in recent years it has been recast by some into a new pseudo-analytical guise.

The first quantitative phylogenetic analysis of Recent scorpions, excluding Buthidae C.L. Koch, was undertaken by Stockwell (1989) but was never published. Stockwell's (1989) matrix of 89 supraspecific terminal taxa and 138 morphological characters incorporated all currently recognised non-buthid genera, a single buthid terminal taxon (a composite of the 50 buthid genera recognised at the time), seven composite fossil 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.

Prendini (2000, 2001, 2003), Prendini *et al.* (2003) and Prendini & Wheeler (2005) pointed out fundamental problems with Stockwell's (1989) analysis, including forced character transformations, the coding of similar character derivations in allegedly unrelated taxa as separate states on the assumption that they evolved independently, and the use of supraspecific terminals rather than exemplar species. These problems reduce confidence in Stockwell's (1989) cladistic findings and, consequently, his revised classification. Stockwell (1992) published only his proposed revisions to the suprageneric classification of North American Chactoidea and Vaejovoidea, however. Others, notably Lourenço (1998a, b, 2000) and Soleglad & Fet (2008), have since published his revisions to the Chactoidea and Vaejovoidea.

Three original family-level phylogenetic analyses based on morphological data appeared since Stockwell (1989). Prendini (2000) treated superfamily Scorpionoidea based on an analysis of 71 exemplar species and 115 characters (three phylogenetically uninformative). Soleglad & Sissom (2001) treated the chactoid family Euscorpiidae Laurie based on an analysis of 11 supraspecific terminal taxa representing genera, and 89 characters (15

characters were phylogenetically uninformative and another 14 were deactivated in the analysis). Soleglad & Fet (2003) treated all extant scorpion families in an analysis based on 60 supraspecific terminal taxa representing genera and 105 characters (12 phylogenetically uninformative), and proposed a radical reworking of the classification: four extant 'parvorders', six extant superfamilies and fourteen extant families were recognised (Table 1).

Prendini & Wheeler (2005) criticised Soleglad & Fet's (2003) phylogenetic analysis on theoretical and empirical grounds, rejected their phylogeny and revised classification, and reverted to a classification based on the most recent peer-reviewed treatments, pending the outcome of a rigorous phylogenetic analysis. Fet & Soleglad (2005) promptly reinstated their previous classification (Soleglad & Fet 2003), ignoring the problems identified by Prendini & Wheeler (2005), but it was not universally accepted. Several authors have since followed the recommendations of Prendini & Wheeler (2005). However, the classification of Soleglad & Fet (2003) continues to be used by others and promoted on amateur websites. The present contribution demonstrates that these endorsements are misguided. Soleglad & Fet's (2003) classification is poorly supported by a reanalysis of their own data, and rapidly disintegrates as some of the most basic problems outlined by Prendini & Wheeler (2005) are addressed. There remains no scientific justification for accepting the results of Soleglad & Fet's (2003) analyses or the revised classification derived from them, nor any requirement to do so based on the rules of nomenclature.

Material and methods

Four separate reanalyses of Soleglad & Fet's (2003) morphological character matrices were conducted to test the support of their data for their phylogeny and revised classification. The first analysis was intended to simulate that conducted by Soleglad & Fet (2003), the actual results of which were never presented. The other three analyses entailed progressive removal of the assumptions of character transformation and taxon monophyly pervasive in their matrix, corrections to the scoring of characters, and the addition of relevant characters from the literature.

Analysis 1: Soleglad & Fet's (2003: 66) original Table 3, comprising 60 supraspecific terminal taxa representing genera and 105 characters (12 phylogenetically uninformative), was analysed with characters 1 and 27 ordered (additive) and characters 19, 41, 42, 60, 82 and 102 partially ordered as described in Soleglad & Fet's (2003: 135–147) Appendix A.

Analysis 2: As for Analysis 1, except with all characters unordered (nonadditive).

Analysis 3: The 60 supraspecific terminal taxa in Soleglad & Fet's (2003) Tables 3 and 4 were replaced with the exemplar species studied by these authors. The composite fossil *Palaeopisthacanthus* Petrunkevitch was deconstructed into observations for the four species from which it was assembled by Soleglad & Fet (2001, 2003): *Compsoscorpius elegans* Petrunkevitch, *Cryptoscorpius americanus* Jeram, *Palaeopisthacanthus schucherti* Petrunkevitch and *Palaeopisthacanthus vogelandurdeni* Jeram. The composite terminal for *Typhlochactas* Mitchell was deconstructed into the six species from which it was assembled by Soleglad & Fet (2003): *Typhlochactas cavicola* Francke, *Typhlochactas granulosus* Sissom & Cokendolpher, *Typhlochactas mitchelli* Sissom, *Typhlochactas reddelli* Mitchell, *Typhlochactas*

rhodesi Mitchell, *Typhlochactas sylvestris* Mitchell & Peck. Other supraspecific terminal taxa based on observations from multiple exemplar species in Soleglad & Fet's (2003: 65, 67) analysis were represented by all exemplar species mentioned in their Taxa Set discussion. Unidentified species and subspecies of particular genera were presumed to be the following based on locality data in Soleglad & Fet's (2003: 6–9) Material Examined section: *Lychas perfidus* (Keyserling) (Fiji), *Lychas scutilus* C.L. Koch (Singapore), *Microbuthus pusillus* Kraepelin (Oman), *Hadogenes gunningi* Purcell (Johannesburg), misidentified as *Hadogenes troglodytes* (Peters), *Liocheles karschii* (Keyserling) (Papua New Guinea), *Scorpio maurus fuscus* (Ehrenberg) (Israel), *Chactas exsul* (Werner) (Panama), *Anuroctonus pococki bajae* Soleglad & Fet (Anza-Borrego, California).

Soleglad & Fet's (2003: 66, 68) Tables 3 and 4 were then fused and the following corrections implemented to the characters. Ordered character 1, portraying 'fundamental' trichobothrial patterns in Soleglad & Fet's (2003) Table 3, was replaced with Soleglad & Fet's (2004) Table 4: 62 trichobothria 'existence' characters representing orthobothriotaxy. State 2 was converted to state 1 in all binary characters from Table 4 in which the putative 'intermediate' petite state was not observed. Among the remaining characters from Table 3, similar character derivations in different taxa were assigned the same state (by merging identical states), removing the assumption that they were independently derived and allowing these hypotheses to be tested by congruence with other characters. Forced reversals, coded as apomorphic states of separate characters, were removed by merging states or characters. Other unjustified instances of forced character transformation were removed by merging additive binary characters and unordering as necessary. States with overlapping variation and characters that were not independent were merged. States were split or

additional characters created when more than one state or character was subsumed. Polymorphic 'states' were removed by scoring appropriately in different exemplar species. Unknown 'states' were removed by scoring with a questionmark. Characters known in and applicable to particular taxa, previously scored unknown or inapplicable by Soleglad & Fet (2003), were scored appropriately. Various other corrections (by no means exhaustive) were also implemented (Table 2). The resulting matrix comprised 81 exemplar species (5 species in 4 extinct genera and 76 species in 57 extant genera), and 161 characters (10 phylogenetically uninformative). All characters were unordered (nonadditive) in this analysis.

Analysis 4: All relevant characters from previous or contemporaneous cladistic analyses of extinct and/or extant scorpion phylogeny (Lamoral 1980; Stockwell 1989; Jeram 1994, 1998; Prendini 2000, 2003; Dunlop & Braddy 2001; Soleglad & Sissom 2001) were incorporated into the matrix prepared for Analysis 3 and scored in the 81 exemplar species. The fusion of the 161 revised characters from Soleglad & Fet's (2003) original matrices with partially or completely overlapping characters from the abovementioned analyses created 174 characters, to which 26 other relevant characters from these analyses, previously omitted from Soleglad & Fet's (2003) matrices, were added. The resulting matrix comprised 81 exemplar species and 200 characters (13 phylogenetically uninformative). All characters were again unordered (nonadditive) in this analysis.

Character data were edited and cladograms prepared using WinClada (Nixon 2002). Characters were weighted equally *a priori*, uninformative characters deactivated, and heuristic searches conducted with equal weighting in TNT (Goloboff *et al.* 2003-2006; 2008). The following options were applied in each of the four analyses. The maximum number of trees held in memory was set to 10,000. A new technology search was performed, starting

with 1,000 random addition sequences and followed by a driven search with 1,000 initial addition sequences. In each case, 100 iterations of the parsimony ratchet (Nixon 1999) were conducted, along with 100 cycles of tree drifting (Goloboff 1999), three rounds of tree fusing (Goloboff 1999), and six cycles of sectorial search, using default parameters. A strict consensus of the resultant trees was then calculated and the support for each node recovered in the consensus assessed with 1,000 replicates of jackknife resampling (Farris *et al.* 1996; Goloboff *et al.* 2003) at a 36% character removal probability.

Results

Analysis 1: An attempt to simulate Soleglad & Fet's (2003) analysis by running their unmodified matrix using the original settings, yielded 197 most parsimonious trees (MPTs) of 307 steps (Fig. 2). One clade portrayed in Soleglad & Fet's (2003) tree and ten suprageneric taxa (one superfamily, three families, three subfamilies, two tribes and one subtribe) in their revised classification and subsequent emendations (Fet & Soleglad 2005; Fet *et al.* 2004a; Soleglad & Fet 2003, 2004, 2008; Soleglad *et al.* 2005; Table 1) were not monophyletic (Table 3). Among those that were, five clades and one subfamily received <50% jackknife support. One superfamily received exactly 50% jackknife support.

Analysis 2: When Soleglad & Fet's (2003) unmodified matrix was analysed with all characters unordered (nonadditive), 79 MPTs of 293 steps were retrieved (Fig. 3). Four clades in Soleglad & Fet's (2003) tree and nine suprageneric taxa (two superfamilies, two families, three subfamilies, one tribe and one subtribe) in their classification were not monophyletic (Table 3). Among those that were, four clades and one tribe received <50% jackknife support.

Analysis 3: When Soleglad & Fet's (2003) supraspecific terminal taxa were converted to

exemplar species, their assumptions of character transformation removed, and some corrections to their character coding implemented (Table 2), 156 MPTs of 401 steps were recovered (Fig. 4). Three clades in Soleglad & Fet's (2003) tree and 11 suprageneric taxa (one superfamily, one family, five subfamilies, three tribes and one subtribe) in their classification were not monophyletic (Table 3). Among those that were, five clades, one family and three subfamilies received <50% jackknife support.

Analysis 4: After fusion of the matrix used for Analysis 3 with other matrices and character data from the literature, 227 MPTs of 498 steps were obtained (Fig. 5). Seven clades in Soleglad & Fet's (2003) tree and 12 suprageneric taxa (two superfamilies, two families, six subfamilies, one tribe and one subtribe) in their classification were not monophyletic (Table 3). Among those that were, two clades, one superfamily and two subfamilies received <50% jackknife support.

When Soleglad & Fet's (2003) original tree (reproduced here as Fig. 6A) is compared with the strict consensus of suprafamilial relationships retrieved by the four reanalyses presented here (Fig. 6B), we see substantial collapse. Nine clades and 18 suprageneric taxa (two superfamilies, four families, eight subfamilies, three tribes and one subtribe) in their tree, revised classification and subsequent emendations were not recovered in at least one analysis (Table 3). Another four clades, one superfamily and two subfamilies received <50% jackknife support in at least one analysis. The following were not monophyletic and/or received <50% jackknife support in the majority of analyses: (Pseudochactida + Buthida + Chaerilida + Iurida), (Buthida + Chaerilida + Iurida), (Chaerilida + Iurida), Iuroidea, (Chactoidea + Scorpionoidea), Chactoidea, Smeringurinae, Smeringurini, Syntropinae, Syntropini,

Syntropina, Vaejovinae, (Brotheinae + Chactinae), (Euscorpiinae + Megacorminae), (Scorpionidae + Urodacidae), Scorpionidae.

The general trend emphasised by these analyses is a progressive decrease in the number of monophyletic clades and suprageneric taxa in Soleglad & Fet's (2003) tree, revised classification and subsequent emendations, associated with removing the assumptions of character transformation and taxon monophyly, correcting the scoring of characters, and adding characters from the literature (Fig. 7A). This finding is unsurprising because many of Soleglad & Fet's (2003) characters were specifically designed to achieve a preconceived result and various characters which might challenge this result were omitted (Prendini & Wheeler 2005). It is noteworthy, however, that more clades and suprageneric taxa received <50% jackknife support in Analysis 1, the attempted simulation of Soleglad & Fet's (2003) assumption-laden analysis, than in Analysis 4 without the assumptions of monophyly and character transformation, and with additional characters (Fig. 7B), indicating that Soleglad & Fet's (2003) tree and classification are poorly supported by their original data matrix.

Discussion

Soleglad & Fet (2003) proposed a radical reworking of the suprageneric classification of extant scorpions based on their phylogenetic analysis of 60 supraspecific terminal taxa, representing genera, scored for 105 morphological characters (Table 1). The 'parvorder' category (Sibley & Monroe 1990; McKenna & Bell 1997) was introduced to scorpion classification and four extant parvorders created within Infraorder Orthosterni Pocock (Buthida Soleglad & Fet; Chaerilida Soleglad & Fet; Iurida Soleglad & Fet; Pseudochactida Soleglad & Fet). Six extant superfamilies, two new (Iuroidea Soleglad & Fet; Pseudochactoidea

Soleglad & Fet, 2003), were recognised and two synonymised (Bothriuroidea Simon; Vaejovoidea). Fourteen extant families were recognised, including a new family, Caraboctonidae Kraepelin (formerly Caraboctoninae Kraepelin of Iuridae Thorell). One family was synonymised (Troglotayosicidae Lourenço) and three were downgraded to subfamilies of other families (Diplocentridae Karsch; Hemiscorpiidae Pocock; Heteroscorpionidae Kraepelin). Three subfamilies, four tribes (one new, Nullibrotheini Soleglad & Fet) and two subtribes (one new, Neochactina Soleglad & Fet) were established within Chactidae Pocock, and various chactoid genera were transferred from one family to another.

Many changes proposed by these authors are controversial, the monophyly and composition of Chactoidea, Iuroidea and their component families, Caraboctonidae, Chactidae, Euscorpiidae, Iuridae, Superstitioniidae Stahnke and Vaejovidae Thorell, especially so (Coddington *et al.* 2004; Prendini & Wheeler 2005; Francke & Prendini 2008). For example, Soleglad & Fet (2003, 2004) placed the North American *Uroctonus* Thorell, previously considered a basal vaejovid (Stockwell 1989; Sissom 1990, 2000a; Lourenço 2000, 2001), in subfamily Uroctoninae Mello-Leitão of the largely Neotropical Chactidae, along with *Anuroctonus* Pocock, another North American chactoid, formerly placed in subfamily Hadrurinae Stahnke of Vaejovidae (Stahnke 1974), or of Iuridae (Stockwell 1989, 1992; Lourenço 2000, 2001; Sissom & Fet 2000), or considered *incertae sedis* in Chactoidea (Francke & Soleglad 1981; Sissom 1990; Coddington *et al.* 2004). In contrast with the findings of Soleglad & Fet (2003), Stockwell's (1989) unpublished phylogenetic analysis, deemed 'important and highly-regarded' by Soleglad *et al.* (2005: 5), supported the placements of *Uroctonus* and *Anuroctonus* in the Vaejovidae and Hadrurinae (the latter placed under Caraboctonidae by Soleglad & Fet 2003), respectively.

Another controversial example is provided by *Belisarius* Simon, a troglomorphic endogean scorpion from the Pyrenees of France and Spain, placed in Chactidae, in an otherwise exclusively Neotropical epigean subfamily Brotheinae Simon, by Soleglad & Fet (2003). Regardless of disagreements concerning its taxonomic rank (reviewed by Coddington *et al.* 2004), most previous authors (Mitchell 1971; Francke 1982; Stockwell 1989, 1992; Lourenço 1998b, 2000, 2001; Sissom & Cokendolpher 1998; Fet & Sissom 2000; Sissom 2000b) either considered a possible relationship to, or grouped *Belisarius* with, other mostly troglomorphic endogean and hypogean scorpions, viz. Typhlochactinae Mitchell and/or *Troglotayosicus* Lourenço, all of which were placed in Superstitioniidae by Soleglad & Fet (2003). A monophyletic group comprising *Belisarius*, *Troglotayosicus* and Typhlochactinae was retrieved in Stockwell's (1989) unpublished phylogenetic analysis.

The phylogenetic position of the troglomorphic Neotropical genus *Troglotayosicus* is also controversial. *Troglotayosicus* was originally placed in Chactidae (Lourenço 1981), where it remained until Stockwell (1992) transferred it to the newly-elevated Superstitioniidae, along with *Belisarius*, based on his unpublished phylogenetic analysis (Stockwell 1989). A new family, Troglotayosicidae Lourenço (as Troglotayosidae), with two monotypic subfamilies, Troglotayosicinae Lourenço (as Troglotayosinae) and Belisariinae Lourenço (as Belisarinae), were subsequently created to accommodate the two genera, their inclusion in the same family justified solely on the basis of their troglomorphic habitus and relictual distribution (Lourenço 1998b). Lourenço (2000, 2001) continued to recognise Troglotayosicidae, in spite of the criticisms of Sissom (2000b c) and Fet & Sissom (2000). Coddington *et al.* (2004) questioned its monophyly, suggesting that *Belisarius* may be more closely related to Euscorpiidae or Chactidae than to *Troglotayosicus*, which they suggested might be a

superstitioniid. Soleglad & Fet (2003) returned *Belisarius* to Chactidae and *Troglotayosicus* to Superstitioniidae, and synonymised Troglotayosicidae with Superstitioniidae. Prendini & Wheeler (2005) then resurrected Troglotayosicidae and Fet & Soleglad (2005) synonymised it again. Lourenço (2006) suggested that *Troglotayosicus* should be retained in Troglotayosicidae or considered *incertae sedis* in Chactoidea, while Botero-Trujillo & Francke (2009), who described the second species of this genus, also recognised Troglotayosicidae.

The Neotropical genus *Chactopsis* Kraepelin presents yet another example of a chactoid genus with controversial phylogenetic placement. *Chactopsis* was first transferred to Euscorpiidae by Soleglad & Sissom (2001), based on an analysis that included insufficient taxa to rigorously test its position, omitted many important characters, and was fundamentally flawed in other respects (Prendini & Wheeler 2005). Soleglad & Fet (2003) continued to regard this genus as a euscorpiid although it was traditionally grouped with the Neotropical chactids (Sissom 1990, 2000c; Lourenço 2000, 2001; Coddington *et al.* 2004), a position confirmed in Stockwell's (1989) unpublished phylogenetic analysis and in a more recent analysis by Florez & Mattoni (2007). Lourenço (2003) also doubted its placement in Euscorpiidae, based on an examination of male genitalia, and subsequently listed it under Chactidae (Lourenço 2005).

Besides removing *Chactopsis* from Chactidae, Soleglad & Fet (2003: 97–102) extensively revised the remaining Neotropical chactid genera, especially those grouped into tribe Brotheini Simon. Three genera were synonymised, a new genus (*Neochactas* Soleglad & Fet) erected, and 48 new combinations proposed, decisions based almost entirely on an assessment of trichobothrial patterns obtained from the literature. No phylogenetic analysis was presented, no other character systems besides trichobothria were considered, and only

seven specimens in six genera and species of Neotropical Chactidae were actually examined (*vide* Soleglad & Fet 2003: 7). Debate has since raged over the validity of one genus that was synonymised, *Auyantepuia* González-Sponga (Lourenco & Souza Araújo 2004; Soleglad & Fet 2005b; Lourenco & Qi 2007), and it is fairly obvious that the other two, *Cayooca* González-Sponga and *Guyanochactas* Lourenço, were synonymised with the wrong genus.

Further revisions to the classification of Scorpionoidea, some contradicting Soleglad & Fet's (2003) earlier actions, were implemented subsequently by Fet *et al.* (2004a) and Soleglad *et al.* (2005). Fet *et al.* (2004a) resurrected subfamilies Bothriurinae Simon, 1880 and Lisposominae Lawrence of Bothriuridae Simon, while Soleglad *et al.* (2005) downgraded Urodacidae Kraepelin to a subfamily of Scorpionidae Latreille, proposed Hemiscorpiidae as a senior synonym of Liochelidae Fet & Bechly and Hormurinae Laurie as a senior synonym of Liochelinae Fet & Bechly, and transferred Heteroscorpioninae Kraepelin to Hemiscorpiidae.

The ranking of the various scorpionoid families and subfamilies by these authors, in direct opposition to the phylogenetic classification proposed by Prendini (2000), is questionable, particularly in view of the justification provided for doing so (Soleglad & Fet 2003: 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 these taxa, rearranged and redefined by Soleglad & Fet (2003), Fet *et al.* (2004a) and Soleglad *et al.* (2005), remains uncertain in spite of previous analyses (Prendini & Wheeler 2005). For example, Prendini (2000, 2003) obtained two alternative placements for *Urodacus* Peters and *Heteroscorpion* Birula, one in which they were monophyletic and another in which they were not. According to the second hypothesis, first proposed by Stockwell (1989), Heteroscorpionidae is sister to (Hemiscorpiidae + Liochelidae), whereas Urodacidae is sister to (Diplocentridae + Scorpionidae). This finding was discussed at length by Soleglad & Sissom (2001: 72), Soleglad & Fet (2003: 115–117) and Soleglad *et al.* (2005), who attempted to re-examine the matter in a flawed reanalysis of Prendini's (2000) data. Given the uncertainty in the relative positions of these taxa, a prudent strategy to retain stability in the current classification, would have been to continue recognising 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, until more data accumulated and their phylogenetic

positions were more robustly supported (Prendini & Wheeler 2005). As it turns out, in this particular example, the addition of data (taxa and characters) resolved the phylogeny in favor of Prendini's (2000) first hypothesis, supporting the recognition of Heteroscorpionidae and Urodacidae as distinct families. In a reanalysis of urodacid phylogeny, Volschenk & Prendini (2008) failed to retrieve the second hypothesis due to increased support for the (Heteroscorpionidae + Urodacidae) sister-group hypothesis achieved by the character combination and phylogenetic position of a basal urodacid, *Aops* Volschenk & Prendini.

In the past five years, Soleglad, Fet and their associates have focused on the suprageneric classification of North American chactoid scorpions, especially Vaejovidae. Fet *et al.* (2004b) proposed *Hoffmannihadrurus* Fet & Soleglad, a new genus of Caraboctonidae, to accommodate two well known species of *Hadrurus* Thorell from mainland Mexico. *Hoffmannihadrurus* has since been twice synonymised (Prendini & Wheeler 2005; Francke & Prendini 2008) and twice revalidated (Fet & Soleglad 2005, 2008).

Proposed changes to vaejovid classification (Graham & Soleglad 2007; Soleglad & Fet 2005a, 2006, 2008) include the creation of a new subfamily (Smeringurinae Soleglad & Fet), three new tribes (Paravaejovini Soleglad & Fet; Smeringurini Soleglad & Fet; Stahnkeini Soleglad & Fet), a new subtribe (Thorellina Soleglad & Fet), seven new genera (*Franckeus* Soleglad & Fet; *Gertschius* Graham & Soleglad; *Hoffmannius* Soleglad & Fet; *Kochius* Soleglad & Fet; *Stahnkeus* Soleglad & Fet; *Thorellius* Soleglad & Fet; *Wernerius* Soleglad & Fet) and 55 new combinations. No phylogenetic analysis justifying these changes, many taken unashamedly from Stockwell's (1989) unpublished PhD dissertation (*vide* Soleglad & Fet 2008: 1–2), has been presented to date. Most of the new vaejovid genera erected are nothing

more than unoriginal names for species groups that have been recognised since the 1970s, but the monophyly of which has yet to be tested.

Conclusions

Most systematists agree that stability is an important attribute of any taxonomic classification; that predictivity is maximised for classifications stable to the addition of new data, equating stability with repeatability; and that changes to a classification should bring stability and be supported by rigorous, unbiased analyses of all available evidence (Nelson 1972, 1973; Gaffney 1979; Kluge 1989; Kluge & Wolf 1993; Nixon & Carpenter 1996; Dominguez & Wheeler 1997; Knapp *et al.* 2004).

The stability of Soleglad & Fet's (2003) classification and subsequent emendations (e.g., Fet & Soleglad 2005, 2008; Fet *et al.* 2004a, 2004b, 2005; Graham & Soleglad 2007; Soleglad & Fet 2004, 2005a, 2006, 2008; Soleglad *et al.* 2005) depends on the rigor of their phylogenetic analyses (in the few cases presented). However, the analyses presented by these authors cannot be termed rigorous or unbiased because they fail to meet the most basic standards in systematics (Prendini & Wheeler 2005): their 'existence approach' to trichobothrial homology, in which the directionality of trichobothrial states is forced by Sankoff optimization (Soleglad & Fet 2001), their 'fundamental character' analyses, in which 'important' characters are isolated and analysed separately from less important characters (Soleglad & Fet 2003; Fet *et al.* 2005), their failure to analyse different sources of evidence simultaneously (Fet *et al.* 2003, 2005; Soleglad & Fet 2003), their use of hypothetical outgroups (Soleglad & Fet 2001, 2004) and supraspecific terminal taxa (Soleglad & Fet 2001, 2003; 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 (Soleglad & Fet 2003; Fet *et al.* 2004a, 2005; Soleglad *et al.* 2005), is nothing more than an elaborate scheme designed to achieve and legitimise a desired result. Prendini & Wheeler (2005) therefore rejected all changes to the suprageneric classification of scorpions proposed by Soleglad, Fet and colleagues in their self-edited online publication since 2001 and, pending a rigorous and unbiased analysis, reverted to a classification reflected by the most recent peer-reviewed, published treatments. In response, Fet & Soleglad (2005) promptly reinstated their previous classification (Soleglad & Fet 2003), ignoring the problems identified by Prendini & Wheeler (2005), but it was not universally accepted. Several authors have since followed the recommendations of Prendini & Wheeler (2005). However, the classification of Soleglad & Fet (2003) continues to be used by others and promoted on amateur websites. The present contribution demonstrates that these endorsements are misguided. Soleglad & Fet's (2003) classification is poorly supported by a reanalysis of their own data, and rapidly disintegrates as some of the most basic problems outlined by Prendini & Wheeler (2005) are addressed. There remains no scientific justification for accepting the results of Soleglad & Fet's (2003) analyses or the revised classification derived from them, nor any requirement to do so based on the rules of nomenclature: the Code 'refrains from infringing upon taxonomic judgment, which must not be made subject to regulation or restraint [and] does not determine the inclusiveness or exclusiveness of any taxon, nor the rank to be accorded to any assemblage of animals' (ICZN 1999: XIX).

The present contribution illustrates the effects of modest corrections to Soleglad & Fet's (2003) character matrix, principally those steps taken to remove the more blatantly

unacceptable assumptions discussed by Prendini & Wheeler (2005). The correction of all remaining flaws in this matrix will not, however, achieve a rigorous analysis of scorpion phylogeny. A serious attempt to assemble the scorpion Tree of Life will require an adequate outgroup taxon sample, including representatives of all other chelicerate lineages, extinct and extant; an extensive ingroup taxon sample, representing all extinct and extant scorpion lineages with appropriate numbers of exemplar species, especially in the many groups that are demonstrably paraphyletic; traditional character systems (e.g. pedipalp trichobothria, carinae, hemispermatophore) to be properly homologised across the entire order and scored in all taxa; new character systems (e.g. internal anatomy, pectinal peg sensillae, sperm structure) to be explored and, if found to be informative, scored in all taxa; the inclusion of DNA sequence data from multiple loci in the nuclear and mitochondrial genomes, preferably including at least one nuclear protein-coding locus.

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Abstract

Soleglad & Fet (2003) presented a phylogenetic analysis of all scorpion families, using supraspecific terminal taxa, and proposed a radical reworking of the classification: four extant ‘parvorders’, six extant superfamilies and fourteen extant families were recognised. Prendini

& Wheeler (2005) criticised Soleglad & Fet's (2003) analysis on theoretical and empirical grounds, rejected their phylogeny and revised classification, and reverted to a classification based on the most recent peer-reviewed treatments, pending the outcome of a rigorous phylogenetic analysis. Fet & Soleglad (2005) promptly reinstated their previous classification (Soleglad & Fet 2003), ignoring the problems identified by Prendini & Wheeler (2005), but it was not universally accepted. Several authors have since followed the recommendations of Prendini & Wheeler (2005). However, the classification of Soleglad & Fet (2003) continues to be used by others and promoted on amateur websites. The present contribution demonstrates that these endorsements are misguided. Soleglad & Fet's (2003) classification is poorly supported by a reanalysis of their own data, and rapidly disintegrates as some of the most basic problems outlined by Prendini & Wheeler (2005) are addressed. Nine clades and 18 suprageneric taxa (two superfamilies, four families, eight subfamilies, three tribes and one subtribe) in their tree, revised classification and subsequent emendations were not recovered in at least one of four reanalyses conducted. Another four clades, one superfamily and two subfamilies received <50% jackknife support in at least one analysis. The following were not monophyletic and/or received <50% jackknife support in the majority of analyses: (Pseudochactida + Buthida + Chaerilida + Iurida), (Buthida + Chaerilida + Iurida), (Chaerilida + Iurida), Iuroidea, (Chactoidea + Scorpionoidea), Chactoidea, Smeringurinae, Smeringurini, Syntropinae, Syntropini, Syntropina, Vaejovinae, (Brotheinae + Chactinae), (Euscorpiinae + Megacorminae), (Scorpionidae + Urodacidae), Scorpionidae. There remains no scientific justification for accepting the results of Soleglad & Fet's (2003) analyses or the revised classification derived from them, nor any requirement to do so based on the rules of nomenclature.

References

BOTERO-TRUJILLO R, FRANCKE OF. 2009. A new species of troglomorphic leaf litter scorpion from Colombia belonging to the genus *Troglotayosicus* (Scorpiones: Troglotayosicidae). Texas Memorial Museum Speleological Monographs 7. Studies on the cave and endogean fauna of North America V: 1–10.

CODDINGTON JA, GIRIBET G, HARVEY MS, PRENDINI L, WALTER DE. 2004. Arachnida. In: Cracraft J, Donoghue M. (Eds.) Assembling the Tree of Life. Oxford University Press. Oxford. p. 296–318.

DOMINGUEZ E, WHEELER QD. 1997. Taxonomic stability is ignorance. Cladistics 13: 367–372.

DUNLOP JA, BRADDY SJ. 2001. Scorpions and their sister-group relationships. In: Fet V, Selden PA. (Eds.) Scorpions 2001. *In Memoriam* Gary A. Polis. British Arachnological Society. Burnham Beeches, Buckinghamshire, UK. p. 1–24.

FARRIS JS, ALBERT VA, KÄLLERSJÖ M, LIPSCOMB D, KLUGE AG. 1996. Parsimony jackknifing outperforms neighbor-joining. Cladistics 12: 99–124.

FET V, GANTENBEIN B, GROMOV AV, LOWE G, LOURENÇO WR. 2003. The first molecular phylogeny of Buthidae (Scorpiones). Euscorpius 4: 1–10.

FET V, SISSOM WD. 2000. Family Troglotayosicidae Lourenço, 1998. In: Fet V, Sissom WD, Lowe G, Braunwalder ME. Catalog of the Scorpions of the World (1758–1998). The New York Entomological Society. New York. p. 501–502.

FET V, SOLEGLAD ME, KOVAŘÍK F. 2004a. Subfamily Lisposominae revisited (Scorpiones: Bothriuridae). Revista Ibérica de Aracnología 10: 195–209.

FET V, SOLEGLAD ME, LOWE G. 2005. A new trichobothrial character for the high-level systematics of Buthoidea (Scorpiones: Buthida). Euscorpius 23: 1–40.

FET V, SOLEGLAD ME, NEFF DPA, STATHI I. 2004b. Tarsal armature in the superfamily Iuroidea (Scorpiones: Iurida). Revista Ibérica de Aracnología 10: 17–40.

FET V, SOLEGLAD ME. 2005. Contributions to scorpion systematics. I. On recent changes in high-level taxonomy. Euscorpius 31: 1–13.

FET V, SOLEGLAD ME. 2008. Cladistic analysis of superfamily Iuroidea, with emphasis on subfamily Hadrurinae (Scorpiones: Iurida). Boletín Sociedad Entomológica Aragonesa 43: 255–281.

FLOREZ E, MATTONI C. 2007. Los escorpiones del género *Chactopsis*: ¿Euscórpiidos o Cháctidos? In: VII Reunión Argentina de Cladística y Biogeografia. Sesiones Regulares. Darwiniana 45 (suppl.): 83–85.

FRANCKE OF, PRENDINI L. 2008. Phylogeny and classification of the giant hairy scorpions, *Hadrurus* Thorell (Iuridae Thorell): A reappraisal. Systematics and Biodiversity 6: 205–223.

FRANCKE OF, SOLEGLAD ME. 1981. The family Iuridae Thorell (Arachnida, Scorpiones). Journal of Arachnology 9: 233–258.

FRANCKE OF. 1982. Studies of the scorpion subfamilies Superstitioninae and Typhlochactinae, with description of a new genus (Scorpiones, Chactidae). Bulletin of the Association for Mexican Cave Studies 8: 51–61/Bulletin of the Texas Memorial Museum 28: 51–61.

GAFFNEY ES. 1979. An introduction to the logic of phylogeny reconstruction. In: Cracraft J, Eldredge N. (Eds.) Phylogenetic Analysis and Palaeontology. Columbia University Press. New York. p. 79–111.

GOLOBOFF PA. 1999. Analyzing large data sets in reasonable times: Solutions for composite optima. Cladistics 15: 415–428.

GOLOBOFF PA, FARRIS JS, KÄLLERSJÖ M., OXELMAN B., RAMÍREZ MJ, SZUMIK CA. 2003. Improvements to resampling measures of group support. Cladistics 19: 324–332.

GOLOBOFF PA, FARRIS JS, NIXON KC. 2003–2006. TNT: Tree Analysis Using New Technology. Version 1.1. Computer software and documentation. Available at: http://www.zmuc.dk/public/Phylogeny/TNT/

GOLOBOFF PA, FARRIS JS, NIXON KC. 2008. TNT, a free program for phylogenetic analysis. Cladistics 24: 774–786.

GRAHAM MR, SOLEGLAD ME. 2007. A new scorpion genus representing a primitive taxon of tribe Stahnkeini, with a description of a new species from Sonora, Mexico (Scorpiones: Vaejovidae). Euscorpius 57: 1–13.

ICZN (INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE). 1999. International Code of Zoological Nomenclature. 4th ed. The International Trust for Zoological Nomenclature c/o The Natural History Museum. London.

JERAM AJ. 1994. Carboniferous Orthosterni and their relationship to living scorpions. Palaeontology 37: 513–550.

JERAM AJ. 1998. Phylogeny, classification and evolution of Silurian and Devonian scorpions. In: Selden PA. (Ed.) Proceedings of the 17th European Colloquium of Arachnology, Edinburgh 1997. British Arachnological Society. Burnham Beeches, Buckinghamshire, UK. p. 17–31.

KLUGE AG, WOLF, AJ. 1993. Cladistics: What's in a word? Cladistics 9: 183–199.

KLUGE AG. 1998. Total evidence or taxonomic congruence: Cladistics or consensus classification. Cladistics 14: 151–158.

KNAPP S, LAMAS G, NIC LUGHADHA E, NOVARINO G. 2004. Stability or stasis in the names of organisms: The evolving codes of nomenclature. Philosophical Transactions of the Royal Society of London, Series B 359: 611–622.

LAMORAL BH. 1980. A reappraisal of the suprageneric classification of recent scorpions and their zoogeography. In: Gruber J. (Ed.) Verhandlungen. 8. Internationaler Arachnologen – Kongress abgehalten ander Universität für Bodenkultur Wien, 7–12 Juli, 1980. H. Egermann. Vienna. p. 439–444.

LOURENÇO WR, QI J-X. 2007. Additions à la faune des scorpions de l'Etat du Amapá, Brésil (Chelicerata, Scorpiones). Revue suisse de Zoologie 114: 3–12.

LOURENÇO WR, SOUZA ARAÚJO J. DE 2004. Nouvelles considérations sur le genre *Auyantepuia* Gonzalez-Sponga (Scorpiones, Chactidae) et description d'une nouvelle espèce pour la région de Manaus, en Amazonie brésilienne. Acta biológica paranaense, Curitiba 33: 1–11.

LOURENÇO WR. 1981. Scorpions cavernicoles de l'Équateur: *Tityus demangei* n. sp. et *Ananteris ashmolei* n. sp. (Buthidae); *Troglotayosicus vachoni* n. gen., n. sp. (Chactidae), scorpion troglobie. Bulletin du Muséum National d'Histoire Naturelle, Paris 3: 635–662.

LOURENÇO WR. 1998a. Designation of the scorpion subfamily Scorpiopsinae Kraepelin, 1905 as family Scorpiopsidae Kraepelin, 1905: Its generical composition and a description of a new species of *Scorpiops* from Pakistan (Scorpiones, Scorpiopsidae). Entomologische Mitteilungen aus dem Zoologischen Museum Hamburg 12: 245–254.

LOURENÇO WR. 1998b. Panbiogéographie, les distribution disjointes et le concept de famille relictuelle chez les scorpions. Biogeographica 74: 133–144.

LOURENÇO WR. 2000. Panbiogéographie, les familles des scorpions et leur répartition

géographique. Biogeographica 76: 21–39.

LOURENÇO WR. 2001. The scorpion families and their geographical distribution. Journal of Venomous Animals and Toxins 7: 1–12. (doi : 10.1590/S0104-79302001000100002)

LOURENÇO WR. 2003. Le genre *Chactopsis* Kraepelin (Scorpiones, Euscorpiidae (ou Chactidae)) en Amazonie Bresilienne. Biogeographica 79: 167–174.

LOURENÇO WR. 2005. Scorpion diversity and endemism in the Rio Negro region of Brazilian Amazonia, with the description of two new species of *Tityus* C.L. Koch (Scorpiones, Buthidae). 18: 203–213.

LOURENÇO WR. 2006. Further considerations on the genus *Troglotayosicus* Lourenço, 1981 (Scorpiones: Troglotayosicidae or *Incertae sedis*). Boletín Sociedad Entomológica Aragonesa 39: 389–395.

MCKENNA MC, BELL SK. 1997. Classification of Mammals above the Species Level. Columbia University Press. New York.

MITCHELL RW. 1971. *Typhlochactas elliotti*, a new eyeless cave scorpion from Mexico (Scorpionida, Chactidae). Annales de Spéléologie 26: 135–148.

NELSON GJ. 1972. Phylogenetic relationship and classification. Systematic Zoology 21: 227–231.

NELSON GJ. 1973. Classification as an expression of phylogenetic relationships. Systematic Zoology 22: 344–359.

NIXON KC. 1999. The Parsimony Ratchet, a new method for rapid parsimony analysis. Cladistics 15, 407–414.

NIXON KC. 2002. WinClada. Version 1.00.08. Computer software and documentation. Available at: http://www.cladistics.com

NIXON KC, CARPENTER JM. 1996. On simultaneous analysis. Cladistics 12: 221–241.

PRENDINI L, CROWE TM, WHEELER WC. 2003. Systematics and biogeography of the family Scorpionidae Latreille, with a discussion of phylogenetic methods. Invertebrate Systematics 17: 185–259.

PRENDINI L, WHEELER WC. 2005. Scorpion higher phylogeny and classification, taxonomic anarchy, and standards for peer review in online publishing. Cladistics 21: 446–494.

PRENDINI L. 2000. Phylogeny and classification of the Superfamily Scorpionoidea Latreille 1802 (Chelicerata, Scorpiones): An exemplar approach. Cladistics 16: 1–78.

PRENDINI L. 2001. Species or supraspecific taxa as terminals in cladistic analysis? Groundplans versus exemplars revisited. Systematic Biology 50: 290–300.

PRENDINI L. 2003. A new genus and species of bothriurid scorpion from the Brandberg Massif, Namibia, with a reanalysis of bothriurid phylogeny and a discussion of the phylogenetic position of *Lisposoma* Lawrence. Systematic Entomology 28: 149–172.

SIBLEY CG, MONROE BL, JR. 1990. Distribution and Taxonomy of Birds of the World. Yale University Press. New Haven, CT.

SISSOM WD, COKENDOLPHER JC. 1998. A new troglobitic scorpion of the genus *Typhlochactas* (Superstitionidae) from Veracruz, Mexico. Journal of Arachnology 26: 285–290.

SISSOM WD, FET V. 2000. Family Iuridae Thorell, 1876. In: Fet V, Sissom WD, Lowe G, Braunwalder ME. Catalog of the Scorpions of the World (1758–1998). The New York Entomological Society. New York. p. 409–420.

SISSOM WD. 1990. Systematics, biogeography and paleontology. In: Polis GA. (Ed.) The Biology of Scorpions. Stanford University Press. Stanford, CA. p. 64–160.

SISSOM WD. 2000a. Family Vaejovidae Thorell, 1876. In: Fet V, Sissom WD, Lowe G, Braunwalder ME. Catalog of the Scorpions of the World (1758–1998). The New York Entomological Society. New York. p. 503–553.

SISSOM WD. 2000b. Family Superstitioniidae Stahnke, 1940. In: Fet V, Sissom WD, Lowe G, Braunwalder ME. Catalog of the Scorpions of the World (1758–1998). The New York Entomological Society. New York. p. 496–500.

SISSOM WD. 2000c. Family Chactidae Pocock, 1893. In: Fet V, Sissom WD, Lowe G, Braunwalder ME. Catalog of the Scorpions of the World (1758–1998). The New York Entomological Society. New York. p. 287–322.

SOLEGLAD ME, FET V, KOVAŘÍK F. 2005. The systematic position of the scorpion genera *Heteroscorpion* Birula, 1903 and *Urodacus* Peters, 1861 (Scorpiones: Scorpionoidea). Euscorpius 20: 1–38.

SOLEGLAD ME, FET V. 2001. Evolution of scorpion orthobothriotaxy: A cladistic approach. Euscorpius 1: 1–38.

SOLEGLAD ME, FET V. 2003. High-level systematics and phylogeny of the extant scorpions (Scorpiones: Orthosterni). Euscorpius 11: ii+1–175.

SOLEGLAD ME, FET V. 2004. The systematics of the scorpion subfamily Uroctoninae (Scorpiones: Chactidae). Revista Ibérica de Aracnología 10: 81–128.

SOLEGLAD ME, FET V. 2005a. A new scorpion genus (Scorpiones: Vaejovidae) from Mexico. Euscorpius 24: 1–13.

SOLEGLAD ME, FET V. 2005b. The genus *Auyantepuia* González-Sponga, 1978 is confirmed as a synonym of *Broteochactas* Pocock, 1893 (Scorpiones: Chactidae). Euscorpius 29: 1–14.

SOLEGLAD ME, FET V. 2006. Contributions to scorpion systematics. II. Stahnkeini, a new

tribe in scorpion family Vaejovidae (Scorpiones: Chactoidea). Euscorpius 40: 1–32.

SOLEGLAD ME, FET V. 2008. Contributions to scorpion systematics. III. Subfamilies Smeringurinae and Syntropinae (Scorpiones: Vaejovidae). Euscorpius 71: 1–115.

SOLEGLAD ME, SISSOM WD. 2001. Phylogeny of the family Euscorpiidae Laurie, 1896: A major revision. In: Fet V, Selden PA. (Eds.) Scorpions 2001. *In Memoriam* Gary A. Polis. British Arachnological Society. Burnham Beeches, Buckinghamshire, UK. p. 25–111.

STAHNKE HL. 1974. Revision and keys to the higher categories of Vejovidae. Journal of Arachnology 1: 107–141.

STOCKWELL SA. 1989. Revision of the phylogeny and higher classification of scorpions (Chelicerata). Unpublished PhD Dissertation. University of California. Berkeley, CA.

STOCKWELL SA. 1992. Systematic observations on North American Scorpionida with a key and checklist of the families and genera. Journal of Medical Entomology 29: 407–422.

VOLSCHENK ES, PRENDINI L. 2008. *Aops oncodactylus* gen. *et* sp. nov., the first troglobitic urodacid (Urodacidae: Scorpiones), with a re-assessment of cavernicolous, troglobitic and troglomorphic scorpions. Invertebrate Systematics 22: 235–257.

Table 1. The suprageneric classification of Recent (extant) scorpions proposed by Soleglad and Fet (2003a) with subsequent emendations (Fet *et al.* 2004a; Fet & Soleglad 2005; Soleglad *et al.* 2005; Soleglad & Fet 2008).

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

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 Brotheinae Simon, 1879
      - Tribe Brotheini Simon, 1879
        - Subtribe Brotheina Simon, 1879
        - Subtribe Neochactina Soleglad and Fet, 2003
      - Tribe Belisariini Lourenço, 1998
    - Subfamily Chactinae Pocock, 1893
      - Tribe Chactini Pocock, 1893
      - Tribe Nullibrotheini Soleglad and Fet, 2003
    - 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
    - Subfamily Smeringurinae Soleglad & Fet, 2008
      - Tribe Paravaejovini Soleglad & Fet, 2008
      - Tribe Smeringurini Soleglad & Fet, 2008
    - Subfamily Syntropinae Kraepelin, 1905
      - Tribe Syntropini Kraepelin, 1905
        - Subtribe Syntropina Kraepelin, 1905
        - Subtribe Thorellina Soleglad & Fet, 2008
      - Tribe Stahnkeini Soleglad & Fet, 2006
    - Subfamily Vaejovinae 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

Table 2. Selected problems with the morphological characters presented in Soleglad & Fet's (2003: 66, 68) Tables 3 and 4, examples of the characters affected, proposed corrections, and the number of characters amended in Analyses 3 and 4.

Problem: Similar stuctures in different taxa assigned to separate characters or states based on putative phylogenetic relationship. Affected: 40 (24%): Tab. 3: char. 10–15, 21, 22, 24, 28, 32–36, 39, 41–44, 46–48, 50, 55, 60, 62, 67, 72, 82, 85, 86, 87, 93, 97, 98, 101, 102, 104, 105. Correction: Characters or states reexamined, merged where homologous. Amended: 38 (23%).

Problem: Forced 'reversal'. Affected: 6 (4%): Tab. 3: char. 37, 38, 41, 47, 48, 60. Correction: Scored with 'plesiomorphic' state. Amended: 6 (4%).

Problem: Other forced transformation (additive binary or ordering). Affected: 56 (34%): Tab. 3: char. 1, 10, 19–21, 27, 41–43, 47, 48, 57, 58, 60, 82, 102; Tab. 4: char. 1, 2, 4, 5, 7, 8, 10, 15, 17, 19, 20, 22, 24–26, 32, 33, 35, 36–39, 41, 42, 45–53, 55–61. Correction: States or characters reexamined, redefined or unordered (multistate) as necessary. Amended: 55 (34%).

Problem: Redundancy and lack of independence. Affected: 25 (15%): Tab. 3: char. 11, 14, 15, 17, 20–22, 25, 29, 36–38, 42, 43, 49, 52, 57, 58, 66, 67; Tab. 4: char. 10, 17, 24, 35, 45. Correction: Dependent characters merged. Amended: 10 (6%).

Problem: Trichobothrial homology across basic pattern types. Affected: 73 (44%): Tab. 3: char. 1–4, 23–29; Tab. 4: char. 1–62. Correction: Revise primary homology assessment. Amended: None.

Problem: States concepts, not observations. Affected: 14 (8%): Tab. 3: char. 1, 32–38, 63–68. Correction: Replaced with real observations. Amended: 14 (8%).

Problem: Other characters subsuming non-homologous variation. Affected: 14 (8%): Tab. 3: char. 13, 19, 27, 28, 31, 36, 60, 63–65, 93, 97, 99, 101. Correction: Additional characters created. Amended: 4 (2%).

Problem: States overlap. Affected: 15 (9%): Tab. 3: char. 12, 22, 32–36, 39, 55, 72, 86, 98, 101, 102, 105. Correction: Overlapping states merged. Amended: 15 (9%).

Problem: States subsume non-homologous variation. Affected: 33 (20%): Tab. 3: char. 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. Correction: Additional states created and scored in exemplars. Amended: 19 (11%).

Problem: Polymorphic 'state'. Affected: 6 (4%): Tab. 3: char. 41, 45, 60, 102, 104, 105. Correction: States scored in exemplars. Amended: 6 (4%).

Problem: Unknown 'state'. Affected: 2 (1%): Tab. 3: char. 57, 73. Correction: Scored with questionmark. Amended: 2 (1%).

Problem: Scored inapplicable in taxa to which applicable. Affected: 56 (34%): Tab. 3: char. 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. Correction: Scored in all taxa to which applicable. Amended: 53 (32%).

Problem: Errors in scoring of certain taxa. Affected: 28 (17%): Tab. 3: char. 4, 8, 10–14, 16, 18, 23, 24, 26–28, 30, 42, 43, 47, 48, 53, 61, 68, 82, 85, 92, 95, 96, 99. Correction: Errors corrected. Amended: 21 (13%).

Total characters affected by at least one problem: 158 (95%). Total characters amended to correct at least one problem: 126 (75%).

Table 3. Clades and suprageneric taxa proposed by Soleglad, Fet and colleagues (Fet & Soleglad 2005; Fet *et al.* 2004a; Soleglad & Fet 2003, 2004, 2008; Soleglad *et al.* 2005) which were not monophyletic (X) or received <50% jackknife support in four reanalyses of Soleglad & Fet's (2003) data under equal weighting (Figs. 2–5; see text for details). Chactoidea received exactly 50% jackknife support in Analysis 1. According to Soleglad *et al.* (2005): [1](Hemiscorpiidae + Scorpionidae); [2]Scorpionidae; [3](Diplocentrinae + Scorpioninae).

Clade or Suprageneric Taxon	Anal. 1	Anal. 2	Anal. 3	Anal. 4
(Pseudochactida + Buthida + Chaerilida + Iurida)	<50%	X	<50%	<50%
(Buthida + Chaerilida + Iurida)	<50%	X	X	X
(Chaerilida + Iurida)	X	X	<50%	<50%
Iuroidea	X	X		X
Iuridae	X	X		
Caraboctoninae			X	
(Chactoidea + Scorpionoidea)		X	X	X
Chactoidea	50%	X	X	X
Vaejovidae	X		<50%	
Smeringurinae	X	X	X	X
Smeringurini	X	X	X	
Syntropinae	X	X	X	<50%
Syntropini	X	<50%	X	
Syntropina	X	X	X	X
Vaejovinae	X	X	X	X
(Chactidae + Euscorpiidae + Superstitioniidae)			X	X
(Chactidae + Euscorpiidae)			<50%	X
Chactidae				X
(Brotheinae + Chactinae)		<50%	<50%	X
Brotheinae			<50%	X
Brotheini			X	X
Chactinae			X	X
Uroctoninae			<50%	X
(Euscorpiinae + Megacorminae)	<50%	<50%	<50%	X
Megacorminae			<50%	X
Superstitioniinae	<50%			<50%
Scorpionoidea				<50%
(Liochelidae + Scorpionidae + Urodacidae)[1]	<50%	<50%		
(Scorpionidae + Urodacidae)[2]	<50%	<50%		X
Scorpionidae[3]	X	X	X	X

Fig. 1. Changes to the suprageneric classification of extant scorpions from 1758 to 2009 and the number of suprageneric taxa recognised in some classifications from the past twenty years.

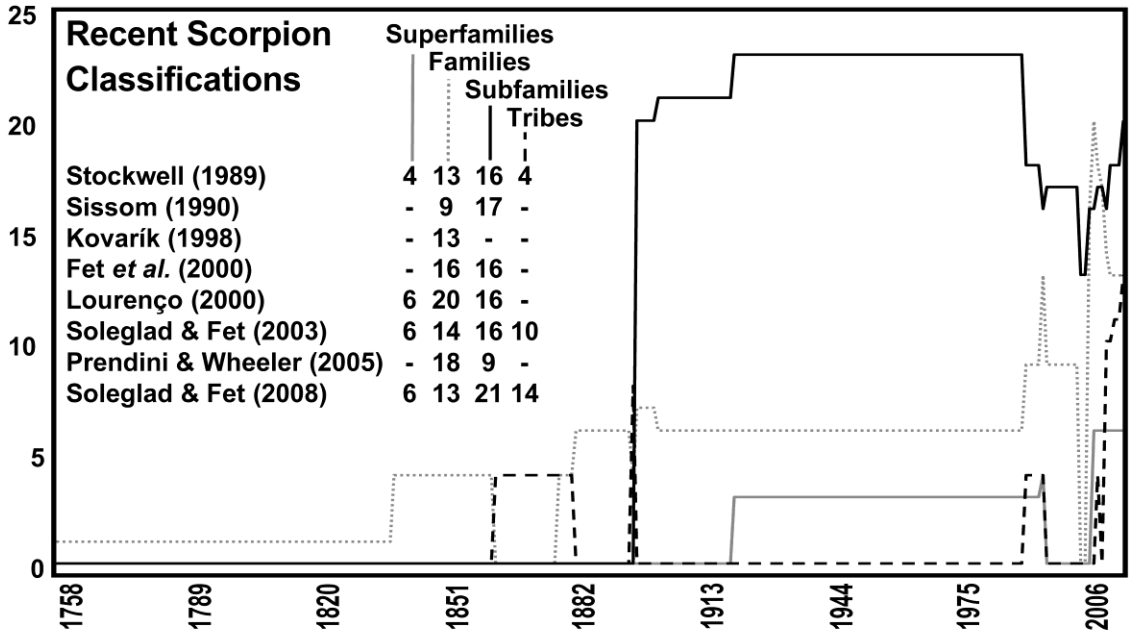

Fig. 2. Results of Analysis 1, Soleglad & Fet's (2003) unmodified matrix of 60 supraspecific terminal taxa and 105 characters, analysed using their original settings: a strict consensus of 197 most parsimonious trees of 307 steps.

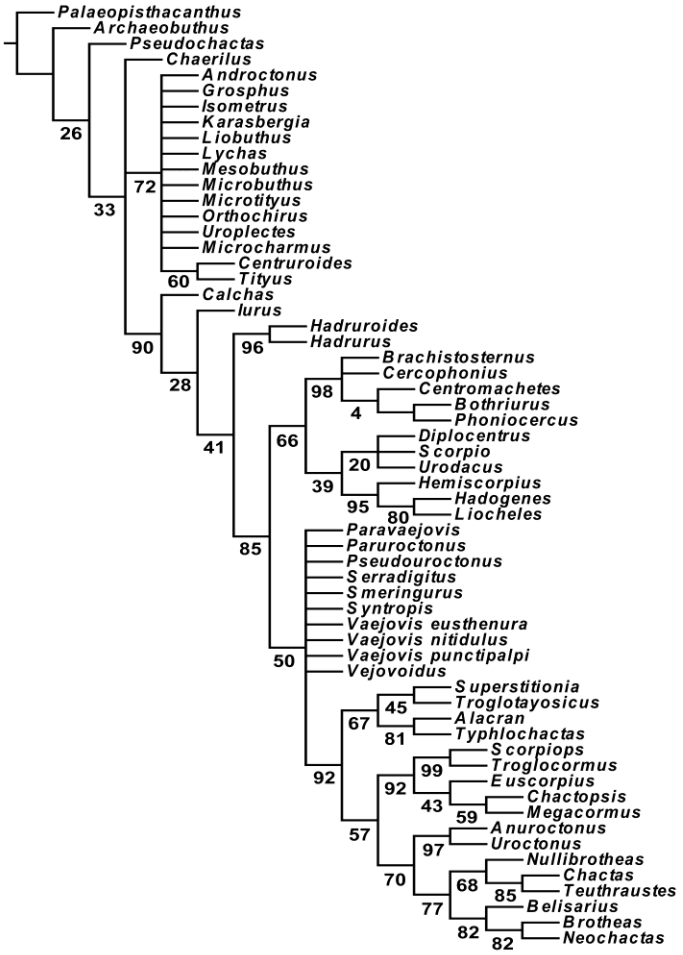

Fig. 3. Results of Analysis 2, Soleglad & Fet's (2003) unmodified matrix of 60 supraspecific terminal taxa and 105 characters, with all characters unordered (nonadditive): a strict consensus of 79 most parsimonious trees of 293 steps.

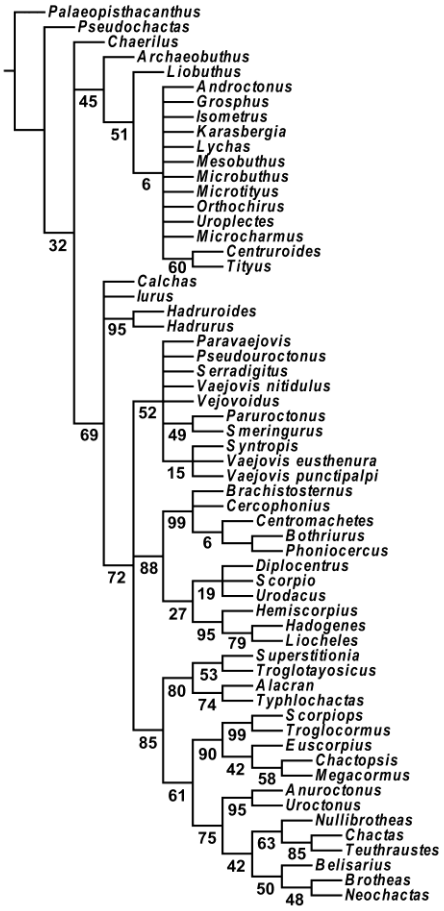

Fig. 4. Results of Analysis 3, Soleglad & Fet's (2003) supraspecific terminal taxa converted to exemplar species, their assumptions of character transformation removed and some corrections to their character coding implemented, creating a matrix of 81 exemplar species and 161 characters, treated unordered (nonadditive): a strict consensus of 156 most parsimonious trees of 401 steps.

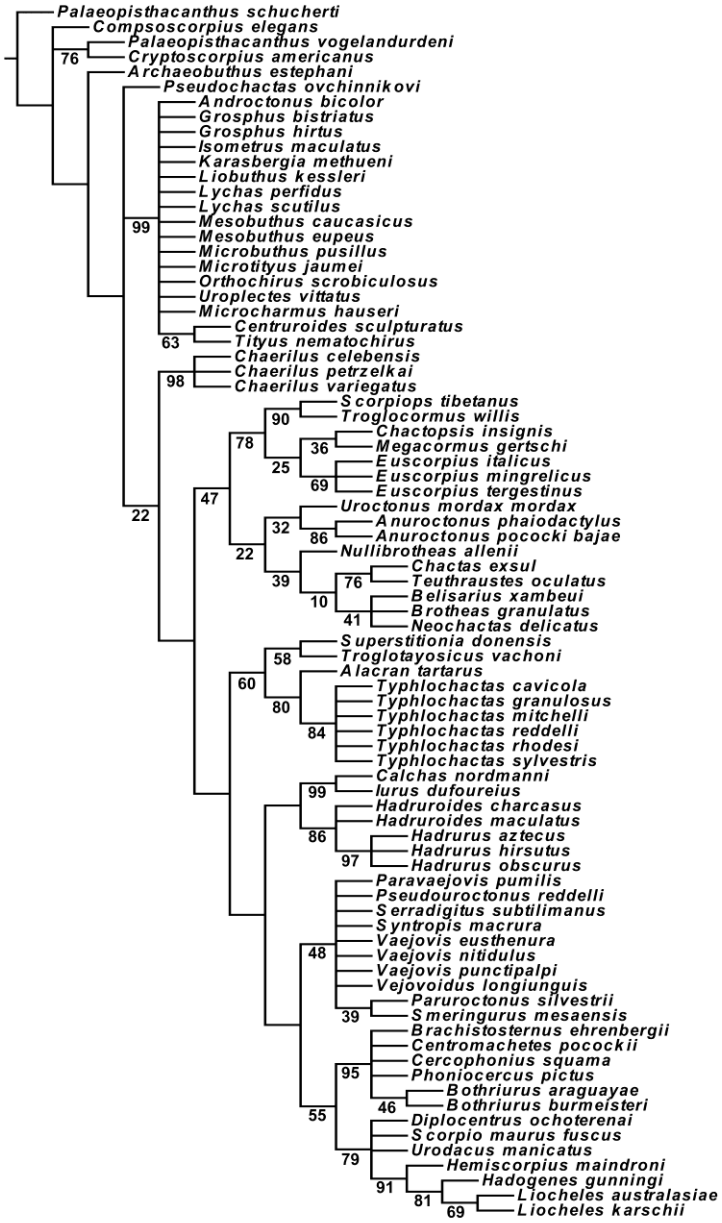

Fig. 5. Results of Analysis 4, the matrix used for Analysis 3 fused with other matrices and character data from the literature to create a matrix of 81 exemplar species and 200 characters, treated unordered (nonadditive): a strict consensus of 227 most parsimonious trees of 498 steps.

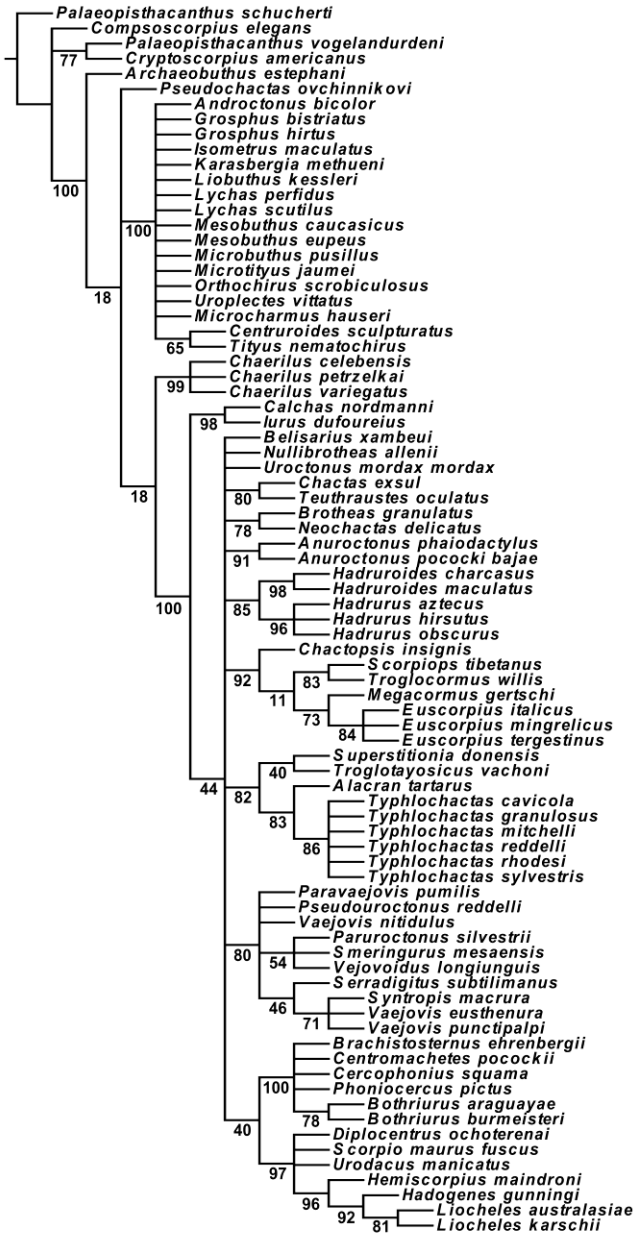

Fig. 6. A. The tree presented by Soleglad & Fet (2003: 71, Fig. 114) as the basis for their revised classification of extant scorpions (Table 1). B. A strict consensus of suprafamilial relationships retrieved by four reanalyses of Soleglad & Fet's (2003) data under equal weighting (Figs. 2–5; see text for details). Dashed lines indicate families which were not monophyletic in at least one analysis. Note: According to Soleglad *et al.* (2005), Liochelidae = Hemiscorpiidae, Scorpionidae = (Diplocentrinae + Scorpioninae) and Urodacidae = Urodacinae.

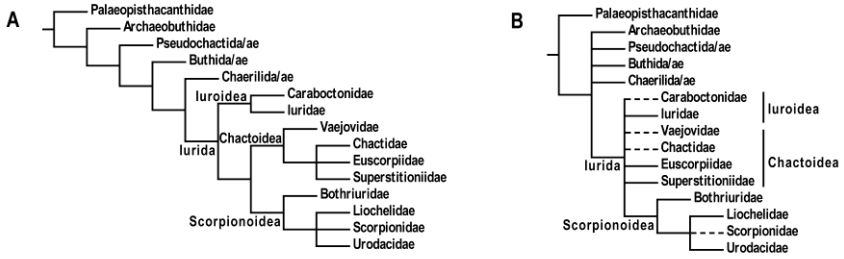

Fig. 7. The number of clades and suprageneric taxa proposed by Soleglad, Fet and colleagues (Fet & Soleglad 2005; Fet *et al.* 2004a; Soleglad & Fet 2003, 2004, 2008; Soleglad *et al.* 2005) which were not monophyletic (A) or received <50% jackknife support (B) in four reanalyses of Soleglad & Fet's (2003) data under equal weighting (Figs. 2–5; see text for details). One superfamily that received exactly 50% jackknife support in Analysis 1 is included.