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# Troglomorphism, trichobothriotaxy and typhlochactid phylogeny (Scorpiones, Chactoidea): more evidence that troglobitism is not an evolutionary dead-end

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**Abstract**

The scorpion family Typhlochactidae Mitchell, 1971 is endemic to eastern Mexico and exclusively troglomorphic. Six of the nine species in the family are hypogean (troglobitic), morphologically specialized for life in the cave environment, whereas three are endogean (humicolous) and comparably less specialized. The family therefore provides a model for testing the hypotheses that ecological specialists (stenotopes) evolve from generalist ancestors (eurytopes) and that specialization (in this case to the cavernicolous habitat) is an irreversible, evolutionary dead-end that ultimately leads to extinction. Due to their cryptic ecology, inaccessible habitat, and apparently low population density, Typhlochactidae are very poorly known. The monophyly of these troglomorphic scorpions has never been rigorously tested, nor has their phylogeny been investigated in a quantitative analysis. We test and confirm their monophyly with a cladistic analysis of 195 morphological characters (142 phylogenetically informative), the first for a group of scorpions in which primary homology of pedipalp trichobothria was determined strictly according to topographical identity (the ‘‘placeholder approach’’). The phylogeny of Typhlochactidae challenges the conventional wisdom that ecological specialization (stenotopy) is unidirectional and irreversible, falsifying Cope’s Law of the unspecialized and Dollo’s Law of evolutionary irreversibility. Troglobitism is not an evolutionary dead-end: endogean scorpions evolved from hypogean ancestors on more than one occasion.

Caves are among the most fascinating environments on Earth, where a specialized underground biota provides evidence of evolutionary adaptations for life under severe conditions: reduction or absence of light, constant (usually very high) humidity, extremely stable temperature, and very limited energy (food) input (Barr, 1968; Poulson and White, 1969; Howarth, 1982, 1983, 1993; Parzefall, 1985; Culver and Sket, 2000; Culver et al., 2003). The energy input to caves is low and usually allochthonous, as there are no primary producers. In spite of these challenges, diverse animals, mostly invertebrates, evolved in cave environments around the world. Cavernicolous environments select for loss of characters that are unnecessary and costly to produce or maintain (e.g. eyes, pigmentation, thickened cuticle), and accentuation of characters that assist in resource location or compensate for the ‘‘unnecessary’’ characters lost (e.g. attenuated appendages, reduced metabolic rate). The cave environment also creates natural barriers, limiting dispersal ability, restricting gene flow, and resulting in the evolution of localized endemics (Crouau-Roy, 1989; Lamoreaux, 2004).

Different cave ecomorphotypes may be recognized, depending on the degree of morphological, physiological, and behavioural specialization to the cave environment (Barr, 1963, 1968; Poulson, 1963; Hamilton-Smith, 1967; Howarth, 1972, 1982, 1983, 1993; Barr and

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Holsinger, 1985; Humphreys, 2000; Prendini, 2001a; Volschenk and Prendini, 2008). Obligate cavernicoles or troglobites are restricted to deep cave environments and are highly stenotopic: they exhibit pronounced troglomorphies, ecomorphological adaptations to hypogean habitats that include the loss or reduction of eyes and pigmentation, attenuation of the appendages, and thinning of the cuticle. Facultative cave-dwellers or troglophiles may be found in all cave habitats, from the entrance to the deep zone, and show intermediate degrees of adaptation, including some troglomorphies. Trogloxenes are eurytopes that exhibit no troglomorphies and are considered occasional visitors to cavernicolous habitats.

Troglomorphism in scorpions is defined on the basis of several morphological characters, exhibited to varying degrees (Prendini, 2001a; Volschenk and Prendini, 2008): anophthalmy, loss or reduction of median and/or lateral ocelli; depigmentation; reduction of sclerotization and carination; attenuation of appendages (legs, pedipalps); loss of spurs and spinules on legs; loss of pectinal fulcra, fusion of pectinal lamellae and reduction in number of pectinal teeth; enlargement of telson. Troglomorphism is exhibited by endogean (humicolous) as well as hypogean (troglobitic) scorpions, however, and does not constitute unequivocal evidence of troglobitism in the absence of evidence that the scorpion is restricted to a cavernicolous habitat (Volschenk and Prendini, 2008). Thirty-seven scorpion species in 23 genera and 12 families, displaying various degrees of troglomorphism, have been reported worldwide but only 23 species, in 16 genera and 10 families, are considered unequivocally troglobitic according to the criteria outlined by Volschenk and Prendini (2008).

Nine troglomorphic chactoid scorpions, previously placed in subfamily Typhlochactinae Mitchell, 1971 (first of Chactidae Pocock, 1893, and more recently of Superstitioniidae Stahnke, 1940), but elevated to family rank by Vignoli and Prendini (2009), are endemic to eastern Mexico (Table 1; Fig. 1). Six of the species in this family are hypogean (troglobitic) and three are considered endogean based on available data (one was extracted from leaf litter using Berlese, the others taken from under stones embedded in litter). The family includes the world's most specialized troglomorphic scorpion, *Sotanochactas elliotti* (Mitchell, 1971), and the world's smallest scorpion, an endogean species, *Typhlochactas mitchelli* Sissom, 1988 (Fig. 2), and holds the record for the greatest depth at which a scorpion has been collected: *Alacran tartarus* Francke, 1982 occurs 750–920 m below the surface in the caves of the Huautla Plateau (Oaxaca) (Francke, 1982; Fig. 3).

As with other obligate cavernicoles, the six hypogean (troglobitic) species of Typhlochactidae are greatly specialized for life in the cave environment (Mitchell, 1968, 1971; Francke, 1982, 1986; Sissom and Cokendolpher, 1998), whereas their three endogean (humicolous) relatives are relatively less specialized (Mitchell and Peck, 1977; Sissom, 1988; Francke et al., 2009). The family therefore provides a model for testing the hypotheses that ecological specialists (stenotopes) evolve from generalist ancestors (eurytopes) and that specialization (in this case to the cavernicolous habitat) is an irreversible evolutionary dead-end that ultimately leads to extinction (Dollo, 1893, 1903, 1922; Cope, 1896; Huxley, 1942; Mayr, 1942, 1988; Simpson, 1944, 1953; Rensch, 1959; Gould, 1970; Sugihara, 1980; Wagner, 1982; Laurent, 1983; Bull and Charnov, 1985; Futuyma and Moreno, 1988; Futuyma, 1998).

Due to their cryptic ecology, inaccessible habitat, and apparently low population density, Typhlochactidae are among the most poorly known scorpions. Prior to the recent revision by Vignoli and Prendini (2009), Francke (1982) presented the most comprehensive treatment of

Table 1
Classification of the scorpion family Typhlochactidae Mitchell, 1971; with list of species and known Mexican states of occurrence

- Family Typhlochactidae Mitchell, 1971, type genus *Typhlochactas* Mitchell, 1971
  - Subfamily Alacraninae Vignoli and Prendini, 2009, type genus *Alacran* Francke, 1982
    - *Alacran* Francke, 1982, type species *A. tartarus* Francke, 1982
      - *Alacran tartarus* Francke, 1982: Oaxaca
  - Subfamily Typhlochactinae Mitchell, 1971, type genus *Typhlochactas* Mitchell, 1971
    - *Sotanochactas* Francke, 1986 type species *S. elliotti* (Mitchell, 1971)
      - *Sotanochactas elliotti* (Mitchell, 1971): San Luis Potosí
    - *Stygochactas* Vignoli and Prendini, 2009, type species *S. granulosus* (Sissom and Cokendolpher, 1998)
      - *Stygochactas granulosus* (Sissom and Cokendolpher, 1998): Veracruz
    - *Typhlochactas* Mitchell, 1971, type species *T. rhodesi* Mitchell, 1968
      - *Typhlochactas cavicola* Francke, 1986: Tamaulipas
      - *Typhlochactas mitchelli* Sissom, 1988: Oaxaca
      - *Typhlochactas reddelli* Mitchell, 1968: Veracruz
      - *Typhlochactas rhodesi* Mitchell, 1968: Tamaulipas
      - *Typhlochactas sissomi* Francke et al., 2009: Queretaro
      - *Typhlochactas sylvestris* Mitchell and Peck, 1977: Oaxaca

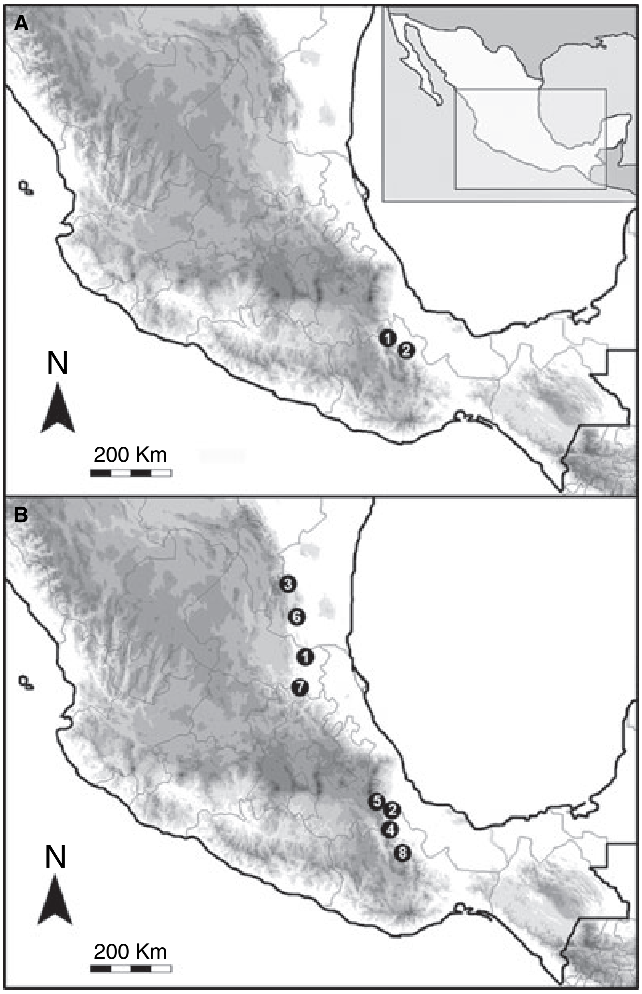

Fig. 1. Map of Mexico showing the known localities of Typhlochactidae Mitchell, 1971. (A) Known localities of Alacraninae Vignoli and Prendini, 2009: Type locality of *Alacran tartarus* Francke, 1982 on the Huautla Plateau, Oaxaca (1); Te Cimutaá, Oaxaca, a new record for the genus possibly representing a new species of *Alacran* Francke, 1982 (2). (B) Type localities of Typhlochactinae Mitchell, 1971: *Sotanochactas elliotti* (Mitchell, 1971), El Sótano de Yerbaniz, San Luis Potosí (1); *Stygochactas granulosus* (Sissom and Cokendolpher, 1998), Sótano de Poncho, Veracruz (2); *Typhlochactas cavicola* Francke, 1986, Cueva del Vandalismo, Tamaulipas (3); *Typhlochactas mitchelli* Sissom, 1988, Cerro Ocote, Oaxaca (4); *Typhlochactas reddelli* Mitchell, 1968, La Cueva del Ojo de Agua de Tlilapan, Veracruz (5); *Typhlochactas rhodesi* Mitchell, 1968, La Cueva de la Mina, Tamaulipas (6); *Typhlochactas sissomi* Francke et al., 2009, Cañada de La Joya, Queretaro (7); *Typhlochactas sylvestris* Mitchell and Peck, 1977, 25 km S Valle Nacional, Oaxaca (8).

the five species known at the time, including a discussion of their phylogenetic position and a hypothesis of phylogenetic relationships among them (figure 26, a tree diagram that was not derived from a quantitative analysis, reproduced here as Fig. 4). Although discussed in the course of various treatments on higher-level scorpion systematics (Stockwell, 1989, 1992; Sissom, 1990; Soleglad and Fet, 2001, 2003; Coddington et al., 2004; Prendini and Wheeler, 2005), the monophyly of these scorpions has never been rigorously tested, nor has their phylogeny been investigated in a quantitative analysis.

We test the monophyly of these remarkable troglomorphic scorpions with a cladistic analysis of 195 morphological characters (142 phylogenetically informative), the first for a group of scorpions in which primary homology of pedipalp trichobothria was determined strictly on topographical identity. The phylogeny obtained in our analyses illuminates understanding of the evolution of troglobitism in typhlochactid scorpions and more generally in troglomorphic animals.

## Material and methods

### Taxon sampling

The cladistic analysis presented is based on 12 terminal taxa (Table 2). Trees were rooted using the outgroup method (Farris, 1982; Nixon and Carpenter, 1993). The ingroup includes all species of Typhlochactidae. Three outgroup taxa were selected based on evidence of a close phylogenetic relationship with the family (Francke, 1982; Stockwell, 1989; Soleglad and Fet, 2003; Coddington et al., 2004; Prendini and Wheeler, 2005): *Superstitionia donensis* Stahnke, 1940, an epigean species (Stahnke, 1940; Williams, 1980); *Troglotayosicus vachoni* Lourenço, 1981, a hypogean (troglobitic) (Lourenço, 1981, 2006) species; and *Troglotayosicus humiculum* Botero-Trujillo and Francke, 2009, an endogean (humicolous) species. The tree was rooted on *S. donensis*.

Material examined is listed in Appendix 1. The female holotype and only known specimen of *T. vachoni* was scored using the literature (Lourenço, 1981, 2006). The holotype could not be found when the first author visited the Museum National d'Histoire Naturelle in 2004, but was rediscovered subsequently.

### Character matrix

Character data were edited and cladograms prepared using WinClada (Nixon, 2002). The character matrix (Table 2; Appendix 2) comprises 196 characters, 47 coded into multistates and 149 coded into binary states. Multistate characters were treated as unordered/nonadditive (Fitch, 1971).

The first 195 characters in the matrix are derived from morphology. The final ''character'' comprising three states of habitat (ecomorphotype), not included in the cladistic analysis, was optimized on the tree *a posteriori*. The three states of this character are distributed among the taxa as follows: epigean (*S. donensis*); endogean (*T. humiculum*, *T. mitchelli*, *T. sissomi*, *T. sylvestris*);

Fig. 2. *Typhlochactas mitchelli* Sissom, 1988, holotype ♂ (AMNH), habitus. (A) Dorsal aspect, visible light. (B) Ventral aspect, ultraviolet light. Scale = 1 mm.

hypogean (*T. vachoni*, *A. tartarus*, *S. elliotti*, *S. granulosus*, *T. cavicola*, *T. reddelli*, *T. rhodesi*).

Fifty-six morphological characters in the matrix were modified from previous analyses of chactoid relationships (Stockwell, 1989; Soleglad and Sissom, 2001; Soleglad and Fet, 2003). Most of the original characters from which these characters were developed were severely criticized by Prendini and Wheeler (2005); they were extensively recoded prior to incorporation in the matrix presented here. Additional characters were added and recoded from Lamoral (1980) and Prendini (2000, 2001b, 2003a, 2004).

Eight sex-specific characters contain question marks for taxa known only from the male (*T. humiculum*, *S. granulosus*, *T. sissomi*) or the female (*T. vachoni*, *T. cavicola*, *T. reddelli*, *T. sylvestris*). Eight characters that could not be scored unequivocally in *T. vachoni* using Lourenço's (1981, 2006) descriptions and illustrations are also registered with question marks in this taxon. Two characters are polymorphic in *S. donensis* and *T. sylvestris*, respectively.

Eighty-two characters record the presence, absence, and relative size (‘‘petite’’ vs full size) of the pedipalp trichobothria, in what is the first-ever attempt to homologize all positionally variable trichobothria in a group of scorpions (Figs 5–8), by setal mapping under ultraviolet light, and based on the assumption that differences in the setal patterns of taxa represent gains or losses rather than ‘‘migration’’ events (*sensu* Vachon, 1974). This ‘‘placeholder approach’’ to trichobothrial homology, introduced by Prendini and Volschenk (2007), contends that two or more trichobothria, macro- or microsetae, occupying different ‘‘positions’’ in different taxa, but observed in identical positions on one and the same taxon, fail the test of conjunction and cannot be homologous (Patterson, 1982, 1988; De Pinna, 1991). Different ‘‘positions’’ observed in the same taxon constitute different

Fig. 3. Type localities and habitats of Typhlochactidae Mitchell, 1971. (A,B) El Sótano de Yerbaniz (San Luis Potosí, Mexico), type locality of *Sotanochactas elliotti* (Mitchell, 1971): entrance (A); descent (B). (C,D) Cueva de Escorpión (Oaxaca, Mexico), type locality of *Alacran tartarus* Francke, 1982: *A. tartarus* ♂ collected from flowstone wall (C); *A. tartarus* ♂, habitus, in life (D). Photos courtesy P. Spouse and A.G. Gluesenkamp.

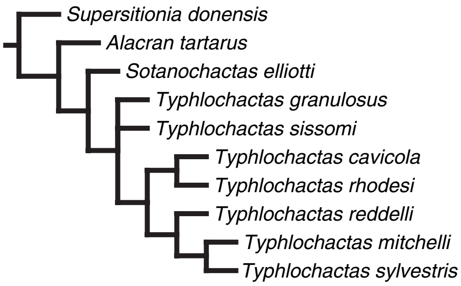

Fig. 4. Previous hypotheses of phylogenetic relationship among the genera and species of Typhlochactidae Mitchell, 1971. Composite of Francke's (1982, p. 59, fig. 26) hypothesis of relationships among *Superstitionia* Stahnke, 1940, *Alacran* Francke, 1982, *Sotanochactas* Francke, 1986 (at the time placed in *Typhlochactas* Mitchell, 1971) and three species of *Typhlochactas* known at the time (*Typhlochactas reddelli* Mitchell, 1968; *Typhlochactas rhodesi* Mitchell, 1968; *Typhlochactas sylvestris* Mitchell and Peck, 1977) to which *Typhlochactas cavicola* Francke, 1986 and *Typhlochactas mitchelli* Sissom, 1988 have been added in accordance with the opinions of previous authors (Francke, 1986; Sissom, 1988). Francke (1986, p. 8) added *T. cavicola* "along the branch leading to *T. rhodesi*". Sissom (1988, p. 370) considered *T. mitchelli* "most similar to *T. sylvestris*". Sissom and Cokendolpher (1998, p. 286) considered *Typhlochactas granulosus* Sissom and Cokendolpher, 1998 "most similar to *T. rhodesi* and *T. reddelli*", which conflicts with Francke's (1982) hypothesis. A phylogenetic position was not proposed for *Typhlochactas sissomi* Francke et al., 2009. These species are therefore placed in a polytomy at the base of *Typhlochactas*.

placeholders which may be expressed as various kinds of setae. For example, the group of five patellar *eb* trichobothria recognized in Vachon's (1974) nomenclatural system also includes four microsetae in some typhlochactids, e.g. *Alacran* (Vignoli and Prendini, 2009), summing to nine placeholders, the differential expression of which leads to the homology scheme presented in Figs 7 and 8 and in Table 3. An illustrated revision of the morphology of typhlochactid scorpions, augmenting the character matrix and descriptions presented here, and applying Vachon's (1974) trichobothrial nomenclature, for comparison with Figs 5–8 and Tables 3 and 4, is provided by Vignoli and Prendini (2009).

### *Cladistic analysis*

Characters were weighted equally *a priori*. Fifty-three uninformative characters, retained in the matrix (Yeates, 1992), were deactivated during the analyses, which are thus based on the 142 informative characters only (Bryant, 1995).

Exact searches with equal weighting were conducted in NONA (Goloboff, 1997a) and TNT (Goloboff et al., 2003–2006, 2008). 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 parameters, in this case, intensity of character weighting (see Prendini, 2000, 2003b, 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. Exact searches were again implemented for analyses with implied weighting, using Pee-Wee (Goloboff, 1997b) and TNT. Results are presented for six values of the concavity constant, *K*.

The support for each node in the tree obtained with equal weighting was assessed with branch support or decay indices (Bremer, 1988, 1994; Donoghue and Sanderson, 1992), calculated in NONA by conducting constrained searches for each node, and by jackknife resampling (Farris et al., 1996; Goloboff et al., 2003) using TNT.

## Results

Analysis of the 142 phylogenetically informative characters located a single most parsimonious tree (MPT) of 312 steps (CI: 57, RI: 56) with equal weighting (Table 5; Fig. 9). A single MPT with the same topology was located by the analyses with implied weighting under six *K* values (Table 5). This topology, obtained by analyses with weighting regimes that minimized length as well as those that maximized fit, is optimal for the data set. Unambiguous synapomorphies and support indices are indicated in this topology in Fig. 9 and the length, fit ($f_i$), CI, and RI of informative characters listed in Table 6.

The topology retrieved by all analyses confirmed the monophyly of Typhlochactidae (Alacraninae + Typhlochactinae) and Typhlochactinae, comprising three genera related to one another as follows: (*Sotanochactas* (*Stygochactas* + *Typhlochactas*)). The topology also confirmed the monophyly of *Troglotayosicus*, *Typhlochactas*, the two hypogean species of *Typhlochactas* from Tamaulipas (*T. cavicola* + *T. rhodesi*) and the two endogean species of *Typhlochactas* from Oaxaca (*T. mitchelli* + *T. sylvestris*). The third endogean *Typhlochactas*, *T. sissomi*, from Queretaro was not monophyletic with the other two endogean species from Oaxaca (*T. mitchelli* + *T. sylvestris*), however, and the hypogean species of Typhlochactidae were rendered paraphyletic by the three endogean species. Typhlochactidae, Typhlochactinae, *Troglotayosicus* and (*T. mitchelli* + *T. sylvestris*) received the highest support.

Table 2
Matrix of 196 characters for nine taxa in the family Typhlochactidae Mitchell, 1971 and three outgroup taxa

| | | | | | |
|---|---|---|---|---|---|
| *Superstitionia donensis* | 000100100[01] | 0011010000 | 0001011010 | 1002122011 | 1001120121 |
| | 1111010010 | 1110101102 | 0200000001 | 0100120001 | 1100011101 |
| | 0100011101 | 1100200000 | 1100000100 | 0100100000 | 2121121100 |
| | 0010001000 | 1100000021 | 1110010011 | 1111111122 | 011100 |
| *Troglotayosicus humiculum* | 1101000011 | 0111000000 | 0001010000 | 0002122011 | 1101121222 |
| | 2211000101 | 1110011001 | 0010010001 | 0010022110 | 0010011101 |
| | 0100000000 | 0100201000 | 1000201110 | 0120110011 | 1011010011 |
| | 11-1111010 | 1?10110021 | ?2?0111010 | 0000000022 | 2-1101 |
| *Troglotayosicus vachoni* | 1101010021 | 010-000000 | 0001010100 | ?002122011 | 1101120121 |
| | 1111000101 | 1110011001 | 0010010001 | 0010022110 | 0010011101 |
| | 0100000000 | 0100201000 | 1000201110 | 0120110000 | ???????100 |
| | 0010001010 | 1?101100?? | 1?20?11010 | 0000000011 | 011102 |
| *Alacran tartarus* | 1100001121 | 1110100000 | 0000100000 | 0110000200 | 0120000000 |
| | 0000101010 | 1101110122 | 1201101001 | 2221022110 | 0011010111 |
| | 0101110002 | 0100202011 | 0100010001 | 110010-011 | 0000000-11 |
| | 11-1020120 | 0110110121 | 1001001000 | 1101100100 | 001012 |
| *Sotanochactas elliotti* | 1100110121 | 1110100011 | 0011001010 | 0012121111 | 1111110111 |
| | 1101001010 | 0001010110 | 1000000110 | 1000021110 | 0011100000 |
| | 1010000001 | 0100201000 | 1011001001 | 0020020111 | 1100010011 |
| | 11-1110120 | 0111011121 | 1001011000 | 1110101110 | 000012 |
| *Stygochactas granulosus* | 1000100121 | 1110000001 | 0000000001 | 0210010200 | 0101110111 |
| | 1111001010 | 0001010101 | 0200000101 | 0100110001 | 1100110000 |
| | 1010000001 | 0100201000 | 1002100100 | 0111010111 | 1100000001 |
| | 1101100120 | 1?11011111 | ?0?1011101 | 2112211122 | 101012 |
| *Typhlochactas cavicola* | 1100100121 | 1110100111 | 0011000010 | 0202122011 | 1101121121 |
| | 2111001010 | 0001010101 | 0200000101 | 0010021110 | 0010011000 |
| | 1010000001 | 0000021100 | 1002100020 | 0111011111 | 1100010001 |
| | 1101100120 | 21101111?? | 1?01?11101 | 2112211122 | 2-1012 |
| *Typhlochactas mitchelli* | 1111210121 | 1110001111 | 1111001012 | 0002122011 | 1101121222 |
| | 2211001010 | 0001010101 | 0200000101 | 1000021110 | 0010011000 |
| | 0010000001 | 0110201000 | 1002100100 | 0111011011 | 1100010000 |
| | 1101100121 | 2110010100 | 0001011101 | 2112211122 | 2-1011 |
| *Typhlochactas reddelli* | 1000010121 | 1110000111 | 0001000000 | ?202122011 | 1101121222 |
| | 2211001010 | 0001010101 | 0200000101 | 0010021110 | 0010011000 |
| | 1010000000 | 0001112000 | 1002100100 | 0111011011 | 1100010011 |
| | 11-1100120 | 21111101?? | 1?01?11101 | 2112211122 | 101012 |
| *Typhlochactas rhodesi* | 1100010121 | 1110101111 | 0011000010 | 0202122011 | 1101110121 |
| | 2211001010 | 0001010101 | 0200000101 | 0010021110 | 0010011000 |
| | 1010000001 | 0000021100 | 1002100020 | 0111011111 | 1100010001 |
| | 1101110121 | 2110110111 | 1001011101 | 2112211122 | 2-1012 |
| *Typhlochactas sissomi* | 1100010121 | 1110110001 | 0011001010 | 0101121011 | 1101120111 |
| | 1111001010 | 0001010121 | 0000000010 | 1000021110 | 0010110000 |
| | 1010000011 | 1000200000 | 1002100020 | 0111011011 | 1100000001 |
| | 1101110120 | 1?11110111 | ?0?1011101 | 2112211121 | 101011 |
| *Typhlochactas sylvestris* | 1111110121 | 1110001111 | 0001001010 | ?002122011 | 1101121222 |
| | 2211001010 | 0001010121 | 1[01]00100000 | 1000021110 | 0010011000 |
| | 0010000001 | 0110201000 | 1002100100 | 0111001011 | 1100010000 |
| | 1101100121 | 20101101?? | 0?01?11101 | 2112211122 | 2-1011 |

Character states are scored 0–2, ? (unknown), and – (inapplicable). Characters that are polymorphic in particular taxa are indicated in square brackets. Refer to Appendix 2 for character descriptions and Table 6 for character statistics.

Based on optimization of the "character" portraying habitat (ecomorphotype: epigean, endogean and hypogean) (Fig. 10), the hypogean condition is ancestral in Typhlochactidae as it also occurs in one of the outgroup taxa, *T. vachoni*. The endogean condition evolved twice independently, once in *T. sissomi* and a second time in the ancestor of *T. mitchelli* and *T. sylvestris*. The endogean condition also evolved independently from the hypogean condition in one of the outgroup taxa, *T. humiculum*.

## Discussion

### *Troglomorphism and troglobitism*

The evolution of troglobites is often considered a unidirectional, irreversible, evolutionary dead-end (Dollo, 1893, 1903, 1922; Cope, 1896; Huxley, 1942; Mayr, 1942, 1988; Simpson, 1944, 1953; Rensch, 1959; Gould, 1970; Sugihara, 1980; Wagner, 1982; Laurent,

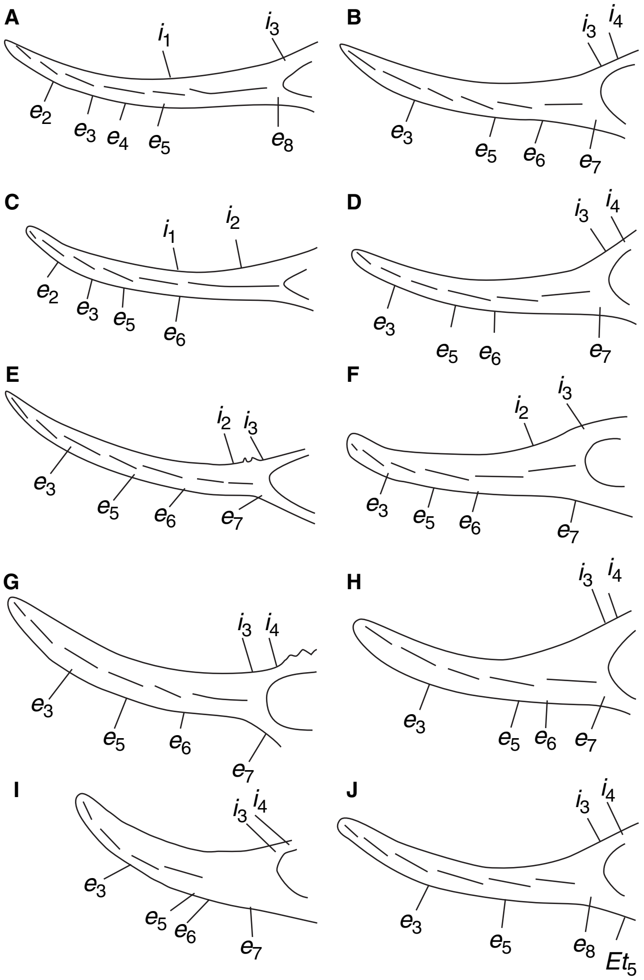

Fig. 5. Sinistral pedipalp chela fixed finger (ventral aspect), showing primary subrows of median denticle row and distribution of trichobothria, homologized according to placeholder approach. (A) *Alacran tartarus* Francke, 1982. (B) *Typhlochactas reddelli* Mitchell, 1968. (C) *Sotanochactas elliotti* (Mitchell, 1971). (D) *Typhlochactas rhodesi* Mitchell, 1968. (E) *Stygochactas granulosus* (Sissom and Cokendolpher, 1998). (F) *Typhlochactas sissomi* Francke et al., 2009. (G) *Typhlochactas cavicola* Francke, 1986. (H) *Typhlochactas sylvestris* Mitchell and Peck, 1977. (I) *Typhlochactas mitchelli* Sissom, 1988. (J) *Superstitionia donensis* Stahnke, 1940. Illustrations modified from originals in Mitchell and Peck (1977), Francke (1982), Sissom (1988) and Sissom and Cokendolpher (1998).

1983; Bull and Charnov, 1985; Futuyma and Moreno, 1988; Futuyma, 1998). Reversal, i.e. the recolonization of endogean or epigean habitats by hypogean taxa, is assumed to be prevented through competitive exclusion by species already occupying, and better adapted to, those habitats (Conway Morris, 1995). Endogean or epigean generalists are thought to possess a wider range of features allowing them to adapt to changing environmental pressures better than hypogean specialists, used to environmental stasis, and for which it may be impossible to reacquire the ancestral state/s necessary to cope with the endogean or epigean habitat; see D'Haese (2000) and Collin and Miglietta (2008) for reviews.

Humphreys (2000) proposed that hypogean species may be able to recolonize epigean and endogean habitats when all potential competitors are removed, and speculated about the existence of epigean and endogean species with hypogean ancestry in the Caribbean region. Epigean and endogean competitors from southern North America, Central America, and northern South America would have been largely eliminated by the thermal pulse following the Chicxulub impact in the Yucatán Peninsula (Hilderbrand, 1993) at the end of the Cretaceous (ca. 65 Mya BP). Some deep cave habitats would probably have been spared the widespread destruction of surface habitats, however, providing a refuge for taxa that may have had epigean and/or endogean relatives prior to the impact.

Volschenk and Prendini (2008) suggested that the unique troglobitic scorpion fauna of Mexico, including several endemic genera that are distantly related to most of the epigean scorpion fauna of the region (and thought to be the result of relatively recent radiations), may represent hypogean relicts of formerly epigean and/or endogean lineages that survived the Chicxulub impact. According to Volschenk and Prendini (2008), the endogean *Typhlochactas* species may represent examples of the recolonization of endogean environments by hypogean ancestors.

In discussing *T. sylvestris*, the first endogean typhlochactid species to be discovered, Mitchell and Peck (1977) proposed precisely the opposite scenario, however. Their scenario was entirely concordant with the conventional view that ecological specialists (stenotopes) evolve from generalist ancestors (eurytopes) and that specialization (in this case to the cavernicolous habitat) is an irreversible evolutionary dead-end. According to Mitchell and Peck (1977, p. 167), the troglomorphies of *T. sylvestris* developed in association with its humicolous habitat and preadapted it for cave life, leading to the subsequent colonization of cavernicolous habitats and the evolution of troglobitic *Typhlochactas* species:

> "Based on the distribution and characteristics of the species of *Typhlochactas*, it is most plausible to argue that the ancestral species inhabited montane litter, where they were widespread. It is entirely possible that these ancestral species may have partially or wholly lost their eyes and pigment as a consequence of adaptation to a cool and humid moist litter habitat because these characteristics appear frequently in other taxa containing 'litter adapted' species such as beetles, collembolans, and millipedes. Such 'preadaptation' may have aided litter inhabitants in cave colonization provided that they could have also withstood behaviourally and physiologically the different set of selection pressures of the cave environments. At the least, the existence of [humicolous] *T. sylvestris* admits to the possibility that the ancestors of the cave species could have been eyeless and depigmented prior to their invasion of the cave

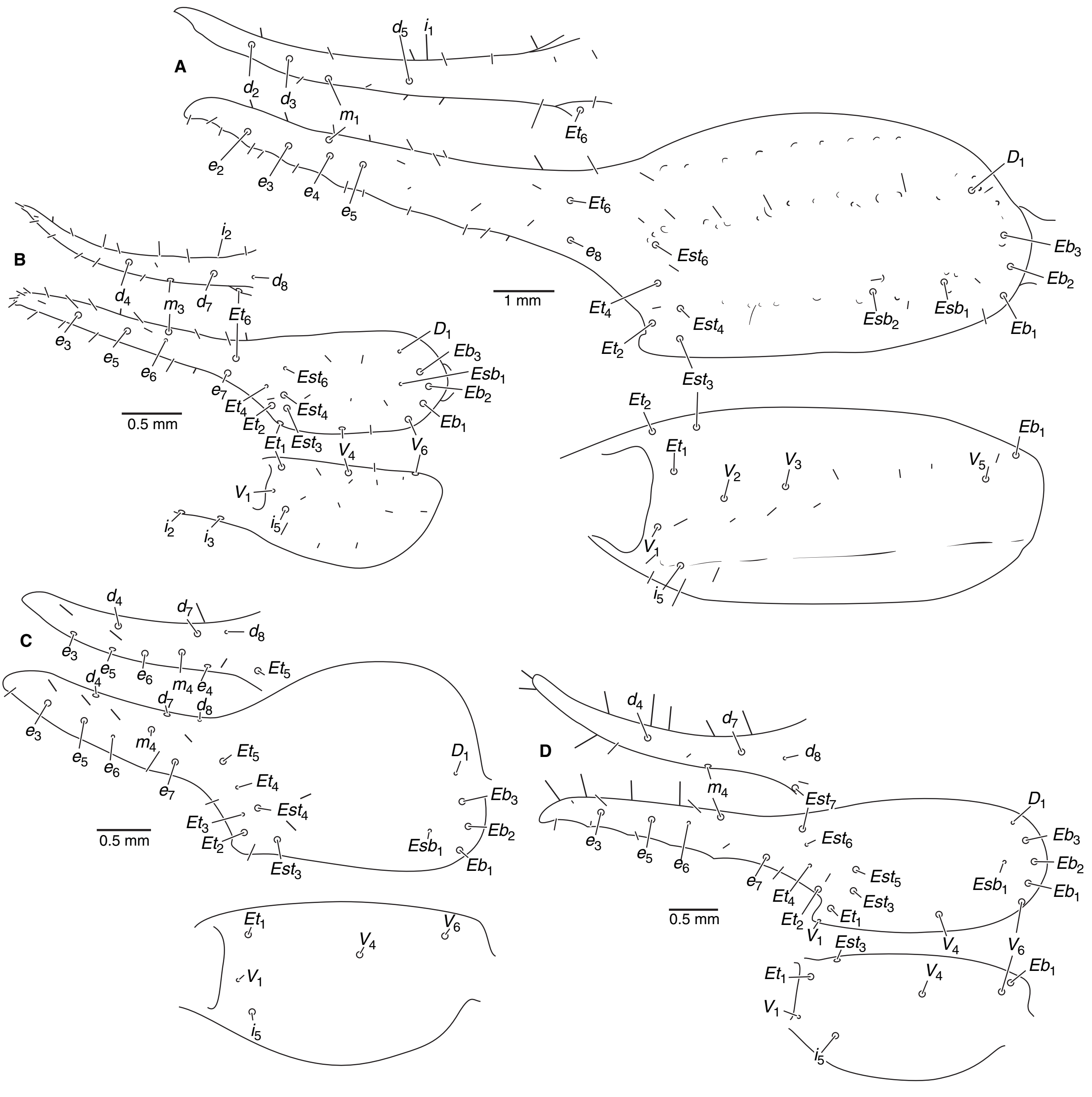

Fig. 6. Sinistral pedipalp chela fixed finger (dorsal aspect), chela (external aspect) and manus (ventral aspect), showing distribution of trichobothria, homologized according to placeholder approach. (A) *Alacran tartarus* Francke, 1982, paratype ♂ (AMNH). (B) *Stygochactas granulosus* (Sissom and Cokendolpher, 1998), juv. ♂ holotype (AMNH) (C) *Typhlochactas sissomi* Francke et al., 2009, subadult ♂ holotype (IBUNAM). (D) *Typhlochactas rhodesi* Mitchell, 1968, holotype ♀ (AMNH). (E) *Sotanochactas elliotti* (Mitchell, 1971), paratype ♂ (WDS). (F) *Typhlochactas cavicola* Francke, 1986, holotype ♀ (AMNH). (G) *Typhlochactas reddelli* Mitchell, 1968, holotype ♀ (AMNH). (H) *Typhlochactas mitchelli* Sissom, 1988, holotype ♂ (AMNH). (I) *Typhlochactas sylvestris* Mitchell and Peck, 1977, holotype ♀ (AMNH). (J) *Superstitionia donensis* Stahnke, 1940, ♂ (AMNH). (K) *Troglotayosicus humiculum* Botero-Trujillo and Francke, 2009, subadult ♂ holotype (IAVH). Scales = 1 mm (A); 0.5 mm (B–K).

environment. On the other hand, the recent discovery of an eyeless diplocentrid scorpion [*Diplocentrus anophthalmus* Francke, 1977] in Yucatán … seem to refute the notion that a scorpion *must* have acquired eyelessness and depigmentation in montane litter prior to cave colonization because no such habitat has been available in Yucatán. To whatever extent the ancestors of *Typhlochactas* may have been 'preadapted' to cave existence, they must have been, at the very least, montane forest litter dwellers. This is the only argument that is consistent with *T. elliotti* showing the greatest degree of cave adaptation, as

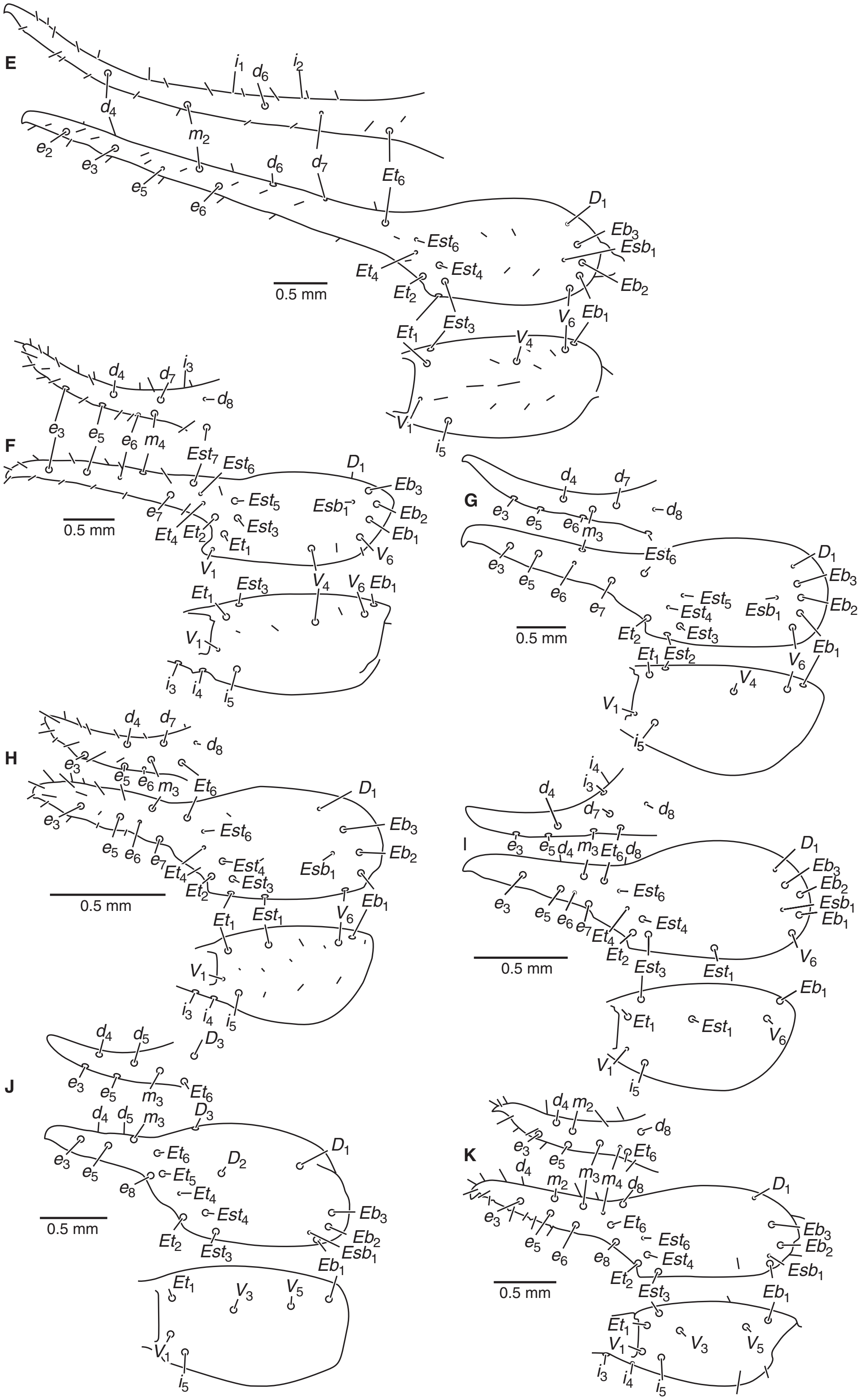

Fig. 6 (*Continued*)

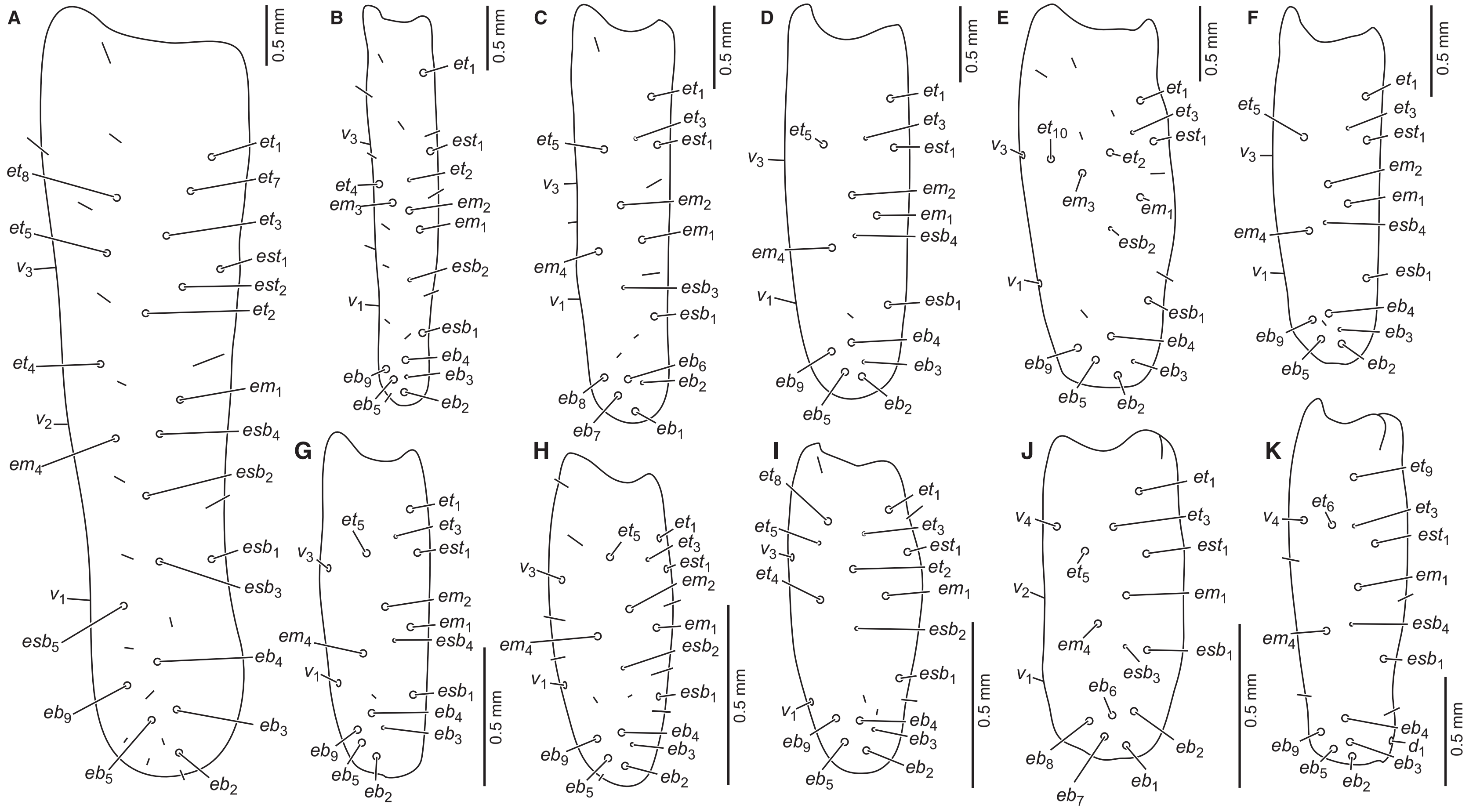

Fig. 7. Sinistral pedipalp patella (external aspect), showing distribution of trichobothria, homologized according to placeholder approach. (A) *Alacran tartarus* Francke, 1982, paratype ♂ (AMNH). (B) *Sotanochactas elliotti* (Mitchell, 1971), paratype ♂ (WDS). (C) *Stygochactas granulosus* (Sissom and Cokendolpher, 1998), juv. ♂ holotype (AMNH). (D) *Typhlochactas rhodesi* Mitchell, 1968, holotype ♀ (AMNH). (E) *Typhlochactas sissomi* Francke et al., 2009, subadult ♂ holotype (IBUNAM). (F) *Typhlochactas cavicola* Francke, 1986, holotype ♀ (AMNH). (G) *Typhlochactas reddelli* Mitchell, 1968, holotype ♀ (AMNH). (H) *Typhlochactas mitchelli* Sissom, 1988, holotype ♂ (AMNH). (I) *Typhlochactas sylvestris* Mitchell and Peck, 1977, holotype ♀ (AMNH). (J) *Superstitionia donensis* Stahnke, 1940, ♂ (AMNH). (K) *Troglotayosicus humiculum* Botero-Trujillo and Francke, 2009, subadult ♂ holotype (IAVH). Scales = 0.5 mm.

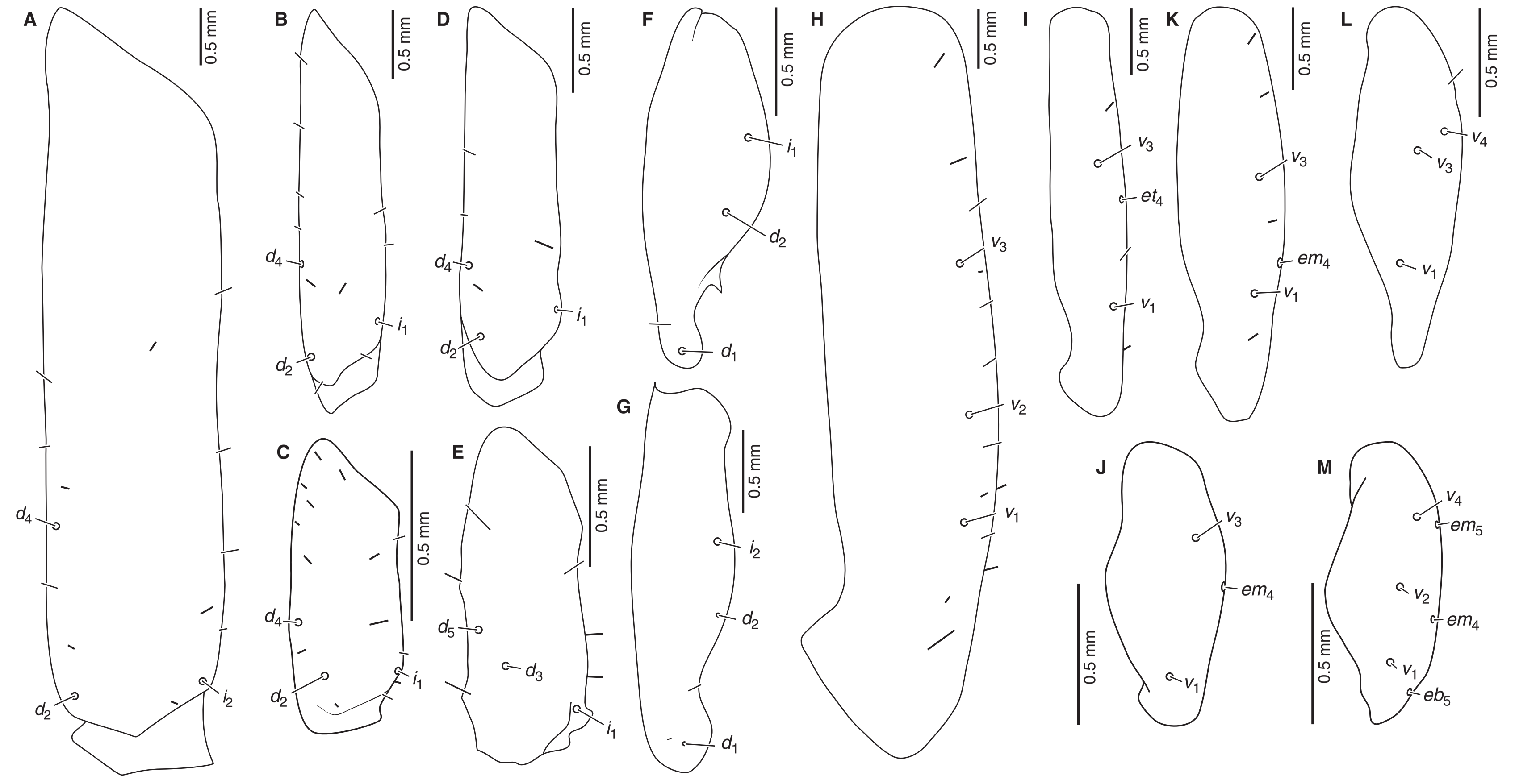

Fig. 8. Sinistral pedipalp femur (dorsal aspect, A–E) and patella (dorsal aspect, F,G; ventral aspect, H–M), showing distribution of trichobothria, homologized according to placeholder approach. (A,H) *Alacran tartarus* Francke, 1982, paratype ♂ (AMNH). (B,I) *Sotanochactas elliotti* (Mitchell, 1971), paratype ♂ (WDS). (C) *Typhlochactas mitchelli* Sissom, 1988, holotype ♂ (AMNH). (D,G,K) *Stygochactas granulosus* (Sissom and Cokendolpher, 1998), juv. ♂ holotype (AMNH). (E,F,L) *Troglotayosicus humiculum* Botero-Trujillo and Francke, 2009, subadult ♂ holotype (IAVH). (J) *Typhlochactas sylvestris* Mitchell and Peck, 1977, holotype ♀ (AMNH). (M) *Superstitionia donensis* Stahnke, 1940, ♂ (AMNH). Scales = 0.5 mm.

Table 3
Trichobothrial homology on pedipalp femur and patella of Typhlochactidae Mitchell, 1971 and related taxa according to Vachon's (1974) nomenclature, as implemented in Vignoli and Prendini (2009)

| | | *Super.* | *Trogl.* | *Alacr.* | *Sotan.* | *Stygo.* | *T. sis.* | *T. cav.*<br>*T. rho.* | *T. red.* | *T. mit.* | *T. syl.* |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Femur | $i_1$ | $i$ | $i$ | | $i$ | $i$ | $i$ | $i$ | $i$ | $i$ | $i$ |
| | $i_2$ | | | $i$ | | | | | | | |
| | $d_1$ | $d$ | | | | | | | | | |
| | $d_2$ | | | $d$ | $d$ | $d$ | $d$ | $d$ | $d$ | $d$ | $d$ |
| | $d_3$ | | $d$ | | | | | | | | |
| | $d_4$ | $e$ | | $e$ | $e$ | $e$ | $e$ | $e$ | $e$ | $e$ | $e$ |
| | $d_5$ | | $e$ | | | | | | | | |
| Patella | $d_1$ | $d_1$ | $d_1$ | $d_1$ | $[d_1]$ | $[d_1]$ | $[d_1]$ | $[d_1]$ | $[d_1]$ | $[d_1]$ | $[d_1]$ |
| | $d_2$ | $d_2$ | $d_2$ | $d_2$ | $[d_2]$ | $[d_2]$ | $[d_2]$ | $[d_2]$ | $[d_2]$ | $[d_2]$ | $[d_2]$ |
| | $i_1$ | $i$ | $i$ | | | | | | | | |
| | $i_2$ | | | $i$ | $i$ | $i$ | $i$ | $i$ | $i$ | $i$ | $i$ |
| | $v_1$ | $v_1$ | $v_1$ | $v_1$ | $v_1$ | $v_1$ | $v_1$ | $v_1$ | $v_1$ | $v_1$ | $v_1$ |
| | $v_2$ | $v_2$ | | $v_2$ | | | | | | | |
| | $v_3$ | | $v_2$ | $v_3$ | $v_2$ | $v_2$ | $v_2$ | $v_2$ | $v_2$ | $v_2$ | $v_2$ |
| | $v_4$ | $v_3$ | $v_3$ | | | | | | | | |
| | $et_1$ | $et_1$ | | $et_1$ | $et_1$ | $et_1$ | $et_1$ | $et_1$ | $et_1$ | $et_1$ | $et_1$ |
| | $et_2$ | | | $em_2$ | $[et_2]$ | | $em_2$ | | | | $em_2$ |
| | $et_3$ | $et_2$ | $[et_2]$ | $et_2$ | | $[et_2]$ | $[et_2]$ | $[et_2]$ | $[et_2]$ | $[et_2]$ | $[et_2]$ |
| | $et_4$ | | | $em_{a1}$ | $et_3$ | | | | | | $em_3$ |
| | $et_5$ | $et_3$ | | $et_3$ | | $et_3$ | | $et_3$ | $et_3$ | $et_3$ | abs. or $[v_3]$ |
| | $et_6$ | | $et_3$ | | | | | | | | |
| | $et_7$ | | | $et_{a1}$ | | | | | | | |
| | $et_8$ | | | $et_{a2}$ | | | | | | | $et_3$ |
| | $et_9$ | | $et_1$ | | | | | | | | |
| | $est_1$ | $est_1$ | $est_1$ | $est_1$ | $est_1$ | $est_1$ | $est_1$ | $est_1$ | $est_1$ | $est_1$ | $est_1$ |
| | $est_2$ | | | $est_a$ | | | | | | | |
| | $em_1$ | $em_1$ | $em_1$ | $em_1$ | $em_1$ | $em_1$ | $em_1$ | $em_1$ | $em_1$ | $em_1$ | $em_1$ |
| | $em_2$ | | | | $em_2$ | $em_2$ | | $em_2$ | $em_2$ | $em_2$ | |
| | $em_3$ | | | | $em_3$ | | $em_3$ | | | | |
| | $em_4$ | $em_2$ | $em_2$ | $em_3$ | | $em_3$ | | $em_3$ | $em_3$ | $em_3$ | |
| | $esb_1$ | $esb_1$ | $esb_1$ | $esb_1$ | $esb_1$ | $esb_1$ | $esb_1$ | $esb_1$ | $esb_1$ | $esb_1$ | $esb_1$ |
| | $esb_2$ | | | $esb_2$ | $[esb_2]$ | | $[esb_2]$ | | | $[esb_2]$ | $[esb_2]$ |
| | $esb_3$ | $[esb_2]$ | | $esb_{a1}$ | | $[esb_2]$ | | | | | |
| | $esb_4$ | | $[esb_2]$ | $em_{a2}$ | | | | $[esb_2]$ | $[esb_2]$ | | |
| | $esb_5$ | | | $esb_{a2}$ | | | | | | | |
| | $eb_1$ | $eb_1$ | | | | $eb_1$ | | | | | |
| | $eb_2$ | $eb_2$ | $eb_1$ | $eb_1$ | $eb_1$ | $[eb_2]$ | $eb_1$ | $eb_1$ | $eb_1$ | $eb_1$ | $eb_1$ |
| | $eb_3$ | | $eb_2$ | $eb_2$ | $[eb_2]$ | | $[eb_2]$ | $[eb_2]$ | $[eb_2]$ | $[eb_2]$ | $[eb_2]$ |
| | $eb_4$ | | $eb_3$ | $eb_3$ | $eb_3$ | | $eb_3$ | $eb_3$ | $eb_3$ | $eb_3$ | $eb_3$ |
| | $eb_5$ | | $eb_4$ | $eb_4$ | $eb_4$ | | $eb_4$ | $eb_4$ | $eb_4$ | $eb_4$ | $eb_4$ |
| | $eb_6$ | $eb_3$ | | | | $eb_3$ | | | | | |
| | $eb_7$ | $eb_4$ | | | | $eb_4$ | | | | | |
| | $eb_8$ | $eb_5$ | | | | $eb_5$ | | | | | |
| | $eb_9$ | | $eb_5$ | $eb_5$ | $eb_5$ | | $eb_5$ | $eb_5$ | $eb_5$ | $eb_5$ | $eb_5$ |

Each row represents trichobothrium in topographically similar position among different taxa. First column, nomenclature according to the "placeholder" approach, as implemented in analyses presented here (Figs 5–8). Petite trichobothria (*sensu* Vachon, 1974) denoted by square brackets. Taxa as follows: *Super.* = *Superstitionia* Stahnke, 1940; *Trogl.* = *Troglotayosicus* Lourenço, 1981; *Alacr.* = *Alacran* Francke, 1982; *Sotan.* = *Sotanochactas* Francke, 1986; *Stygo.* = *Stygochactas* Vignoli and Prendini, 2009; *T. sis.* = *Typhlochactas sissomi* Francke et al., 2009; *T. cav.* = *Typhlochactas cavicola* Francke, 1986; *T. rho.* = *Typhlochactas rhodesi* Mitchell, 1968; *T. red.* = *Typhlochactas reddelli* Mitchell, 1968; *T. mit.* = *Typhlochactas mitchelli* Sissom, 1988; *T. syl.* = *Typhlochactas sylvestris* Mitchell and Peck, 1977. All taxa bilaterally symmetrical except *T. sylvestris*, which has an extra trichobothrium on the dextral pedipalp patella. The trichobothrial patterns of *T. cavicola* and *T. rhodesi* are identical.

> well as *T. sylvestris* the least (as reflected by slenderness of body and general appendage attenuation)."

As pointed out by Volschenk and Prendini (2008), it seems more plausible that the ancestors of endogean *Typhlochactas* species were troglobites that recolonized the endogean environment, because all other endogean scorpions (with the exception of *Belisarius xambeui* Simon, 1879) are pigmented and possess well developed ocelli, suggesting that the troglomorphies of endogean *Typhlochactas* species were inherited from hypogean

Table 4
Trichobothrial homology on pedipalp chela of Typhlochactidae Mitchell, 1971 and related taxa according to Vachon's (1974) nomenclature, as implemented in Vignoli and Prendini (2009)

| | | *Super.* | *Trogl.* | *Alacr.* | *Sotan.* | *Stygo.* | *T. sis.* | *T. cav.*<br>*T. rho.* | *T. red.* | *T. mit.* | *T. syl.* |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Chela | $i_1$ | | | *it* | *it* | | | | | | |
| | $i_2$ | | | | *ib* | *it* | *it* | | | | |
| | $i_3$ | *it* | *it* | *ib* | | *ib* | *ib* | *it* | *it* | *it* | *it* |
| | $i_4$ | *ib* | *ib* | | | | | *ib* | *ib* | *ib* | *ib* |
| | $i_5$ | $V_2$ | $V_2$ | $V_2$ | $V_2$ | $V_2$ | $V_2$ | $V_2$ | $V_2$ | $V_2$ | $V_2$ |
| | $V_1$ | $V_1$ | $V_1$ | $V_1$ | [$V_1$] | [$V_1$] | [$V_1$] | [$V_1$] | [$V_1$] | [$V_1$] | [$V_1$] |
| | $V_2$ | | | $V_a$ | | | | | | | |
| | $V_3$ | $V_3$ | $V_3$ | $V_3$ | | | | | | | |
| | $V_4$ | | | | $V_3$ | $V_3$ | $V_3$ | $V_3$ | $V_3$ | | |
| | $V_5$ | $V_4$ | $V_4$ | $V_4$ | | | | | | | |
| | $V_6$ | | | | $V_4$ | $V_4$ | $V_4$ | $V_4$ | $V_4$ | $V_4$ | $V_4$ |
| | $Eb_1$ | $Eb_1$ | $Eb_1$ | $Eb_1$ | $Eb_1$ | $Eb_1$ | $Eb_1$ | $Eb_1$ | $Eb_1$ | $Eb_1$ | $Eb_1$ |
| | $Eb_2$ | $Eb_2$ | $Eb_2$ | $Eb_2$ | $Eb_2$ | $Eb_2$ | $Eb_2$ | $Eb_2$ | $Eb_2$ | $Eb_2$ | $Eb_2$ |
| | $Eb_3$ | $Eb_3$ | $Eb_3$ | $Eb_3$ | $Eb_3$ | $Eb_3$ | $Eb_3$ | $Eb_3$ | $Eb_3$ | $Eb_3$ | $Eb_3$ |
| | $Esb_1$ | [*Esb*] | [*Esb*] | *Esb* | [*Esb*] | [*Esb*] | [*Esb*] | [*Esb*] | [*Esb*] | [*Esb*] | [*Esb*] |
| | $Esb_2$ | | | *Em* | | | | | | | |
| | $D_1$ | *Db* | [*Db*] | *Db* | [*Db*] | [*Db*] | [*Db*] | [*Db*] | [*Db*] | [*Db*] | [*Db*] |
| | $D_2$ | $Et_5$ | | | | | | | | | |
| | $D_3$ | *db* | | | | | | | | | |
| | $Et_1$ | $Et_1$ | $Et_1$ | $Et_1$ | $Et_1$ | $Et_1$ | $Et_1$ | $Et_1$ | $Et_1$ | $Et_1$ | $Et_1$ |
| | $Et_2$ | $Et_2$ | $Et_2$ | $Et_2$ | $Et_2$ | $Et_2$ | $Et_2$ | $Et_2$ | $Et_2$ | $Et_2$ | $Et_2$ |
| | $Et_3$ | | | | | | [$Et_4$] | | | | |
| | $Et_4$ | [$Et_4$] | | $Et_4$ | [$Et_4$] | [$Et_4$] | [$Et_5$] | [$Et_4$] | | [$Et_4$] | [$Et_4$] |
| | $Et_5$ | *esb* | | | | | *Dt* | | | | |
| | $Et_6$ | *Dt* | $Et_5$ | *Dt* | *Dt* | *Dt* | | | | *Dt* | *Dt* |
| | $Est_1$ | | | | | | | | | $V_3$ | $V_3$ |
| | $Est_2$ | | | | | | | | *Est* | | |
| | $Est_3$ | *Est* | *Est* | *Est* | *Est* | *Est* | *Est* | *Est* | *Est* | *Est* | *Est* |
| | $Est_4$ | $Et_3$ | $Et_3$ | $Et_3$ | $Et_3$ | $Et_3$ | $Et_3$ | | [$Et_4$] | $Et_3$ | $Et_3$ |
| | $Est_5$ | | | | | | | $Et_3$ | [$Et_5$] | | |
| | $Est_6$ | | [$Et_4$] | $Et_5$ | [$Et_5$] | [$Et_5$] | | [$Et_5$] | *Dt* | [$Et_5$] | [$Et_5$] |
| | $Est_7$ | | | | | | | *Dt* | | | |
| | $d_2$ | | | *dt* | | | | | | | |
| | $d_3$ | | | *dst* | | | | | | | |
| | $d_4$ | *dt* | *dt* | | *dt* | *dt* | *dt* | *dt* | *dt* | *dt* | *dt* |
| | $d_5$ | *dst* | | *db* | | | | | | | |
| | $d_6$ | | | | *dst* | | | | | | |
| | $d_7$ | | | | [*db*] | *dst* | *dst* | *dst* | *dst* | *dst* | *dst* |
| | $d_8$ | | *db* | | | [*db*] | [*db*] | [*db*] | [*db*] | [*db*] | [*db*] |
| | $m_1$ | | | *dsb* | | | | | | | |
| | $m_2$ | | *dst* | | *dsb* | | | | | | |
| | $m_3$ | *dsb* | *dsb* | | | *dsb* | | | *dsb* | *dsb* | *dsb* |
| | $m_4$ | | [*Dt*] | | | | *dsb* | *dsb* | | | |
| | $e_2$ | | | *et* | *et* | | | | | | |
| | $e_3$ | *et* | *et* | *est* | *est* | *et* | *et* | *et* | *et* | *et* | *et* |
| | $e_4$ | | | *em* | | | | | | | |
| | $e_5$ | *est* | *est* | *esb* | [*esb*] | *est* | *est* | *est* | *est* | *est* | *est* |
| | $e_6$ | | *esb* | | *eb* | [*esb*] | [*esb*] | [*esb*] | [*esb*] | [*esb*] | [*esb*] |
| | $e_7$ | | | | | *eb* | *eb* | *eb* | *eb* | *eb* | *eb* |
| | $e_8$ | *eb* | *eb* | *eb* | | | | | | | |

Each row represents trichobothrium in topographically similar position among different taxa. First column, nomenclature according to the "placeholder" approach, as implemented in analyses presented here (Figs 5–8). Petite trichobothria (*sensu* Vachon, 1974) denoted by square brackets.Taxa as follows: *Super.* = *Superstitionia* Stahnke, 1940; *Trogl.* = *Troglotayosicus* Lourenço, 1981; *Alacr.* = *Alacran* Francke, 1982; *Sotan.* = *Sotanochactas* Francke, 1986; *Stygo.* = *Stygochactas* Vignoli and Prendini, 2009; *T. sis.* = *Typhlochactas sissomi* Francke et al., 2009; *T. cav.* = *Typhlochactas cavicola* Francke, 1986; *T. rho.* = *Typhlochactas rhodesi* Mitchell, 1968; *T. red.* = *Typhlochactas reddelli* Mitchell, 1968; *T. mit.* = *Typhlochactas mitchelli* Sissom, 1988; *T. syl.* = *Typhlochactas sylvestris* Mitchell and Peck, 1977. The trichobothrial patterns of *T. cavicola* and *T. rhodesi* are identical.

Table 5
Statistical differences among the most parsimonious trees (MPTs) obtained by analysis under implied weighting (IW) with six values for the concavity constant ($K$), arranged in order of decreasing fit

| | MPT | Steps | Fit ($F_i$) | Rescaled fit (%) | CI | RI |
|---|---|---|---|---|---|---|
| IW: $K = 6$ | 1 | 312 | 1241.9 | 52 | 57 | 56 |
| IW: $K = 5$ | 1 | 312 | 1217.1 | 51 | 57 | 56 |
| IW: $K = 4$ | 1 | 312 | 1183.1 | 50 | 57 | 56 |
| IW: $K = 3$ | 1 | 312 | 1133.0 | 49 | 57 | 56 |
| IW: $K = 2$ | 1 | 312 | 1047.0 | 47 | 57 | 56 |
| IW: $K = 1$ | 1 | 312 | 898.4 | 43 | 57 | 56 |

ancestors rather than vice versa. Volschenk and Prendini (2008, p. 249) noted further that this hypothesis was supported partly by the terminal placement of *T. sylvestris*, relative to *Alacran*, *Sotanochactas*, and two of the troglobitic species of *Typhlochactas* in Francke's (1982) figure 26, but that it awaited rigorous testing using modern cladistic methods, a complete taxon sample of *Typhlochactas* and additional characters.

A basal placement for the endogean species would be required to support the hypothesis of Mitchell and Peck (1977). However, as demonstrated in our analyses, that is not the case. The hypogean species of Typhlochactidae were rendered paraphyletic by the three endogean species, which are situated relatively distal in the phylogeny (Fig. 9). According to the optimization of habitat (ecomorphotype: epigean, endogean, and hypogean) on the tree, the hypogean condition is ancestral in Typhlochactidae and the endogean condition evolved twice independently from the hypogean condition: once in *T. sissomi* and a second time in the ancestor of *T. mitchelli* and *T. sylvestris* (Fig. 10). The endogean condition also evolved independently from the hypogean condition in one of the outgroup taxa, *T. humiculum*.

Desutter-Grandcolas (1993, 1994, 1997) demonstrated a similar pattern of recolonization of epigean habitats by troglobitic ancestors in Central American crickets. As in this and other cladistic tests of adaptational hypotheses (Coddington, 1986a,b, 1988; Siddall et al., 1993; Blaxter et al., 1998; Nielsen, 1998; D'Haese, 2000; Collin and Miglietta, 2008), our findings challenge the conventional wisdom that ecological specialization (stenotopy) is unidirectional and irreversible, and provide another empirical example that falsifies Cope's (1896) law of the unspecialized and Dollo's (1893, 1903, 1922) law of evolutionary irreversibility (Huxley, 1942; Mayr, 1942, 1988; Simpson, 1944, 1953; Rensch, 1959; Gould, 1970; Sugihara, 1980; Wagner, 1982; Laurent, 1983; Bull and Charnov, 1985; Futuyma and Moreno, 1988; Futuyma, 1998). The phylogeny of Typhlochactidae demonstrates that troglobitism is not an evolutionary dead-end: endogean scorpions evolved from hypogean ancestors on more than one occasion.

### *Trichobothriotaxy*

Since Vachon's (1974) seminal publication, pedipalp trichobothria have been regarded as an important character system for scorpion higher-level systematics. Primary homology assessment of trichobothria remains contentious, however (Lamoral, 1979; Francke and Soleglad, 1981; Francke, 1982; Stockwell, 1989; Sissom, 1990; Prendini, 2000; Prendini and Wheeler, 2005; Prendini et al., 2006; Francke and Prendini, 2008). The assumption of trichobothrial "migration", invoked by Vachon (1974) to account for positional differences between putatively homologous trichobothria, is increasingly questioned (Prendini and Volschenk, 2007). As pointed out by Francke and Soleglad (1981, p. 238) and Francke (1982, pp. 59, 60), there is neither evidence nor a plausible explanation—one that would account not only for movement of the setae, but also their associated bipolar neurons—for migration. In contrast, there is abundant evidence for the loss or gain of trichobothria (e.g. Vachon, 1974).

The apparent "migration" (different positions) of some putatively homologous trichobothria can, to some extent, be explained as an inaccurate interpretation of changes in the shape or length of the pedipalp segment on which they occur (Prendini, 2000), including allometry, a possible example of which was offered by Francke (1982, p. 60). Many positional differences cannot be explained on the basis of allometric changes in the shape or length of the pedipalp segments, however. None is more difficult to explain in the current Vachonian paradigm than when two or more trichobothria, considered homologous (and therefore assigned the same designation, e.g. $esb_1$) in different orthobothriotaxic taxa, despite occupying different "positions", are observed in identical positions on one and the same neobothriotaxic taxon, a fairly common occurrence. Such observations fail the test of conjunction, which asserts that if two or more structures are found in the same organism, they cannot be homologous (Patterson, 1982, 1988; De Pinna, 1991) and prove, beyond doubt, that trichobothria situated in different positions in different taxa are not necessarily homologous. These observations call into question the legitimacy of many characters concerning the relative positions of trichobothria used in analyses of scorpion phylogeny over the past two decades. In our opinion, each trichobothrial position (placeholder) must be treated as a character, and detailed mapping of the distribution of trichobothria, macro-, and microsetae, as presented here, is required for primary homology assessment of placeholders.

The performance of the placeholder approach in the present study, as evidenced by two metrics, is encouraging. First, the average $f_i$ and CI for 50 phylogenetically informative placeholder characters (8.2 and 71,

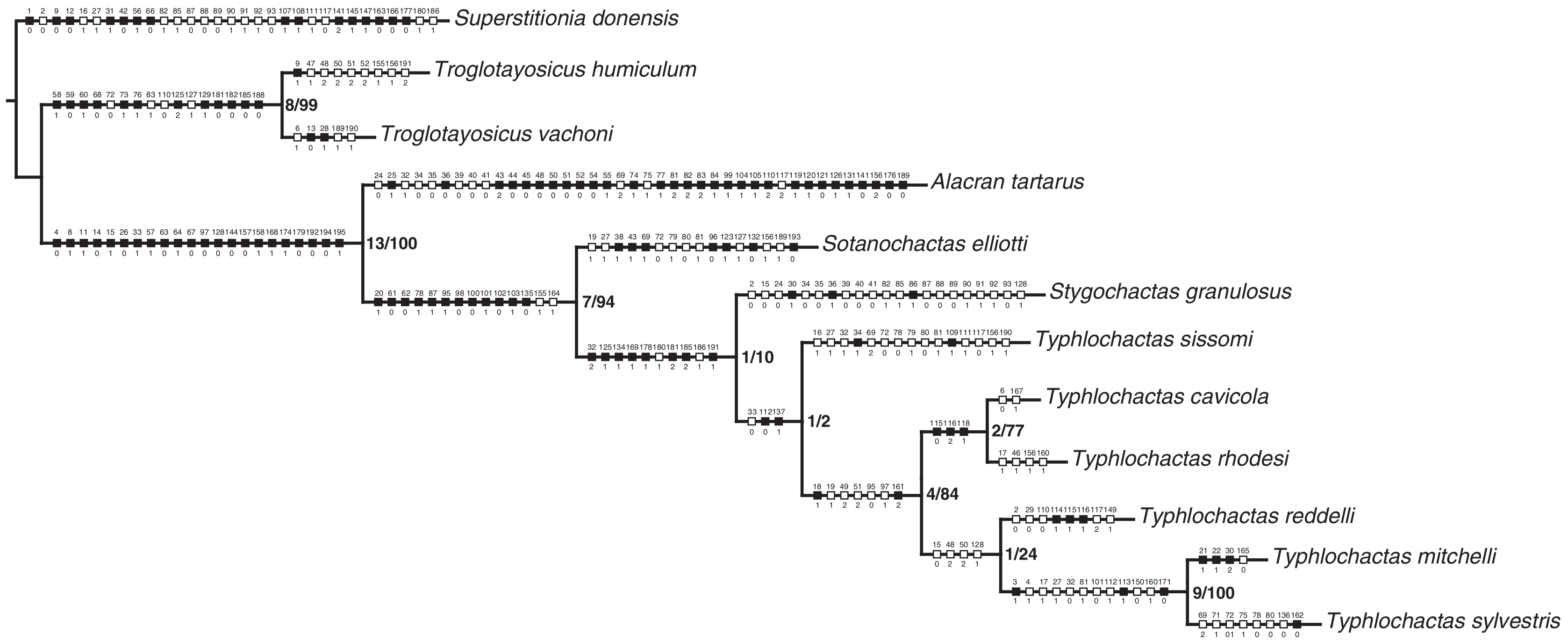

Fig. 9. Single most parsimonious tree (312 steps, CI: 57, RI: 56) obtained by cladistic analysis of 143 morphological characters scored for nine taxa in the family Typhlochactidae Mitchell, 1971 and three outgroup taxa under weighting regimes that maximized fit and minimized length. This topology was 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 numbers in front of each node give the branch support values (left) and jackknife percentages (right). Refer to Table 2 for character matrix and Appendix 2 for character descriptions.

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 maximized fit and minimized length (Fig. 9)

| Char. | Steps | $f_i$ | CI | RI | Char. | Steps | $f_i$ | CI | RI | Char. | Steps | $f_i$ | CI | RI |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 2 | 3 | 6 | 33 | 0 | 65 | 2 | 7.5 | 50 | 0 | 137 | 5 | 7.5 | 40 | 0 |
| 3 | 1 | 10 | 100 | 100 | 67 | 1 | 10 | 100 | 100 | 138 | 1 | 10 | 100 | 100 |
| 4 | 2 | 7.5 | 50 | 75 | 68 | 1 | 10 | 100 | 100 | 139 | 1 | 10 | 100 | 100 |
| 5 | 5 | 5 | 40 | 0 | 69 | 4 | 6 | 50 | 0 | 142 | 3 | 7.5 | 66 | 80 |
| 6 | 4 | 5 | 25 | 25 | 70 | 3 | 7.5 | 66 | 0 | 146 | 4 | 6 | 25 | 0 |
| 7 | 2 | 7.5 | 50 | 0 | 71 | 3 | 6 | 33 | 0 | 148 | 3 | 7.5 | 33 | 0 |
| 8 | 1 | 10 | 100 | 100 | 72 | 3 | 5 | 33 | 33 | 149 | 1 | 5 | 100 | 100 |
| 11 | 1 | 10 | 100 | 100 | 75 | 2 | 7.5 | 50 | 0 | 150 | 2 | 6 | 100 | 100 |
| 14 | 1 | 10 | 100 | 100 | 76 | 1 | 7.5 | 100 | 100 | 151 | 1 | 7.5 | 100 | 100 |
| 15 | 3 | 6 | 33 | 50 | 77 | 1 | 10 | 100 | 100 | 152 | 1 | 7.5 | 100 | 100 |
| 16 | 2 | 7.5 | 50 | 0 | 79 | 2 | 10 | 50 | 0 | 153 | 1 | 10 | 100 | 100 |
| 17 | 2 | 7.5 | 50 | 50 | 80 | 3 | 10 | 33 | 0 | 154 | 1 | 7.5 | 100 | 100 |
| 18 | 1 | 10 | 100 | 100 | 81 | 4 | 6 | 50 | 33 | 155 | 4 | 7.5 | 50 | 0 |
| 19 | 2 | 7.5 | 50 | 80 | 82 | 3 | 10 | 66 | 0 | 156 | 1 | 5 | 100 | 100 |
| 20 | 1 | 10 | 100 | 100 | 85 | 2 | 10 | 50 | 0 | 157 | 3 | 10 | 33 | 33 |
| 23 | 4 | 5 | 25 | 25 | 87 | 3 | 7.5 | 66 | 66 | 158 | 2 | 10 | 50 | 0 |
| 24 | 2 | 7.5 | 50 | 0 | 88 | 2 | 10 | 50 | 0 | 159 | 2 | 10 | 50 | 0 |
| 26 | 1 | 10 | 100 | 100 | 90 | 2 | 6 | 50 | 0 | 160 | 2 | 7.5 | 100 | 100 |
| 27 | 4 | 5 | 25 | 25 | 91 | 2 | 7.5 | 50 | 0 | 161 | 2 | 7.5 | 50 | 0 |
| 29 | 4 | 5 | 25 | 25 | 92 | 2 | 6 | 50 | 0 | 164 | 1 | 6 | 100 | 100 |
| 32 | 4 | 6 | 50 | 50 | 93 | 2 | 6 | 50 | 0 | 165 | 4 | 5 | 50 | 0 |
| 33 | 2 | 7.5 | 50 | 50 | 94 | 2 | 7.5 | 50 | 0 | 167 | 2 | 6 | 50 | 0 |
| 34 | 3 | 7.5 | 66 | 0 | 95 | 2 | 6 | 50 | 50 | 168 | 4 | 10 | 25 | 0 |
| 35 | 2 | 7.5 | 50 | 0 | 98 | 1 | 7.5 | 100 | 100 | 169 | 3 | 10 | 33 | 33 |
| 37 | 4 | 6 | 50 | 0 | 100 | 1 | 10 | 100 | 100 | 171 | 2 | 10 | 50 | 0 |
| 38 | 3 | 7.5 | 66 | 0 | 101 | 2 | 10 | 50 | 80 | 174 | 1 | 10 | 100 | 100 |
| 39 | 2 | 7.5 | 50 | 0 | 103 | 1 | 7.5 | 100 | 100 | 178 | 1 | 10 | 100 | 100 |
| 40 | 2 | 7.5 | 50 | 0 | 106 | 2 | 7.5 | 50 | 0 | 179 | 1 | 10 | 100 | 100 |
| 41 | 2 | 7.5 | 50 | 0 | 111 | 2 | 7.5 | 50 | 0 | 180 | 2 | 7.5 | 50 | 66 |
| 46 | 4 | 6 | 50 | 0 | 112 | 2 | 7.5 | 50 | 66 | 181 | 2 | 10 | 100 | 100 |
| 47 | 3 | 6 | 33 | 50 | 113 | 1 | 7.5 | 100 | 100 | 182 | 1 | 10 | 100 | 100 |
| 48 | 3 | 7.5 | 66 | 66 | 114 | 1 | 7.5 | 100 | 100 | 183 | 2 | 7.5 | 50 | 50 |
| 49 | 3 | 7.5 | 66 | 50 | 115 | 2 | 7.5 | 100 | 100 | 184 | 3 | 7.5 | 66 | 66 |
| 50 | 3 | 7.5 | 66 | 66 | 116 | 2 | 7.5 | 100 | 100 | 185 | 2 | 10 | 100 | 100 |
| 51 | 3 | 7.5 | 66 | 75 | 117 | 4 | 7.5 | 50 | 0 | 186 | 2 | 7.5 | 50 | 66 |
| 52 | 4 | 6 | 50 | 50 | 118 | 1 | 7.5 | 100 | 100 | 187 | 2 | 7.5 | 50 | 50 |
| 53 | 2 | 7.5 | 50 | 0 | 122 | 2 | 10 | 50 | 0 | 188 | 1 | 10 | 100 | 100 |
| 57 | 1 | 10 | 100 | 100 | 124 | 2 | 6 | 100 | 100 | 189 | 3 | 7.5 | 66 | 0 |
| 58 | 1 | 10 | 100 | 100 | 125 | 2 | 10 | 100 | 100 | 190 | 4 | 6 | 50 | 0 |
| 59 | 1 | 10 | 100 | 100 | 127 | 2 | 7.5 | 50 | 50 | 191 | 4 | 6 | 50 | 60 |
| 60 | 1 | 10 | 100 | 100 | 128 | 3 | 7.5 | 33 | 50 | 192 | 1 | 10 | 100 | 100 |
| 61 | 1 | 10 | 100 | 100 | 130 | 2 | 7.5 | 50 | 0 | 194 | 1 | 10 | 100 | 100 |
| 62 | 1 | 10 | 100 | 100 | 133 | 3 | 7.5 | 66 | 66 | 195 | 1 | 10 | 100 | 100 |
| 63 | 1 | 10 | 100 | 100 | 134 | 1 | 10 | 100 | 100 | | | | | |
| 64 | 1 | 10 | 100 | 100 | 136 | 2 | 10 | 50 | 50 | | | | | |

respectively) is greater than the averages for 81 phylogenetically informative characters pertaining to other aspects of scorpion morphology (7.8 and 66, respectively; Table 6). Second, there is a large degree of congruence between the topology in Fig. 9 and that of Francke (1982), reproduced here in Fig. 4.

### *Typhlochactid phylogeny*

The phylogenetic relationships of typhlochactid scorpions have remained enigmatic since the first two species of *Typhlochactas* were described (Francke, 1982). Mitchell (1968) created subfamily Typhlochactinae to accommodate them and placed it within Chactidae Laurie, 1896. Following the description of two additional species of *Typhlochactas* (Mitchell, 1971; Mitchell and Peck, 1977), and of the genus *Alacran*, Francke (1982, p. 57) postulated that three characters ignored by Mitchell (1968) are actually synapomorphic for the two genera. Francke (1982) followed Mitchell (1968) in discounting a close phylogenetic relationship between them and *Belisarius xambeui*, a troglomorphic endogean species from the Pyrenees of France and Spain, and instead proposed a close relationship to *Superstitionia*

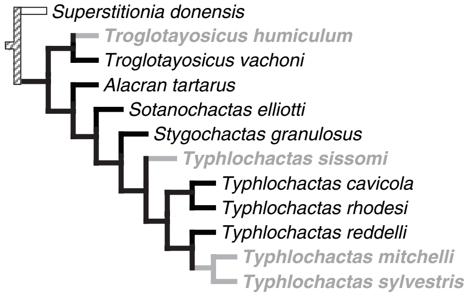

Fig. 10. Habitat (ecomorphotype) optimized on the single most parsimonious tree obtained by cladistic analysis of 143 morphological characters scored for nine taxa in the family Typhlochactidae Mitchell, 1971 and three outgroup taxa. Branch leading to epigean (lapidicolous) taxon indicated in white: *Superstitionia donensis* Stahnke, 1940. Branches leading to endogean (humicolous) taxa indicated in grey: *Troglotayosicus humiculum* Botero-Trujillo and Francke, 2009; *Typhlochactas mitchelli* Sissom, 1988; *Typhlochactas sissomi* Francke et al., 2009; *Typhlochactas sylvestris* Mitchell and Peck, 1977. Branches leading to hypogean (troglobitic) taxa indicated in black: *Troglotayosicus vachoni* Lourenço, 1981; *Alacran tartarus* Francke, 1982; *Sotanochactas elliotti* (Mitchell, 1971); *Stygochactas granulosus* (Sissom and Cokendolpher, 1998); *Typhlochactas cavicola* Francke, 1986; *Typhlochactas reddelli* Mitchell, 1968; *Typhlochactas rhodesi* Mitchell, 1968. Ambiguous optimization shaded.

*donensis* Stahnke, 1940, an epigean scorpion commonly found under stones in the south-western USA and Mexico (Stahnke, 1940; Williams, 1980), placed at the time in a monotypic subfamily, Superstitioniinae Stahnke, 1940, of Chactidae. Francke (1982) downgraded Typhlochactinae to a tribe, Typhlochactini Mitchell, 1971, of Superstitioniinae, included *A. tartarus* in Typhlochactini; and placed *Superstitionia* in tribe Superstitionini Stahnke, 1940. Reluctant to recognize Chactidae as defined at the time, Francke (1982) placed Superstitioniinae *incertae sedis* in superfamily Chactoidea Pocock, 1893.

Stockwell (1992) elevated Superstitioniinae to family rank for the first time and included within it *Belisarius xambeui* and another troglomorphic taxon, *Troglotayosicus vachoni* from Los Tayos Cave, Ecuador, at the time both placed in Chactidae, based on results of an unpublished cladistic analysis (Stockwell, 1989). Sissom and Cokendolpher (1998) tentatively agreed with the recognition of Superstitioniidae at family rank, based on Francke's (1982) diagnosis of the subfamily, but expressed reservations about including *Troglotayosicus* and *Belisarius* in the family without firm evidence. A new family, Troglotayosicidae Lourenço, 1998, and two monotypic subfamilies, Troglotayosicinae Lourenço, 1998 and Belisariinae Lourenço, 1998, were meanwhile created to accommodate *Troglotayosicus* and *Belisarius* respectively, their inclusion in the same family justified solely on their troglomorphic habitus and relictual distribution (Lourenço, 1998). Whereas most subsequent authors (Lourenço, 2000, 2001; Lourenço and Sissom, 2000; Sissom, 2000; Soleglad and Fet, 2003; Coddington et al., 2004; Fet and Soleglad, 2005; Prendini and Wheeler, 2005; Sissom and Hendrixson, 2005) recognized *Superstitionia*, *Alacran*, *Sotanochactas*, and *Typhlochactas* in Superstitioniidae, after its initial elevation by Stockwell (1992), there remains little agreement about the taxonomic placements of *Troglotayosicus* and *Belisarius*.

Our analyses unanimously confirmed the monophyly of the nine ingroup species (Fig. 9). The many apomorphies (besides troglomorphies) supporting their monophyly, as distinct from *Superstitionia* and the other genera variously placed in Superstitioniidae by previous authors (viz. *Belisarius* and *Troglotayosicus*), justifies their elevation to family rank by Vignoli and Prendini (2009), in accordance with the original views of Mitchell (1968, pp. 770, 771). The many apomorphies respectively supporting the branches leading to *A. tartarus* and the monophyletic group comprising the remaining species likewise justifies their placement in two subfamilies, Alacraninae and Typhlochactinae (Table 1) by Vignoli and Prendini (2009).

Francke (1982, p. 59, fig. 26) presented a hypothesis of phylogenetic relationships among *Superstitionia*, *Alacran* and the four species of *Typhlochactas* known at the time (a tree diagram that was not derived from a quantitative analysis, reproduced here as Fig. 4), to which Francke (1986, p. 8) added *T. cavicola* along the branch leading to *T. rhodesi*. Sissom (1988, p. 370) considered *T. mitchelli* most similar to *T. sylvestris*, while Sissom and Cokendolpher (1998, p. 286) considered *T. granulosus* most similar to *T. rhodesi* and *T. reddelli*, conflicting with Francke's (1982) hypothesis.

The topology obtained by our analyses was entirely congruent with Francke's (1982) figure 26 (Fig. 4). The sister-group relationship of *T. cavicola* and *T. rhodesi* confirms the views of Francke (1986, p. 8) concerning these species, and the sister-group relationship of *T. mitchelli* and *T. sylvestris* confirms the views of Sissom (1988, p. 370). The phylogenetic position of *T. granulosus* does not support the opinion of Sissom and Cokendolpher (1998, pp. 286) that this species is most similar to *T. rhodesi* and *T. reddelli*, however. As with Francke's (1986) creation of *Sotanochactas* to accommodate *T. elliotti*, the many apomorphies supporting the branch leading to *T. granulosus* versus the monophyletic group comprising the remaining species of *Typhlochactas* (Fig. 9) justifies their placement in separate genera and hence the creation of *Stygochactas*, to accommodate *T. granulosus* (Table 1), by Vignoli and Prendini (2009).

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## Appendix 1

Material examined for phylogenetic analysis of the family Typhlochactidae Mitchell, 1971.

Specimens deposited in the following collections: American Museum of Natural History, New York (AMNH), including the Ambrose Monell Cryocollection for Molecular and Microbial Research (AMCC); California Academy of Sciences, San Francisco (CAS); Instituto de Biología, Universidad Nacional Autonóma de México, Mexico City (IBUNAM); Instituto de Investigación de Recursos Biológicos Alexander Von Humboldt, Villa de Leyva, Colombia (IAvH); Museum of Comparative Zoology, Harvard University, Cambridge, MA (MCZ); Muséum National d'Histoire Naturelle, Paris (MNHN); W. David Sissom Private Collection, Canyon, TX (WDS).

***Superstitionia donensis*** **Stahnke, 1940: Mexico:** *Baja California*: Municipio de Ensenada: Laguna Manuela, 34 miles NNW on road to Miller's Landing [28°12′ N 114°08′ W], 500 ft, S.C. Williams & M.A. Cazier, 22.VI.1968, 1 ♂, 1 ♀ (MCZ 12359). *Baja California Sur*: Municipio de Mulegé: Vizcaino Desert, 48 miles NW San Ignacio [27°38′ N 113°22′ W], S.C. Williams & C. Mullinex, 30.XI.1973, 1 ♂, 1 ♀ (CAS). *Sonora*: Municipio de Hermosillo: Bay New Kino, 16 km NW on dirt road, 28°55.249′ N 112°02.572′ W, 116 m, E. González, 2.VII.2006, UV detection at night, 1 ♀ (AMCC [LP 7679]). **USA:** *Arizona*: Pinal County: Superstition Mountains, 33°25′43″ N 111°25′03″ W, D. Vernier, XI.2003, 1 ♂, 2 ♀ (AMCC [LP 3420]). *California*: San Benito County: Griswold Hills, Griswold Creek Canyon, New Idria Road, 3.7 miles S intersection with Panoche Road, 36°33′20.8″ N 120°50′27.0″ W, 390 m, L. Prendini, J. Huff & W. Savary, 15.IX.2007, 5 ♂ (AMNH). San Diego County: Anza-Borrego Desert State Park: Culp Valley Camp, 33°13.421′ N 116°27.267′ W, 1033 m, L. Prendini & R. Mercurio, 30.VIII.2005, UV light detection, 2 ♂, 1 ♀ (AMNH). *Nevada*: Clark County: Christmas Mountains, 35°15′39.55″ N 114°44′21.97″ W, 3910 ft, R.C. West, 12.X.2007, under fallen yucca trunks, 1 ♀ (AMCC [LP 7689]). Nye County: Mercury, Nevada Test Site [37°07′ N 116°03′ W], B.Y.U.–A.E.C. Code CBA7©, 30.X.1961, 1 ♀ (AMNH), B.Y.U.–A.E.C. Code JAL8©, 11.X.1961, 1 ♂ (AMNH). *New Mexico*: Hidalgo County: Granite Gap, Peloncillo Mountains, 32°05′43.1″ N 108°58′13.7″ W, 1367 m, L. Prendini & J. Huff, 4.IX.2007, 2 ♂, 1 ♀ (AMNH).

***Troglotayosicus humiculum*** **Botero-Trujillo and Francke, 2009: Colombia:** *Nariño Department*: Reserva Natural La Planada, permanent plot, 01°15′ N 78°15′ W, 1885 m, G. Oliva, 2–4.V.2001, Winkler trap, subadult ♂ holotype (IAVH-E 100809).

***Alacran tartarus*** **Francke, 1982: Mexico:** *Oaxaca*: Município de San Miguel: Sótano de San Agustín [18°06′23″ N 96°47′53″ W, −720 m], San Agustín, 5 km SE Huautla de Jiménez, 1979 San Agustín Expedition members of the Huautla Project, Spring 1979, holotype ♀, juv. ♂ paratype (AMNH); Sótano de San Agustín Section, Sistema Huautla, A. G. Grubbs, J. H. Smith & F. Holliday, V.1985, 2 ♀ (WDS); Sótano Li Nita [18°08′51″ N 96°47′56″ W, −812 m], San Agustín, 5 km SE Huautla de Jiménez, B. Steele & S. Zeman, 1980 Río Iglesia Expedition, 29.III.1980, paratype ♂ (AMNH), M. Minton, L. Wilk & R. Simmons, 1.IV.1981, 1 ♀ (AMNH); Sótano Li Nita [18°08′51″ N

96°47′56″ W], San Agustín, 5 km SE Huautla de Jiménez, White Room Lead, −871 m, M. Minton, 22.III.1981, 1 juv. ♀ (AMNH); Sótano Agua de Carrizo [18°08′16″ N 96°47′39″ W, −760 m], 5 km ESE Huautla de Jiménez, A.G. Grubbs, B. Stone, J. Smith, T. Johnson & M. McEachern, 23.V.1978, juv. ♀ paratype (AMNH); Cueva de Escorpión, San Miguel Dolina, 5 km SE Huautla de Jiménez, R. Jameson & P. Mothes, I.1978, paratype ♀ (MNHN); Cueva de Escorpión, 18°06′23″ N 96°47′53″ W, 1561 m, A. Gluesenkamp, P. Sprouse & C. Savvas, 18.IX.2004, 1 ♂ (AMNH), leg (AMCC [LP 3499]).

***Sotanochactas elliotti*** **(Mitchell, 1971): Mexico:** *San Luis Potosí*: Munícipio de Ciudad Valles: El Sótano de Yerbaniz, 21 km N Ciudad Valles, Sierra de El Abra [22°11′07″ N 98°59′12″ W], ca 250 m, W.R. Elliott, 31.VII.1969, subad. ♂ holotype (AMNH), W.R. Elliott, 27.III.1970, juv. ♀ paratype (MNHN RS 5376); R.W. Mitchell, 4.VII.1970, paratype ♂ (WDS).

***Stygochactas granulosus*** **(Sissom and Cokendolpher, 1998): Mexico:** *Veracruz*: Munícipio Tlaquilpa: Sótano de Poncho [18°37′N 97°07′W, −73 m] P. Sprouse, 22.III.1995, juv. ♂ holotype, 1 ad., pedipalp chela only (AMNH).

***Typhlochactas cavicola*** **Francke, 1986: Mexico:** *Tamaulipas*: Munícipio de Guemez: Cueva del Vandalismo [23°51′54″ N 99°26′45″ W], ca 2600 m, 1 km SE Rancho Nuevo, D. Honea, 15.III.1982, holotype ♀ (AMNH).

***Typhlochactas mitchelli*** **Sissom, 1988: Mexico:** *Oaxaca*: Munícipio de San José Tenango: Cerro Ocote [18°08′58″ N 96°43′59″ W], 5 miles S San José de Tenango, A. Grubbs, A. Cressler & P. Smith, IV.1987, holotype ♂, paratype ♂, subad. ♀ paratype (AMNH).

***Typhlochactas reddelli*** **Mitchell, 1968: Mexico:** *Veracruz*: Munícipio de Tlilapan: La Cueva del Ojo de Agua de Tlilapan, Tlilapan, ca 5 km S Orizaba [18°48′23″ N 97°05′59″ W], 1400 m, J. Reddell, J. Fish & T. R. Evans, 4.VIII.1967, holotype ♀ (AMNH); Cueva Ojo de Agua, Tlilapan, R. Sanchez, 8.II.1990, 1 juv. ♀ (IBUNAM), I. Vazquez, 30.III.1990, under rock, 1 juv. ♂ (IBUNAM), under rock, dark zone, 1 juv. ♀ (IBUNAM).

***Typhlochactas rhodesi*** **Mitchell, 1968: Mexico:** *Tamaulipas*: Munícipio de Gómez Farias: La Cueva de la Mina, Sierra de Guatemala [23°06′06″ N 99°12′56″ W], 1600 m, 24.III.1967, R. W. & R. Mitchell, K. Pittard, D. Falls & V. Colvin, holotype ♀ (AMNH), R. W. Mitchell, F. Abernethy & W. Rhodes, 29–30.VIII.1966, subad. ♀ paratype (AMNH), R.W. Mitchell, F. Abernethy & W. Rhodes, 29.VIII.1967, paratype ♀ (MNHN RS 4760).

***Typhlochactas sissomi*** **Francke et al., 2009: Mexico:** *Queretaro*: Munícipio de Jalpan: Cañada de La Joya, 21°27′23″ N 99°08′26″ W, 1944 m, H. Montaño & A. Valdez, 12.VI.2004, rock-rolling, subad. ♂ holotype (IBUNAM T-0308), leg (AMCC [LP 2949]).

***Typhlochactas sylvestris*** **Mitchell and Peck, 1977: Mexico:** *Oaxaca*: Munícipio de Valle Nacional: Valle Nacional, 25 km S along Highway 175 (Oaxaca–Tuxtepec) [17°36′43″ N 96°25′09″ W], 1200 m, S.B. Peck, 21.V.1971, Berlese sample #204, holotype ♀ (AMNH).

## Appendix 2

List of 196 characters for nine taxa in the family Typhlochactidae Mitchell, 1971 and three outgroup taxa. Fifty-four characters, indicated by †, were deactivated in all analyses. Character 196 was optimized on the phylogeny *a posteriori*. Refer to Table 2 for character matrix. Characters from previous analyses that correspond partially or entirely to those in the present matrix are as follows (author/number): L80 = Lamoral (1980); S89 = Stockwell (1989); P00 = Prendini (2000); P0103 = Prendini (2001b, 2003a); S&S01 = Soleglad and Sissom (2001); S&F03.5 = Soleglad and Fet (2003), Table 5; P04 = Prendini (2004). Character definitions and interpretations of primary homology used here do not necessarily correspond with those in previous analyses; previous usage is provided merely for historical continuity and as a guide to the literature.

### *Pigmentation*

1. †Carapace, tergites, pedipalps and metasoma (e.g. pedipalpal and metasomal carinae): pigmented/infuscated (0); not pigmented/infuscated (1).

### *Chelicerae*

2. Fixed finger, median and basal teeth: fused into a bicusp (conjoined on a "trunk") (0); separate, not fused into a bicusp (not conjoined on a "trunk") (1) [S&S01/9; S&F03.5/44].

3. Fixed finger, number of teeth: four (subdistal present) (0); three (subdistal absent) (1).

4. Movable finger, distal tooth alignment (internal distal and external distal teeth): opposable, internal distal tooth completely overlaps external distal tooth in dorsal view, U-shape in anterior aspect (0); not opposable, internal distal tooth does not overlap or at most partially overlaps external distal tooth in dorsal view, V-shape in anterior aspect (1) [L80/21; P00/11; S&S01/1, 6; S&F03.5/39].

5. Movable finger, dorsal edge, number of subdistal teeth: two (0); one (1); none (2) [L80/10; S89/31, 32; P00/10; S&S01/3; S&F03.5/41].

### *Carapace*

6. Anteromedian projection (epistome): absent or obsolete (0); present, well developed (1).

7. Anteromedian longitudinal sulcus: present (0); absent or obsolete (1).

8. Lateral ocelli, "first" (anterior) ocellus: present, large (0); absent (1) [S89/21, 25; P00/1; S&F03.5/102].

9. †Lateral ocelli, "second" (ventromedian) ocellus: present, large (similar in size to 'first' ocellus) (0); present, greatly reduced (much smaller than "first" ocellus) (1); absent (2) [S89/21, 25; P00/1; S&F03.5/102].

10. †Lateral ocelli, "third" (posterior) ocellus: present, slightly to greatly reduced (slightly to much smaller than "first" and "second" ocelli) (0); absent (1); polymorphic (0 1) [S89/21, 25; P00/1; S&F03.5/102].

11. Lateral ocelli, "fourth" (dorsomedian) ocellus: present, greatly reduced (much smaller than "first" ocellus) (0); absent (1) [S89/21, 25; P00/1; S&F03.5/102].

12. †Median ocelli: present (0); absent (1) [S89/24].

### *Pedipalp chela dentition*

13. †Chela fingers dentition, median denticle row, primary subrows alignment: straight (0); oblique (1) [S89/46; S&S01/28; S&F03.5/47].

14. Chela fingers dentition, median denticle row, oblique primary subrows: not imbricated (0); imbricated (1); inapplicable (–) [P04/7].

15. Chela movable finger dentition, median denticle row, primary subrows: similar in length (0); basal row noticeably longer (1).

16. Chela movable finger dentition, median denticle row, first (terminal) primary subrow: absent (0); one (occasionally two) granules (1) [S&F03.5/55, P04/6].

17. Chela movable finger dentition, fourth external denticle: present (0); absent (1) [S&S01/33].

18. Chela movable finger dentition, fifth external denticle: present (0); absent (1) [S&S01/33].

19. Chela movable finger dentition, sixth external denticle: present (0); absent (1) [S&S01/33].

20. Chela movable finger dentition, seventh external denticle: present (0); absent (1) [S&S01/33].

21. †Chela movable finger dentition, fifth internal denticle: present (0); absent (1) [S&S01/33].

22. †Chela movable finger dentition, sixth internal denticle: present (0); absent (1) [S&S01/33].

23. Chela movable finger dentition, seventh internal denticle: present (0); absent (1) [S&S01/33].

24. Chela movable finger dentition, eighth internal denticle: present (0); absent (1) [S&S01/33].

25. †Chela movable finger dentition, internal denticles development relative to external denticles: internal denticles larger than external denticles (0); internal denticles smaller than external denticles (1).

26. Chela movable finger dentition, internal denticle development: all internal denticles similar in size (0); basal four internal denticles significantly larger (1) [S&F03.5/54].

27. Chela fixed finger, distal diastema (notch) to accommodate terminal denticle of movable finger: present, well developed (0); weakly developed or absent (1).

28. †Chela movable finger, distal diastema (notch) to accommodate terminal denticle of fixed finger: absent or weakly developed (0); present, well developed (1).

29. Chela fingers, terminus: fixed finger, terminal denticle considerably larger than preceding denticles, hook-like, fingertips interlocking unevenly when closed, movable finger markedly displaced to exterior (0); fixed finger, terminal denticle slightly larger than preceding denticles, fingertips interlocking evenly when closed, movable finger at most slightly displaced to exterior (1).

## Pedipalp chela ornamentation

30. †Chela fixed finger, proximal half: smooth (0); dorsal surface granular (1); dorsal, lateral and internal surfaces granular (2).

31. †Chela fingers, curvature and closure (♂): fingers straight, fit together evenly, no gap evident when closed (0); fixed finger curved dorsally, movable finger curved ventrally, fingers fit together unevenly, distinct gap evident when closed (1); unknown (?).

32. Chela manus, internal surface, granulation along distal margin from base of movable finger to base of fixed finger: no prominent granules (0); row of prominent, isolated granules from base of movable finger to base of fixed finger (1); pair of prominent, isolated granules situated close together at base of fixed finger (2).

33. Chela manus, internal surface, granulation near movable finger condyle: no prominent granules (0); one very prominent, isolated granule (1).

34. Chela manus, dorsal secondary carina: distinct (strongly sclerotized, protruding above intercarinal surfaces) (0); obsolete (weakly sclerotized, if at all, not protruding above intercarinal surfaces) (1); absent (2) [P00/22; S&S01/24].

35. Chela manus, digital carina: distinct (strongly sclerotized, protruding above intercarinal surfaces) (0); absent (1).

36. †Chela manus, external secondary carina: distinct (strongly sclerotized, protruding above intercarinal surfaces) (0); obsolete (weakly sclerotized, if at all, not protruding above intercarinal surfaces) (1); absent (2).

37. Chela manus, ventroexternal carina: distinct (strongly sclerotized, protruding above intercarinal surfaces) (0); obsolete (weakly sclerotized, if at all, not protruding above intercarinal surfaces) (1); absent (2).

38. Chela manus, ventromedian carina: absent (0); obsolete (weakly sclerotized, if at all, not protruding above intercarinal surfaces) (1); distinct (strongly sclerotized, protruding above intercarinal surfaces) (2) [P00/28; S&S01/26].

39. Chela manus, ventromedian carina, one to three proximal granules in profile: present (0); absent (1).

40. Chela manus, ventrointernal carina: distinct (strongly sclerotized, protruding above intercarinal surfaces) (0); absent (1) [P00/29, 30; S&S01/27].

41. Chela manus, ventromedian and ventrointernal carinae, relative development: ventromedian carina stronger than ventrointernal carina (0); ventromedian and ventrointernal carinae similarly developed (1).

## Pedipalp patella ornamentation

42. †Patella internal surface, dorsal process (“dorsal patellar spur”): well developed projection comprising one or more prominent, spiniform granules (0); projection absent or very weakly developed, comprising at most a low granule (1) [P00/18; S&S01/15–17; S&F03.5/97, 98].

43. †Patella, (dorsal) internomedian carina (“dorsal patellar spur carina”): absent, at most one or two granules besides dorsal process (“dorsal patellar spur”) (0); present, row of multiple granules (1); fully developed, granular row (2) [S89/41, 42; S&F03.5/96].

44. †Patella, (dorsal) externomedian carina: obsolete (weakly sclerotized, if at all, not protruding above intercarinal surfaces) (0); absent (1).

45. †Patella, (ventral) externomedian carina: obsolete (weakly sclerotized, if at all, not protruding above intercarinal surfaces) (0); absent (1).

46. Patella, dorsoexternal carina: distinct (strongly sclerotized, protruding above intercarinal surfaces) (0); obsolete (weakly sclerotized, if at all, not protruding above intercarinal surfaces) (1); absent (2).

47. Patella, dorsointernal carina: obsolete (weakly sclerotized, if at all, not protruding above intercarinal surfaces) (0); absent (1).

48. Patella, ventrointernal carina: distinct (strongly sclerotized, protruding above intercarinal surfaces) (0); obsolete (weakly sclerotized, if at all, not protruding above intercarinal surfaces) (1); absent (2).

49. Patella, ventroexternal carina: distinct (strongly sclerotized, protruding above intercarinal surfaces) (0); obsolete (weakly sclerotized, if at all, not protruding above intercarinal surfaces) (1); absent (2).

## Pedipalp femur ornamentation

50. Femur, dorsoexternal carina: distinct (strongly sclerotized, protruding above intercarinal surfaces) (0); obsolete (weakly sclerotized, if at all, not protruding above intercarinal surfaces) (1); absent (2).

51. Femur, dorsointernal carina: distinct (strongly sclerotized, protruding above intercarinal surfaces) (0); obsolete (weakly sclerotized, if at all, not protruding above intercarinal surfaces) (1); absent (2).

52. Femur, ventrointernal carina: distinct (strongly sclerotized, protruding above intercarinal surfaces) (0); obsolete (weakly sclerotized, if at all, not protruding above intercarinal surfaces) (1); absent (2).

53. Femur, ventroexternal carina: distinct (uninterrupted row of granules) (0); absent (no granules) (1).

## Pedipalp trichobothria

54. †Femur, trichobothrium $i_1$: absent (0); present, full size (1).

55. †Femur, trichobothrium $i_2$: absent (0); present, full size (1).

56. †Femur, trichobothrium $d_1$: absent (0); present, full size (1).

57. Femur, trichobothrium $d_2$: absent (0); present, full size (1).

58. Femur, trichobothrium $d_3$: absent (0); present, full size (1).

59. Femur, trichobothrium $d_4$: absent (0); present, full size (1).

60. Femur, trichobothrium $d_5$: absent (0); present, full size (1).

61. Patella, trichobothrium $d_1$: present, petite (0); present, full size (1).

62. Patella, trichobothrium $d_2$: present, petite (0); present, full size (1).

63. Patella, trichobothrium $i_1$: absent (0); present, full size (1).

64. Patella, trichobothrium $i_2$: absent (0); present, full size (1).
65. Patella, trichobothrium $v_2$: absent (0); present, full size (1).
66. †Patella, trichobothrium $v_3$: absent (0); present, full size (1).
67. Patella, trichobothrium $v_4$: absent (0); present, full size (1).
68. Patella, trichobothrium $et_1$: absent (0); present, full size (1).
69. Patella, trichobothrium $et_2$: absent (0); present, petite (1); present, full size (2).
70. Patella, trichobothrium $et_3$: absent (0); present, petite (1); present, full size (2).
71. Patella, trichobothrium $et_4$: absent (0); present, full size (1).
72. Patella, trichobothrium $et_5$: absent (0); present, petite (1); present, full size (2); polymorphic (0 1).
73. Patella, trichobothrium $et_6$: absent (0); present, full size (1).
74. †Patella, trichobothrium $et_7$: absent (0); present, full size (1).
75. Patella, trichobothrium $et_8$: absent (0); present, full size (1).
76. Patella, trichobothrium $et_9$: absent (0); present, full size (1).
77. †Patella, trichobothrium $est_2$: absent (0); present, full size (1).
78. Patella, trichobothrium $em_2$: absent (0); present, full size (1).
79. Patella, trichobothrium $em_3$: absent (0); present, full size (1).
80. Patella, trichobothrium $em_4$: absent (0); present, full size (1).
81. Patella, trichobothrium $esb_2$: absent (0); present, petite (1); present, full size (2).
82. Patella, trichobothrium $esb_3$: absent (0); present, petite (1); present, full size (2).
83. Patella, trichobothrium $esb_4$: absent (0); present, petite (1); present, full size (2).
84. †Patella, trichobothrium $esb_5$: absent (0); present, full size (1).
85. Patella, trichobothrium $eb_1$: absent (0); present, full size (1).
86. †Patella, trichobothrium $eb_2$: absent (0); present, petite (1); present, full size (2).
87. Patella, trichobothrium $eb_3$: absent (0); present, petite (1); present, full size (2).
88. Patella, trichobothrium $eb_4$: absent (0); present, full size (1).
89. Patella, trichobothrium $eb_5$: absent (0); present, full size (1).
90. Patella, trichobothrium $eb_6$: absent (0); present, full size (1).
91. Patella, trichobothrium $eb_7$: absent (0); present, full size (1).
92. Patella, trichobothrium $eb_8$: absent (0); present, full size (1).
93. Patella, trichobothrium $eb_9$: absent (0); present, full size (1).
94. Chela, trichobothrium $i_1$: absent (0); present, full size (1).
95. Chela, trichobothrium $i_2$: absent (0); present, full size (1).
96. †Chela, trichobothrium $i_3$: absent (0); present, full size (1).
97. Chela, trichobothrium $i_4$: absent (0); present, full size (1).
98. Chela, trichobothrium $V_1$: present, petite (0); present, full size (1).
99. †Chela, trichobothrium $V_2$: absent (0); present, full size (1).
100. Chela, trichobothrium $V_3$: absent (0); present, full size (1).
101. Chela, trichobothrium $V_4$: absent (0); present, full size (1).
102. Chela, trichobothrium $V_5$: absent (0); present, full size (1).
103. Chela, trichobothrium $V_6$: absent (0); present, full size (1).
104. †Chela, trichobothrium $Esb_1$: present, petite (0); present, full size (1).
105. †Chela, trichobothrium $Esb_2$: absent (0); present, full size (1).
106. Chela, trichobothrium $D_1$: present, petite (0); present, full size (1).
107. †Chela, trichobothrium $D_2$: absent (0); present, full size (1).
108. †Chela, trichobothrium $D_3$: absent (0); present, full size (1).
109. †Chela, trichobothrium $Et_3$: absent (0); present, petite (1).
110. Chela, trichobothrium $Et_4$: absent (0); present, petite (1); present, full size (2).
111. Chela, trichobothrium $Et_5$: absent (0); present, full size (1).
112. Chela, trichobothrium $Et_6$: absent (0); present, full size (1).
113. Chela, trichobothrium $Est_1$: absent (0); present, full size (1).
114. †Chela, trichobothrium $Est_2$: absent (0); present, full size (1).
115. Chela, trichobothrium $Est_4$: absent (0); present, petite (1); present, full size (2).
116. Chela, trichobothrium $Est_5$: absent (0); present, petite (1); present, full size (2).
117. Chela, trichobothrium $Est_6$: absent (0); present, petite (1); present, full size (2).
118. Chela, trichobothrium $Est_7$: absent (0); present, full size (1).
119. †Chela, trichobothrium $d_2$: absent (0); present, full size (1).
120. †Chela, trichobothrium $d_3$: absent (0); present, full size (1).
121. †Chela, trichobothrium $d_4$: absent (0); present, full size (1).
122. Chela, trichobothrium $d_5$: absent (0); present, full size (1).
123. †Chela, trichobothrium $d_6$: absent (0); present, full size (1).
124. Chela, trichobothrium $d_7$: absent (0); present, petite (1); present, full size (2).
125. Chela, trichobothrium $d_8$: absent (0); present, petite (1); present, full size (2).
126. †Chela, trichobothrium $m_1$: absent (0); present, full size (1).
127. Chela, trichobothrium $m_2$: absent (0); present, full size (1).
128. Chela, trichobothrium $m_3$: absent (0); present, full size (1).
129. Chela, trichobothrium $m_4$: absent (0); present, petite (1); present, full size (2).
130. Chela, trichobothrium $e_2$: absent (0); present, full size (1).
131. †Chela, trichobothrium $e_4$: absent (0); present, full size (1).
132. †Chela, trichobothrium $e_5$: present, petite; present, full size (1).
133. Chela, trichobothrium $e_6$: absent (0); present, petite (1); present, full size (2).
134. Chela, trichobothrium $e_7$: absent (0); present, full size (1).
135. Chela, trichobothrium $e_8$: absent (0); present, full size (1).
136. Patella, trichobothrium $v_1$, position relative to trichobothrium $esb_1$: proximal to (0); level with (1); distal to (2).
137. Chela, trichobothrium $d_4$, position relative to trichobothrium $e_5$: distal to (0); level with (1); inapplicable (–).

## *Legs*

138. Legs I–IV, prolateral pedal spurs: present (0); absent (1) [L80/11; S89/90; P00/64; S&F03.5/60].
139. Legs I and II, retrolateral pedal spurs: present (0); absent (1) [L80/11; S89/90; P00/63; S&F03.5/60].
140. Legs III and IV, retrolateral pedal spurs: present (0); absent (1) [L80/11; S89/90; P00/63; S&F03.5/60].
141. †Basitarsi I–III, retrolateral spinules or spinule clusters: absent (0); short distal row (1); long, well developed continuous row (2) [S&S01/85].
142. Basitarsus (IV), retrolateral spinules or spinule clusters: absent (0); distal spinules or spinule clusters only (1) [S&S01/85].
143. †Basitarsi I and II, retroventral spinules or spinule clusters: absent (0); short distal row (1); long row (2) [S&S01/86].
144. Basitarsus III, retroventral spinules or spinule clusters: absent (0); short distal row (1) [S&S01/86].
145. †Basitarsus IV, retroventral spinules or spinule clusters: absent (0); distal spinules or spinule clusters only (1) [S&S01/86].
146. Basitarsi I and II, proventral spinules or spinule clusters: absent (0); short subdistal row (1); long row, at least half length of segment (2) [S&S01/87].
147. †Basitarsi III and IV, proventral spinules or spinule clusters: absent (0); short distal row (1) [S&S01/87].
148. Basitarsi, ventral and lateral surfaces, spinules, type: simple, isolated spinules (0); loose clusters of elongated spinules (1); inapplicable (–) [S&S01/85–87].
149. Telotarsi, ventral surface, spinules or spinule clusters, curved proximal row: present (0); absent (1).
150. Telotarsi, ventral surface, spinules or spinule clusters, straight ventromedian row: present (0); absent (1) [L80/9; S89/93, 94, 97; P00/68, 70; S&S01/83, 84, 88, 89; S&F03.5/57; S&F03.5/58].
151. Telotarsi, ventral surface, spinules or spinule clusters, number of ventrodistal pairs: more than three (0); none (1) [S89/97; S89/100; S&S01/83; S&F03.5/62].
152. Telotarsi, ventral surface, spinules or spinule clusters, rows flanking pseudonychium (dactyl): absent (0); present (1).

153. Telotarsi, ventral surface, spinules, type: simple, isolated spinules (0); loose clusters of elongated spinules (1); inapplicable (–) [L80/9; S89/93, 94, 97; P00/68, 70; S&S01/83, 84, 88, 89; S&F03.5/57; S&F03.5/58].

154. Telotarsi, ventral macrosetae, arrangement: irregularly arranged, "non-flanking" (0); regularly arranged into pair of distinct ventrosubmedian rows (1) [L80/9; S89/93, 94, 97; P00/68, 70; S&S01/83, 84, 88, 89; S&F03.5/57; S&F03.5/58].

155. Telotarsi, ventral macrosetae, development: thin, acuminate (0); subspiniform (1) [L80/9; S89/93, 94, 97; P00/68, 70; S&S01/83, 84, 88, 89; S&F03.5/57; S&F03.5/58].

156. Telotarsi, ventrosubmedian ("flanking") setal pairs, number: 3–5 (0); 6–8 (1); more than 10 (2) [S89/93, 94; P00/70; S&S01/88].

## Sternum

157. Sternum, vertical compression: absent, length greater than or equal to posterior width (0); minimal, length less than width (1) [S&S01/70; S&F03.5/67].

158. Sternum apex, shape: pointed (0); rounded (1) [S&F03.5/69].

159. Sternum lateral lobes, development: strongly convex (lobes create deep cleft medially) (0); weakly convex (lobes create shallow cleft medially) (1); flat (2) [S&F03.5/69].

## Tergites

160. Tergite VII, dorsosubmedian carinae, longitudinal development: vestigial (few posterior granules) (0); absent (1).

161. Tergite VII, dorsolateral carinae, longitudinal development: distinct, complete (0); vestigial (few posterior granules) (1); absent (2).

## Genital opercula

162. †Genital opercula (♀), sclerites, extent of fusion: entirely fused, no indication of suture (0); entirely fused, but loosely connected by membrane along entire length of suture (1); separated for most of length, loosely connected by membrane at extreme anterior edge only (2); unknown (?) [L80/12; S89/105–107; P00/80; S&S01/71; S&F03.5/82].

## Pectines

163. †Pectinal fulcra, development: well developed (0); absent (1) [S&S01/73; S&F03.5/104].

164. Pectinal lamellae, sutures, transverse suture between second (subdistal) and third marginal lamellae: present, lamellae separated (0); absent, lamellae fused (1) [S&F03.5/105].

165. Pectinal lamellae, sutures, longitudinal suture between second (subdistal) marginal lamella and second (subdistal) or second and third medial lamellae: present, lamellae separated (0); absent, lamellae fused (1).

166. †Pectinal lamellae, sutures, transverse suture between second (subdistal) and third medial lamellae: present, lamellae separated (0); absent, lamellae fused (1).

167. Pectinal lamellae, sutures, transverse suture between third and fourth medial lamellae: present, lamellae separated (0); absent, lamellae fused (1).

168. Pectinal lamellae, sutures, transverse suture between fourth and fifth medial lamellae: present, lamellae separated (0); absent, lamellae fused (1).

169. Pectines, proximal medial lamella (scape), angle (♂): acute, less than 90° (0); approximately 90° (1); obtuse, greater than 90° but less than 180° (2); unknown (?).

170. †Pecten development, length, expressed relative to length of coxa of leg IV (♂): long, distal edge reaching beyond distal edge of coxa (0); moderate, distal edge reaching to, but not beyond, distal edge of coxa (1); unknown (?) [S&F03.5/103].

171. Pecten development, length, expressed relative to length of coxa of leg IV (♀): moderate, distal edge reaching to, but not beyond, distal edge of coxa (0); short, distal edge not reaching to distal edge of coxa (1); unknown (?) [S&F03.5/103].

172. †Pectinal teeth, number (♂): 5 (0); 6 (1); 7 (2); unknown (?) [S&F03.5/103].

173. †Pectinal teeth, number (♀): 5 (0); 6 (1); 7 (2); unknown (?) [S&F03.5/103].

174. Pectinal teeth, shape: curved, slightly overlapping (0); straight, non-overlapping (1).

## Sternites

175. †Sternite V, posteromedian surface (♂): unmodified (0); smooth, raised surface (1); unknown (?).

176. †Sternite VII, ventrolateral carinae: present (0); absent (1).

177. †Stigmata, shape: oval (0); round (1) [L80/20; S&F03.5/101].

## Metasoma

178. Metasomal segments I–III, dorsosubmedian carinae: distinct (strongly sclerotized, protruding above intercarinal surfaces) (0); obsolete (weakly sclerotized, if at all, not protruding above intercarinal surfaces) (1).

179. Metasomal segments I–III, dorsosubmedian carinae, distal granules: not noticeably larger than preceding granules (0); significantly larger than preceding granules (1).

180. Metasomal segment IV, dorsosubmedian carinae: distinct (strongly sclerotized, protruding above intercarinal surfaces) (0); obsolete (weakly sclerotized, if at all, not protruding above intercarinal surfaces) (1).

181. Metasomal segments I–III, dorsolateral carinae: distinct (strongly sclerotized, protruding above intercarinal surfaces) (0); obsolete (weakly sclerotized, if at all, not protruding above intercarinal surfaces) (1); absent (2).

182. Metasomal segment IV, dorsolateral carinae: distinct (strongly sclerotized, protruding above intercarinal surfaces) (0); absent (1).

183. Metasomal segment V, dorsosolateral carinae: distinct (strongly sclerotized, protruding above intercarinal surfaces) (0); obsolete (weakly sclerotized, if at all, not protruding above intercarinal surfaces) (1).

184. Metasomal segments I, dorsolateral carinae, longitudinal development: present, complete (0); present, incomplete (1); absent (2).

185. Metasomal segments II and III, dorsolateral carinae, longitudinal development: present, complete (0); present, incomplete (1); absent (2).

186. Metasomal segment I, median lateral carinae, longitudinal development: present, incomplete (0); absent (1).

187. Metasomal segment II, median lateral carinae, longitudinal development: present, incomplete (0); absent (1).

188. Metasomal segment III and IV, median lateral carinae, longitudinal development: present, incomplete (0); absent (1) [S&F03.5/87; P0103/42; P04/24].

189. Metasomal segment I, ventrolateral carinae: distinct (strongly sclerotized, protruding above intercarinal surfaces) (0); obsolete (weakly sclerotized, if at all, not protruding above intercarinal surfaces) (1); absent (2).

190. Metasomal segments II–IV, ventrolateral carinae: distinct (strongly sclerotized, protruding above intercarinal surfaces) (0);

obsolete (weakly sclerotized, if at all, not protruding above intercarinal surfaces) (1); absent (2).

191. Metasomal segment V, ventrolateral carinae: distinct (strongly sclerotized, protruding above intercarinal surfaces) (0); obsolete (weakly sclerotized, if at all, not protruding above intercarinal surfaces) (1); absent (2).

192. Metasomal segment V, ventrolateral carinae, longitudinal development: complete (0); restricted to distal third of segment (1); inapplicable (–).

193. †Metasomal segment V, ventromedian carina: obsolete (weakly sclerotized, if at all, not protruding above intercarinal surfaces) (0); absent (1).

## *Telson*

194. Telson vesicle, width relative to metasomal segment V, distal width: broader than (0); similar to (1).

195. Telson vesicle, anterodorsal lateral lobes: present (0); absent (1).

## *Habitat*

196. †Ecomorphotype: epigean (0); endogean (1); hypogean (2).