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Phylogeny and classification of the giant hairy scorpions, *Hadrurus* Thorell (Iuridae Thorell): a reappraisal

Abstract The ‘giant hairy scorpions’, genus *Hadrurus* Thorell, are the largest and most conspicuous scorpions in North America, but their systematics has long been confused. A new genus, *Hoffmannihadrurus* Fet *et al.* was recently created to accommodate the two species endemic to mainland Mexico, *Hadrurus aztecus* Pocock and *Hadrurus gertschi* Soleglad. In the present contribution, we review the taxonomic history of *Hadrurus*, re-evaluate the phylogenetic relationships among its component species with an analysis based on morphological characters and a taxon sample representing the known morphological variation, and assess the validity of the new genus. Seven independent analyses of the morphological character matrix, under weighting regimes that minimised length as well as those that maximised fit, each located a single most parsimonious tree with the following scheme of relationships: (*Iurus* ((*Caraboctonus* + *Hadruroides*) (*H. aztecus* ((*H. gertschi* + *H. pinteri*) (*H. concolorous* + *H. hirsutus*)) ((*H. obscurus* + *H. spadix*) (*H. a. arizonensis* (*H. a. austrinus* + *H. a. pallidus*)))))). This topology supports the monophyly of Caraboctoninae, Caraboctonini, Hadrurini, the ‘*arizonensis*’ subgroup, *H. arizonensis* and *H. concolorous*. It does not support the monophyly of *Hoffmannihadrurus*, *Hadrurus*, the ‘*aztecus*’ group, the ‘*hirsutus*’ group, and the ‘*hirsutus*’ subgroup, all of which were rendered paraphyletic by the grouping of *H. gertschi* with *H. pinteri*, rather than with *H. aztecus*. The results unequivocally demonstrate that the creation of a new genus for the mainland Mexican species was unfounded. We therefore propose the following new synonymy: *Hoffmannihadrurus* Fet *et al.*, 2004 = *Hadrurus* Thorell, 1876, syn. nov.

Introduction

North American scorpions of the genus *Hadrurus* Thorell (Family Iuridae Thorell) are the largest in the New World, attaining a length of *c.* 12–13 cm and a mass of 20–25 g. In Mexico, these scorpions are known as ‘matacaballos’ (horse killers), although their venom has low toxicity to mammals (Hoffmann, 1931; Williams, 1970). In the USA, they are called ‘giant hairy scorpions’.

The eight species and two subspecies of *Hadrurus* (Table 1) are fossorial, seldom wandering far from the entrances to their burrows. Consequently, these scorpions were relatively rare in collections before the advent of ultraviolet (UV) light detection collecting techniques (Sissom *et al.*, 1990). The paucity of specimens in collections hindered progress on their taxonomy and confusion remains today regarding the taxonomic status of certain populations, and the phylogenetic relationships among the species. In the latest treatment (Fet *et al.*, 2004), a new genus, *Hoffmannihadrurus* Fet *et al.* was created to accommodate the two species endemic to mainland Mexico. The aim of the present contribution is to review the taxonomic history of these scorpions, re-evaluate their phylogenetic relationships with an analysis based on morphological characters and a taxon sample representing the known morphological variation, and assess the validity of the new genus.

Taxonomic history

Wood (1863) described two scorpions from ‘Lower California’, *Buthus hirsutus* Wood, 1863 and *Buthus emarginaticeps* Wood, 1863. Thorell (1876) recognised these taxa as distinct from *Buthus* Leach and created *Hadrurus* Thorell. Pocock (1902) added *Hadrurus aztecus* Pocock from ‘Jalapa, Mexico’, and synonymised *H. emarginaticeps* with *H. hirsutus*. Ewing (1928) described *Hadrurus hirsutus* var. *arizonensis* Ewing, from Pima County, Arizona. Hoffmann (1931) reported *H. aztecus* from the states of Puebla and Guerrero (later shown to

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H. arizonensis Ewing, 1928	Mexico (SON, BC), USA (AZ, CA, NV, UT)
H. a. arizonensis Ewing, 1928	Mexico (SON), USA (AZ, CA, NV, UT)
H. a. austrinus Williams, 1970	Mexico (BC)
H. a. pallidus Williams, 1970	Mexico (SON, BC), USA (AZ, CA)
H. aztecus Pocock, 1902	Mexico (OAX, PUE, VER?)
H. concolorous Stahnke, 1969[1]	Mexico (BC, BCS)
H. gertschi Soleglad, 1976	Mexico (GRO)
H. hirsutus (Wood, 1863)	Mexico (BCS)
H. obscurus Williams, 1970	Mexico (BC), USA (CA, NV)
H. pinteri Stahnke, 1969	Mexico (BC, BCS)
H. spadix Stahnke, 1940	USA (AZ, CA, CO, ID, NV, OR, UT)

Table 1 List of *Hadrurus* Thorell species, subspecies, authors, dates, known countries and states of occurrence (from Sissom & Fet, 2000). Abbreviations for states as follows: AZ (Arizona), BC (Baja California), BCS (Baja California Sur), CA (California), CO (Colorado), GRO (Guerrero), ID (Idaho), NV (Nevada), OAX (Oaxaca), OR (Oregon), PUE (Puebla), SON (Sonora), UT (Utah), VER (Veracruz).

[1] Sissom and Fet (2000) considered the name of *H. concolorous* to be an 'Incorrect Original Spelling' in the meaning of the International Code of Zoological Nomenclature (2000), and amended it to *H. concolor* indicating that 'concolorous' is an English adjective, and the correct Latin word is 'concolor'. However, Acosta and Fet (2005) considered that it was an unjustified emendation and restored *concolorous* as the proper specific epithet. Fet *et al.* (2001, 2004) used *concolor* in their publications, but the original name is used in the present text.

be two different species). Stahnke (1940) described *Hadrurus spadix* Stahnke from northern Arizona.

Stahnke (1945) presented the first revision of *Hadrurus*, in which *H. arizonensis* was elevated to the rank of species, *H. hirsutus* reported from Arizona and California (misidentifications), and *H. aztecus* reported from Puebla, Oaxaca and Guerrero (two species mixed). Stahnke (1945) indicated that the colour of the carapace, dorsal and ventral mesosoma of *Hadrurus* is diagnostic for species, and relied solely on colour differences in his key to their identification.

Stahnke (1969) updated his revision of the genus, adding *Hadrurus concolorous* Stahnke from Baja California Sur, *Hadrurus pinteri* Stahnke from Baja California, and *Hadrurus thayeri* Stahnke from the Los Cabos region, Baja California Sur. Stahnke (1969) continued to report *H. hirsutus* from southwestern Arizona, southern California and Mexico (misidentified specimens without specific localities), and reported *H. aztecus* from 'extreme southern Arizona'. Stahnke's (1969) key to the species was also based exclusively on colour patterns.

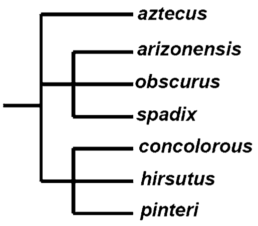

Figure 1 Phylogenetic relationships within *Hadrurus* Thorell hypothesised by Williams (1970). Williams (1970) most likely did not examine *H. aztecus* Pocock and studied only one adult male and one adult female of *H. gertschi* Soleglad.

Williams (1970) presented another revision of *Hadrurus*, which incorporated a large amount of new material collected with UV light detection methods during his extensive fieldwork in the North American deserts. Williams (1970) clarified that *H. hirsutus* was endemic to southern Baja California Sur, synonymised *H. thayeri* with it, and described *Hadrurus obscurus* Williams from southern California. Williams (1970) defined three subspecies of *H. arizonensis*, once again based on colour variation, of which *H. arizonensis pallidus* Williams accommodated the previously misidentified *H. hirsutus* from south-western Arizona and southern California. Finally, Williams (1970) recognised three subgroups within *Hadrurus*: (1) *H. aztecus*; (2) (*H. arizonensis* + *H. obscurus* + *H. spadix*); (3) (*H. concolorous* + *H. hirsutus* + *H. pinteri*). Williams' (1970, p. 31) statement that 'within each subgroup the members share such characteristics in common that a closer relation by descent is apparent' implies a hypothesis of phylogenetic relationship, which we have presented diagrammatically in Fig. 1.

Soleglad (1976) presented an analysis of the taxonomy of the genus based on the trichobothrial pattern of the pedipalp chela and recognized *Hadrurus gertschi* Soleglad from the Mexican state of Guerrero as distinct from *H. aztecus* from the states of Oaxaca and Puebla. Soleglad (1976, p. 117) defined two species groups, each containing two subgroups:

> Two species, *H. aztecus* and *H. gertschi*, lack internal accessory trichobothria. Due to this characteristic plus their close geographical proximity and likewise distant range from other species, I have placed them in the '*aztecus*' group. However, since the two species *have little in common except for the lack of internal accessory trichobothria*, I have placed them in separate subgroups, the '*aztecus*' subgroup and the '*gertschi*' subgroup. The other group, which I call the '*hirsutus*' group, has at least two internal accessory trichobothria and sometimes as many as seven. Within this group I recognize two subgroups based entirely on the presence or absence of external accessory trichobothria. The first subgroup, which has one to four external accessory trichobothria, is called the '*hirsutus*' subgroup; the other subgroup, called the '*arizonensis*' subgroup, does not have external accessory trichobothria; in coming up with differentiae for the species, *only the presence or absence* of accessory trichobothria were considered to be of primary importance. Positional differences in the trichobothria were seldom relied upon, and were avoided entirely in most cases. [italics added]

Soleglad (1976) also implied, using pedipalp chelal trichobothrial patterns alone, that *H. concolorous* and *H. hirsutus* are sister species, and likewise that *H. obscurus* and *H. spadix* are sister species. Soleglad's (1976) implied hypothesis of phylogenetic relationships among the species of *Hadrurus* is presented diagrammatically in Fig. 2.

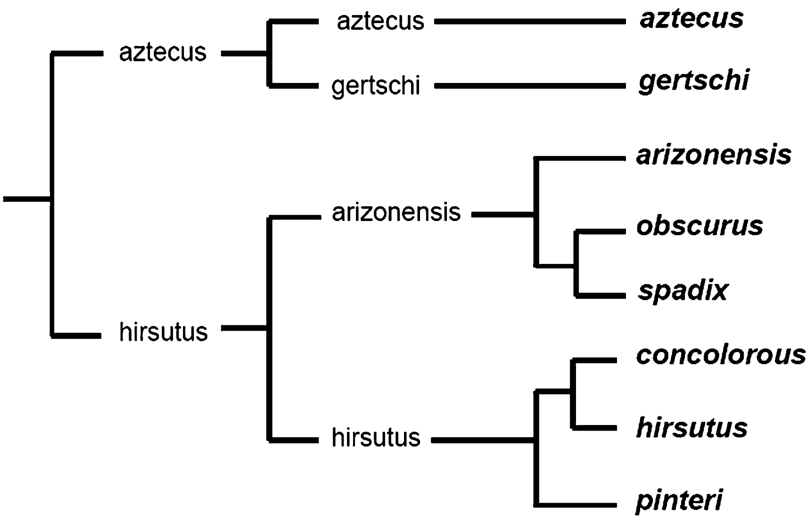

Figure 2 Phylogenetic relationships within *Hadrurus* Thorell hypothesised by Soleglad (1976), indicating the groups and subgroups recognised.

Three taxonomic characters either ignored or overlooked by Soleglad (1976), in proposing phylogenetic relationships among the species of *Hadrurus*, are noteworthy: (1) the males of *H. aztecus*, *H. concolorous* and *H. pinteri* possess well-developed subaculear glands on the dorsal aspect of the telson; (2) although *H. gertschi* and the '*hirsutus*' subgroup possess external accessory trichobothria on the pedipalp chela manus, *H. concolorous* and *H. hirsutus* possess one or two (usually one, always located in the *Et* region), whereas *H. gertschi* and *H. pinteri* possess three or four (usually one in the *Et* region, and two or three in the *Esb–Est* region); (3) both *H. gertschi* and *H. pinteri* possess more than 20 trichobothria on the ventral surface of the chela manus, forming a double row in the distal three-quarters in *H. gertschi*, and a double row in the distal third in *H. pinteri*, whereas the other species possess fewer than 20 trichobothria on the ventral surface, arranged in a single row.

In a monograph on the scorpions of the Baja California Peninsula, Williams (1980) indicated that several species of *Hadrurus* found there are extremely variable in colouration. In some cases, darker forms are associated with darker (e.g. volcanic) substrata, but in others there is no clear association, and melanistic forms occur in sympatry with non-melanistic forms. In view of these observations, caution should be exercised when using colouration in the systematics of *Hadrurus*.

Fet *et al.* (2001) presented a phylogenetic analysis of the '*hirsutus*' group of *Hadrurus*, based on morphology and mitochondrial DNA sequences, the aims of which were to determine the phylogenetic support for the two subgroups defined by Soleglad (1976) within the '*hirsutus*' group (i.e. the '*hirsutus*' and '*arizonensis*' subgroups) and to evaluate the monophyly of species complexes within the two subgroups. Fet *et al.* (2001) constructed a matrix of 16 morphological characters and four 'biogeographical-based' characters (discussed in some detail by Prendini & Wheeler, 2005), scored for seven terminal taxa (Table 2), and gathered nineteen 369 base-pair fragments of the 16S rDNA gene from eleven samples of *H. arizonensis*, four samples of *H. obscurus*, and one sample each of *H. concolorous*, *H. hirsutus*, *H. pinteri* and *H. spadix*, for the analysis.

H. pinteri	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
H. concolorous	1	0	1	1	1	0	0	1	0	1	0	0	1	1	0	0	1	0	1	0
H. hirsutus	1	0	1	1	1	0	0	1	0	1	0	0	1	1	1	1	1	0	2	0
H. spadix	1	1	2	2	2	2	1	0	0	2	0	1	1	0	1	0	1	1	4	4
H. obscurus	1	1	2	2	2	2	2	0	0	2	0	2	1	0	1	0	1	1	4	3
H. arizonensis arizonensis	1	1	2	0	1	1	0	1	1	2	1	0	1	0	1	0	1	1	3	2
H. arizonensis pallidus	1	1	2	0	1	1	0	1	1	2	2	0	1	0	1	0	1	1	3	1

Table 2 Matrix of 20 characters for the '*hirsutus*' group of *Hadrurus* Thorell presented by Fet *et al.* (2001). Character states are scored 0–4. Refer to Appendix 1 for character descriptions.

Analysis of the morpho-biogeographical matrix, on the basis of which Fet *et al.* (2001, p. 139) claimed to have 'demonstrated the monophyly' of the '*hirsutus*' and '*arizonensis*' subgroups, retrieved the cladogram reproduced in Fig. 3. The molecular data, analysed separately using four methods (UPGMA, neighbor-joining, maximum likelihood and parsimony), and simultaneously with the morpho-biogeographical data in a direct-optimization parsimony analysis, consistently retrieved the following scheme of relationships, demonstrating a paraphyletic '*hirsutus*' subgroup: (*H. pinteri* ((*H. concolorous* + *H. hirsutus*) (*H. arizonensis* (*H. spadix* + *H. obscurus*)))). Unlike Fet *et al.* (2001, p. 153), we do not regard 'supported but ladderized' (their terminology for paraphyletic) as evidence of monophyly. It is noteworthy that the simultaneous analysis of all data gathered by these authors falsified the hypothesis of a monophyletic '*hirsutus*' subgroup. Based on molecular evidence alone, Fet *et al.* (2001) synonymised subspecies *H. arizonensis pallidus* with the nominotypical form.

A critique of the morpho-behavioral characters employed by Fet *et al.* (2001) is presented in Appendix 1. The analysis

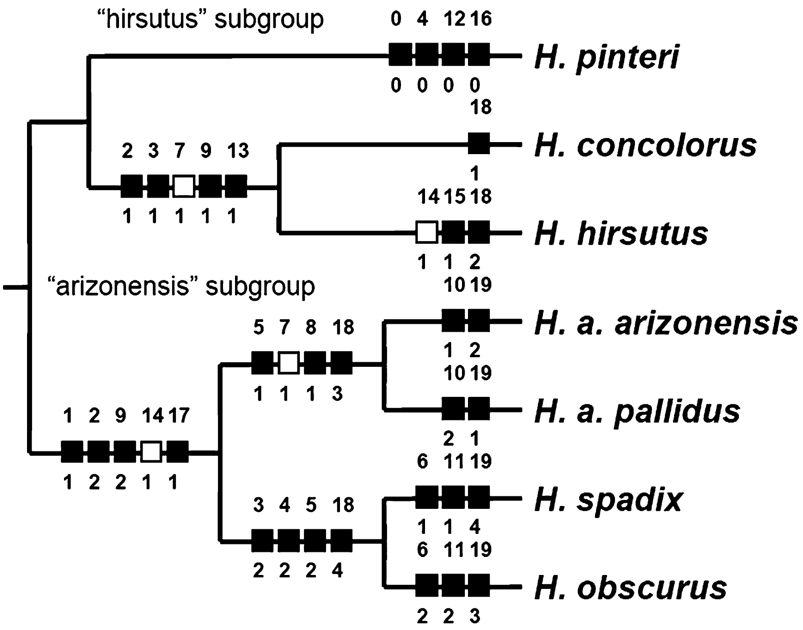

Figure 3 Cladogram of the '*hirsutus*' group of *Hadrurus* Thorell presented by Fet *et al.* (2001). Characters and states optimised with delayed transformation (DELTRAN). Characters indicated with bars. Solid bars indicate uniquely derived apomorphic states, whereas empty bars indicate parallel derivations of apomorphic states. The number above each bar gives the character number. Refer to Table 2 for character matrix and Appendix 1 for character descriptions.

presented by Fet *et al.* (2001) may be further criticised on the peculiar method of rooting that was employed, and which calls into question the results obtained (Fig. 3). No data were provided for the '*aztecus*' group of *Hadrurus*, containing the two mainland Mexican species (*H. aztecus* and *H. gertschi*), and considered sister to the '*hirsutus*' group by Williams (1970) and Soleglad (1976). According to Fet *et al.* (2001, p. 142):

> The ideal outgroup for '*hirsutus*' group analysis would be a member of its *presumed* sister group, the '*aztecus*' group (either *H. aztecus* or *H. gertschi*), but neither species was available for DNA sampling. However, for morphology we did conduct a detailed analysis of all *Hadrurus* species (not presented in this paper), where, by *declaring* the '*aztecus*' group as an outgroup, we were able to establish the '*hirsutus*' subgroup as monophyletic within the '*hirsutus*' group. Thus, the '*hirsutus*' subgroup is a legitimate outgroup for morphology analysis as presented in this paper. For initial molecular analysis, *Vaejovis spinigerus* (Wood) (Vaejovidae), a 'chactoid' species, was first chosen as an outgroup to the 19 *Hadrurus* sequences. All resulting trees supported *H. pinteri* as an outgroup (however, monophyly of the '*hirsutus*' subgroup *was not supported*). Therefore, for the final molecular analysis, we used *H. pinteri* as the outgroup. [italics added]

An unpublished analysis that is rooted on a taxon, the affinities and monophyly of which have not been tested (i.e. the '*aztecus*' group), cannot be used to justify the ingroup for a separate, subsequent analysis. Use of the '*hirsutus*' subgroup as outgroup for a morphological analysis of the '*hirsutus*' group (a more inclusive clade) is not only logically absurd, but contradicted by the molecular analyses of Fet *et al.* (2001), which retrieved a paraphyletic '*hirsutus*' subgroup. The choice of different outgroups for the morphological and molecular analyses presented by Fet *et al.* (2001) is also unconventional. Their initial outgroup for the molecular analyses, *Vaejovis spinigerus* Wood (family Vaejovidae Thorell), is not even confamilial with *Hadrurus*.

In their latest paper on the systematics of *Hadrurus*, Fet *et al.* (2004) used their alleged evidence of a monophyletic '*hirsutus*' group (Fet *et al.*, 2001) to justify monophyly of the '*aztecus*' group, and proposed a new genus, *Hoffmannihadrurus* Fet *et al.*, to accommodate its component species in two new combinations: *Hoffmannihadrurus aztecus* (Pocock) and *Hoffmannihadrurus gertschi* (Soleglad). The '*aztecus*' group was originally defined (Soleglad, 1976) by the absence of internal accessory trichobothria on the pedipalp chela, a plesiomorphy, based on outgroup comparison with other iurid genera, and neither Fet *et al.* (2001) nor Fet *et al.* (2004) presented a phylogenetic analysis to test the monophyly of the '*aztecus*' group, and hence the monophyly of their putative new genus, *Hoffmannihadrurus*.

Materials and methods

Taxa. The cladistic analysis presented here is based on 15 terminal taxa (Table 4). The ingroup includes all species, subspecies and known colour variations of *Hadrurus* (Williams, 1970; Fet *et al.*, 2001), treated as separate terminal taxa to test their relationships directly (see Prendini, 2001 for rationale).

Trees were rooted using the outgroup method (Watrous & Wheeler, 1981; Farris, 1982; Nixon & Carpenter, 1993). The generally accepted higher classification of the family Iuridae, to which *Hadrurus* belongs, follows Francke and Soleglad (1981; Table 3), ranks notwithstanding. Fet *et al.* (2004) followed Soleglad and Fet (2003) in recognising subfamily Caraboctoninae at family rank, and tribes Caraboctonini and Hadrurini at subfamily rank. Nonetheless, the phylogenetic relationships implied by this scheme of classification remain the same. For the reanalysis of *Hadrurus* phylogeny presented below, we included three outgroup taxa: *Iurus dufoureius*

Family Iuridae Thorell, 1876
- Subfamily Iurinae Thorell, 1876:
    - *Calchas* Birula, 1899 (1 species: Greece, Turkey)
    - *Iurus* Thorell, 1876 (1 species, 2 subspecies: Greece, Turkey)
- Subfamily Caraboctoninae Kraepelin, 1905
    - Tribe Caraboctonini Kraepelin, 1905:
        - *Caraboctonus* Pocock, 1893 (1 species: Chile)
        - *Hadruroides* Pocock, 1893 (9 species: Bolivia, Ecuador, Perú)
    - Tribe Hadrurini Stahnke, 1974:
        - *Hadrurus* Thorell, 1876 (8 species, 3 subspecies: México, USA)

Table 3 The currently accepted higher classification and geographical distribution of the scorpion family Iuridae Thorell.

(Brullé); *Caraboctonus keyserlingi* Pocock, the type species of *Caraboctonus*; *Hadruroides charcasus* (Karsch), the type species of *Hadruroides*.

We follow Francke and Soleglad (1981) and others in excluding *Anuroctonus* Pocock from Iuridae, and hence from our analysis of *Hadrurus* phylogeny, for the following reasons. Stahnke (1974) considered *Anuroctonus* to be the sister-group of *Hadrurus*, based on the shared presence of accessory trichobothria (neobothriotaxy) on the ventral surfaces of the pedipalp chela manus and patella in the two genera. However, Vachon (1974) provided ample evidence that neobothriotaxy per se evolved independently in many groups of scorpions and cannot be considered synapomorphic. Francke and Soleglad (1981) reviewed Stahnke's (1974) hypothesis of relationship between *Anuroctonus* and *Hadrurus*, failed to corroborate it, and removed *Anuroctonus* from Iuridae, placing it *incertae sedis* within Chactoidea. Francke and Soleglad (1981) proposed several putative synapomorphies for Caraboctoninae instead. Sissom (1990) followed Francke and Soleglad (1981) in retaining *Anuroctonus* as *incertae sedis* within Chactoidea. Stockwell (1992), however, returned *Anuroctonus* to Iuridae, and resurrected Stahnke's (1974) putative sister-group relationship between *Hadrurus* and *Anuroctonus*, based on an unpublished phylogenetic analysis (Stockwell, 1989) in which the group was supported primarily by the presence of accessory trichobothria. Stockwell's (1992) decision was questioned by Sissom and Fet (2000). In the most recent development, Soleglad and Fet (2003, 2004) transferred *Anuroctonus* from Iuridae to Chactidae Pocock, and placed it in subfamily Uroctoninae Mello-Leitão, as the sister-group of *Uroctonus* Thorell (which was transferred from Vaejovidae to Chactidae by these authors), on the basis of a different set of putative synapomorphies. Prendini and Wheeler (2005) presented a detailed critique of the work of Soleglad and Fet (2003, 2004), demonstrating that several of these putative synapomorphies fail the test of primary homology, and concluded that there is no justification for accepting the analytical results or revised classification of these authors (and, by extension, their decisions on the taxonomic placement of *Anuroctonus*). Given that the phylogenetic position of *Anuroctonus* remains ambiguous, and that *Hadrurus* shares more potential synapomorphies with Caraboctonini than either of these taxa shares with *Anuroctonus*, we exclude *Anuroctonus* from the analysis presented below, and instead include exemplar species of the two genera of Caraboctonini, *Caraboctonus* and *Hadruroides*, as outgroups, while acknowledging that the phylogenetic position of *Anuroctonus* merits further investigation. The tree is rooted on *Iurus dufoureius*. Material examined for outgroup taxa is listed in Appendix 2.

Characters. The morpho-biogeographical character matrix presented by Fet *et al.* (2001; Table 2) was re-evaluated in the course of the present investigation (Appendix 1). Several characters (including the 'biogeographical-based' characters) were abandoned or recoded, and additional characters, many of which are pertinent to relationships among the outgroup taxa, added and often recoded from Williams (1970), Soleglad (1976), Lamoral (1980), Stockwell (1989), Prendini (2000, 2003, 2004), Soleglad and Sissom (2001), Soleglad and Fet (2001, 2003) and Fet *et al.* (2004). The revised character list is presented in Appendix 3.

The revised character matrix (Table 4) comprises 61 characters, 11 coded into multistates and 50 coded into binary states. Twenty-nine of these characters (9–19, 21–23, 25, 27, 31, 33, 34, 37, 39–41, 43, 45, 52, 54, 55, 60) are uninformative, but were retained in the matrix because they contribute to its completeness and future utility, e.g. in diagnostic keys (Yeates, 1992). These characters were deactivated during the analyses, which are thus based on the 32 informative characters only. Multistate characters were treated as unordered/nonadditive (Fitch 1971), 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).

Cladistic analysis. Character data were edited and cladograms prepared using WinClada, version 1.00.08 (Nixon, 2002). Ambiguous optimisations were resolved using accelerated transformation (ACCTRAN) or Farris optimisation, which favours reversals over parallelisms to explain homoplasy (Farris, 1970; Swofford & Maddison, 1987, 1992) and therefore maximises homology (Griswold *et al.*, 1998). The 29 uninformative characters were deactivated during all the analyses; hence tree statistics are calculated from phylogenetically informative characters only (Bryant, 1995).

Characters were not weighted *a priori*. Analyses with equal weighting were conducted using the 'parsimony ratchet' (Nixon, 1999) in NONA version 2.0 (Goloboff, 1997a), according to the following command sequence: **nix = 50; hold/3; nix[10; nix-10 50 20;** preceded by **hold10000; hold/100; mult∗100;** and followed by **max∗;**. The 'strength' or 'factor' of the ratchet (i.e. the proportion of characters reweighted) was set to 50% (command **nix = 50**). Fifty initial iterations of the ratchet (command **nix 50**) were conducted. SPR branch-swapping was applied in the first ten iterations, followed by TBR branch-swapping in the remaining 40 (command **nix-10**). Three starting trees were held in memory at each iteration (command **hold/3**) and, every 10 iterations, one

Iurus d. dufoureius	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	–	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	–	0	0	0	0	0	0	0	0	0	0	0	0
Caraboctonus keyserlingi	0	0	0	0	0	0	0	1	1	1	1	1	2	1	1	1	1	1	1	2	0	1	1	1	1	1	1	0	1	1	1	0	1	1	0	0	1	0	0	1	1	1	1	1	1	0	0	0	–	1	0	1	0	1	1	1	1	0	0	1	0
Hadruroides charcasus	2	2	1	0	0	0	0	1	1	1	1	1	1	1	0	1	1	1	1	2	1	1	1	1	1	1	1	0	1	1	1	0	1	2	0	0	1	0	0	1	1	1	1	1	1	0	0	0	–	1	0	1	0	1	1	1	1	0	0	1	0
Hadrurus a. arizonensis	2	0	0	1	0	0	0	0	1	1	1	1	2	1	0	1	1	1	1	1	0	1	1	2	1	2	1	1	2	2	1	0	1	2	0	1	1	0	0	1	1	0	1	2	1	1	1	1	0	0	1	1	1	1	1	0	0	0	1	1	0
Hadrurus a. austrinus	2	0	1	1	0	1	0	0	1	1	1	1	2	1	0	1	1	1	1	1	0	1	1	2	1	2	1	1	2	2	1	0	1	2	0	1	1	0	0	1	1	0	1	2	1	1	1	1	0	0	1	1	1	1	1	0	0	0	0	1	0
Hadrurus a. pallidus	2	0	1	1	0	1	0	0	1	1	1	1	2	1	0	1	1	1	1	1	0	1	1	2	1	2	1	1	2	2	1	0	1	2	0	1	1	0	0	1	1	0	1	2	1	1	1	1	0	0	1	1	1	1	1	0	0	0	1	1	0
Hadrurus aztecus	2	0	0	0	0	0	0	1	1	1	1	1	2	1	0	1	1	1	1	1	0	1	1	2	1	2	1	1	2	2	1	0	1	2	0	1	1	0	0	1	1	0	1	1	1	0	1	1	1	0	1	1	1	1	1	0	0	0	0	1	1
Hadrurus concolorous 1	2	1	0	0	0	0	1	0	1	1	1	1	2	1	0	1	1	1	1	1	0	1	1	2	1	2	1	1	2	2	1	0	1	2	1	1	1	0	0	1	1	0	1	2	1	1	1	1	0	0	1	1	1	1	1	0	0	0	0	1	1
Hadrurus concolorous 2	2	2	1	0	0	1	1	0	1	1	1	1	2	1	0	1	1	1	1	1	0	1	1	2	1	2	1	1	2	2	1	0	1	2	1	1	1	0	0	1	1	0	1	2	1	1	1	1	0	0	1	1	1	1	1	0	0	0	0	1	1
Hadrurus gertschi	2	0	0	0	1	0	2	1	1	1	1	1	2	1	0	1	1	1	1	1	0	1	1	2	1	2	1	1	2	2	1	1	1	2	1	1	1	1	0	1	1	0	1	1	1	0	1	1	1	0	1	1	1	1	1	0	0	0	0	1	0
Hadrurus hirsutus	2	1	0	0	0	0	1	0	1	1	1	1	2	1	0	1	1	1	1	1	0	1	1	2	1	2	1	1	2	2	1	0	1	2	1	1	1	0	0	1	1	0	1	2	1	1	1	1	0	0	1	1	1	1	1	0	0	0	0	1	0
Hadrurus obscurus 1	1	0	0	0	0	0	0	0	1	1	1	1	2	1	0	1	1	1	1	1	0	1	1	2	1	2	1	1	2	2	1	0	1	2	0	1	1	0	0	1	1	0	1	2	1	1	1	1	0	0	1	1	1	1	1	0	0	1	1	1	0
Hadrurus obscurus 2	2	0	0	0	0	0	0	0	1	1	1	1	2	1	0	1	1	1	1	1	0	1	1	2	1	2	1	1	2	2	1	0	1	2	0	1	1	0	0	1	1	0	1	2	1	1	1	1	0	0	1	1	1	1	1	0	0	1	1	1	0
Hadrurus pinteri	0	0	0	0	1	0	2	0	1	1	1	1	2	1	0	1	1	1	1	1	0	1	1	2	1	2	1	1	2	2	1	1	1	2	1	1	1	1	1	1	1	0	1	2	1	1	1	1	0	0	1	1	1	1	1	0	0	1	0	1	1
Hadrurus spadix	0	0	0	0	0	0	0	0	1	1	1	1	2	1	0	1	1	1	1	1	0	1	1	2	1	2	1	1	2	2	1	0	1	2	0	1	1	0	0	1	1	0	1	2	1	1	1	1	0	0	1	1	1	1	1	0	0	1	1	1	0

Table 4 Revised matrix of 61 characters for the eight species of *Hadrurus* Thorell and three outgroup taxa. Character states are scored 0–2 and – (inapplicable). Refer to Appendix 3 for character descriptions.

of the best trees located at that stage in the search was randomly selected for continued swapping (command **nix[10**). When the 50 initial iterations were completed, a further 20 iterations were conducted (command **nix 50 20**).

Implied character weighting (Goloboff, 1993, 1995) was conducted to assess the effects of weighting against homoplasious characters, and the resultant topologies compared with those obtained by analysis with equal weighting. In varying the weighting regime applied to the data, we provide a 'sensitivity analysis' (Wheeler, 1995), i.e. an assessment of the relative robustness of clades to different analytical parameters, in this case, method and intensity of character weighting (see Prendini, 2000, 2004; Prendini *et al.*, 2003). If a group is monophyletic only under a very specific combination of parameters, less confidence may be placed in the supposition that the data robustly support its monophyly than may be placed in a group that is monophyletic under a wider range and combination of parameters.

Pee-Wee version 3.0 (Goloboff, 1997b) was used for analyses with implied weighting, applying the command sequence: **hold10000; hold/10; mult*100;** (hold 10000 trees in memory; hold ten starting trees in memory; perform tree-bisection-reconnection (TBR) branch-swapping on 100 random addition replicates). Additional swapping on up to 1000 trees that are up to 5% longer than the shortest trees (command **jump 50;**) was performed to help the swapper move between multiple local optima ('islands' *sensu* Maddison, 1991). Finally, trees found with this command were again swapped with TBR, using the command **max*;** to retain only optimal trees. Analyses with implied weighting investigated the use of six values for the concavity constant, *K*, spanning the input range permitted by Pee-Wee (command: **conc N;**).

The relative degree of support for each node in the tree obtained with equal weighting was assessed with branch support or decay indices (Bremer, 1988, 1994; Donoghue & Sanderson 1992). Branch support indices up to 14 extra steps (setting the maximum number of trees held in memory to 10000) were calculated with NONA, by means of the following command sequence: **h10000; bsupport 14;**. Obtaining accurate branch support values required 14 successive searches to be conducted, starting by searching for trees only one step longer than the shortest, and continuing with searches for progressively longer trees until values had been obtained for nodes with the greatest support.

Results

Analysis of the 32 informative characters located a single most parsimonious tree under equal weighting and implied weighting with six *K* values (Table 5; Fig. 4), with the following scheme of relationships: (*Iurus* ((*Caraboctonus* + *Hadruroides*) (*H. aztecus* ((*H. gertschi* + *H. pinteri*) (*H. concolorous* + *H. hirsutus*)) ((*H. obscurus* + *H. spadix*) (*H. a. arizonensis* (*H. a. austrinus* + *H. a. pallidus*)))))). This topology, obtained by the seven independent analyses under weighting regimes that minimised length as well as those that maximised fit (Table 5), is regarded as the optimal hypothesis

	MPT	Steps	Fit (F_i)	Rescaled fit	CI	RI
IW: $K=6$	1	57	298.6	73	71	74
IW: $K=5$	1	57	295.6	72	71	74
IW: $K=4$	1	57	291.5	72	71	74
IW: $K=3$	1	57	285.5	72	71	74
EW	1	57	285.5	72	71	74
IW: $K=2$	1	57	275.2	71	71	74
IW: $K=1$	1	57	257.4	69	71	74

Table 5 Summary of statistical differences among the most parsimonious trees (MPTs) obtained by analysis under equal weighting (EW) and implied weighting (IW) with six values for the concavity constant (*K*), arranged in order of decreasing fit.

of phylogenetic relationships among the taxa in question. Synapomorphies are indicated on this topology in Fig. 4, and the length, fit (f_i), consistency indices, and retention indices of informative characters listed in Table 6.

This topology supports the monophyly of Caraboctoninae, Caraboctonini, Hadrurini, the '*arizonensis*' subgroup, *H. arizonensis* and *H. concolorous*. It does not support the monophyly of *Hoffmannihadrurus*, *Hadrurus*, the '*aztecus*' group, the '*hirsutus*' group and the '*hirsutus*' subgroup, all of which were rendered paraphyletic by the grouping of *H. gertschi* with *H. pinteri*, rather than with *H. aztecus*. In addition, the terminals of *H. obscurus* collapsed to form a zero-length branch with *H. spadix*, suggesting that there are no unambiguous morphological characters supporting the monophyly of *H. obscurus* as distinct from *H. spadix*.

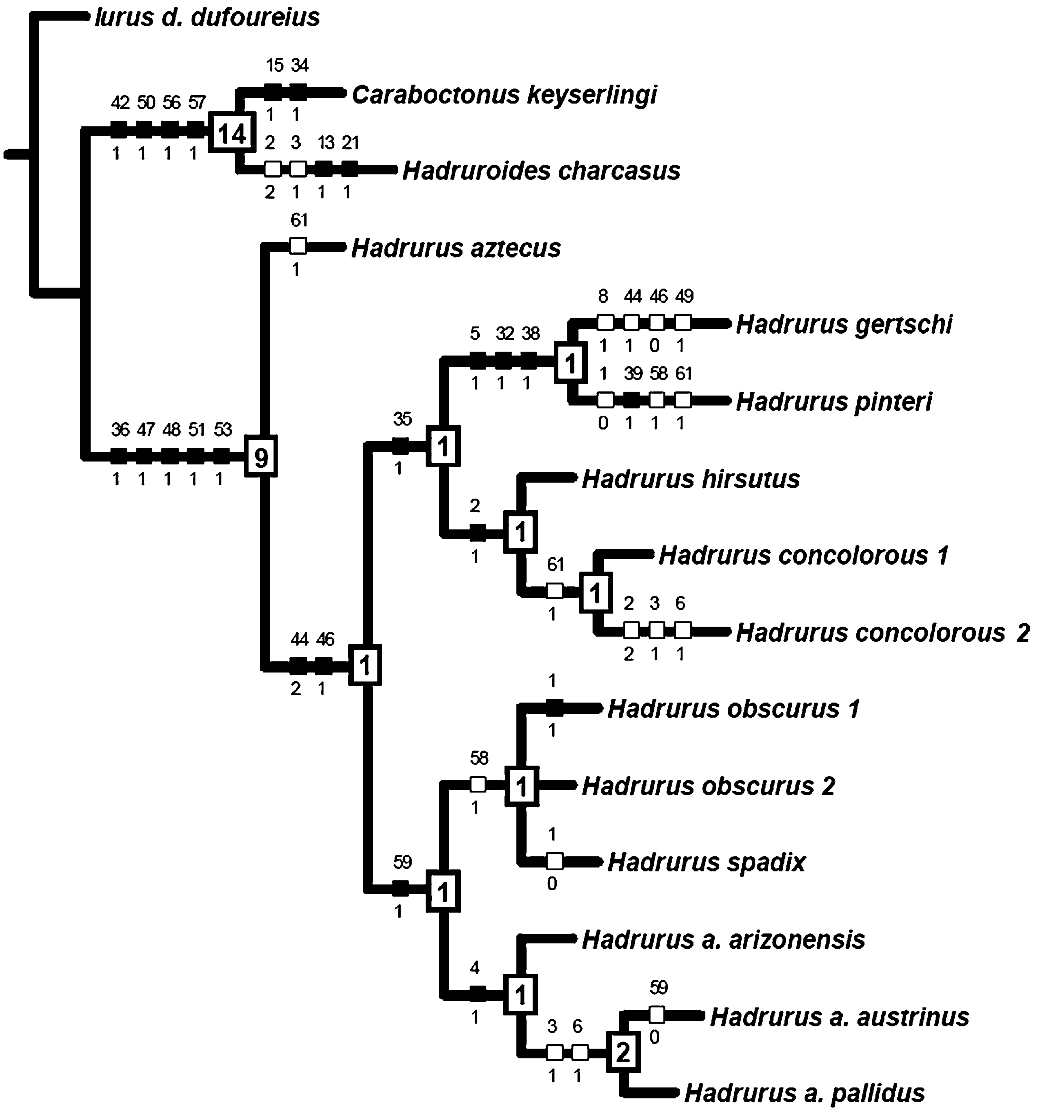

Figure 4 The single most parsimonious tree obtained by cladistic analysis of 32 morphological characters scored for the eight species of *Hadrurus* Thorell and three outgroup taxa under weighting regimes that maximised fit and minimised length. This topology was retrieved by analyses with equal weighting and implied weighting with $K=1$–6 (Table 5). Unambiguous synapomorphies are indicated with bars. Solid bars indicate uniquely derived apomorphic states, whereas empty bars indicate parallel derivations of apomorphic states. The number above each bar gives the character number, the number below gives the character state, and the number at each node gives the branch support value. Zero-length branches are collapsed. Refer to Table 4 for character matrix and Appendix 3 for character descriptions.

Character	Steps	f_i	CI	RI
1	5	5	40	0
2	3	7.5	66	50
3	3	6	33	33
4	1	10	100	100
5	1	10	100	100
6	2	7.5	50	50
7	2	10	100	100
19	3	6	33	33
23	2	10	100	100
25	2	10	100	100
27	2	10	100	100
28	1	10	100	100
29	2	10	100	100
31	2	10	100	100
34	1	10	100	100
35	1	10	100	100
37	1	10	100	100
41	1	10	100	100
43	1	10	100	100
45	3	7.5	66	66
46	2	7.5	50	75
47	1	10	100	100
48	1	10	100	100
49	2	7.5	50	0
50	1	10	100	100
55	1	10	100	100
56	1	10	100	100
57	1	10	100	100
58	2	7.5	50	66
60	2	7.5	50	75
61	3	6	33	33

Table 6 Length (steps), fit (f_i), consistency indices (CI), and retention indices (RI) of informative characters on the most parsimonious tree obtained by analysis under weighting regimes that maximised fit and minimised length (Fig. 4).

Discussion

The results presented here agree in most respects with previous hypotheses of relationship for the taxa in question (Figs 1–3), in supporting the monophyly of Caraboctoninae, Caraboctonini, Hadrurini, the '*arizonensis*' subgroup (*H. obscurus* + *H. spadix*), (*H. concolorous* + *H. hirsutus*) and the monophyletic group containing the three *Hadrurus* species endemic to the Baja California Peninsula, *H. concolorous*, *H. hirsutus* and *H. pinteri*. The results unequivocally demonstrate that the creation by Fet *et al.* (2004) of a new genus, *Hoffmannihadrurus*, for the two mainland Mexican species of *Hadrurus*, *H. aztecus* and *H. gertschi*, was unfounded. The two species are not monophyletic. *Hadrurus gertschi* instead groups with *H. pinteri*, rendering *Hoffmannihadrurus* and the redefined *Hadrurus* paraphyletic. The recognition and diagnosis of *Hoffmannihadrurus* by Fet *et al.* (2004, p. 22) was based entirely on three characters:

(1) Chela fixed finger internal accessory trichobothria present in *Hadrurus*, but absent in *Hoffmannihadrurus*. This is character 46 in our revised character matrix (Table 4; Appendix 3). According to the optimal tree retrieved in the present analyses (Fig. 4), the absence of internal accessory trichobothria on the pedipalp chela fixed finger is plesiomorphic in *H. aztecus* and undergoes an autapomorphic reversal (interpreted as loss of the trichobothria) in *H. gertschi*, falsifying this character state as a diagnostic synapomorphy of *Hoffmannihadrurus*.

(2) Trichobothria *ib* and *it* situated suprabasally on fixed finger in *Hadrurus* (Fet *et al.* 2004, p. 40, Figs 60–64), but situated basally in *Hoffmannihadrurus* (Fet *et al.* 2004, p. 40, Fig. 59). This somewhat subjective distinction in trichobothrial position merits further evaluation from several perspectives. First, comparison of Fig. 59, illustrating the combined positions of trichobothria *ib* and *it* in *H. aztecus* and *H. gertschi* according to Fet *et al.* (2004), with Fig. 64, illustrating their positions in *H. spadix*, reveals no meristic difference between fixed finger length and distance from the tip of the finger to the trichobothria. An examination of real specimens showed that both trichobothria are situated basal to the basal enlarged denticle of the median denticle row on the fixed finger in *H. gertschi*, *ib* is situated basal and *it* equal to or slightly distal to the denticle in *H. aztecus*, and *it* is situated slightly basal to the denticle in *H. spadix*. Therefore, if the positions of these trichobothria are defined relative to the basal denticle of the median denticle row, the distinction between *H. aztecus*, *H. gertschi*, and other species of *Hadrurus* is less obvious than suggested by Fet *et al.* (2004). Second, a pattern of allometric growth may be observed at the base of the finger, among the species in which trichobothria *ib* and *it* are situated suprabasally. The first (basal) subrow of the median denticle row is 1.5–2 times longer than the second and third subrows in these species, but equal to or slightly shorter than the second and third rows in the species in which these trichobothria are situated basally. Third, the supposed homology of the internal trichobothria is open to interpretation when accessory trichobothria are present (for further discussion of this controversial issue, see Prendini and Wheeler, 2005). Finally, it must be pointed out that the sister-group Caraboctonini possess no internal accessory trichobothria, and *ib* and *it* are located relatively basally (see Francke & Soleglad, 1980, Figs 12 and 30), suggesting that this character state would be symplesiomorphic in *Hoffmannihadrurus*. In spite of these issues, we coded the basal and suprabasal positions of these trichobothria as proposed by Fet *et al.* (2004), to test the veracity of the basal condition as a potential synapomorphy for *Hoffmannihadrurus*. However, we treated the two trichobothria as separate characters 44 and 45 in our revised character matrix (Table 4; Appendix 3), based on the different position of trichobothrium *it* in the outgroup *Iurus*. Only character 44 (trichobothrium *ib*) portrays the distinction between the basal and suprabasal positions proposed by Fet *et al.* (2004). According to the optimal tree retrieved in the present analyses (Fig. 4), the basal position of trichobothrium *ib* is plesiomorphic in *H. aztecus* and undergoes an autapomorphic reversal in *H. gertschi*, falsifying this character state as a diagnostic synapomorphy of *Hoffmannihadrurus*.

(3) Ridges of fused spinule clusters of leg tarsus and basitarsus well defined in *Hadrurus*, even in early developmental stages, but 'not well defined, essentially obsolete in early developmental stages' in *Hoffmannihadrurus* (Fet *et al.* 2004). This character, included in our revised character matrix as character 49 (Table 4; Appendix 3), also has several problems. First, Fet *et al.* (2004) did not examine juveniles of *H. gertschi*, but instead extrapolated from juveniles of *H. aztecus* on the untested assumption that the two species form a monophyletic group. Second, all *Hadrurus* species, including *H. aztecus* and *H. gertschi*, are fossorial and the spinule clusters and their associated microscopic ridges, are subject to wear depending on the hardness of the substrate and the time since the last moult. A recently moulted individual is expected to display better defined ridges than one that has been repeatedly enlarging its burrow since its last moult, regardless of age (or instar). Describing a scanning electron micrograph, Fet *et al.* (2004, p. 20) stated: 'we see that in an adult *H. gertschi* only a subtle trace of the ridges are visible on the extreme base of the fused spinule' [*sic*]. During the present investigation, we examined eight adult specimens of *H. gertschi*, in several of which, the ridges were clearly visible under moderate magnification (220×) using a dissecting microscope (more difficult to discern in specimens under ethanol than in air-dried specimens). Following our observations, we question the evidential basis for the distinction between the ridges proposed by Fet *et al.* (2004). In spite of these doubts, we included this character in our revised character matrix to test its potential as a synapomorphy for *Hoffmannihadrurus*. As with the other putatively diagnostic characters proposed by Fet *et al.* (2004), the obsolete condition was plesiomorphic in *H. aztecus* and underwent an autapomorphic reversal in *H. gertschi* (Fig. 4), falsifying this character state as a diagnostic synapomorphy of *Hoffmannihadrurus*.

The most surprising result of our reanalysis is the close phylogenetic relationship between *H. gertschi* and *H. pinteri*, supported by three unambiguous synapomorphies (state 1 of characters 5, 32 and 38; Fig. 4), and the relative distance of *H. aztecus* from the other taxa, including *H. gertschi*, all of which are united by state 2 of character 44 and state 1 of character 46 (Appendix 3). Williams (1970) apparently examined only two specimens of '*H. aztecus*' from mainland Mexico, an adult male from Mezcala, Guerrero (undoubtedly *H. gertschi* and not *H. aztecus*, based on distribution and the absence of telson glands) and an adult female from 'Mexico' without additional locality details, and which is probably also *H. gertschi* judging by the infuscation of the carapace and tergites in Williams' (1970) Figs 11 and 35. Williams (1970) correctly noted the close phylogenetic relationship between *H. arizonensis*, *H. obscurus* and *H. spadix*, and between *H. concolorous*, *H. hirsutus* and *H. pinteri*, but failed to place *H. gertschi* (his '*H. aztecus*') correctly. Soleglad (1976) separated *H. aztecus* and *H. gertschi* for the first time, and identified the '*arizonensis*' subgroup correctly, despite defining it on the basis of a symplesiomorphy. However, Soleglad (1976) failed to include *H. gertschi* in the '*hirsutus*' subgroup although he was aware that it also possessed external accessory trichobothria on the pedipalp chela manus (one of three synapomorphies supporting this clade). Soleglad's (1976) '*aztecus*' group, defined on the basis of a symplesiomorphy, is not monophyletic. Similarly, the genus *Hoffmannihadrurus*, proposed by Fet *et al.* (2004) for the '*aztecus*' group, is also not monophyletic and is hereby rejected. We propose the following new synonymy: *Hoffmannihadrurus* Fet *et al.*, 2004 = *Hadrurus* Thorell, 1876, syn. nov.

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Appendix 1

Annotated list of 20 characters for the '*hirsutus*' group of *Hadrurus* Thorell presented by Fet *et al.* (2001). Character states are scored 0–4. Refer to Table 2 for character matrix.

Trichobothria-based characters, the chela

0. External accessory trichobothrium on fixed finger: yes, *H. pinteri* (0); no (1). This character is autapomorphic for *H. pinteri* and therefore uninformative.
1. External accessory trichobothria on palm: yes, '*hirsutus*' subgroup (0); no, '*arizonensis*' subgroup (1).
2. External accessory trichobothria number: 3–4, *H. pinteri* (0); 1–2, *H. hirsutus* and *H. concolorous* (1); none, '*arizonensis*' subgroup (2). There are several problems with the coding of characters 1 and 2. Firstly, the *arizonensis* subgroup is scored twice, whereas for character 2 it should have been scored inapplicable. As a consequence of implicitly weighting the same character twice relative to other characters, two synapomorphies (state 1 of character 1 and state 2 of character 2) supported the monophyly of the '*arizonensis*' subgroup in the cladogram of Fet *et al.* (2001; Fig. 3). However, the chosen outgroup, the '*aztecus*' group comprises one species with (*H. gertschi*) and one without (*H. aztecus*) external accessory trichobothria, hence this character would have optimised ambiguously. Furthermore, the same character appears as a synapomorphy (state 1 of character 2) for the '*hirsutus*' subgroup. Character 2 can be further subdivided as indicated in Appendix 3 (characters 32, 35).
3. Internal accessory trichobothria number: 5–6, *H. pinteri* and *H. arizonensis* (0); 4–5, *H. hirsutus* and *H. concolorous* (1); 2–3, *H. spadix* and *H. obscurus* (2). In the cladogram of Fet *et al.* (2001), states 1 and 2 of character 3 respectively support the monophyly of (*H. hirsutus* + *H. concolorous*) and (*H. spadix* + *H. obscurus*). Soleglad's (1976, p. 125) Table 2 provides the following figures for trichobothrial counts [range (mean), sample size] for the taxa in question: *H. hirsutus*: 4–5 (4.06), $n = 8$; *H. concolorous*: 3–5 (4.09), $n = 16$; *H. pinteri*: 5–6 (5.69), $n = 8$; *H. arizonensis*: 4–7 (5.54), $n = 94$; *H. spadix*: 2–3 (2.17), $n = 58$; *H. obscurus*: 2–4 (2.94), $n = 18$. The ranges of *H. hirsutus* and *H. pinteri* fall entirely within the range of *H. arizonensis*, questioning the basis for scoring them differently. The ranges of *H. concolorous* and *H. obscurus* also overlap, yet they were scored differently. We therefore reject the coding used by Fet *et al.* (2001) for this character and score only the presence or absence of accessory trichobothria in the revised matrix (Table 3, character 46).
4. Ventral trichobothria number: 22+, *H. pinteri* (0); 16–20, *H. arizonensis*, *H. hirsutus* and *H. concolorous* (1); 14–16, *H. spadix* and *H. obscurus* (2). In the cladogram of Fet *et al.* (2001), state 0 of character 4 (more than 22 ventral trichobothria) is autapomorphic for *H. pinteri*, state 1 (16–20 ventral trichobothria) is homoplasious, and state 2 (14–16 ventral trichobothria) synapomorphic for (*H. spadix* + *H. obscurus*). The outgroup Caraboctonini possess only four ventral trichobothria, however, implying that the presence of more than four ventral trichobothria is synapomorphic for the species of *Hadrurus*. Furthermore, the range and mean of trichobothrial counts for the ventral series of chelal trichobothria reported by Soleglad (1976, p. 125, table 2) are as follows: *H. arizonensis*: 16–22 (19.12); *H. aztecus*: 17–19 (17.91); *H. concolorous* 16–20 (17.53); *H. gertschi*: 20–25 (21.14); *H. hirsutus* 15–16 (15.75); *H. obscurus* 13–17 (14.89); *H. pinteri* 22–27 (24.64); *H. spadix* 13–17 (15.04). Soleglad (1976) reported trichobothrial counts higher than 20 for *H. arizonensis arizonensis* and *H. arizonensis pallidus*, yet according to Fet *et al.* (2004) the range for *H. arizonensis* is 16–20. Fet *et al.* (2004) also increased the lower range for *H. hirsutus* from 15 to 16, and restricted the upper and lower ranges for *H. spadix* and *H. obscurus* to 14–16 instead of 13–17. It is also unclear as to why *H. hirsutus* was not scored the same as *H. spadix* and *H. obscurus* given on their overlapping ranges. We presume this was part of the 'filtering' process alluded to by Fet *et al.* (2001, p. 146). To avoid such inevitably ad hoc procedures, we instead propose a simple presence or absence of accessory trichobothria (Table 3, character 36) and add an additional character, previously identified by Soleglad (1976, pp. 119–120, figs. 4, 8, 12, 16, 20, and 24), for the arrangement of the ventral trichobothria (Table 3, character 38).
5. *Est*/palm-length ratio: inapplicable (0); 0.445–0.526 (0.486), *H. arizonensis* (1); 0.360–0.456 (0.408), *H. spadix* and *H. obscurus* (2). The *Est*/palm-length ratio was used by Soleglad (1976) to separate *H. arizonensis* from *H. spadix* and *H. obscurus*. There are several problems with this character as coded by Fet *et al.* (2001). First, this character is applicable to the other species of the genus, all of which possess trichobothrium *Est* on the chela. Fet *et al.* (2001) simply did not measure and calculate it in these species. Second, inapplicable entries should be scored '-' or '?' not '0' (for discussion, see Prendini & Wheeler 2005). Third, the ranges overlap and this character therefore fails the test of primary homology. It was therefore omitted from the revised character matrix.
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). The *esb–eb*/*esb–Et*$_5$ trichobothrial distance ratio was used by Soleglad (1976) to separate *H. obscurus* from *H. spadix*. This character suffers from the same problems as the previous character (character 5) and was also omitted from the revised character matrix.

Setae-based character

7. Numerous setae between inferior median carinae, metasomal segments I–III: yes, *H. spadix*, *H. obscurus* and *H. pinteri* (0); no (1). In the resulting cladogram of Fet *et al.* (2001), the absence of numerous ventral submedian setae on metasomal segments I–III was homoplasious for the

species in which these macrosetae are absent. We have nonetheless included it as character 58, and added an additional metasomal setation character (character 59), first noted by Williams (1970).

Coloration/patterns-based characters

8. Chelal fingers pigmented, reddish to black: yes (0); no, *H. arizonensis* (1). This character is autapomorphic for *H. arizonensis* and was uninformative in the analysis by Fet *et al.* (2001). However, it provides a synapomorphy for the subspecies of *H. arizonensis* and was therefore included in the revised matrix (character 4).
9. Coloration and patterns on carapace and mesosoma: carapace and mesosoma entirely melanic, no significant variability, *H. pinteri* (0); carapace and mesosoma variable, from complete concolourous to melanic pattern on carapace posterior half and mesosoma, never in interocular area, *H. concolorous* and *H. hirsutus* (1); melanic pattern on carapace connecting median tubercle and lateral eyes, carapace posterior and mesosoma variable, *H. spadix*, *H. obscurus* and *H. arizonensis* (2). The coding and scoring of this character applied by Fet *et al.* (2001) are unacceptable. First, as observed by Williams (1970, pp. 44, fig. 14), the carapace and mesosoma of *H. spadix* are completely melanic (we prefer the term 'infuscated'), and this species should have been scored the same as *H. pinteri.* According to Fet *et al.* (2001, pp. 142), *H. spadix* exhibits a melanic wedge-shaped pattern on the carapace but it is 'masked out by the totally melanic pattern'. We question how it is possible to observe a melanic wedge-shaped pattern that is 'masked out' on an entirely melanic carapace. Second, we doubt the homology of the 'variable' patterns assigned to states 1 and 2. Given the diversity of patterns observed on the carapaces of *Hadrurus* species (*vide* Fet *et al.* 2001, p. 143, figs. 2–12), we disagree with the coding presented by Fet *et al.* (2001) in characters 9–11. We recoded the variation as presented in characters 1–3 and 10 in the revised matrix.
10. Melanic crescent-shaped pattern on carapace: no (0); yes, carapace posterior and mesosoma melanic, *H. a. arizonensis* (1); yes, carapace posterior and mesosoma without melanic pattern, *H. a. pallidus* (2). This character was created by Fet *et al.* (2001) to separate the two subspecies of *H. arizonensis*. Although there is some variation in this character, e.g. see Williams (1970, pp. 44–45, figs. 14–21), we incorporated it in character 3 of the revised matrix, and scored it in separate terminals representing the three subspecies of *H. arizonensis*.
11. Melanic wedge-shaped pattern on carapace: no (0); yes, interocular area melanic, *H. spadix* (1); yes, interocular area clear to some degree, *H. obscurus* (2). This character was recoded as character 1 in the revised matrix. As indicated above, the melanic wedge-shaped pattern is not discernible in *H. spadix*, the carapace of which is entirely infuscated.

Species	♂	♀	**Source**
H. arizonensis arizonensis	32–37	24–31	Williams (1970, 1980)
H. arizonensis austrinus	35–41	28–32	Williams (1970, 1980)
H. arizonensis pallidus	32–37	24–31	Williams (1970)
H. aztecus	33–40	29–32	Soleglad (1976)
H. concolorous	34–40	27–33	Williams (1970, 1980)
H. gertschi	29–35	25–29	This study[1]
H. hirsutus	28–35	22–27	Williams (1970, 1980)
H. obscurus	34–37	24–30	Williams (1970)
H. pinteri	38–44	28–35	Williams (1970, 1980)
H. spadix	35–40	26–33	Stahnke (1945)

Table 7 Pectinal tooth count ranges for males and females of the species of *Hadrurus* Thorell (see Fig. 5).

[1] The frequencies found among specimens deposited at IBUNAM are: males: 29 teeth ($n = 1$), 30 (3), 31 (4), 32 (2), 33 (3), 34 (3) and 35 (2); females: 25 teeth (1), 26 (6), 27 (5) and 28 (6). Soleglad (1976) reported a tooth count of 29.

12. Marbled melanic patterns on metasoma and chelal palms: yes, *H. pinteri* (0); no (1). We consider the infuscation of the metasoma and chela to be separate characters and they were coded as such in the revised character matrix (Table 3, characters 5, 7).
13. Melanic pattern on lateral and ventral aspect of metasomal segment V: no (0); yes, variable, depending on local geographic races, *H. concolorous* and *H. hirsutus* (1). This character is incorporated into character 7 in the revised matrix.

Aculear glands-based character

14. Aculear glands present on telson of sexually mature males: yes, *H. pinteri* and *H. concolorous* (0); no (1). The absence of telson glands in adult males of *H. hirsutus* is homoplasious in the cladogram of Fet *et al.* (2001) because glands are present in its sister species, *H. concolorous*. The glands are also present in *H. aztecus* but absent in *H. gertschi* (Table 3, character 61).

Pectinal tooth count-based character

15. Gross pectinal tooth count ranges for males and females: normal ranges, male 32–44 (37), female 24–35 (29) (0); reduced ranges, male 28–35 (32), female 22–27 (24) (a reduction of approximately 14–17%), *H. hirsutus* (1). In the cladogram by Fet *et al.* (2001), character state 1 (reduced pectinal tooth count ranges) is autapomorphic for *H. hirsutus*. The first problem is that Caraboctonini possess lower ranges (usually less than 20 pectinal teeth),

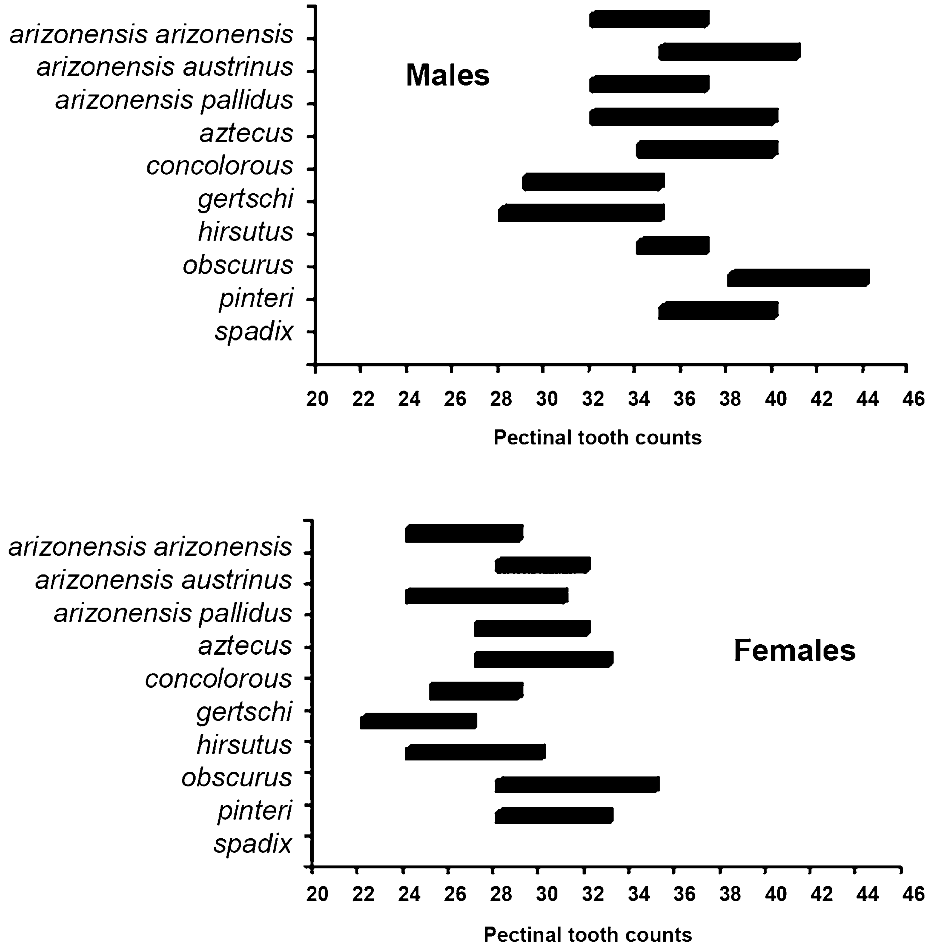

Figure 5 Pectinal tooth count ranges for species and subspecies of *Hadrurus* Thorell (see Table 7).

calling into question the definition of 'normal'. Pectinal tooth count ranges for both sexes of all *Hadrurus* species are provided in Table 7. Among the species with 'normal' ranges, Fet *et al.* (2001) consider *H. arizonensis arizonensis*, with tooth counts of 32–37 in males and 24–31 in females, to be at the low end, and *H. pinteri*, with tooth counts of 38–44 in males and 28–35 in females, to be at the high end. The counts for *H. gertschi* vary from 31–33 in males and 26–29 in females, spanning the variation in both. Figure 5 illustrates the futility of this character as a taxonomic or phylogenetic concept and it was therefore excluded from the revised matrix.

Biogeographical-based characters

16. Sympatric/allopatric/parapatric distribution: sympatric, *H. pinteri* (with *H. concolorous* 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. concolorous*, and *H. hirsutus* (0); United States area: *H. arizonensis, H spadix* and *H. obscurus* (1).
18. Specific parapatric subareas, connected: inapplicable, *H. pinteri* (0); Baja area, Baja Sur subarea: *H. concolorous* (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). Characters 16–19 merely restate the ideas of allopatric speciation and are quite meaningless in a cladistic context (Prendini & Wheeler 2005). It is remarkable that, in character 16, *H. pinteri* was scored state 0, sympatric with *H. concolorous* and, to a limited degree, *H. arizonensis*, yet *H. concolorous* and *H. arizonensis* were both scored state 1, allopatric. Sympatry is a symmetrical relationship: if *H. pinteri* is sympatric with *H. concolorous*, then *H. concolorous* must also be sympatric with *H. pinteri* (see Williams, 1970, pp. 54, 56, figs. 42 and 45 for the distributions of these two species).

Appendix 2

Material examined for phylogenetic analysis of the eight species of *Hadrurus* Thorell and three outgroup taxa. Specimens deposited in the following collections: American Museum of Natural History (AMNH), New York; Centro de Investigación Científica y de Educación Superior de Ensenada, (CICESE) Baja California; Instituto de Biología, Universidad Nacional Autonóma de México (IBUNAM), Mexico City; Muséum National d'Histoire Naturelle (MNHN), Paris; Museum für Naturkunde der Humboldt-Universität, Berlin (ZMB); Zoologisches Museum der Universität Hamburg (ZMH).

***Iurus dufoureius asiaticus* Brullé, 1832: GREECE:** Samos Island, Potamos waterfalls, Karlovasi, 27.vi.2003, V. Vignoli, 1 ♀ (AMNH LP 2327). **TURKEY:** 1 ♂ (MNHN RS 3007), Keyserling, 1 ♀ (ZMB 4186), Lindberg, 1 ♂ (MNHN RS 3008), 1965, M. Tsabar, 1 juv. ♂ (MNHN RS 5167); Alanya, 31.v.2001, J. Ove Rein, captive bred 15.ix.2001, mother collected 31.v.2001, 1 ♀ (AMNH LP 2308); Ancient ruin city of Anemouryon, near Anamur, *c.* 250 km E Antalya, 36°01′27.4″N 32°48′09.5″E, S. Huber, *c.* 35 m, 1 juv. (AMNH LP 4218); Aydin-Söke, Davutlar, 28.v.2005, H. Koç, 800 m, 1 ♂ (AMNH LP 4335), 1 ♂ (AMNH LP 4337), 1 ♀ (AMNH LP 4336); Campsite near Fethye, 8.vii.1987, M. Paulschinger, 2 ♂ (ZMH A90/87); Cennet sinkhole, near Silifke, c. 350 km E Antalya, 36°27′08.2″N 34°06′22.3″E, 6.iv.2005, S. Huber, *c.* 100 m, 1 juv. (AMNH LP 4217); Isparta, Sütgüler, 14.vi.2002, ex A. Karataş, 1 ♀ (AMNH LP 2244); Korikos, Silifke, ii.1946, Kosswig, 1 subad. ♂, 1 juv. ♀ (MNHN RS 3009), 1 subad. ♂, 1 juv. (MNHN RS 5169); Ovacik, 6–7 km from Göcek/Mekri, 16.iv.1930, R. Delmas, 2 ♀, 13 juv. (ZMH).

***Caraboctonus keyserlingi* Pocock, 1893: CHILE:** 20.v.2002, ex R. Mercurio, 1 ♂ (AMNH LP 1960A). **Region III (Atacama):** La Herradura, W of Parque Nacional Llanos de Challe, 28°06.034′S 71°09.258′W, 10.xi.2003, L. Prendini, C. Mattoni & J. Ochoa, 35 m, UV detection on cool, dark, breezy night; very humid near beach, coastal sand flats, rocky hill and soils of intermediate hardness between, arid chaparral with cacti and other succulents, specimen on rocky ground, 1 ♀ (AMNH LP 2420). **Region IV (Coquimbo):** 2.7 km E of turnoff to Salamanca, 5 km N of Los Vilos, 31°52.178′S 71°28.008′W, 3.xi.2003, L. Prendini, C. Mattoni & J. Ochoa, 27 m, UV light detection, cool, humid night, cloudy, no wind, coastal chaparral with cacti and Bromeliaceae on steep, rocky, N-facing slope, clayey loam soil, most specimens in rocky ravine among boulders and leaf litter, 1 ♀, 2 juv. (AMNH LP 2389); 3.5 km E of turnoff to Salamanca, 5 km N of Los Vilos, 31°52.226′S 71°27.452′W, 3.xi.2003, L. Prendini, C. Mattoni & J. Ochoa, 30 m, UV light detection, cool, humid night, cloudy, no wind, coastal chaparral with cacti on steep, rocky, N-facing slope, clayey loam soil, most specimens in rocky ravine among boulders and leaf litter, 2 subad. (AMNH LP 2390); Los Vilos, 2.7 km from turnoff to Salamanca, 31°52.178′S 71°28.008W, 3.xi.2003, L. Prendini, C. I, Mattoni, J. A. Ochoa, 27 m, 1 ♂, 1 ♀ (AMNH); Monumento Natural Pichasca, 3 km N of San Pedro de Pichasca, 30°23.815′S 70°52.895′W, 5.xi.2003, L. Prendini, C. Mattoni & J. Ochoa, 786 m, UV detection, cool, windless night, full moon, very dry chaparral with tall cacti and chollas, granitic loam with rocky ravines, 4 juv. (AMNH LP 2396); Pichidangui, Terraza Costema, Frente cam Demento, 10.x.1976, J. Manroviel, M. Carrasco & J. Linderman, inclinacion mont 15°, 3 ♂, 2 ♀ (AMNH); Punta Teatinos, *c.* 10 km N of La Serena, 29°49.341′S 71°17.397′W, 7.xi.2003, L. Prendini, C. Mattoni & J. Ochoa, 0 m, UV detection, cool, still night, full moon, high humidity near beach, rocky hill near beach, granite boulders with sandy loam soil, chaparral vegetation, 1 subad. (AMNH LP 2410). **Region V (Valparaíso):** Aguas Claras, near Zapallar, 1.xii.2004, J.S. Ascher, under stones, 2 ♂, 1 ♀ (AMNH LP 3686); Parque Nacional La Campana: Palmas de Ocoa: Sendero Quillay trail from campsite, 32°56.048′S 71°04.562′W, 12.xi.2003, L. Prendini, C. Mattoni & J. Ochoa, 494 m, UV detection, warm, still night, no moon, dry savanna vegetation with palms, dense brush on slopes, large boulders in places, dry leaf litter layer, specimen collected along trail in rocky areas, 1 subad. (AMNH LP 2428).

***Hadruroides charcasus* (Karsch, 1879): PERU:** vi.1999, ex R.D. Gaban, 2 ♀, 1 subad. ♀ (AMNH LP 1555), 16.v.2000, ex T. Gearheart, 1 ♀ (AMNH LP 1575). **Departamento Lambayeque:** N Lambayeque, 13.xi.1970, 2 ♂, 2 ♀, 1 subad. ♂, 6 juv. (AMNH); Puchaca Alto, Dist. Incawasi, 20.xi.2004, J.C. Chaparro & J.A. Ochoa, 1 subad. ♂ (AMNH LP 6269B).

***Hadrurus arizonensis arizonensis* Ewing, 1928: MEXICO: Baja California:** Bataques, 1 ♀ (IBUNAM); Colonia Progreso, 1 ♀ (IBUNAM); Isla Angel de La Guarda, 17.ii.1986, L. Cervantes & F. Arias, sea level, 1 ♂, 1 ♀ (IBUNAM). **Sonora:** Altar, 1971, H. Araiza, 2 ♂, 2 ♀ (IBUNAM); Sonoyta, 95 km NW, off Route 2, W of Microondas Cerro Lava, 32°06.175′N 113°47.105′W, 28.vi.2005, R. Mercurio & E. González, 273 m, UV detection at night, 1 ♂ (AMNH LP 5088), 1 subad. ♂ (AMNH LP 4460). **USA: Arizona:** Tucson, Bopp Road, N of Ajo Road, iv.2004, R. Barnhill, night collecting, 1 subad. ♀ (AMNH LP 3048); Tucson, Bopp Road, N of Ajo Road, iv.2004, R. Barnhill, night collecting, 1 ♀ (AMNH LP 3047), 1 ♀ (AMNH LP 3083). **California:** 10 km N of 138 between Pearblossum and Little Rock, E of 110th Street, 34°36′07.8′N 117°54′29.7′W, 19.viii.2004, K. Bamba, M. McCoy, W. Savary & R. Mercurio, 809 m, 1 ♀ (AMNH LP 3190); Death Valley National Park: Saratoga Springs, 35°40.843′N 116°25.264′W, 1.ix.2005, R. Mercurio & L. Prendini, 83 m, UV light detection, 1 juv. ♀ (AMNH LP 4974); Desert studies Center, Zzyx, W side of Soda Dry lake, 17.ix.1995, W.E. Savary & S. Angold, 1 ♂ (AMNH LP 4401); Trona Pinnacles, 28.v.1997, W.E. Savary, D. Ubick & G. Pratt, 1 ♀ (AMNH LP 1638), 1 juv. (AMNH LP 4359); Whitewater Canyon, off I10, Whitewater Canyon Road, S Whitewater Trout Farm, 33°58′14.2″N 116°39′09.0″W, 19.viii.2004, M. McCoy, W. Savary, R. Mercurio & K. Bamba, 584 m, 1 ♂ (AMNH LP 3192).

***Hadrurus arizonensis austrinus* Williams, 1970: MEXICO: Baja California:** Punta Bufeo, S end of airstrip, 29°54′N 114°28′W, 28.v.2004, R. Mercurio, M. Nishiguchi *et al.*, 10 m, UV light detection, 1 ♂, 1 ♀, 1 juv. (AMNH LP 3469); Punta Bufeo, *c.* 2 km S, 29°54.150′N 114°26.800′W, 14.vii.2005,

E. González, W.E. Savary, L. Prendini & R. Mercurio, 2 m, UV detection at night, 1 juv. (AMNH LP 4454); 4 km S turnoff to Punta Bufeo from road to San Felipe, 29°51.433′N 114°26.500′W, 14.vii.2005, E. González, W.E. Savary, L. Prendini & R. Mercurio, 28 m, UV detection at night, 3 juv. (AMNH LP 4457); Rancho Ines, 9 km NW, 29.vii.1998, W. Clark, 1 ♂, 1 ♀ (CICESE).

***Hadrurus arizonensis pallidus* Williams, 1970: MEXICO: Baja California:** Los Algodones, sand dunes 10 km SW, 32°40.649′N 114°48.153′W, 16.vii.2005, L. Prendini, E. González, W.E. Savary & R. Mercurio, 47 m, UV detection at night, 2 juv. (AMNH LP 4452); NW Laguna Salada, S of Route 2, 32°34.51′N 115°44.60′W, 16.v.2004, R. Mercurio, M. Nishiguchi *et al.*, 11 m, UV light detection, 2 ♂, 1 juv. (AMNH LP 3470); San Felipe, sand dunes 11 km S, 30°57.312′N 114°47.734′W, 15.vii.2005, E. González, W.E. Savary, L. Prendini & R. Mercurio, 11 m, UV detection at night, 3 juv. (AMNH LP 4456). **Sonora:** Cedo dunes, Puerto Peñasco, 10.x.2002, M. Nishiguchi *et al.*, 11–12 pm, UV lighting, 1 ♀ (AMNH LP 2168); Cerro Prieto, Puerto Peñasco, 24.xi.1965, C. Beutelspacher, 1 ♀ (IBUNAM); Cholla Bay, near Puerto Peñasco, 7.x.1967, N. Hadley, sea level, 1 ♂, 1 ♀ (IBUNAM); Cholla Bay, near Puerto Peñasco, 15.x.1966, S.C. Williams, sea level, 1 ♀ (IBUNAM); Estero Morúa, 30 km SSE Puerto Peñasco, 20.i.1970, W. Lopez-Forment, 1 juv. (IBUNAM); Isla San Pedro Nolasco, 28.ix.1970, R.M.L., 1 ♀ (IBUNAM); Microondas Cerro Prieto, 5 km NW, Reserva de la Biosfera and Parque Nacional El Pinacate, 32°14.011′N 114°04.037′W, 27–28.vi.2005, E. González & R. Mercurio, 256 m, UV detection at night, 2 juv. (AMNH LP 4458); New Kino Bay, 16 km NW dirt road, 28°55. 249′N 112°02.572′W, 2.vii.2006, E. González, 116 m, UV detection at night, 1 juv. (AMNH LP 6328); Sonoyta, 95 km NW, off Route 2, W of Microondas Cerro Lava, 32°06.175′N 113°47.105′W, 28.vi.2005, R. Mercurio & E. González, 273 m, UV detection at night, 1 ♀ (AMNH LP 5087). **USA: Arizona:** Black Mountains, 1.5 mi S Oatman, Route 66, 34°59.255′N 114°25.723′W, 2.iv.2004, R.C. West, *c.* 2200 ft, steep western talus slopes, under rocks, cacti, creosote, 1 ♀ (AMNH LP 2962); Goldwater Bombing Range, County 14 1/4 Street and 5 1/2 Street East, B, 32°37.438′N 114°32.303′W, 25.vi.2000, J. Bigelow, 2 ♂ (AMNH LP 1813). **California:** 12 km NW Palm Springs, S of 111, 2 km E of Snow Creek Road, 33°54′35.5″N 116°39′15.0″W, 18.viii.2004, M. McCoy, W. Savary, R. Mercurio & K. Bamba, 345 m, 1 ♂ (AMNH LP 3421); Between Borrego Springs and La Casa del Zorro, just off Borrego Springs Road, 33°12.828′N 116°22.505′W, 30.viii.2005, R. Mercurio & L. Prendini, 211 m, UV light detection, 1 ♂ (AMNH LP 5045).

***Hadrurus aztecus* Pocock, 1902: MEXICO: Oaxaca:** Cuicatlan, 7 km on road to Ixcatlan, 17°81.523′N 97°00.539′W, 8.xi.2005, O.F. Francke, A. Jaimes, M. Cordova & G. Montiel, 702 m, 1 ♀, 1 juv. (IBUNAM); Dominguillo, 24.v.1998, C. Duran, 1 ♂ (IBUNAM); Valerio Trujano, 19.viii.2004, J.M. Rosas, 1 ♀ (IBUNAM); Tomellin, 17°45.180′N 96°57.237′W, 23.vii.2002, L. Prendini, O. Francke, E. González & J. Ponce, 605 m, desert, excavated from burrows in road verge, 1 ♂ (AMNH LP 2041), 1 subad. ♂, 1 subad. ♀, 2 juv. ♀ (AMNH LP 2042), 3 juv. ♀ (AMNH LP 2043). **Puebla:** El Riego, ix.1960, J. Julia, 1 ♂ (IBUNAM); San Bartolo Teontepec, 9.xii.1992, G. Ortega & E. Barrera, 1 juv. (IBUNAM); Tehuacan, 20.iii.1996, 1 ♂ (IBUNAM); Zapotitlan Salinas, 16.xi.1998, E. González-Santillan, 1500 m, 1 juv. (IBUNAM).

***Hadrurus concolorous* Stahnke, 1969: MEXICO: Baja California:** 4 km along gravel road to Calamajué from junction with Route 1, 29°15.116′N 114°08.366′W, 13.vii.2005, R. Mercurio & L. Prendini, 623 m, UV detection at night, 1 ♀ (AMNH LP 4542); Bahia de Los Angeles, 18.viii.1964, A. Villalobos, 1 ♀ (IBUNAM); Balandra, 12 km NE La Paz, 26.x.1994, F.A. Cervantes, 50 m, 1 ♀ (IBUNAM); Ejido Meliton Albañez, viii.2004, H. Carmona, 1 ♂ (IBUNAM); Isla Coronados, 26.i.1967, L. Cervantes & F. Arias, 2 juv. (IBUNAM); Isla del Carmen, 5.ii.2006, W. Lopez-Forment, 1 juv. (IBUNAM); Isla Espiritu Santo, 1.iii.2002, W. Lopez-Forment, 1 ♀, 1 juv. (IBUNAM); Isla San Jose, ix.1986–i.1987, L. Cervantes, 1 ♂ (IBUNAM); Isla San Jose, 30.v.1994, F. A. Cervantes, 5 m, 1 ♂, 1 juv. (IBUNAM); Isla San Marcos, 1.v.2005, W. Lopez-Forment, 1 ♂ (IBUNAM); La Paz, 5 km S, 20.xi.1974, W. Lopez-Forment, 1 ♀ (IBUNAM); Loreto, 30 km SW, 31.xii.1979, W. Lopez-Forment, 1 ♀ (IBUNAM); Misión San Borja, 28°44.607′N 113°45.233′W, 13.vii.2005, E. González & W.E. Savary, 433 m, UV detection at night, 1 juv. (AMNH LP 4453); Mision Santa Dolores, 10.xi.2003, W. Clark, 1 ♀ (CICESE); Punta Prieta, 37 km N, off Route 1, 29°15.116′N 114°10.100′W, 13.vii.2005, L. Prendini & R. Mercurio, 588 m, UV detection at night, 4 juv. (AMNH LP 4541); Rancho San Fernando, 40 km S La Paz, xi.1972, J.M. Alcocer, 1 ♂, 2 juv. (IBUNAM). **Baja California Sur:** Ciudad Constitución, 32 km SW, 24°55′17′N 111°58′5.5′W, 11.vii.2004, O. Francke, W. Savary, E. González & A. Valdez, 26 m, UV light detection at night, 1 juv. (AMNH LP 3126); El Cayuco Fish Camp, sand dunes S, 24°34.666′N 111°40.633′W, 11.vii.2005, W.E. Savary, E. González, L. Prendini & R. Mercurio, 6 m, UV detection at night, 1 subad. ♀, 5 juv. (AMNH LP 4535); El Tecolote, 24°20.259′N 110°18.580′W, 21.v.2004, R. Mercurio, M. Nishiguchi *et al.*, 2 m, UV light detection, 1 ♀ (AMNH LP 3471); Guerrero Negro, 11 km SE, W side Route 1, 27°54.916′N 113°55.333′W, 4.vii.2005, L. Prendini & R. Mercurio, 18 m, UV detection at night, 1 subad. ♂, 1 juv. (AMNH LP 4536); Juncalito, 25°49.892′N 111°19.691′W, 20.v.2004, R. Mercurio, M. Nishiguchi *et al.*, 5 m, UV light detection, 1 ♀ (AMNH LP 3472); La Paz, 75 km NW, 24°05′56.2′N 110°45′41′W, 7.vii.2004, O. Francke, E. González & A. Valdez, 256 m, UV light detection at night, 1 juv. (AMNH LP 3127); La Paz, *c.* 20 km N junction Route 1 and road to San Juan de la Costa, 24°13.383′N 110°35.766′W, 9.vii.2005, L. Prendini, E. González & R. Mercurio, 20 m, UV detection at night, 2 juv. (AMNH LP 4533); La Paz, *c.* 10 km SE on BCS 286 to San Juan de los Planes, 24°08.433′N 110°15.333′W, 9.vii.2005, L. Prendini & R. Mercurio, 106 m, UV detection at night, 1 juv. (AMNH LP 4539); Loreto, S, *c.* 3 km along gravel road to San Javier, from junction with Route 1, 25°59.800′N 111°19.250′W, 8.vii.2005, E. González, R. Mercurio, W.E. Savary & L. Prendini, 38 m, UV detection at night, 1 juv. (AMNH LP 4540); Loreto, S, *c.* 8 km along gravel road to San Javier, from junction with Route 1, 25°59.733′N 111°25.116′W, 8.vii.2005, L. Prendini, E. González, R. Mercurio & W.E. Savary, 120 m, UV detection at night, 1 juv. (AMNH LP 4532); Loreto, 25 km S on gravel road, *c.* 250 m E Route 1, 25°48.666′N 111°19.266′W, 7.vii.2005, W.E. Savary, L. Prendini, R. Mercurio & E. González, 6 m, UV detection at night, 4 juv. (AMNH LP 4537); Loreto, 25 km S, on gravel road just off Route 1, 25°48.666′N 111°19.266′W, 7.vii.2005, E. González, W.E. Savary, L. Prendini & R. Mercurio, 6 m, UV detection at night, 1 subad. ♀ (AMNH LP 4534); Microondas San Lucas, 27°11.550′N 112°14.150′W, 5.vii.2005, W.E. Savary & R. Mercurio, 185 m, UV detection at night, 1 juv. (AMNH LP 4455); Mulegé, sand dunes *c.* 4 km S, 26°53.166′N 111°56.550′W, 6.vii.2005, W.E. Savary & R. Mercurio, 3 m, UV detection at night, 1 juv. (AMNH LP 4459); San Ángel dunes, 27°14′05′N 113°13′46.5′W, 14.vii.2004, O. Francke, W. Savary, E. González & A. Valdez, 25 m, UV light detection at night, 1 juv. (AMNH LP 3128); San Miguel de Comondú, 26°02′26.7′N 111°49′55.3′W, 12.vii.2004, O. Francke, W. Savary, E. González & A. Valdez, 220 m, UV light detection at night, 1 juv. (AMNH LP 3129).

Hadrurus gertschi **Soleglad, 1976: MEXICO: Guerrero:** Atenango del Rio, 19.viii.2000, O.F. Francke, M. Capes, E. González-Santillan & O. Delgado, 3 ♂, 2 ♀ (IBUNAM); Balsas, 1 ♀ (IBUNAM); Comala, 2.5 km N, 22.iv.2000, E. González-Santillan, 700 m, 1 juv. (IBUNAM); Copalillo/Rio Papalutla, 20.viii.2000, M. Capes & E. González-Santillan, 1 ♂ (IBUNAM); entre Comala and Atenango, 23.iv.2000, E. González-Santillan, 700 m, 1 ♀ (IBUNAM); Mezcala, 11.viii.1990, C. Velazquez, 3 ♂ (IBUNAM); Placeres del Oro, viii.2004, E. González-Santillan, 1 ♂, 1 ♀ (IBUNAM); Rivera del rio Amacuzac, Atenango del Rio, 17.viii.2000, M. Capes & E. González, 1 ♂ (AMNH LP 1810); Valerio Trujano, vii.1967, H. Perez R., 1 ♂ (IBUNAM); Valerio Trujano, 1 km N, 12.vi.1962, J. Julia, 1 ♀ (IBUNAM).

Hadrurus hirsutus **(Wood, 1863): MEXICO: Baja California Sur:** Bahia Chileno, 22°57′51.1′N 109°48′39.5′W, 21.i.2005, H. Carmona, 62 m, 1 ♀ (IBUNAM); Cabo San Lucas, 20.i.2006, W. Lopez-Forment, 1 ♂ (IBUNAM); Cabo San Lucas, 15 mi. E, 1.vi.1999, M.E. Soleglad, 1 juv. (AMNH LP 1675); La Paz, 75 km NW, 24°05′56.2′N 110°45′41′W, 7.vii.2004, O. Francke, E. González & A. Valdez, 256 m, UV light detection at night, 1 ♂ (AMNH LP 3131); La Paz, 18 km SE, 24°02′45.9″N 110°08′51.9″W, 8.vii.2004, O. Francke, E. González & A. Valdez, 625 m, UV light detection at night, 1 juv. (AMNH LP 3130); San José del Cabo, 17.ix.1986, M. Correa, 2 ♀ (IBUNAM); San José del Cabo, *c.* 10 km S off Route 1, 22°59.766′N 119°44.216′W, 10.vii.2005, W.E. Savary, E. González & R. Mercurio, 50 m, UV detection at night, 3 juv. (AMNH LP 4538); Santiago, 23°26′24.5″N 109°43′34.6″W, 9.vii.2004, O. Francke, E. González & A. Valdez, 225 m, UV light detection at night, 2 juv. (AMNH LP 3132).

Hadrurus obscurus **Williams, 1970: USA: California:** Anza-Borrego Desert State Park: Culp Valley Camp, 33°13.421′N 116°27.267′W, 30.viii.2005, L. Prendini & R. Mercurio, 1033 m, UV light detection, 1 subad. ♂, 2 juv. (AMNH LP 4973); Mountain Springs Canyon, China Lake Naval Weapons Station, 28.v.1997, W.E. Savary, D. Ubick & G. Pratt, 1 ♀, 1 juv. (AMNH LP 4366); Tungsten Hills, Tungsten Road, near Tungsten Mine, 37°21.364′N 118°31.706′W, 6.ix.2005, L. Prendini & R. Mercurio, 1536 m, UV light detection, 1 subad. ♂ (AMNH LP 5046).

Hadrurus pinteri **Stahnke, 1969: MEXICO: Baja California:** El Rincon, 18.ii.2001, W. Clark, 1 juv. (CICESE); Mision San Fernando, 2 km E, 30.vii.1998, W. Clark, 1 ♂ (CICESE); Santa Catarina, 1 km NE, 17.i.2001, W. Clark, 1 ♀ (CICESE); Bahia Concepcion near El Coyote, 26°40′N 111°50′W, 17.ii.1966, V. Roth, 1 ♂ (AMNH); Isla Danzante, 4.vii.1962, R. Banks, 1 ♀ (AMNH). **Baja California Sur:** Loreto, S, *c.* 8 km along gravel road to San Javier, from junction with Route 1, 25°59.733′N 111°25.116′W, 8.vii.2005, L. Prendini, E. González, R. Mercurio & W.E. Savary, 120 m, UV detection at night, 1 ♂ (AMNH LP 5090); Microondas San Lucas, 27°11.550′N 112°14.150′W, 5.vii.2005, W.E. Savary & R. Mercurio, 185 m, UV detection at night, 1 ♂ (AMNH LP 5089); San Ignacio, 3 km S on road to La Laguna, 27°16.533′N 112°53.366′W, 12.vii.2005, E. González, W.E. Savary, L. Prendini & R. Mercurio, 167 m, UV detection at night, 1 ♀ (AMNH LP 5091); San Miguel de Comondú, 26°02′26.7″N 111°49′55.3″W, 12.vii.2004, O. Francke, W. Savary, E. González & A. Valdez, 220 m, UV light detection at night, 3 juv. (AMNH LP 3134); near San Miguel, 27°56′5.8″N 113°54′23.1″W, 16.vii.2004, O. Francke, W. Savary, E. González & A. Valdez, 25 m, UV light detection at night, 1 juv. (AMNH LP 3133).

Hadrurus spadix **Stahnke, 1940: USA: Arizona:** Oatman, 2 mi. S on Route 66, 3.iv.2003, R.C. West, 1 ♀ (AMNH LP 2444). **California:** Avawatz Mountains, 36°30′37.5″N 116°18′33.6″W, 27.v.1997, W.E. Savary, D. Ubick & G. Pratt, 1290 m, 1 juv. (AMNH LP 4396); Death Valley National Park: Grapevine Canyon, Saline Valley Road, 36°33.591′N 117°35.219′W, 4.ix.2005, R. Mercurio & L. Prendini, 1290 m, UV light detection, 1 juv. (AMNH LP 5039); Death Valley National Park: Mesquite Springs Campground, 36°57.783′N 117°22.257′W, 3.ix.2005, L. Prendini & R. Mercurio, 529 m, UV light detection, 2 juv. (AMNH LP 4975); **Nevada:** ex T. Gearheart, 1 ♂ (AMNH LP 1791), 1 ♀ (AMNH LP 1790) Between Garfield Flat Road and Black Dyke Mountain, W of Mina, 17.viii.2005, L. Iacovelli, UV light detection at night, 1 ♂ (AMNH LP 4777), 1 ♂ (AMNH LP 4778); Hawthorne, 3–10 mi. N along I-95 near Walker Lake, 38°37′14.5′N 118°44′23.1′W, 23.viii.2006, J. Huff, 1321 m, collected along rocky-sandy slopes and along flat patches of the same substrate, sparse vegetation, collected at night using UV, 2 ♀, 1 subad. ♀ (AMNH LP 6295); Mercury (Nevada Test Site), 21.vi.1961, 3 ♂, 3 ♀ (IBUNAM); Sparks, Pyramid Way (Hwy 447), *c.* 22 mi. from McCarran Blvd. across from shooting range, 39°51′19.1′N 119°39′21.5′W, 22.viii.2006, J. Huff & J. Courting, 1295 m, collected on sandy soil with sparse vegetation using UV at night, 2 ♀, 2 subad. ♂ (AMNH LP 6296).

Appendix 3

Revised list of 61 characters for the eight species of *Hadrurus* Thorell and three outgroup taxa. Character states are scored 0–2 and - (inapplicable). Twenty-nine uninformative characters, indicated by †, were excluded from all analyses. Refer to Table 4 for character matrix. Previous character numbers as follows (author/number): L80 = Lamoral (1980); S89 = Stockwell (1989); P00 = Prendini (2000); FSB01 = Fet *et al.* (2001); S&S01 = Soleglad & Sissom (2001); S&F01 = Soleglad & Fet (2001); P03 = Prendini (2003); S&F03.4 = Soleglad & Fet (2003), Table 4; S&F03.5 = Soleglad & Fet (2003), Table 5; P04 = Prendini (2004).

Colouration

1. Carapace, interocular surface, infuscation: entirely infuscated (0); partially infuscated (1); triangle lacking infuscation between lateral and median ocelli (2). Previous characters: FSB01/9–11 (part).
2. Carapace, circumocular surfaces, infuscation: infuscated to lateral ocelli (0); infuscation not reaching lateral ocelli (1); not infuscated (2). Previous characters: FSB01/9–11 (part).
3. Carapace, posterior (posterolateral and posteromedian) surfaces, infuscation: infuscated (0); not infuscated (1). Previous characters: FSB01/9–11 (part).
4. Pedipalp chela fingers, colouration: reddish or brownish, darker than manus (0); light yellow, similar to manus (1). Previous characters: FSB01/8.
5. Pedipalp chela manus, infuscation: absent (0); present (1). Previous characters: FSB01/12 (part).
6. Mesosomal tergites, infuscation: entirely to mostly infuscated (except for lateral and posterior edges) (0); little to no infuscation (1). Previous characters: FSB01/9 (part).
7. Metasomal segments, infuscation: not infuscated (0); segment V infuscated only (1); infuscated (at least ventrally) on all segments (2). Previous characters: FSB01/12 (part), 13.
8. Metasoma, ventral surface, carinae, infuscation: not infuscated (0); infuscated (1).

Chelicerae

†9. Cheliceral fixed finger, subdistal and median teeth: U-spaced (0); V-spaced (1). Previous characters: L80/19.

†10. Cheliceral movable finger, distal denticle alignment (inner and outer distal teeth): subequal, with distal external tooth only slightly smaller than distal internal tooth, and opposable, i.e. forming a bicusp (ventral approximately equal to dorsal) (0); unequal, with distal external tooth considerably smaller than distal internal tooth, aligned longitudinally and not opposable (ventral extends considerably beyond dorsal) (1). Previous characters: L80/21 (part), P00/11, S&S01/1, S&F03.5/39.

†11. Cheliceral movable finger, dorsal edge, number of subdistal teeth: one (0); two (1). Previous characters: L80/10; S89/31, 32; P00/10; S&S01/3.

†12. Cheliceral movable finger, ventral edge, serrula: present (0); absent (1). Previous characters: L80/10; S89/31, 32; S89/37–39; P00/10; S&S01/3, 7; S&F03.5/41.

†13. Cheliceral movable finger, ventral edge, large denticle, position: medial (0); suprabasal (1); basal (2).

Carapace

†14. Carapace, anterior margin: sublinear, with median notch, lateral ocular carinae well developed (0); convex, without median notch, lateral ocular carinae inconspicuous (1).

†15. Lateral ocelli, number: three (0); four (1). Previous characters: S89/21, 25; P00/1 (part); S&F03.5/102.

Pedipalps

†16. Pedipalp patella, internal projections (‘spurs’): dorsal and ventral projections similarly developed (0); absent (1). Previous characters: S&S01/15–17.

†17. Pedipalp chela, subdigital carina: absent (0); present, vestigial (1). Previous characters: S89/40 (corrected); P00/19; S&S01/20, 23; S&F03.5/91.

†18. Pedipalp chela, ventromedian carina: absent (0); weak to obsolete, present only in proximal half (1). Previous characters: S&S01/26; P00/28.

†19. Pedipalp chela fingers, median denticle row, primary subrows, orientation: oblique, imbricated (0); oblique, not imbricated (1). Previous characters: P04/7.

20. Pedipalp chela, movable finger, number of internal denticles: 10–14 (0); nine (1); seven (2).

†21. Pedipalp chela finger dentition, inner and outer accessory denticles [supernumary granules *sensu* Sissom (1990)]: absent (0); present (1). Previous characters: S&S01/30, 33; S&F03.5/49, 51, 52.

Trichobothria

†22. Pedipalp femur, trichobothrium *d* position: external surface (0); dorsal surface (1). Previous characters: S&S01/39.

†23. Pedipalp patella, external surface, trichobothrium et_2, size: smaller than other trichobothria (‘petite’) (0); similar to other trichobothria (1). Previous characters: S&S01/49, S&F01/45, S&F03.4/45; S&F03.5/25.

24. Pedipalp patella, external surface, number of trichobothria in *em* series: two (0); three (single accessory trichobothrium) (1); more than ten (more than eight accessory trichobothria) (2). Previous characters: L80/17; S89/60–68; P00/45; S&S01/51, 54–56, 59–65; S&F03.5/30, 36.

†25. Pedipalp patella, external surface, trichobothrium eb_2, size: smaller than other trichobothria (‘petite’) (0); similar to other trichobothria (1). Previous characters: S&S01/49; S&F01/35; S&F03.4/35; S&F03.5/25.

26. Pedipalp patella, ventral surface, number of trichobothria: one (0); three (1); more than three (2), Previous characters: L80/1, 17; S89/52, 56–59; P00/42, 43; S&S01/52, 53; S&F03.5/35.

†27. Pedipalp patella, ventral surface, trichobothrium v_1 position: suprabasal (0); basal (1). Previous characters: S&S01/50.

28. Pedipalp patella, ventral series trichobothria, positions: one (v_3) positioned externally (0); more than two positioned externally (1); inapplicable (-). Previous characters: S89/53–55; P00/44; S&S01/48; S&F03.5/23, 24.

29. Pedipalp chela, trichobothrium *Db*, position: manus, ventroexternal surface, distal third (0); manus, dorsoexternal surface, distal third (1); manus, dorsoexternal surface, proximal third (2). Previous characters: S89/81, 83–85; P00/51, 52; S&F03.5/19.

30. Pedipalp chela, trichobothrium *Dt*, position: manus, external surface, distal third (0); near base of fixed finger, dorsal surface (1); manus, dorsal surface, proximal third (2). Previous characters: S89/81, 83–85; P00/52; S&F03.5/19.

†31. Pedipalp chela manus, external surface, trichobothrium *Est*, size: smaller than other trichobothria ('petite') (0); similar to other trichobothria (1). Previous characters: S&S01/47; S&F01/17; S&F03.4/17; S&F03.5/17.

32. Pedipalp chela manus, external surface, accessory trichobothria in *Esb–Est* series: absent (0); present (1). Previous characters: L80/14; P00/53; FSB01/1, 2 (part); S&F03.5/33.

†33. Pedipalp chela manus, trichobothrium Et_1, position: external surface (0); ventral surface (1).

†34. Pedipalp chela, trichobothrium Et_5, position: on manus, near to trichobothrium Et_4 (0); basal on fixed finger, removed from Et_4 (1); suprabasal on fixed finger, considerably removed from Et_4 (2). Previous characters: S&F03.5/15, 22.

35. Pedipalp chela manus, external surface, accessory trichobothria in *Et* series: absent (0); present (1). Previous characters: L80/14; P00/53; FSB01/1, 2 (part); S&F03.5/33.

36. Pedipalp chela manus, ventral surface, number of trichobothria: four (0); more than four (1). Previous characters: L80/14; S89/75, 76; P00/49; FSB01/4, 5; S&S01/57; S&F03.5/32.

†37. Pedipalp chela manus, ventral surface, trichobothrium V_2, size: smaller than other trichobothria ('petite') (0); similar to other trichobothria (1). Previous characters: S&S01/47; S&F01/24; S&F03.4/24; S&F03.5/17.

38. Pedipalp chela manus, ventral surface, arrangement of trichobothria: in a single row (0); forming a double row in at least the distal third (1).

†39. Pedipalp chela, fixed finger, external accessory trichobothrium: absent (0); present (1). Previous characters: FSB01/0.

†40. Pedipalp chela, fixed finger, trichobothria *eb–et* and *db–dt* positions: confined to distal one-third to two-thirds of finger (0); evenly distributed across most of finger (1). Previous characters: S89/73; P00/58, 60–62; S&S01/42, 58; S&F03.5/13.

†41. Pedipalp chela, fixed finger, trichobothrium *esb*, size: smaller than other trichobothria ('petite') (0); similar to other trichobothria (1). Previous characters: S&S01/47; S&F01/10; S&F03.4/10; S&F03.5/17.

42. Pedipalp chela, fixed finger, trichobothrium *esb*, position: approximately in line with to slightly below *eb–est–et* axis (usually making an obtuse angle, dorsally, with *eb* and *est–et*) (0); considerably below *eb–est–et* axis (usually making an acute angle, dorsally, with *eb* and *est–et*) (1). Previous characters: P00/62; S&F03.5/20, 21.

†43. Pedipalp chela, fixed finger, trichobothrium *eb*, position: medial to distal third (0); proximal third (1). Previous characters: P00/61.

44. Pedipalp chela, trichobothrium *ib* position: on manus, behind movable finger condyle (0); basal on fixed finger (1); suprabasal on fixed finger (2). Previous characters: S89/71, 72; P00/48; S&S01/40, 41; S&F03.5/10.

†45. Pedipalp chela, fixed finger, trichobothrium *it* position: distal (0); basal to suprabasal (1). Previous characters: S89/70–72; P00/47; S&S01/40, 41; S&F03.5/11, 14.

46. Pedipalp chela, internal surface, number of trichobothria: two (no accessory trichobothria) (0); more than two (2–7 accessory trichobothria) (1). Previous characters: L80/14; S89/69; P00/46; FSB01/3; S&F03.5/34.

Legs

47. Basitarsus, pedal spurs, spination: smooth, lacking spinules (0); pectinate, with conspicuous spinules (1).

48. Telotarsus, ventromedian surface, armature: with conspicuous, concentrated spinule clusters ('tarsal tufts') (0); with fused spinule clusters (1). Previous characters: L80/9; S89/93, 94, 97 (part); P00/70; S&S01/84, 86–88.

49. Telotarsus, fused spinule clusters, ultrastructure: with well developed ridges (0); with obsolete ridges (1); inapplicable (-).

50. Posttarsus, dactyl (unguicular spine), development: sharp, pronounced (0); blunt, reduced (1). Previous characters: S89/98.

Mesosoma

51. Genital papillae (♂): present, visible at posterior edge of genital operculum (0); absent (1). Previous characters: S&S01/72; S&F03.5/81.

†52. Genital operculum, sclerites (♀): loosely connected (0); separated for most of length (1). Previous characters: L80/12 (part); S89/105–107; P00/80; S&F03.5/82.

53. Accessory 'genital operculum': absent (0); present (1). Previous characters: S89/108.

†54. Testis: straight (0); coiled (1). Previous characters: S89/104.

†55. Seminal vesicle, size: normal (0); enlarged (1).

56. Hemispermatophore, truncal flexure: present (0); absent (1). Previous characters: S89/114, 115; P00/83; S&F03.5/78.

57. Respiratory spiracles (stigmata), shape: slit-like (0); oval (1). Previous characters: L80/20 (part); S&F03.5/101.

Metasoma and telson

58. Metasomal segments I–III, ventral intercarinal surfaces, setation: sparsely setose (0); densely setose (1). Previous characters: FSB01/7.
59. Metasomal segment III, dorsal carinae, setation (♂): sparsely setose (0); densely setose (1).

†60. Metasomal segment IV, median lateral carinae: absent (0); present, partial (1). Previous characters: S&F03.5/87; P03/42; P04/24.

61. Telson, pair of subaculear glands (♂): absent (0); present (1). Previous characters: FSB01/14.