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SYSTEMATIC REVISION OF THE
TROGLOMORPHIC NORTH AMERICAN
SCORPION FAMILY TYPHLOCHACTIDAE
(SCORPIONES: CHACTOIDEA)

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ABSTRACT

The scorpion family Typhlochactidae Mitchell, 1971, endemic to eastern Mexico, comprises nine troglomorphic species specialized for life in hypogean and endogean habitats. Due to their cryptic ecology, inaccessible habitat, and apparently low population density, Typhlochactidae are poorly known. Only 29 specimens have been collected in 40 years. Four species are known from a single specimen, two species are known only from the male and three only from the female. We provide an illustrated revision of the family based on a reexamination of most specimens in the world's collections, including new specimens collected after the original descriptions and older specimens not previously described. Based on results of a recent cladistic analysis, Typhlochactidae are elevated, for the first time, from their former rank as subfamily, first of Chactidae and, more recently, of Superstitioniidae. Alacraninae, new subfamily is created to accommodate *Alacran* Francke, 1982. *Stygochactas*, new genus, is created to accommodate *Typhlochactas granulatus* Sissom and Cokendolpher, 1998 in a new combination. *Sotanochactas* Francke, 1986, *Stygochactas* and *Typhlochactas* Mitchell, 1971 are retained in subfamily Typhlochactinae Mitchell, 1971. Diagnoses of the family and subfamilies are presented, followed by a key to the genera and species, revised diagnoses of the genera, revised diagnoses and descriptions, tabulated meristic data, and distribution maps of the species. Descriptions and diagnoses are illustrated with ultraviolet fluorescence and visible light photographs, providing a visual atlas to the morphology of these remarkable scorpions. A review of their taxonomic history is provided, the importance of trichobothriotaxy for their systematics discussed, and several misconceptions in the literature clarified.

INTRODUCTION

Since discovery of the first two troglobite scorpions, I have fully expected that we would find others ... and until more species and more localities of these eyeless cave scorpions are known, it is not possible to speculate on their evolutionary history. I think one may predict, however, that these scorpions will assume considerable importance in considerations on phylogeny in the Scorpionida. (Mitchell, 1971: 147)

Troglomorphism, morphological specialization to hypogean and endogean habitats, in scorpions is defined on the basis of several characters that may be exhibited to differing 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. 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 (table 1), are considered unequivocally tro-

globitic according to the criteria outlined by Volschenk and Prendini (2008).

The scorpion family Typhlochactidae Mitchell, 1971, as defined below, is endemic to eastern Mexico (fig. 1) and exclusively troglomorphic, lacking ocelli and pigmentation, among other typical troglomorphies. Due to their cryptic ecology, inaccessible habitat (figs. 2, 3), and apparently low population density, Typhlochactidae remain one of the most poorly known families of scorpions. Only 29 specimens have been collected in 40 years (table 2). Four of nine described species are known from a single specimen, three from three specimens, one from four, and one from 11. Two species are known only from the male and three only from the female. Given the very small number of specimens available for most species, sexual dimorphism, intraspecific and ontogenetic variation is often unknown.

Francke (1982a) presented the most comprehensive treatment of the five typhlochactid species known at the time. Only three papers dealing exclusively with typhlochactid scorpions appeared in the two decades thereafter (Francke, 1986; Sissom, 1988; Sissom and Cokendolpher, 1998). Since the 1970s, typhlochactid scorpions were mentioned in various taxonomic checklists and

TABLE 1

Scorpion families and genera containing species reported to be troglomorphic in the literature

(Simon, 1879; Pocock, 1894; Vachon, 1945; Fage, 1946; Auber, 1959; Vandel, 1964; Mitchell, 1968, 1971; Reddell and Mitchell, 1971; Gertsch and Soleglad, 1972; González-Sponga, 1974; Francke, 1977, 1978, 1981, 1982a, 1986; Mitchell and Peck, 1977; Lourenço, 1981, 1994, 1995, 2000, 2006, 2007a, 2007b; Lourenço and Francke, 1985; Sissom, 1986, 1988, 2000b; Sissom and Cokendolpher, 1998; Kovařík, 2000; Armas, 2001; Soleglad and Sissom, 2001; Volschenk et al., 2001; Armas and Palacios-Vargas, 2002; Vignoli and Kovařík, 2003; Lourenço et al., 2004; Rojas-Runjaic, 2004; Sissom and González Santillán, 2004; Soleglad and Fet, 2005; Francke and Savary, 2006; Levy, 2007; Lourenço and Goodman, 2008; Volschenk and Prendini, 2008; Botoero-Trujillo and Francke, 2009; Francke, 2009; Francke et al., 2009) and the number of species considered unequivocally troglobitic according to the criteria of Volschenk and Prendini (2008)

Family	Genus	Troglomorphic	Troglobitic
Akravidae Levy, 2007	<i>Akrav</i> Levy, 2007	1	1
Buthidae C. L. Koch, 1837	<i>Tityus</i> C. L. Koch, 1836	1	
	<i>Troglotityobuthus</i> Lourenço, 2000	1	
	<i>Trogloorhopalurus</i> Lourenço et al., 2004	1	1
Chactidae Pocock, 1893	<i>Broteochactas</i> Pocock, 1893	1	
	<i>Chactas</i> Gervais, 1844	1	
Chaerilidae Pocock, 1893	<i>Chaerilus</i> Simon, 1877	3	2
Diplocentridae Karsch, 1880	<i>Diplocentrus</i> Peters, 1861	4	3
	<i>Heteronebo</i> Pocock, 1899	1	
Euscorpidae Laurie, 1896	<i>Troglocormus</i> Francke, 1981	2	2
Liochelidae Fet & Bechly, 2001	<i>Liocheles</i> Sundevall, 1833	1	1
	<i>Opisthacanthus</i> Peters, 1861	1	
Pseudochactidae Gromov, 1998	<i>Troglokhammouanus</i> Lourenço, 2007	1	
Troglotayosicidae Lourenço, 1998	<i>Belisarius</i> Simon, 1879	1	
	<i>Troglotayosicus</i> Lourenço, 1981	2	1
Typhlochactidae Mitchell, 1971	<i>Alacran</i> Francke, 1982	1	1
	<i>Sotanochactas</i> Francke, 1986	1	1
	<i>Stygochactas</i> , new genus	1	1
	<i>Typhlochactas</i> Mitchell, 1971	6	3
Urodacidae Pocock, 1893	<i>Aops</i> Volschenk & Prendini, 2008	1	1
Vaejovidae Thorell, 1876	<i>Vaejovis</i> C. L. Koch, 1836 ¹	2	1
	<i>Pseudouroctonus</i> Stahnke, 1974 ¹	2	2
	<i>Uroctonus</i> Thorell, 1876	1	1

¹At least one undescribed species in each of these genera is troglobitic.

catalogs (Díaz Najera, 1975; Francke, 1985; Nenilin and Fet, 1992; Kovařík, 1998; Sissom, 1990, 2000b; Beutelspacher Baigts, 2000; Lourenço, 2000, 2001; Lourenço and Sissom, 2000; Sissom and Hendrixson, 2005; Dupré, 2007), works on troglobitic scorpions (González-Sponga, 1974; Lourenço, 1981, 1994; Lourenço and Francke, 1985; Armas, 1994, 2001; Locket, 1995; Volschenk et al., 2001; Vignoli and Kovařík, 2003; Lourenço et al., 2004; Rojas-Runjaic, 2004; Lourenço and Goodman, 2008; Volschenk and Prendini, 2008), and broader treatments on scorpion systematics (Stockwell, 1989, 1992; Soleglad and Fet, 2001, 2003b; Coddington et al., 2004; Prendini and Wheeler, 2005). No single work covered all species in the family

and compared their morphology directly, however. That omission, taken together with their obvious importance for understanding the phylogeny of chactoid scorpions (Mitchell, 1971; Francke, 1982a) and the publication of errors concerning their morphology by Soleglad and Fet (2001, 2003b), justified the need for a reinvestigation of their morphology and systematics.

This paper, the second in a series investigating the systematics of Typhlochactidae, presents an illustrated revision of the family based on a reexamination of most specimens in the world's collections, including new specimens collected after the original descriptions and older specimens not previously described, among them the only adult male

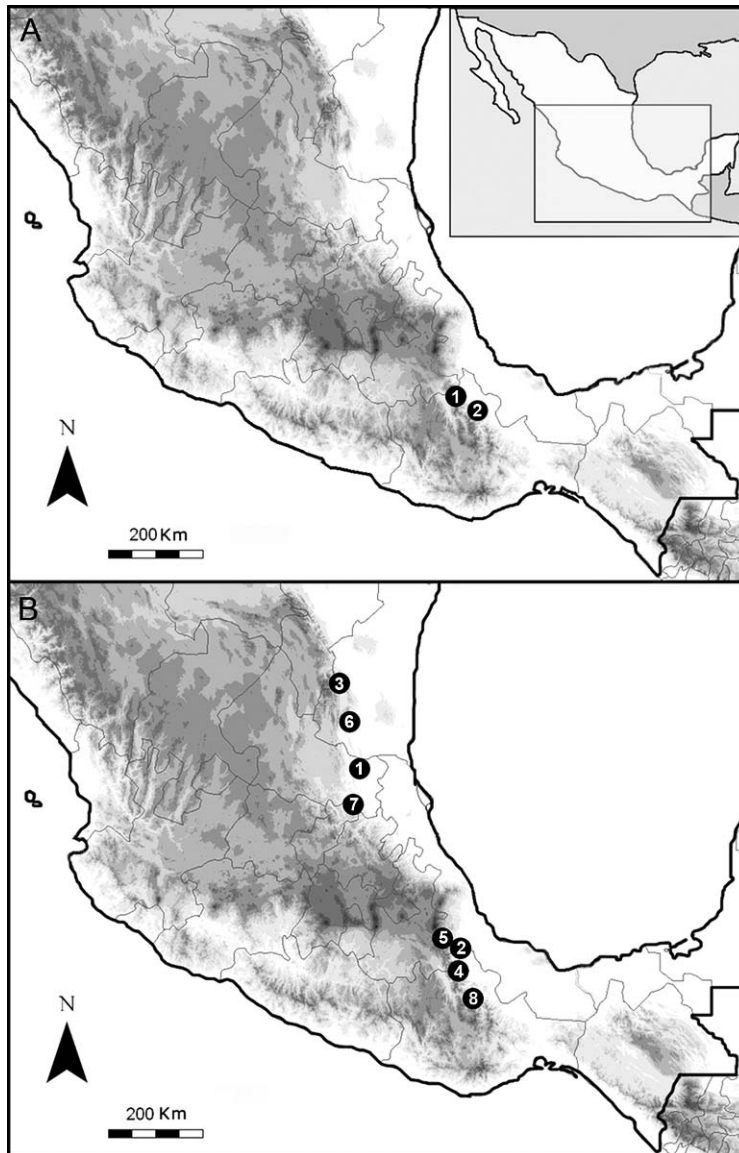


Fig. 1. Map of Mexico, showing the known localities of Typhlochactidae Mitchell, 1971. **A.** Known localities of Alacraninae, new subfamily: Type locality of *Alacran tartarus* Francke, 1982, on the Huautla Plateau, Oaxaca (1); Te Cimutaá Cave, Oaxaca, a new record for the genus possibly representing 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 granulatus* (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).

specimen of *Sotanochactas elliotti* (Mitchell, 1971). Based on results of a recent cladistic analysis (Prendini et al., 2009), Typhlochactidae are elevated, for the first time, from their former rank as subfamily, first of Chactidae and, more recently, of Superstitioniidae. Alacraninae, new subfamily is created to accommodate *Alacran* Francke, 1982. *Stygochactas*, new genus, is created to accommodate *Typhlochactas granulatus* Sissom and Cokendolpher, 1998, in a new combination. *Sotanochactas* Francke, 1986, *Stygochactas* and *Typhlochactas* Mitchell, 1971, are retained in subfamily Typhlochactinae Mitchell, 1971. Diagnoses of the family and subfamilies are presented, followed by a key to the genera and species, revised diagnoses of the genera, revised diagnoses and descriptions, tabulated meristic data, and distribution maps of the species. Descriptions and diagnoses are illustrated with ultraviolet fluorescence (UV) and visible light photographs, providing a visual atlas to the morphology of these remarkable scorpions. A review of their taxonomic history is provided, the importance of trichobothriotaxy for their systematics discussed, and several misconceptions in the literature clarified.

TAXONOMIC HISTORY

The phylogenetic relationships of the troglomorphic scorpions that form the subject of this paper have remained enigmatic since the first two species of *Typhlochactas* were described (Francke, 1982a). Mitchell (1968: 773) created subfamily Typhlochactinae to accommodate two troglobites, *Typhlochactas reddelli* Mitchell, 1968, from La Cueva del Ojo de Agua de Tlilapan, Veracruz, and *Typhlochactas rhodesi* Mitchell, 1968, from La Cueva de la Mina, Tamaulipas and with “less than absolute justification,” placed the subfamily within Chactidae Laurie, 1896. At the time, Mitchell (1968: 770, 771) noted the following:

The problem of family assignment of these scorpions is a perplexing one. To place these animals in a presently existing family, it is necessary to ignore certain features, long important in scorpion taxonomy, while at the same time giving more weight to other features than perhaps is justified. Based upon the

characteristics by which certain scorpion families are separated, there would seem to be sufficient justification for creating a new family for these scorpions ... These eyeless scorpions, ... on this basis alone, would appear to be distinct at the family level. However, I object to the creation of higher taxa based solely or primarily upon “cave-associated” features such as eyelessness. Elsewhere, I have suggested elimination of some taxa created primarily on the basis of the “troglobite facies”. Such classification has frequently served to obscure true relationships between troglobite and epigean species ... It should now be apparent why family placement of these scorpions is difficult and, in the present state of scorpion systematics, why any assignment is somewhat less than satisfactory and open to question. One must resort to a process of elimination in an attempt to relate these scorpions to others. I must emphasise that the following argument ignores the eyes, basitarsal spurs, and distinctness of the median and basal teeth of the superior margin of the fixed cheliceral finger.

The generic concept within this group of troglomorphic scorpions was almost as problematic as their phylogenetic placement. According to Mitchell (1968: 775):

One could probably present a cogent argument for separating [*T. reddelli* and *T. rhodesi*] into different genera. However, the almost identical trichobothrial patterns of the two species seem to argue against creating separate genera.

Typhlochactas Mitchell, 1971 was not designated as the type genus of Typhlochactinae until the description of a third troglobite, *Typhlochactas elliotti* Mitchell, 1971 from El Sótano de Yurbaniz, San Luis Potosí. The argument for separate genera became stronger with the discovery of this species, which differed from *T. reddelli* and *T. rhodesi* in numerous respects, besides trichobothrial pattern. Mitchell (1971: 145) observed:

Based upon criteria presently used in diagnosing scorpion genera, one could probably justify a new genus for *T. elliotti*, but this would probably necessitate separating *T. rhodesi* and *T. reddelli* into separate genera at the same time. This is what the future may well hold for these scorpions.

Typhlochactas sylvestris Mitchell and Peck, 1977, the fourth species to be described in

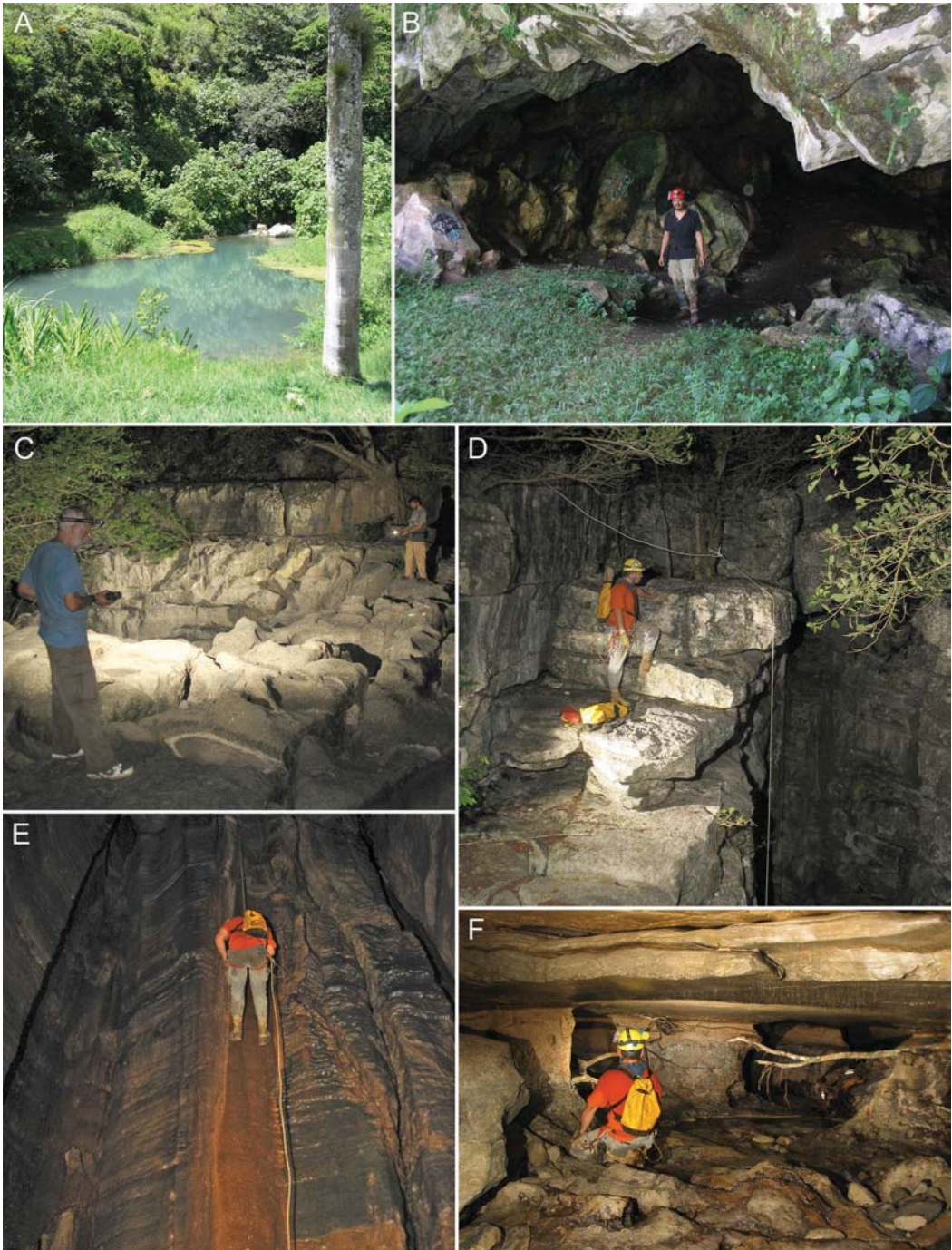


Fig. 2. Type localities and habitats of Typhlochactidae Mitchell, 1971. **A, B.** La Cueva del Ojo de Agua de Tlilapan (Veracruz, Mexico), type locality of *Typhlochactas reddelli* Mitchell, 1968: lake in front of entrance (A); entrance (B). **C–F.** El Sótano de Yerbaniz (San Luis Potosí, Mexico), type locality of *Sotanochactas elliotti* (Mitchell, 1971): entrance (C, D); descent (E); horizontal tunnel (F). Photos courtesy P. Spouse and A. G. Gluesenkamp.



Fig. 3. Type localities and habitats of Typhlochactidae Mitchell, 1971. **A, B.** La Cueva de la Mina (Tamaulipas, Mexico), type locality of *Typhlochactas rhodesi* Mitchell, 1968: entrance (A); main chamber (B). **C–F.** Cueva de Escorpión (Oaxaca, Mexico), type locality of *Alacran tartarus* Francke, 1982: lake in front of entrance (C); descent (D); *A. tartarus* ♂ (AMNH) collected from flowstone wall (E); *A. tartarus* ♂ (AMNH) habitus, in life (F). Photos courtesy P. Spouse and A. G. Gluesenkamp.

TABLE 2
List of Typhlochactidae Mitchell, 1971 species, authorities, Mexican states, municipalities, localities of occurrence, habitat, specimens and depositories
 Abbreviations as follows: OAX = Oaxaca; QRO = Queretaro; SLP = San Luis Potosí; TAM = Tamaulipas; VER = Veracruz

	State	Municipio	Localities	Habitat	Holotype	Paratypes	Other
Alacraninae, new subfamily							
<i>Alacran tartarus</i> Francke, 1982	OAX	San Miguel	Sótano de San Agustín Sótano Li Nita Sótano Agua de Carrizo Cueva de Escorpión Te Cimutaá Cave	cave cave cave cave cave	1 ♀ 1 ♂ 1 subad. ♀ 1 ♀ 1 ♂ 1 ♀ ²	1 juv. ♂ 1 ♂ 1 subad. ♀ 1 ♀ 1 ♂ 1 ♀ ²	2 ♀ ¹ 1 ♀, 1 juv. ♀ 1 ♂ 1 ♀ ²
<i>Alacran</i> sp.		Valle Nacional	Te Cimutaá Cave	cave			1 ♂ 1 ♀ ²
Typhlochactinae Mitchell, 1971							
<i>Sotanochactas elliotii</i> (Mitchell, 1971)	SLP	Ciudad Valles	El Sótano de Yerbaniz	cave	1 subad. ♂ 1 juv. ♂	1 ♂ ¹ , 1 juv. ♀ ³	1 ad. (chela only)
<i>Stygochactas granulatus</i> (Sissom and Cokendolpher, 1998)	VER	Tlaquilpa	Sótano de Poncho	cave	1 ♀	1 ♂, 1 subad. ♀	1 juv. ♂ ² , 2 juv. ♀ ²
<i>Typhlochactas cavicola</i> Francke, 1986	TAM	Guemez	Cueva del Vandalismo	cave	1 ♀	1 ♂, 1 subad. ♀	1 juv. ♂ ² , 2 juv. ♀ ²
<i>Typhlochactas mitchelli</i> Sissom, 1988	OAX	San José Tenango	Cerro Ocote	under stones buried in litter	1 ♂	1 ♂, 1 subad. ♀	1 juv. ♂ ² , 2 juv. ♀ ²
<i>Typhlochactas reddelli</i> Mitchell, 1968	VER	Tlilapan	La Cueva del Ojo de Agua de Tlilapan	cave	1 ♀	1 subad. ♀	1 juv. ♂ ² , 2 juv. ♀ ²
<i>Typhlochactas rhodesi</i> Mitchell, 1968	TAM	Gómez Farias	La Cueva de la Mina	cave	1 ♀	1 ♀ ³ , 1 subad. ♀	1 juv. ♂ ² , 2 juv. ♀ ²
<i>Typhlochactas sissomi</i> Francke et al., 2009	QRO	Jalpan	Cañada de La Joya	under stone	1 subad. ♂ ²	1 subad. ♀	1 juv. ♂ ² , 2 juv. ♀ ²
<i>Typhlochactas sylvestris</i> Mitchell and Peck, 1977	OAX	Valle Nacional	Valle Nacional, 25 km S	litter	1 ♀	1 subad. ♀	1 juv. ♂ ² , 2 juv. ♀ ²

¹Deposited in the W. David Sissom private collection, Canyon, TX.

²Deposited at the Instituto de Biología, Universidad Nacional Autónoma de México, Mexico City.

³Deposited at the Muséum National d'Histoire Naturelle, Paris. All other specimens deposited at the American Museum of Natural History, New York.

this group of scorpions, was collected with Berlese from montane forest litter, 25 km S of Valle Nacional, Oaxaca, unlike the first three species, collected from deep inside caves. At this point in the taxonomic history of these scorpions, Mitchell & Peck (1977: 164) noted:

No diagnosis of the genus *Typhlochactas* ... can be entirely satisfactory. Each species presents its own unique features, features of considerable importance in scorpion taxonomy Thus, it seems at present that there are but two reasonable alternatives, maintain a single genus—perhaps one so heterogeneous as to be artificial, or separate each species into its own genus.

A monotypic genus, *Alacran* Francke, 1982, was subsequently created to accommodate *Alacran tartarus* Francke, 1982, a large troglobite collected in four deep caves in the Sistema Huautla, Oaxaca, and which differed from the other four species in many important characters. In spite of the differences between *Alacran* and *Typhlochactas*, Francke (1982a) recognized a close phylogenetic relationship between the two genera, while following Mitchell (1968) in discounting a close relationship between them and *Belisarius xambeui* Simon, 1879, a troglomorphic endogean species from the Pyrenees of France and Spain and, at the time, the only other eyeless scorpion known. Francke (1982a: 57) postulated that the three characters ignored by Mitchell (1968: 770, 771) are synapomorphic for *Alacran* and *Typhlochactas*, and proposed that the two genera are closely related to *Superstitionia donensis* Stahnke 1940, an epigeal scorpion from the southwestern United States and Mexico (Stahnke, 1940; Williams, 1980), placed at the time in a monotypic subfamily, Superstitioniinae Stahnke, 1940 (as Superstitioniinae), of Chactidae. Francke (1982a) 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 (1982a) placed Superstitioniinae incertae sedis in superfamily Chactoidea Pocock, 1893 (a putatively monophyletic

group comprising Chactidae Laurie, 1896, Iuridae Thorell, 1876, and Vaejovidae Thorell, 1876). Francke (1986) continued to recognize Superstitioniinae as incertae sedis in Chactoidea although Francke (1985) listed it as a subfamily of Chactidae.

Typhlochactas cavicola Francke, 1986, collected in Cueva del Vandalismo, Tamalipas, was the sixth species in the group to be described. In light of the discoveries of *Alacran*, *T. cavicola* and *T. sylvestris*, Francke (1986) reassessed generic limits within the group. Francke (1986: 5) recognized the important differences between *T. elliotti* and the other species of *Typhlochactas* noted earlier by Mitchell (1971: 145), and created a monotypic genus, *Sotanochactas* Francke, 1986, to accommodate it:

These species [*Alacran*, *T. cavicola* and *T. sylvestris*] ... have indeed assisted in clarifying the systematic relationships within the tribe Typhlochactini Mitchell. *Typhlochactas rhodesi* Mitchell, *Typhlochactas reddelli* Mitchell, *T. sylvestris* and *T. cavicola* form a compact monophyletic group of species, and the differences between this group and *Typhlochactas elliotti* Mitchell are such that the recognition of a new genus is now justified.

Typhlochactas mitchelli Sissom, 1988, the fifth species of *Typhlochactas* to be described, was the second in the genus to be collected from montane forest litter. This species was collected on Cerro Ocote, Oaxaca, in the same mountain range as the type locality of *T. sylvestris*. Unlike the holotype of *T. sylvestris*, collected with Berlese (Mitchell and Peck, 1977), the holotype and paratypes of *T. mitchelli* were taken from under stones buried deep in litter (A.G. Grubbs, personal commun.).

Sissom (1988, 1990) and Beutelspacher Baigts (2000) followed Francke (1985) in recognizing Superstitioniinae as a subfamily of Chactidae and Typhlochactini as a tribe of Superstitioniinae. Stockwell (1992) meanwhile elevated Superstitioniinae to family rank for the first time, and included within it *Belisarius xambeui* and another troglomorphic taxon, *Troglotayosicus vachoni* Lourenço, 1981, from Los Tayos Cave, Ecuador, at the time both placed in Chactidae, based on results of an unpublished

cladistic analysis of scorpion higher phylogeny (Stockwell, 1989).

Typhlochactas granulosus Sissom and Cokendolpher, 1998, the sixth species of the genus to be described, was collected in Sótano de Poncho, Veracruz. Sissom and Cokendolpher (1998) tentatively agreed with Stockwell's (1992) recognition of Superstitioniidae at family rank, based on Francke's (1982a) diagnosis of the subfamily, but expressed reservations about including *Troglotayosicus* and *Belisarius* in the family without firm evidence.

A new family, Troglotayosicidae Lourenço, 1998 (as Troglotayosidae), and two monotypic subfamilies, Troglotayosicinae Lourenço, 1998 (as Troglotayosinae), and Belisariinae Lourenço, 1998 (as Belisarinae), were meanwhile created to accommodate *Troglotayosicus* and *Belisarius* respectively, their inclusion in the same family justified solely on the basis of their troglomorphic habitus and relictual distribution (Lourenço, 1998).

Whereas most subsequent authors (Lourenço, 2000, 2001; Lourenço and Sissom, 2000; Sissom, 2000b; Sissom and Hendrixson, 2005; Soleglad and Fet, 2003; Coddington et al., 2004; Prendini and Wheeler, 2005; Fet and Soleglad, 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*.

According to Sissom (2000a, 2000b) and Fet and Sissom (2000), the transferral of *Troglotayosicus* and *Belisarius* from Chactidae to Superstitioniidae was weakly justified, and Troglotayosicidae was not supported by solid characters. Lourenço (2000, 2001) continued to recognise *Troglotayosicus* and *Belisarius* as Troglotayosicidae, however. Coddington et al. (2004) also questioned the monophyly of Troglotayosicidae, suggesting that *Belisarius* may be more closely related to Euscorpidae Laurie, 1896 (and, less plausibly, to Chactidae), than to *Troglotayosicus*, which these authors suggested might be a superstitioniid.

Soleglad and Fet (2003) returned *Belisarius* to Chactidae and *Troglotayosicus* to Superstitioniidae, and synonymized Troglotayosicidae with Superstitioniidae, based on a cladistic analysis of scorpion higher phylog-

eny criticized by Prendini and Wheeler (2005). Prendini and Wheeler (2005) rejected all changes to the suprageneric classification of scorpions proposed by Soleglad, Fet, and colleagues in their self-edited online publication since 2001 and, pending a rigorous and unbiased analysis, reverted to a classification reflected by the most recent peer-reviewed, published treatments which recognized, inter alia, both Superstitioniidae and Troglotayosicidae. In response, Fet and Soleglad (2005) promptly reinstated their previous classification (Soleglad and Fet, 2003), ignoring the problems identified by Prendini and Wheeler (2005), but it was not universally accepted. Lourenço (2006), for example, suggested that *Troglotayosicus* should be retained in Troglotayosicidae or considered incertae sedis in Chactoidea, while Botero-Trujillo and Francke (2009), who described the second species of *Troglotayosicus*, also recognised Troglotayosicidae.

In the most recent contributions on the systematics of these scorpions, Francke et al. (2009) described a new species of *Typhlochactas*, the third putatively endogean species, taken from under a stone in Cañada de La Joya, Queretaro, while Prendini et al. (2009) tested the monophyly and phylogenetic relationships among the nine troglomorphic species with a quantitative cladistic analysis, the first ever conducted in this group of scorpions. The analysis of Prendini et al. (2009), based on 142 phylogenetically informative morphological characters (appendix 1), including eighty-two trichobothrial characters defined strictly on positional homology (the "placeholder approach"; tables 3, 4), confirmed the monophyly of the nine ingroup species (fig. 4). 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, in accordance with the original views of Mitchell (1968: 770, 771). In the present contribution, we therefore elevate Typhlochactidae, for the first time, from their former rank as subfamily; create Alacraninae, new subfamily to accommodate *A. tartarus*; and retain the remaining genera and species in subfamily

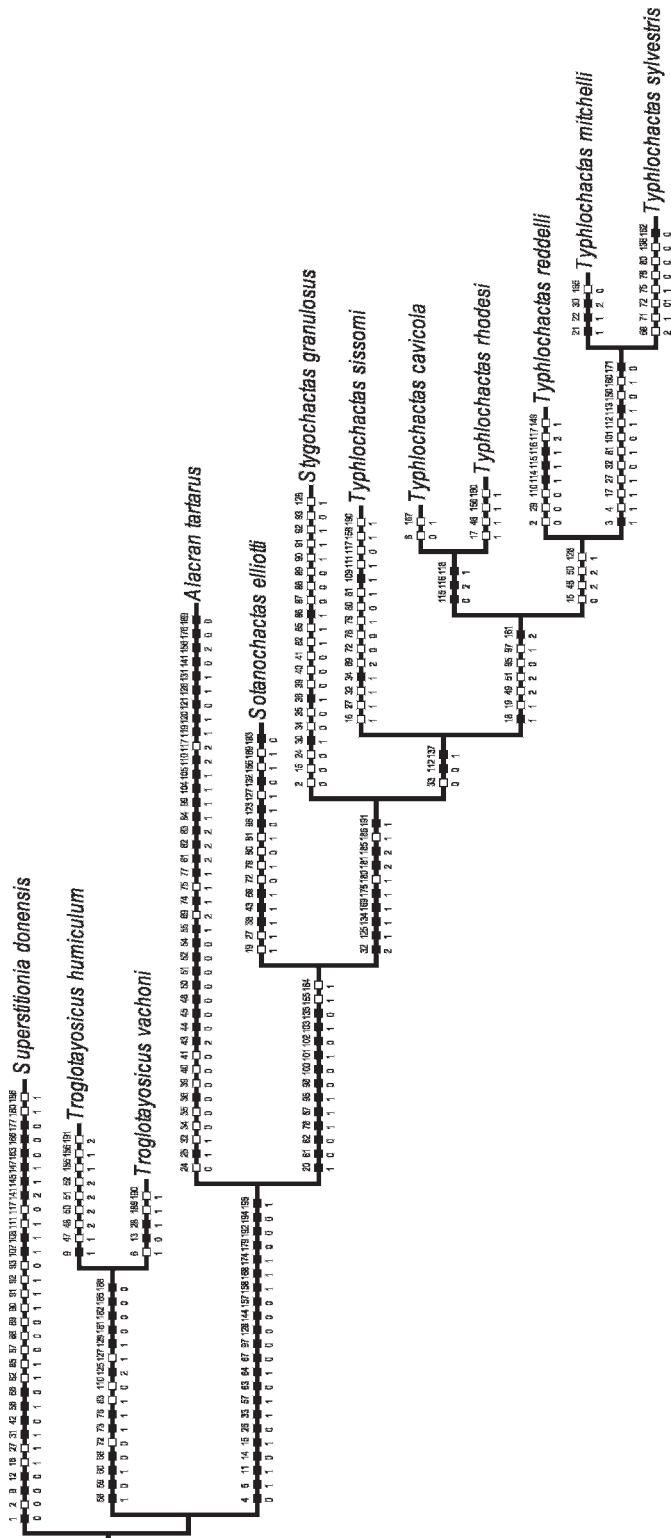


Fig. 4. Single most parsimonious tree (312 steps, CI: 57, RI: 56) obtained by cladistic analysis of 142 morphological characters (appendix 1) scored for nine taxa in the family Typhlochaetidae Mitchell, 1971, and three outgroup taxa under weighting regimes that maximized fit and minimized length (Prendini et al., 2009). 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.

Typhlochactinae. As with Francke's (1986) creation of *Sotanochoctas* to accommodate *T. elliotti*, the many apomorphies supporting the branch leading to *T. granulatus* versus the monophyletic group comprising the remaining species of *Typhlochactas* in the analysis of Prendini et al. (2009), justifies their placement in separate genera. We therefore create *Stygochoctas*, new genus to accommodate *T. granulatus* in a new combination. Based on evidence put forth below, the holotype of *S. granulatus* is a juvenile and the adult, a complete specimen of which has yet to be discovered, may be similar in size to adult *A. tartarus* (which measure 60–70 mm in length), thus representing the second large-bodied species in the family.

MATERIAL AND METHODS

Material examined is deposited in the following collections: American Museum of Natural History, New York (AMNH); Instituto de Biología, Universidad Nacional Autónoma de México, Mexico City (IBUNAM); Muséum National d'Histoire Naturelle, Paris (MNHN); W. David Sissom private collection, Canyon, TX (WDS). All except one of the specimens examined are preserved in 75% ethanol; a leg from a specimen of *A. tartarus* from Cueva de Escorpión, a leg from the *Alacran* specimen from Te Cimutaá Cave, and a leg from the holotype of *T. sissomi* are preserved for DNA isolation in the Ambrose Monell Cryocollection for Molecular and Microbial Research (AMCC) at the AMNH.

Measurements follow Stahnke (1970) and were recorded (in mm) with an ocular micrometer. Color designation follows Smithe (1974, 1975, 1981). Morphological nomenclature follows Hjelle (1990) and Sissom (1990) for pedipalp segmentation; Soleglad and Sissom (2001) for pedipalp chela finger dentition; Soleglad and Fet (2003a) (modified) for sternum; Jacob et al. (2004) for hemispermatophore; Stahnke (1970), Sissom (1990), and Prendini (2000) for remaining features, except trichobothria. Trichobothrial notation follows Vachon (1974) but we adopt a reinterpretation of *Typhlochactas* trichobothrial patterns presented by Prendini and Wheeler (2005) and extend this to the other

genera. Furthermore, the trichobothrial notation used in the taxonomic revision does not necessarily imply homology among the different species (i.e., trichobothria with the same designation in different species are not necessarily homologous); see Prendini et al. (2009), tables 3, 4 and appendix 1 for trichobothrial notation defined strictly on positional homology (the “placeholder approach”).

The morphological examination and measurements were conducted using a Nikon SMZ-1500 stereomicroscope with the aid of visible and UV light, which provides more detailed information regarding the external morphology of the epicuticle (Volschenk, 2005). Photographs were taken under UV and visible light using a Microptics™ ML-1000 digital imaging system. Four of the type specimens (two holotypes and two paratypes) were seriously damaged and some morphological characters of these specimens were difficult to assess. Some preserved specimens did not fluoresce under UV light and were illustrated using visible light instead.

Distribution maps were produced using ArcView GIS Version 8.3 (Environmental Systems Research Institute, Redlands, California) by superimposing georeferenced point locality records on spatial datasets of topography (contour intervals of 500 m) and the boundaries of Mexican states.

ON ‘PETITE’ TRICHOBOTHRIA IN TYPHLOCHACTIDAE

So-called “petite” trichobothria are relatively smaller than other trichobothria on the pedipalps of a scorpion, readily identified, and therefore traditionally considered important “landmarks” for primary homology assessment of other “full-sized” trichobothria (Vachon, 1974; Sissom, 1990; Prendini, 2000; Soleglad and Fet, 2001; Prendini and Wheeler, 2005; Prendini et al., 2006). Petite trichobothria are identified not solely by the reduced diameter of the areola (the pit or follicle in which the seta resides), as suggested by Soleglad and Fet (2001), but also by the reduced length (and often diameter) of the seta itself.

Most scorpions have a standard complement of petite trichobothria. For example, in

the Type A trichobothrial pattern (Buthidae), femoral d_2 , i_3 and i_4 , patellar d_5 , and chelal Eb_3 and Et_4 (manus) and esb (fixed finger) are usually petite (Vachon, 1974; Prendini and Wheeler, 2005; Prendini et al., 2006). In the Type C trichobothrial pattern (most “non-buthids”), patellar esb_2 and chelal Esb and Et_4 (manus) are usually petite. Exceptions to these “fundamental” patterns have been termed “abnormal” by some. In a discussion on “abnormal occurrences” of petite trichobothria in Recent scorpions, Soleglad and Fet (2001: 31, 32) claimed that the presence of “five additional” petite trichobothria, beyond the usual Type C complement of three, is unique to *T. mitchelli*, and attributed the phenomenon to the “incredibly small size” of this species:

In the remarkable small litter scorpion *Typhlochactas mitchelli* Sissom (Sissom, 1988) (Superstitionidae), no less than five additional petite orthobothriotaxic trichobothria are present: for the chela we find Db , Et_5 and esb ; and for the patella, db and dt ... we consider the petite condition exhibited in *T. mitchelli* to be localized to this species and probably due, in part, to the species incredibly small size (adults total length 8.49–8.99 mm.). In line [sic] with this suspicion, other unusual character loss and/or reduction is also found in this species: loss of some denticles on both the fixed and movable fingers of the chelicerae and loss of basal inner accessory denticles on the chelal fingers.

As we demonstrate below, however, 12 petite trichobothria (nine “additional” to the usual Type C complement of three) occur in all eight species of subfamily Typhlochactinae, including *S. granulatus*, the adults of which are probably similar in size to *A. tartarus*, based on estimates from the single adult pedipalp chela known (see below) and *T. sylvestris*, the holotype of which is similar in size to the holotype and paratypes of *T. mitchelli*. There are five petite trichobothria on the patella (d_1 , d_2 , et_2 , esb_2 , eb_2) and seven on the chela (Db , Esb , Et_4 , Et_5 , V_1 , db , esb) of all typhlochactine scorpions.

We were not the first to make these observations, but merely confirmed them across Typhlochactinae. These petite trichobothria were previously illustrated (often with different designations) in *T. reddelli*, *T. rhodesi* and *S. elliotti* by Mitchell (1968,

1971) and Francke (1982a, 1986), in *T. sylvestris* by Mitchell and Peck (1977) and Francke (1982a, 1986), in *T. mitchelli* by Sissom (1988), and in *S. granulatus* by Sissom and Cokendolpher (1998). Mitchell (1968, 1971), Mitchell and Peck (1977), and Francke (1982a) denoted them only with a shorter seta, whereas Francke (1986), Sissom (1988), and Sissom and Cokendolpher (1998) denoted them with a shorter seta and a smaller areola, following the convention of Vachon (1974). Sissom (1988: 369, 370) and Sissom and Cokendolpher (1998: 288, 289) explicitly mentioned some of the trichobothria they recognized as petite in *T. mitchelli* (patellar db , dt ; chelal Db , Esb , Et_4 , Et_5 , esb) and *S. granulatus* (patellar d_1 , d_2 ; chelal Db , Esb , Et_4 , Et_5 , V_1 , esb), respectively.

The putative “abnormal occurrence” of these petite trichobothria provides several synapomorphies for Typhlochactinae (Prendini et al., 2009; fig. 4). None of the “additional” petite trichobothria was scored as such in the “*Typhlochactas*” terminal (an explicit composite of all species in the genus plus *Sotanochactas*) of Soleglad and Fet’s (2003b: 451, table 3) trichobothrial character matrix, however.

Surprisingly, there are no petite trichobothria on the pedipalps of *Alacran*. Not even the three landmark petite trichobothria on the external surfaces of the chela manus (Esb , Et_4) and patella (esb_2) of most Type C scorpions (Vachon, 1974) are petite, although they were scored as such in the *Alacran* terminal of Soleglad and Fet’s (2003b: 451, table 3) trichobothrial character matrix. The areolae and setae of Esb , Et_4 and esb_2 are similar in dimensions to those of other trichobothria on the pedipalps of *A. tartarus*, as first illustrated by Francke (1982a: 58, figs. 5–11). Prendini and Wheeler (2005: 469, fig. 12) mistakenly followed Soleglad and Fet (2003b: 40, fig. 80) in illustrating pedipalp patellar trichobothrium esb_2 as petite in *A. tartarus*. The absence of petite trichobothria in *Alacran*, compared to their presence in *Stygochactas*, the adult pedipalp chelae of which are similar in dimensions, falsifies Soleglad and Fet’s (2001: 31, 32) hypothesis that the presence of “additional” petite trichobothria is in any way related to the size of a scorpion.

TABLE 3
Trichobothrial homology on pedipalp femur and patella of Typhlochaetidae Mitchell, 1971 and related taxa according to Vachon's (1974) nomenclature
 Each row in table represents trichobothrium in topographically similar position among different taxa. First column denotes nomenclature according to the "placeholder" approach (Prendini et al., 2009), for comparison with fig. 4 and appendix 1. Petite trichobothria (*sensu* Vachon, 1974) denoted with square brackets. Taxa as follows: *Super.* = *Superstitionia* Stahnke, 1940; *Trogl.* = *Troglotayosicus* Lourenço, 1981; *Alacr.* = *Alacran* Francke, 1982; *Sotan.* = *Sotanochaetas* Francke, 1986; *Stygo.* = *Stygochaetas*, new genus; *T. sis.* = *Typhlochaetas sissomi* Francke et al., 2009; *T. cav.* = *Typhlochaetas cavicola* Francke, 1986; *T. rho.* = *Typhlochaetas rhodesi* Mitchell, 1968; *T. red.* = *Typhlochaetas reddelli* Mitchell, 1968; *T. mit.* = *Typhlochaetas mitchelli* Sissom, 1988; *T. syl.* = *Typhlochaetas 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

	<i>Super.</i>	<i>Trogl.</i>	<i>Alacr.</i>	<i>Sotan.</i>	<i>Stygo.</i>	<i>T. sis.</i>	<i>T. rho.</i>	<i>T. red.</i>	<i>T. mit.</i>	<i>T. syl.</i>
Femur	<i>i</i> ₁	<i>i</i>	<i>i</i>	<i>i</i>	<i>i</i>	<i>i</i>	<i>i</i>	<i>i</i>	<i>i</i>	<i>i</i>
	<i>i</i> ₂									
	<i>d</i> ₁	<i>d</i>	<i>d</i>	<i>d</i>	<i>d</i>	<i>d</i>	<i>d</i>	<i>d</i>	<i>d</i>	<i>d</i>
	<i>d</i> ₂									
	<i>e</i> ₁	<i>e</i>	<i>e</i>	<i>e</i>	<i>e</i>	<i>e</i>	<i>e</i>	<i>e</i>	<i>e</i>	<i>e</i>
Patella	<i>d</i> ₁	<i>d</i> ₁	<i>d</i> ₁	[<i>d</i> ₁]	[<i>d</i> ₁]	[<i>d</i> ₁]	[<i>d</i> ₁]	[<i>d</i> ₁]	[<i>d</i> ₁]	[<i>d</i> ₁]
	<i>d</i> ₂	<i>d</i> ₂	<i>d</i> ₂	[<i>d</i> ₂]	[<i>d</i> ₂]	[<i>d</i> ₂]	[<i>d</i> ₂]	[<i>d</i> ₂]	[<i>d</i> ₂]	[<i>d</i> ₂]
	<i>i</i> ₁	<i>i</i>	<i>i</i>	<i>i</i>	<i>i</i>	<i>i</i>	<i>i</i>	<i>i</i>	<i>i</i>	<i>i</i>
	<i>v</i> ₁	<i>v</i> ₁	<i>v</i> ₁	<i>v</i> ₁	<i>v</i> ₁	<i>v</i> ₁	<i>v</i> ₁	<i>v</i> ₁	<i>v</i> ₁	<i>v</i> ₁
	<i>v</i> ₂	<i>v</i> ₂	<i>v</i> ₂	<i>v</i> ₂	<i>v</i> ₂	<i>v</i> ₂	<i>v</i> ₂	<i>v</i> ₂	<i>v</i> ₂	<i>v</i> ₂
	<i>v</i> ₃	<i>v</i> ₃	<i>v</i> ₃	<i>v</i> ₃	<i>v</i> ₃	<i>v</i> ₃	<i>v</i> ₃	<i>v</i> ₃	<i>v</i> ₃	<i>v</i> ₃
	<i>e</i> ₁	<i>e</i> ₁	<i>e</i> ₁	<i>e</i> ₁	<i>e</i> ₁	<i>e</i> ₁	<i>e</i> ₁	<i>e</i> ₁	<i>e</i> ₁	<i>e</i> ₁
	<i>e</i> ₂			[<i>e</i> ₂]	[<i>e</i> ₂]	[<i>e</i> ₂]	[<i>e</i> ₂]	[<i>e</i> ₂]	[<i>e</i> ₂]	[<i>e</i> ₂]
	<i>e</i> ₃	<i>e</i> ₃	<i>e</i> ₃	<i>e</i> ₃	<i>e</i> ₃	<i>e</i> ₃	<i>e</i> ₃	<i>e</i> ₃	<i>e</i> ₃	<i>e</i> ₃
	<i>e</i> ₄			<i>e</i> _{a1}	<i>e</i> ₃					<i>e</i> _{m3}
	<i>e</i> ₅			<i>e</i> ₃						abs. or [<i>v</i> ₃]
	<i>e</i> ₆									
	<i>e</i> ₇			<i>e</i> _{a1}						
	<i>e</i> ₈			<i>e</i> _{a2}						
	<i>e</i> ₉		<i>e</i> ₁							<i>e</i> _{f3}
<i>e</i> _{st1}	<i>e</i> _{st1}	<i>e</i> _{st1}	<i>e</i> _{st1}	<i>e</i> _{st1}	<i>e</i> _{st1}	<i>e</i> _{st1}	<i>e</i> _{st1}	<i>e</i> _{st1}	<i>e</i> _{st1}	<i>e</i> _{st1}
<i>e</i> _{st2}			<i>e</i> _{st2}							
<i>e</i> _{m1}	<i>e</i> _{m1}	<i>e</i> _{m1}	<i>e</i> _{m1}	<i>e</i> _{m1}	<i>e</i> _{m1}	<i>e</i> _{m1}	<i>e</i> _{m1}	<i>e</i> _{m1}	<i>e</i> _{m1}	<i>e</i> _{m1}
<i>e</i> _{m2}			<i>e</i> _{m2}	<i>e</i> _{m2}	<i>e</i> _{m2}	<i>e</i> _{m2}	<i>e</i> _{m2}	<i>e</i> _{m2}	<i>e</i> _{m2}	<i>e</i> _{m2}
<i>e</i> _{m3}			<i>e</i> _{m3}	<i>e</i> _{m3}	<i>e</i> _{m3}	<i>e</i> _{m3}	<i>e</i> _{m3}	<i>e</i> _{m3}	<i>e</i> _{m3}	<i>e</i> _{m3}

TABLE 3
(Continued)

	Super.	Trogl.	Alacr.	Sotan.	Stygo.	T. sis.	T. cav.	T. red.	T. mit.	T. syl.
<i>em</i> ₄	<i>em</i> ₂	<i>em</i> ₂	<i>em</i> ₃		<i>em</i> ₃		<i>em</i> ₃	<i>em</i> ₃	<i>em</i> ₃	
<i>esb</i> ₁	<i>esb</i> ₁	<i>esb</i> ₁	<i>esb</i> ₁	<i>esb</i> ₁	<i>esb</i> ₁	<i>esb</i> ₁	<i>esb</i> ₁	<i>esb</i> ₁	<i>esb</i> ₁	<i>esb</i> ₁
<i>esb</i> ₂			<i>esb</i> ₂	[<i>esb</i> ₂]	[<i>esb</i> ₂]	[<i>esb</i> ₂]	[<i>esb</i> ₂]	[<i>esb</i> ₂]	[<i>esb</i> ₂]	[<i>esb</i> ₂]
<i>esb</i> ₃	[<i>esb</i> ₂]	[<i>esb</i> ₂]	<i>esb</i> _{a1}							
<i>esb</i> ₄			<i>em</i> _{a2}							
<i>esb</i> ₅			<i>esb</i> _{a2}							
<i>eb</i> ₁	<i>eb</i> ₁	<i>eb</i> ₁	<i>eb</i> ₁	<i>eb</i> ₁	<i>eb</i> ₁	<i>eb</i> ₁	<i>eb</i> ₁	<i>eb</i> ₁	<i>eb</i> ₁	<i>eb</i> ₁
<i>eb</i> ₂	<i>eb</i> ₂	<i>eb</i> ₂	<i>eb</i> ₂	[<i>eb</i> ₂]	[<i>eb</i> ₂]	[<i>eb</i> ₂]	[<i>eb</i> ₂]	[<i>eb</i> ₂]	[<i>eb</i> ₂]	[<i>eb</i> ₂]
<i>eb</i> ₃		<i>eb</i> ₃	<i>eb</i> ₃	<i>eb</i> ₃	<i>eb</i> ₃	<i>eb</i> ₃	<i>eb</i> ₃	<i>eb</i> ₃	<i>eb</i> ₃	<i>eb</i> ₃
<i>eb</i> ₄		<i>eb</i> ₄	<i>eb</i> ₄	<i>eb</i> ₄	<i>eb</i> ₄	<i>eb</i> ₄	<i>eb</i> ₄	<i>eb</i> ₄	<i>eb</i> ₄	<i>eb</i> ₄
<i>eb</i> ₅										
<i>eb</i> ₆	<i>eb</i> ₃				<i>eb</i> ₃					
<i>eb</i> ₇	<i>eb</i> ₄				<i>eb</i> ₄					
<i>eb</i> ₈	<i>eb</i> ₅				<i>eb</i> ₅					
<i>eb</i> ₉		<i>eb</i> ₅	<i>eb</i> ₅	<i>eb</i> ₅	<i>eb</i> ₅	<i>eb</i> ₅	<i>eb</i> ₅	<i>eb</i> ₅	<i>eb</i> ₅	<i>eb</i> ₅

Soleglad and Fet (2003b: 37, fig. 66) also failed to illustrate the fifth trichobothrium on the ventral surface of the pedipalp chela of *A. tartarus*, with implications for the scheme of chela trichobothrial homology among the genera they placed in Superstitioniidae.

SYSTEMATICS

TYPHLOCHACTIDAE Mitchell, 1971

Typhlochactinae Mitchell, 1971: 135; type genus *Typhlochactas* Mitchell, 1971.

Typhlochactinae: Mitchell, 1968: 774 (nomen nudum); Soleglad, 1976: 299, 301; Mitchell and Peck, 1977: 159; Francke, 1982a: 51, 57; Sissom and Cokendolpher, 1998: 285; Sissom, 2000b: 497; Soleglad and Fet, 2003b: 28, 30, 36, 51, 76, 82, 106, 107, 109, 141–143, fig. 116, tab. 9; Prendini and Wheeler, 2005: 448, 462, 472, 473, 492, tab. 2, 10; Fet and Soleglad, 2005: 12; Volschenk and Prendini, 2008: 243.

DIAGNOSIS: Typhlochactidae may be separated from all other scorpion families on the basis of the following combination of characters. Carapace, tergites, pedipalps, and metasoma not pigmented or infuscated. Cheliceral movable finger, external distal tooth smaller than internal distal tooth; ventral surface with serrula; ventral edge smooth, without teeth. Carapace without median or lateral ocelli; anterior margin without median notch (emargination). Pedipalp chela fingers, median denticle row comprising oblique, nonoverlapping primary subrows. Pedipalp patella, internal surface, dorsal and ventral processes absent or very weakly developed, comprising at most a low granule. Pedipalp femur trichobothrium *e* situated on dorsal surface or dorsoexternal carina; trichobothrium *d* situated proximal to or level with trichobothrium *i*. Pedipalp patella trichobothrium *i* situated on dorsal surface; ventral surface with two or three trichobothria. Pedipalp chela trichobothrium *Db* situated proximally; trichobothrium *Dt* situated distally. Legs without tibial spurs, retrolateral pedal spurs, and often without prolateral pedal spurs; basitarsi I–IV without retroventral or retrolateral rows of spinules or spinule clusters; III and IV without proventral rows of spinules or spinule clusters; telotarsi, laterodistal lobes truncate,

TABLE 4
Trichobothrial homology on pedipalp chela of Typhlochaetidae Mitchell, 1971 and related taxa according to Vachon's (1974) nomenclature

Each row in table represents trichobothrium in topographically similar position among different taxa. First column denotes nomenclature according to the "placeholder" approach (Prendini et al., 2009), for comparison with fig. 4 and appendix 1. Petite trichobothria (*sensu* Vachon, 1974) denoted with square brackets. Taxa as follows: *Super.* = *Superstitio* Stahnke, 1940; *Trogl.* = *Troglotayosicus* Lourenço, 1981; *Alacr.* = *Alacran* Francke, 1982; *Sotan.* = *Sotanochaeta* Francke, 1986; *Stygo.* = *Stygochaeta*, new genus; *T. sis.* = *Typhlochaeta sissomi* Francke et al., 2009; *T. cav.* = *Typhlochaeta cavicola* Francke, 1986; *T. rho.* = *Typhlochaeta rhodesi* Mitchell, 1968; *T. red.* = *Typhlochaeta reddelli* Mitchell, 1968; *T. mit.* = *Typhlochaeta mitchelli* Sissom, 1988; *T. syl.* = *Typhlochaeta sylvestris* Mitchell and Peck, 1977. The trichobothrial patterns of *T. cavicola* and *T. rhodesi* are identical

	<i>Super.</i>	<i>Trogl.</i>	<i>Alacr.</i>	<i>Sotan.</i>	<i>Stygo.</i>	<i>T. sis.</i>	<i>T. cav</i> <i>T. rho.</i>	<i>T. red.</i>	<i>T. mit.</i>	<i>T. syl.</i>
Chela										
<i>i</i> ₁	<i>it</i>	<i>it</i>	<i>it</i>	<i>it</i>	<i>it</i>	<i>it</i>	<i>it</i>	<i>it</i>	<i>it</i>	<i>it</i>
<i>b</i> ₁	<i>ib</i>	<i>ib</i>	<i>ib</i>	<i>ib</i>	<i>ib</i>	<i>ib</i>	<i>ib</i>	<i>ib</i>	<i>ib</i>	<i>ib</i>
<i>i</i> ₃	<i>V</i> ₂	<i>V</i> ₂	<i>V</i> ₂	<i>V</i> ₂	<i>V</i> ₂	<i>V</i> ₂	<i>V</i> ₂	<i>V</i> ₂	<i>V</i> ₂	<i>V</i> ₂
<i>i</i> ₄	<i>V</i> ₁	<i>V</i> ₁	<i>V</i> ₁	<i>V</i> ₁	<i>V</i> ₁	<i>V</i> ₁	<i>V</i> ₁	<i>V</i> ₁	<i>V</i> ₁	<i>V</i> ₁
<i>i</i> ₅	<i>V</i> ₃	<i>V</i> ₃	<i>V</i> ₃	<i>V</i> ₃	<i>V</i> ₃	<i>V</i> ₃	<i>V</i> ₃	<i>V</i> ₃	<i>V</i> ₃	<i>V</i> ₃
<i>V</i> ₁	<i>V</i> ₄	<i>V</i> ₄	<i>V</i> ₄	<i>V</i> ₄	<i>V</i> ₄	<i>V</i> ₄	<i>V</i> ₄	<i>V</i> ₄	<i>V</i> ₄	<i>V</i> ₄
<i>V</i> ₂	<i>Eb</i> ₁	<i>Eb</i> ₁	<i>Eb</i> ₁	<i>Eb</i> ₁	<i>Eb</i> ₁	<i>Eb</i> ₁	<i>Eb</i> ₁	<i>Eb</i> ₁	<i>Eb</i> ₁	<i>Eb</i> ₁
<i>V</i> ₃	<i>Eb</i> ₂	<i>Eb</i> ₂	<i>Eb</i> ₂	<i>Eb</i> ₂	<i>Eb</i> ₂	<i>Eb</i> ₂	<i>Eb</i> ₂	<i>Eb</i> ₂	<i>Eb</i> ₂	<i>Eb</i> ₂
<i>V</i> ₄	<i>Eb</i> ₃	<i>Eb</i> ₃	<i>Eb</i> ₃	<i>Eb</i> ₃	<i>Eb</i> ₃	<i>Eb</i> ₃	<i>Eb</i> ₃	<i>Eb</i> ₃	<i>Eb</i> ₃	<i>Eb</i> ₃
<i>V</i> ₅	[<i>Esb</i>]	[<i>Esb</i>]	<i>Esb</i>	[<i>Esb</i>]	[<i>Esb</i>]	[<i>Esb</i>]	[<i>Esb</i>]	[<i>Esb</i>]	[<i>Esb</i>]	[<i>Esb</i>]
<i>V</i> ₆	<i>Em</i>	<i>Em</i>	<i>Em</i>	<i>Em</i>	<i>Em</i>	<i>Em</i>	<i>Em</i>	<i>Em</i>	<i>Em</i>	<i>Em</i>
<i>Eb</i> ₁	<i>Db</i>	[<i>Db</i>]	<i>Db</i>	[<i>Db</i>]	[<i>Db</i>]	[<i>Db</i>]	[<i>Db</i>]	[<i>Db</i>]	[<i>Db</i>]	[<i>Db</i>]
<i>Eb</i> ₂	<i>E</i> ₁₅	<i>E</i> ₁₅	<i>E</i> ₁₅	<i>E</i> ₁₅	<i>E</i> ₁₅	<i>E</i> ₁₅	<i>E</i> ₁₅	<i>E</i> ₁₅	<i>E</i> ₁₅	<i>E</i> ₁₅
<i>Eb</i> ₃	<i>alb</i>	<i>alb</i>	<i>alb</i>	<i>alb</i>	<i>alb</i>	<i>alb</i>	<i>alb</i>	<i>alb</i>	<i>alb</i>	<i>alb</i>
<i>Esb</i> ₁	<i>E</i> ₁	<i>E</i> ₁	<i>E</i> ₁	<i>E</i> ₁	<i>E</i> ₁	<i>E</i> ₁	<i>E</i> ₁	<i>E</i> ₁	<i>E</i> ₁	<i>E</i> ₁
<i>Esb</i> ₂	<i>E</i> ₂	<i>E</i> ₂	<i>E</i> ₂	<i>E</i> ₂	<i>E</i> ₂	<i>E</i> ₂	<i>E</i> ₂	<i>E</i> ₂	<i>E</i> ₂	<i>E</i> ₂
<i>D</i> ₁	[<i>E</i> ₄]	[<i>E</i> ₄]	<i>E</i> ₄	[<i>E</i> ₄]	[<i>E</i> ₄]	[<i>E</i> ₄]	[<i>E</i> ₄]	[<i>E</i> ₄]	[<i>E</i> ₄]	[<i>E</i> ₄]
<i>D</i> ₂	<i>esb</i>	<i>esb</i>	<i>esb</i>	<i>esb</i>	<i>esb</i>	<i>esb</i>	<i>esb</i>	<i>esb</i>	<i>esb</i>	<i>esb</i>
<i>D</i> ₃	<i>D</i> ₁	<i>D</i> ₁	<i>D</i> ₁	<i>D</i> ₁	<i>D</i> ₁	<i>D</i> ₁	<i>D</i> ₁	<i>D</i> ₁	<i>D</i> ₁	<i>D</i> ₁
<i>E</i> ₁	<i>E</i> ₁	<i>E</i> ₁	<i>E</i> ₁	<i>E</i> ₁	<i>E</i> ₁	<i>E</i> ₁	<i>E</i> ₁	<i>E</i> ₁	<i>E</i> ₁	<i>E</i> ₁
<i>E</i> ₂	<i>E</i> ₂	<i>E</i> ₂	<i>E</i> ₂	<i>E</i> ₂	<i>E</i> ₂	<i>E</i> ₂	<i>E</i> ₂	<i>E</i> ₂	<i>E</i> ₂	<i>E</i> ₂
<i>E</i> ₃	[<i>E</i> ₄]	[<i>E</i> ₄]	<i>E</i> ₄	[<i>E</i> ₄]	[<i>E</i> ₄]	[<i>E</i> ₄]	[<i>E</i> ₄]	[<i>E</i> ₄]	[<i>E</i> ₄]	[<i>E</i> ₄]
<i>E</i> ₄	<i>Est</i>	<i>Est</i>	<i>Est</i>	<i>Est</i>	<i>Est</i>	<i>Est</i>	<i>Est</i>	<i>Est</i>	<i>Est</i>	<i>Est</i>
<i>E</i> ₅	<i>Est</i>	<i>Est</i>	<i>Est</i>	<i>Est</i>	<i>Est</i>	<i>Est</i>	<i>Est</i>	<i>Est</i>	<i>Est</i>	<i>Est</i>
<i>E</i> ₆	<i>Est</i>	<i>Est</i>	<i>Est</i>	<i>Est</i>	<i>Est</i>	<i>Est</i>	<i>Est</i>	<i>Est</i>	<i>Est</i>	<i>Est</i>
<i>Est</i> ₁	<i>Est</i>	<i>Est</i>	<i>Est</i>	<i>Est</i>	<i>Est</i>	<i>Est</i>	<i>Est</i>	<i>Est</i>	<i>Est</i>	<i>Est</i>
<i>Est</i> ₂	<i>Est</i>	<i>Est</i>	<i>Est</i>	<i>Est</i>	<i>Est</i>	<i>Est</i>	<i>Est</i>	<i>Est</i>	<i>Est</i>	<i>Est</i>
<i>Est</i> ₃	<i>Est</i>	<i>Est</i>	<i>Est</i>	<i>Est</i>	<i>Est</i>	<i>Est</i>	<i>Est</i>	<i>Est</i>	<i>Est</i>	<i>Est</i>
<i>Est</i> ₄	<i>Est</i>	<i>Est</i>	<i>Est</i>	<i>Est</i>	<i>Est</i>	<i>Est</i>	<i>Est</i>	<i>Est</i>	<i>Est</i>	<i>Est</i>

TABLE 4
(Continued)

	Super.	Trogl.	Alacr.	Sotan.	Stygo.	T. sis.	T. cav T. rho.	T. red.	T. mit.	T. syl.
<i>Est5</i>				[<i>Et5</i>]	[<i>Et5</i>]		<i>Et3</i>	[<i>Et5</i>]	[<i>Et5</i>]	[<i>Et5</i>]
<i>Est6</i>		[<i>Et4</i>]	<i>Et5</i>	[<i>Et5</i>]	[<i>Et5</i>]		[<i>Et5</i>]	<i>Dt</i>	[<i>Et5</i>]	[<i>Et5</i>]
<i>Est7</i>							<i>Dt</i>			
<i>d2</i>			<i>dt</i>							
<i>d3</i>			<i>dst</i>							
<i>d4</i>	<i>dt</i>	<i>dt</i>		<i>dt</i>	<i>dt</i>	<i>dt</i>	<i>dt</i>	<i>dt</i>	<i>dt</i>	<i>dt</i>
<i>d5</i>	<i>dst</i>		<i>db</i>							
<i>d6</i>				<i>dst</i>						
<i>d7</i>				[<i>db</i>]	<i>dst</i>	<i>dst</i>	<i>dst</i>	<i>dst</i>	<i>dst</i>	<i>dst</i>
<i>d8</i>		<i>db</i>			[<i>db</i>]	[<i>db</i>]	[<i>db</i>]	[<i>db</i>]	[<i>db</i>]	[<i>db</i>]
<i>m1</i>										
<i>m2</i>		<i>dst</i>	<i>dsb</i>							
<i>m3</i>	<i>dsb</i>	<i>dsb</i>		<i>dsb</i>	<i>dsb</i>	<i>dsb</i>	<i>dsb</i>	<i>dsb</i>	<i>dsb</i>	<i>dsb</i>
<i>m4</i>		[<i>Dt</i>]								
<i>e2</i>			<i>et</i>	<i>et</i>						
<i>e3</i>	<i>et</i>	<i>et</i>	<i>est</i>	<i>est</i>	<i>et</i>	<i>et</i>	<i>et</i>	<i>et</i>	<i>et</i>	<i>et</i>
<i>e4</i>			<i>em</i>							
<i>e5</i>	<i>est</i>	<i>est</i>	<i>esb</i>	[<i>esb</i>]	<i>est</i>	<i>est</i>	<i>est</i>	<i>est</i>	<i>est</i>	<i>est</i>
<i>e6</i>		<i>esb</i>		<i>eb</i>	[<i>esb</i>]	[<i>esb</i>]	[<i>esb</i>]	[<i>esb</i>]	[<i>esb</i>]	[<i>esb</i>]
<i>e7</i>					<i>eb</i>	<i>eb</i>	<i>eb</i>	<i>eb</i>	<i>eb</i>	<i>eb</i>
<i>e8</i>	<i>eb</i>	<i>eb</i>	<i>eb</i>							

each with two pairs of terminal macrosetae, usually without ventromedian row of spinules, and with somewhat irregular, paired ventrosubmedian rows of macrosetae. Sternum Type 2, pentagonal; apex rounded; lateral lobes flat; not longitudinally compressed. Pectinal lamellae fused to some degree; fulcra absent; teeth straight, nonoverlapping. Genital opercula (male), medial edges closely adpressed, genital papillae only visible at posterior edges or in posterior third; genital opercula (female), sclerites fused, usually loosely connected by membrane along entire length of suture. Respiratory spiracles (stigmata) small, rounded. Metasomal segments I–III, dorsosubmedian carinae, distal granules not noticeably larger than preceding granules; segment IV, dorsolateral carina termination conspicuously flared, straight. Telson without anterodorsal lateral lobes. Hemispermatophore lamelliform; capsule weakly developed; spiniform processes absent.

INCLUDED TAXA: Comprising two subfamilies: Alacraninae, comprising one genus, *Alacran* Francke, 1982, monotypic; Typhlochactinae, comprising three genera, *Sotanochactas* Francke, 1986, monotypic, *Stygochactas*, new genus, monotypic, and *Typhlochactas* Mitchell, 1971, with six species (table 2).

DISTRIBUTION: Endemic to Mexico. Recorded from five states: Oaxaca, Queretaro, San Luis Potosí, Tamaulipas, Veracruz (fig. 1).

Key to identification of the subfamilies, genera, and species of Typhlochactidae Mitchell, 1971

(Additional diagnostic differences summarized in table 5.)

- 1. Pedipalp patella with three trichobothria on ventral surface and 21 (rarely 19 or 20) on external surface *Alacran tartarus* (Alacraninae)
- Pedipalp patella with two trichobothria on ventral surface and 14 (rarely 15) on external surface 2 (Typhlochactinae)
- 2. Pedipalp chela fingers more than twice length of manus *Sotanochactas elliotti*
- Pedipalp chela fingers similar in length to manus 3
- 3. Prolateral pedal spurs absent 4

- Prolateral pedal spurs present 6
- 4. Cheliceral fixed finger, median and basal teeth fused into a bicusp *Stygochactas granulosus*
- Cheliceral fixed finger, median and basal teeth separate, not fused 5
- 5. Cheliceral movable finger with four dorsal teeth *Typhlochactas cavicola*
- Cheliceral movable finger with five dorsal teeth *Typhlochactas rhodesi*
- 6. Cheliceral fixed finger, median and basal teeth fused into a bicusp *Typhlochactas reddelli*
- Cheliceral fixed finger, median and basal teeth separate, not fused 7
- 7. Cheliceral fixed finger with four teeth *Typhlochactas sissomi*
- Cheliceral fixed finger with three teeth 8
- 8. Cheliceral movable finger with four dorsal teeth *Typhlochactas sylvestris*
- Cheliceral movable finger with three dorsal teeth *Typhlochactas mitchelli*

ALACRANINAE, new subfamily

Type genus, *Alacran* Francke, 1982.

DIAGNOSIS: Alacraninae, the sister group of Typhlochactinae (fig. 4), may be separated from the latter on the basis of the following combination of characters. Size moderate to large, total length (adult), 60–70 mm. Cheliceral fixed finger, median and basal teeth not fused into a bicusp; movable finger with five dorsal teeth (two subdistal teeth present). Carapace, anterior margin, median projection (epistome) absent; median longitudinal sulcus obsolete. Pedipalp femur dorsoexternal, dorsointernal, and ventrointernal carinae, patella dorsoexternal, externomedian, ventroexternal, ventrointernal and internomedian carinae, and chela external secondary, ventroexternal and ventrointernal carinae, well developed. Pedipalp chela, fixed and movable fingers, median denticle row comprising six and seven oblique primary subrows, respectively; internal denticles smaller than external denticles; fixed finger, terminal denticle considerably larger than preceding denticles, hooklike, fingertips interlocking unevenly when closed. Pedipalp patella with 25–27 trichobothria, three situated on dorsal surface, 19–21 (including 6–8 accessory trichobothria) on external surface, and three on ventral surface. Chela with 29 trichobothria, 11 (including an accessory

TABLE 5

Discrete diagnostic characters separating the genera and species of Typhlochactidae Mitchell, 1971 (modified from Sissom and Cokendolpher, 1998)

Abbreviations as follows: *A. tar.* = *Alacran tartarus* Francke, 1982; *S. ell.* = *Sotanochactas elliotti* (Mitchell, 1971); *S. gra.* = *Stygochactas granulatus* (Sissom and Cokendolpher, 1998); *T. cav.* = *Typhlochactas cavicola* Francke, 1986; *T. mit.* = *Typhlochactas mitchelli* Sissom, 1988; *T. red.* = *Typhlochactas reddelli* Mitchell, 1968; *T. rho.* = *Typhlochactas rhodesi* Mitchell, 1968; *T. sis.* = *Typhlochactas sissomi* Francke et al., 2009; *T. syl.* = *Typhlochactas sylvestris* Mitchell and Peck, 1977; abs. = absent; pres. = present

Character	<i>A. tar.</i>	<i>S. ell.</i>	<i>S. gra.</i>	<i>T. cav.</i>	<i>T. mit.</i>	<i>T. red.</i>	<i>T. rho.</i>	<i>T. sis.</i>	<i>T. syl.</i>
Cheliceral fixed finger, median and basal teeth, bicusp	abs.	abs.	pres.	abs.	abs.	pres.	abs.	abs.	abs.
Cheliceral fixed finger, teeth (subdistal: 0, 1)	4 (1)	4 (1)	4 (1)	4 (1)	3 (0)	4 (1)	4 (1)	4 (1)	3 (0)
Cheliceral movable finger, dorsal teeth (subdistal: 0, 1, 2)	5 (2)	4 (1)	4 (1)	4 (1)	4 (1)	5 (2)	5 (2)	5 (2)	3 (0)
Chela fixed finger, primary subrows	6	6	7	6	4–5	6	6	6	5
Chela movable finger, primary subrows	7	5	7	5	5–6	7	6	6	6
Chela fixed finger <i>e</i> trichobothrial count	5	4	4	4	4	4	4	4	4
Chela manus <i>E</i> trichobothrial count	11	10	10	10	10	10	10	10	10
Chela manus <i>V</i> trichobothrial count	5	4	4	4	4	4	4	4	4
Patella <i>e</i> trichobothrial count	19–21	14	14	14	14	14	14	14	14–15
Patella <i>v</i> trichobothrial count	3	2	2	2	2	2	2	2	2
Prolateral pedal spurs	pres.	abs.	abs.	abs.	pres.	pres.	abs.	pres.	pres.
Telotarsal spinules, ventromedian row	abs.	abs.	abs.	abs.	pres.	abs.	abs.	abs.	pres.

trichobothrium) situated on fixed finger and 18 (including one accessory trichobothrium on external surface and another on ventral surface) situated on manus. All trichobothrial areolae small, similar in diameter, trichobothrial setae similar in length (none “petite”). Chela fixed finger, dorsal and external trichobothria situated in distal half of finger. Leg basitarsi with prolateral pedal spurs, retrolateral surfaces without spinules distally; telotarsi each with more than 10 thin, acuminate macrosetae in paired ventro-submedian rows, without ventromedian row of spinules. Sternite VII, ventrolateral carinae weakly developed. Metasomal segments I–IV, dorsosubmedian and ventrolateral carinae well developed; segment V, dorsolateral and ventrolateral carinae well developed. Telson (adult) vesicle markedly globose; aculeus very short.

INCLUDED TAXA: Monotypic genus, *Alacran* Francke, 1982.

DISTRIBUTION: Endemic to Mexico. Recorded from Oaxaca (fig. 1A).

Alacran Francke, 1982

Alacran Francke, 1982a: 51–53, 57, 59–61, fig. 26; type species *Alacran tartarus* Francke, 1982.

Alacran: Francke, 1985: 5, 16, 19; Lourenço and Francke, 1985: 4; Francke, 1986: 8; Sissom, 1990: 109, 113; Nenilin and Fet, 1992: 10; Stockwell, 1992: 410, 412, 414, 419, figs. 24, 31, 32; Armas, 1994: 19; Kovařík, 1998: 142; Sissom and Cokendolpher, 1998: 285; Beutelspacher Baigts, 2000: 6, 13–16, 18, 48, 50, 51, 151, fig. 10, graph 1, tables 1, 2; Lourenço, 2000: 25; Lourenço and Sissom, 2000: 118; Sissom, 2000b: 496–498; Lourenço, 2001: 4; Soleglad and Sissom, 2001: 40; Soleglad and Fet, 2003a: 17, 32; 2003b: 13, 28, 32, 36, 48, 51, 67, 72, 82, 106–109, 136, 138, 141, 162, 164, tables 3, 4, 9; fig. 116; Prendini and Wheeler, 2005: 463, 468, 476–478, tables 3–5, 10; Fet and Soleglad, 2005: 12; Sissom and Hendrixson, 2005: 130; Dupré, 2006: 2; Francke and Savary, 2006: 29; Graham and Fet, 2006: 2, 7; Volschenk and Prendini, 2008: 249; Kamenz and Prendini, 2008: 10 (table 2), 34, 44.

DIAGNOSIS: As for subfamily.

INCLUDED TAXA: Single species, *Alacran tartarus* Francke, 1982.

DISTRIBUTION: Specimens of *Alacran* have been collected from five caves in the state of Oaxaca, southeastern Mexico (Cueva de Escorpión, Sótano Agua de Carrizo, Sótano Li Nita, Sótano de San Agustín, Te Cimutáá Cave). *Alacran tartarus* is known from the first four of these caves which occur in the Sistema Huautla (Reddell, 1981), a large

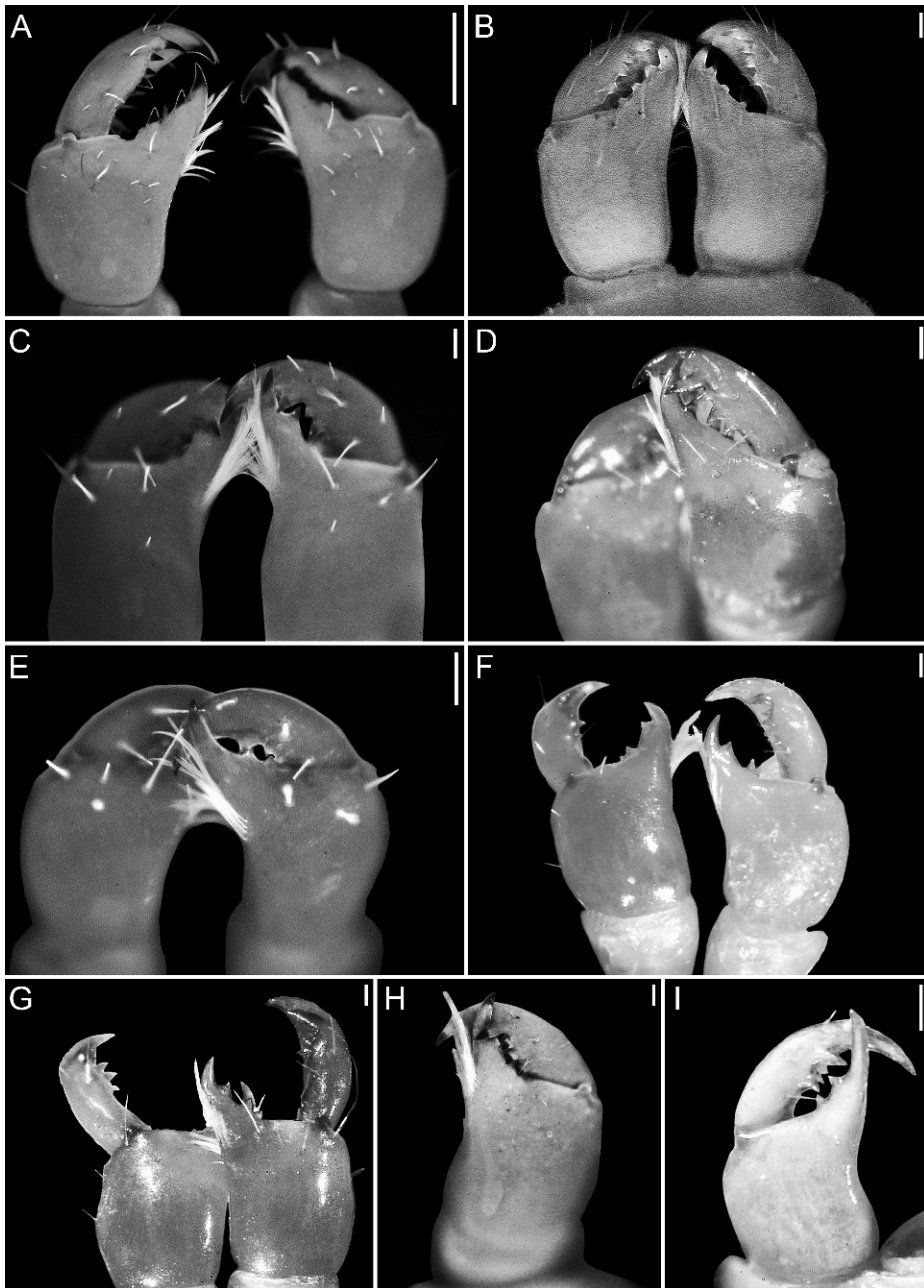


Fig. 5. Typhlochaetidae Mitchell, 1971, chelicerae, dorsal aspect. A. *Alacran tartarus* Francke, 1982, paratype ♂ (AMNH). B. *Sotanochactas elliotti* (Mitchell, 1971), paratype ♂ (WDS). C. *Stygochactas granulatus* (Sissom and Cokendolpher, 1998), juv. ♂ holotype (AMNH). D. *Typhlochactas cavicola* Francke, 1986, holotype ♀ (AMNH). E. *Typhlochactas mitchelli* Sissom, 1988, holotype ♂ (AMNH). F. *Typhlochactas reddelli* Mitchell, 1968, holotype ♀ (AMNH). G. *Typhlochactas rhodesi* Mitchell, 1968, holotype ♀ (AMNH). H. *Typhlochactas sissomi* Francke et al., 2009, subad. ♂ holotype (IBUNAM), dextral chelicera. I. *Typhlochactas sylvestris* Mitchell and Peck, 1977, holotype ♀ (AMNH), sinistral chelicera. Scales: A = 1 mm; B–H = 0.1 mm.

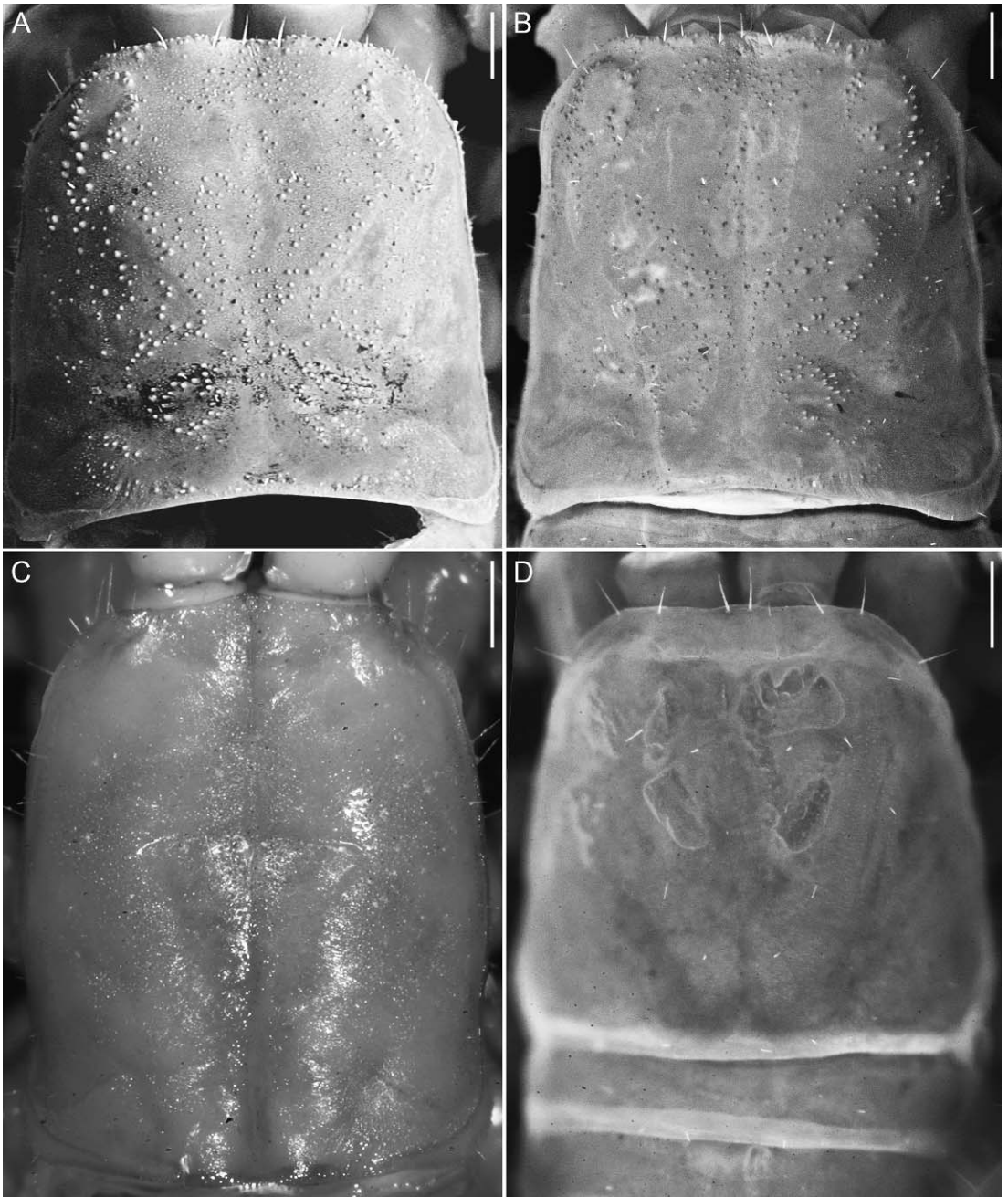


Fig. 6. Typhlochactidae Mitchell, 1971, carapace, dorsal aspect. **A.** *Alacran tartarus* Francke, 1982, paratype ♂ (AMNH). **B.** *Alacran tartarus* Francke, 1982, ♀ (WDS). **C.** *Sotanochactas elliotti* (Mitchell, 1971), paratype ♂ (WDS). **D.** *Stygochactas granulatus* (Sissom and Cokendolpher, 1998), juv. ♂ holotype (AMNH). Scales: A, B = 1 mm; C, D = 0.5 mm.

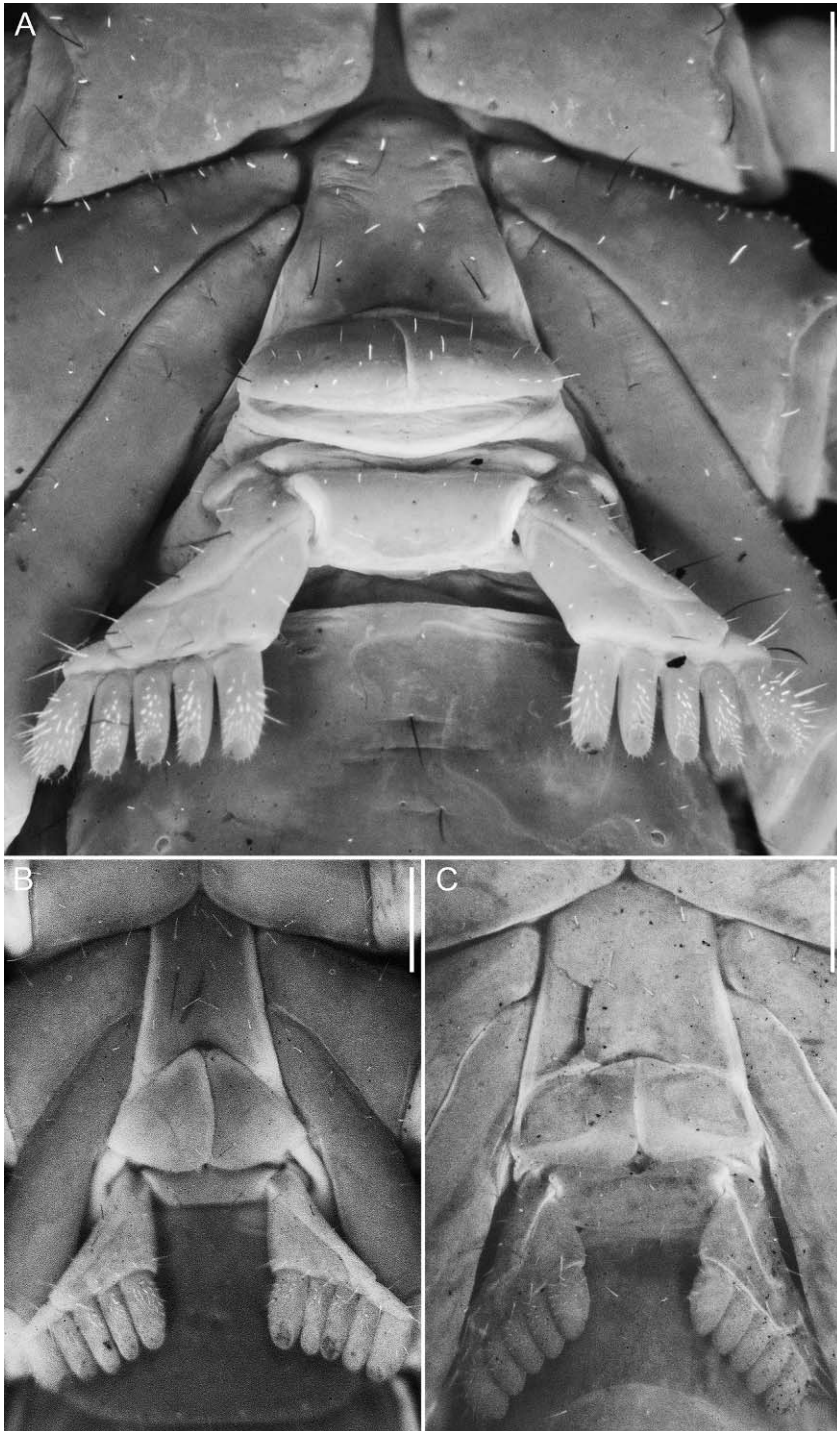


Fig. 7. Typhlochactidae Mitchell, 1971, sternum, genital operculum and pectines, ventral aspect. **A.** *Alacran tartarus* Francke, 1982, ♀ (WDS). **B.** *Sotanochactas elliotti* (Mitchell, 1971), paratype ♂ (WDS). **C.** *Typhlochactas rhodesi* Mitchell, 1968, holotype ♀ (AMNH). Scales: A = 1 mm; B, C = 0.5 mm.

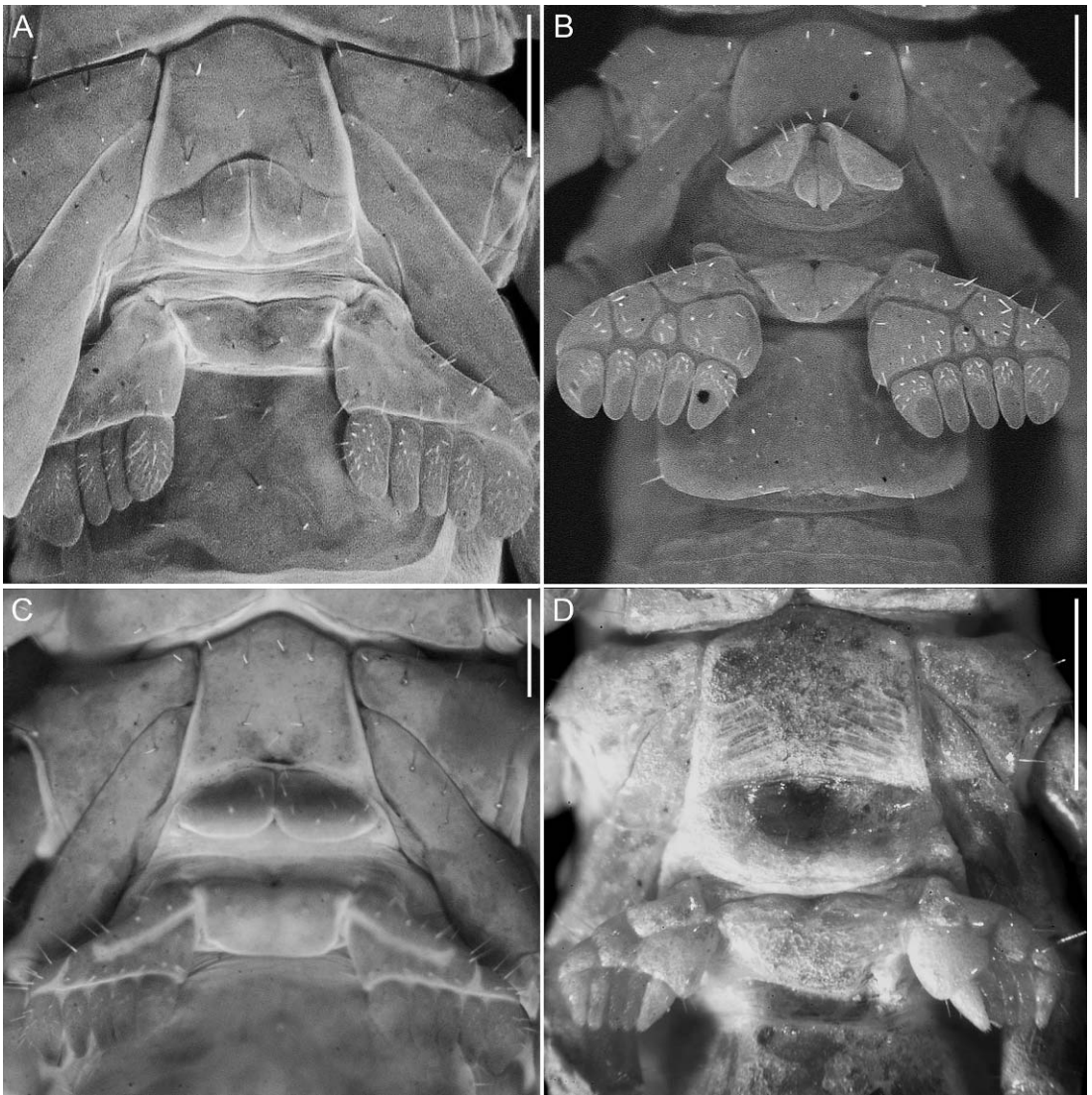


Fig. 8. Typhlochactidae Mitchell, 1971, sternum, genital operculum and pectines, ventral aspect. **A.** *Stygochactas granulatus* (Sissom and Cokendolpher, 1998), juv. ♂ holotype (AMNH). **B.** *Typhlochactas mitchelli* Sissom, 1988, holotype ♂ (AMNH). **C.** *Typhlochactas cavicola* Francke, 1986, holotype ♀ (AMNH). **D.** *Typhlochactas sylvestris* Mitchell and Peck, 1977, holotype ♀ (AMNH). Scales = 0.5 mm.

integrated karstic system of very deep caves on the Huautla Plateau (ca. 2000 m elevation) of the Sierra Mazateca, northern Oaxaca (fig. 1A). The fifth cave, Te Cimutaá, is a new record for the genus and may represent a new species.

ECOLOGY: *Alacran tartarus*, an obligate troglobite, inhabits some of the deepest caves in the world (fig. 3C, D). This species has

been collected at depths of 720–916 m below the surface (Francke, 1982a), the deepest records at which a scorpion has been found, and an order of magnitude greater than the next deepest record (–75 m) for a troglobitic scorpion, *Sotanochactas elliotti* from El Sótano de Yerbaniz (Francke, 1982a). The large size of *Alacran* (60–70 mm) is remarkable given the depths at which these scorpions

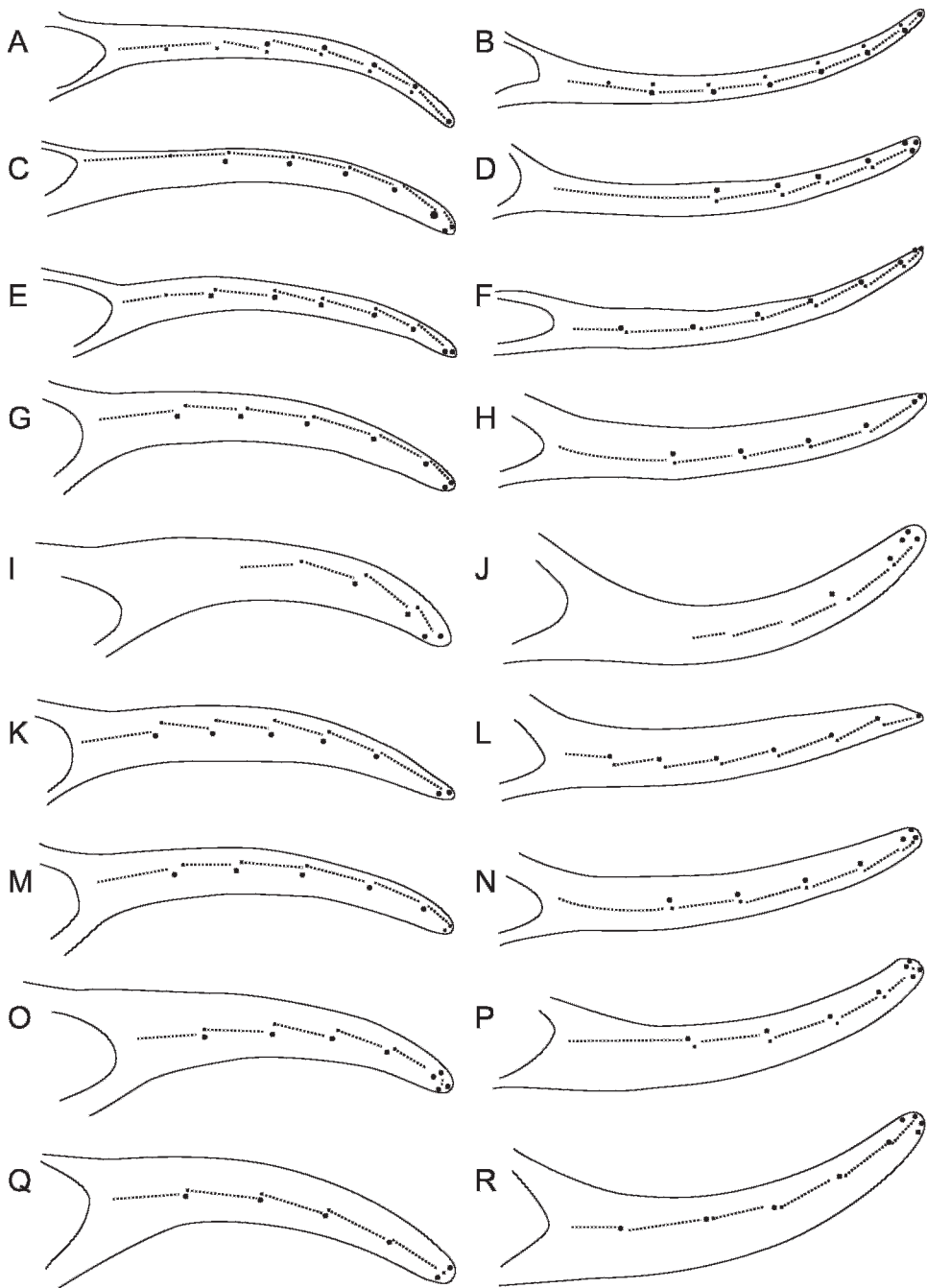


Fig. 9. Typhlochactidae Mitchell, 1971, dextral pedipalp chela fixed (left) and movable (right) fingers, dentition patterns. **A, B.** *Alacran tartarus* Francke, 1982. **C, D.** *Sotanochactas elliotti* (Mitchell, 1971). **E, F.** *Stygochactas granulatus* (Sissom and Cokendolpher, 1998). **G, H.** *Typhlochactas cavicola* Francke, 1986. **I, J.** *Typhlochactas mitchelli* Sissom, 1988. **K, L.** *Typhlochactas reddelli* Mitchell, 1968. **M, N.** *Typhlochactas rhodesi* Mitchell, 1968. **O, P.** *Typhlochactas sissomi* Francke et al., 2009. **Q, R.** *Typhlochactas sylvestris* Mitchell and Peck, 1977.

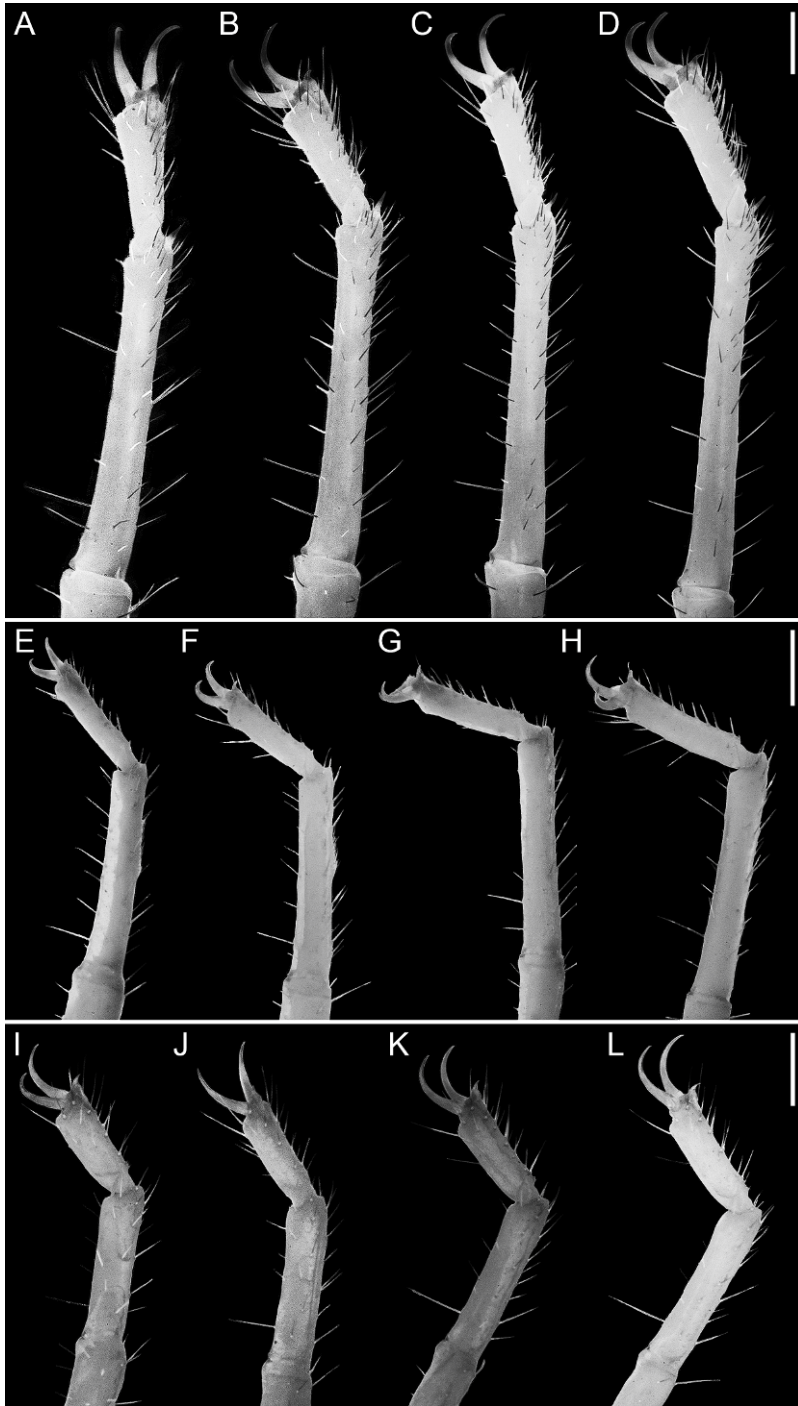


Fig. 10. Typhlochactidae Mitchell, 1971, sinistral legs I-IV, basitarsi and telotarsi, retrolateral aspect. A-D. *Alacran tartarus* Francke, 1982, ♀ (WDS). E-H. *Sotanochactas elliotti* (Mitchell, 1971), paratype ♂ (WDS). I-L. *Stygochactas granulatus* (Sissom and Cokendolpher, 1998), juv. ♂ holotype (AMNH). Scales: A = 0.1 mm; B, C = 0.5 mm.

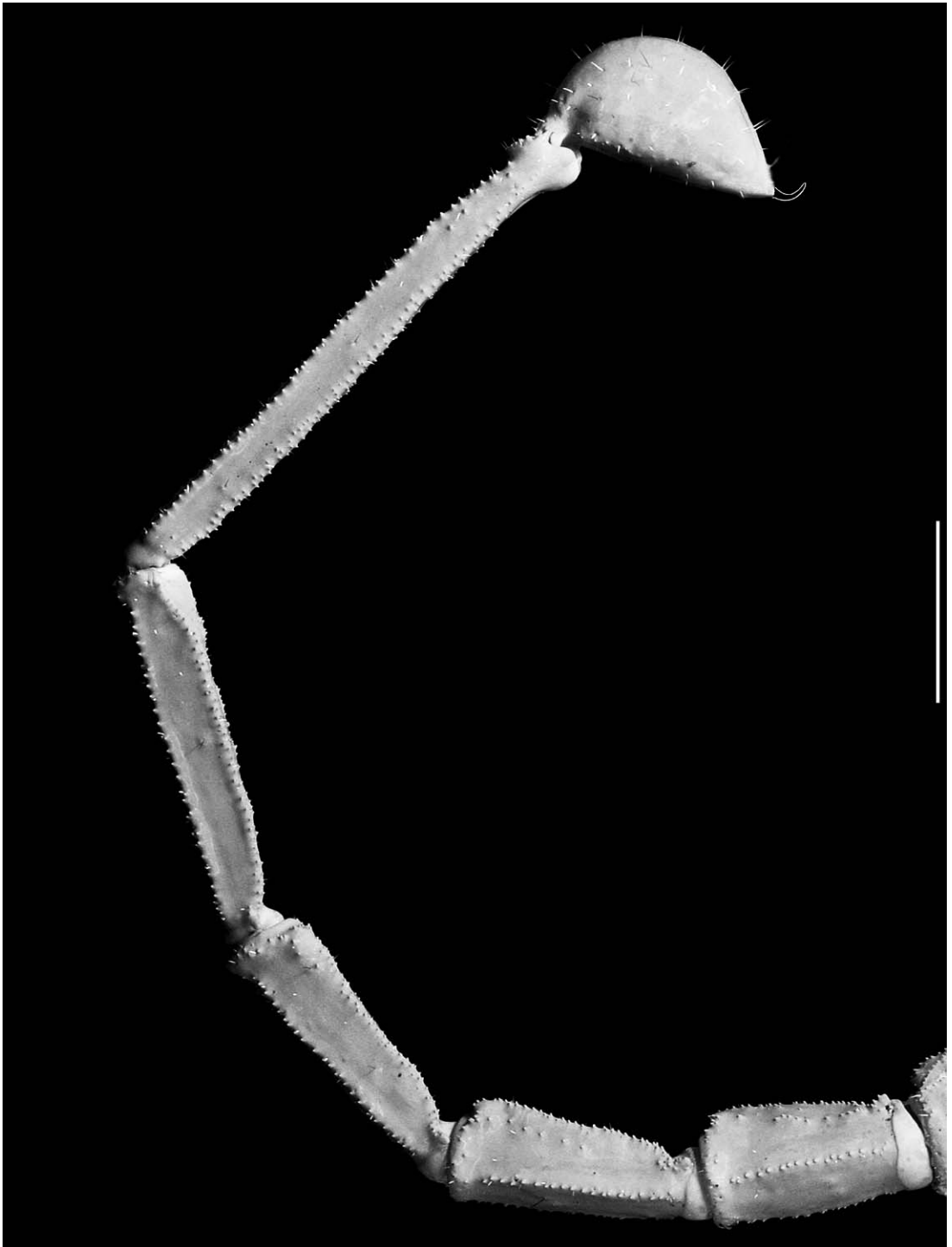


Fig. 11. *Alacran tartarus* Francke, 1982, paratype ♂ (AMNH), metasoma and telson, lateral aspect. Scale = 5 mm.

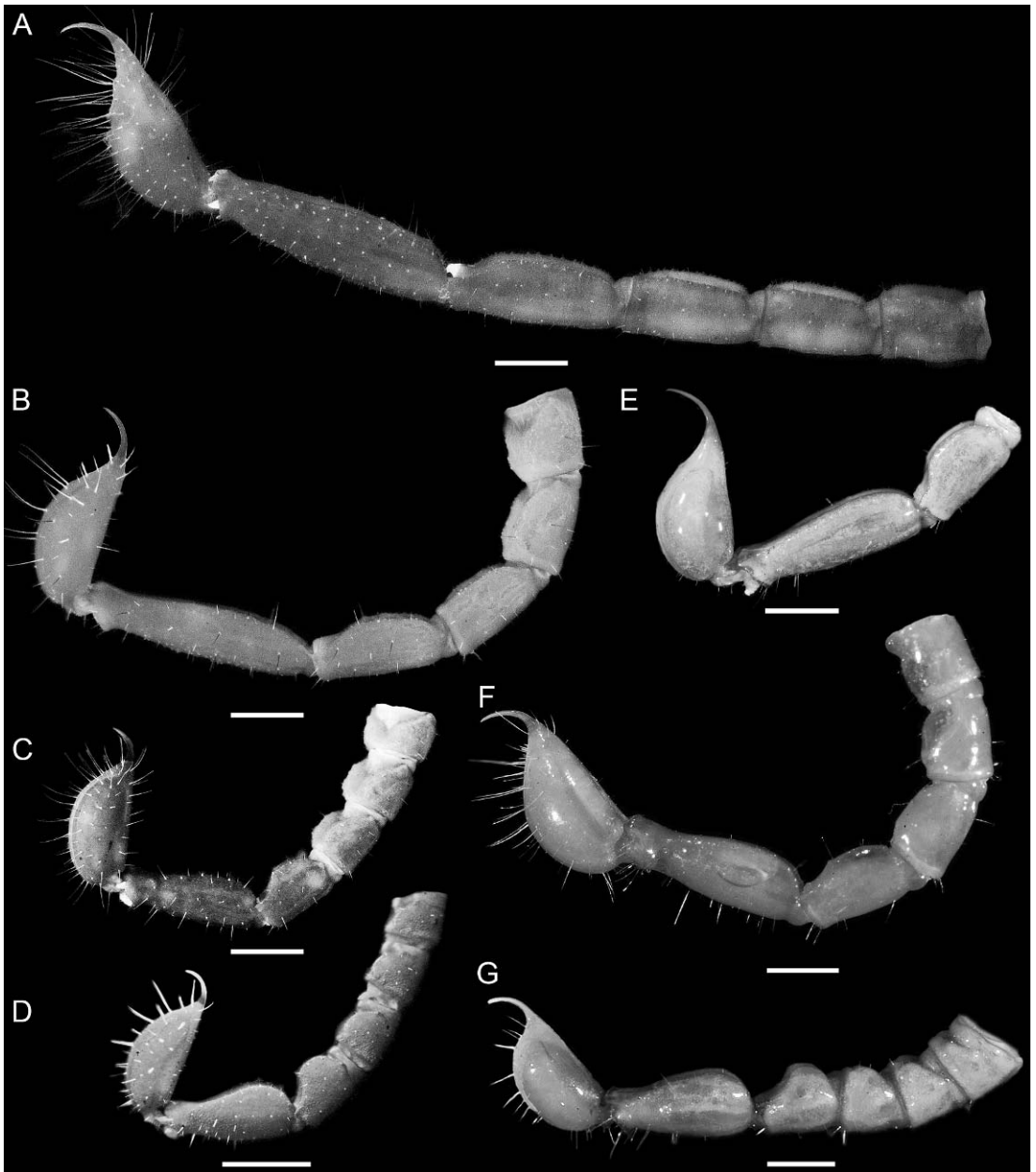


Fig. 12. Typhlochactinae Mitchell, 1971, metasoma and telson, lateral aspect. **A.** *Sotanochactas elliotti* (Mitchell, 1971), paratype ♂ (WDS). **B.** *Stygochactas granulatus* (Sissom and Cokendolpher, 1998), juv. ♂ holotype (AMNH). **C.** *Typhlochactas cavicola* Francke, 1986, holotype ♀ (AMNH). **D.** *Typhlochactas mitchelli* Sissom, 1988, holotype ♂ (AMNH). **E.** *Typhlochactas reddelli* Mitchell, 1968, holotype ♀ (AMNH), segments IV, V and telson only. **F.** *Typhlochactas rhodesi* Mitchell, 1971, holotype ♀ (AMNH). **G.** *Typhlochactas sylvestris* Mitchell and Peck, 1977, holotype ♀ (AMNH). Scales = 1 mm.

ons live and the amounts of energy that must be transported there to support them (Francke, 1982a). Most species of Typhlochactinae follow the usual trend toward small size in troglobitic arthropods and are less than 25 mm in length. *Alacran* appears to be amphibious: the second specimen from Cueva de Escorpión was collected on a wet flowstone wall (fig. 3E, F) and the specimen from Te Cimutaá Cave was found underwater in a small stream (A.G. Gluesenkamp and P. Sprouse, personal commun.).

Alacran tartarus Francke, 1982

(Figs. 1A, 3C–F, 4, 5A, 6A, 6B, 7A, 9A, 9B, 10A–D, 11, 13–16; table 6)

Alacran tartarus Francke, 1982a: 51–57, 59, figs. 1–17, 27, 32; table 1.

Alacran tartarus: Lourenço and Francke, 1985: 5 (table 1); Polis, 1990: 252; Nenilin and Fet, 1992: 28; Armas, 1994: 19, 21; Lourenço, 1994: 182, 183; Lockett, 1995: 191; Kovařík, 1998: 142; Sissom and Cokendolpher, 1998: 289; Beutelspacher Baigts, 2000: 18, 20, 47, 51, 143, 151, map 20; Fet and Sissom, 2000: 496, 497; Lourenço and Sissom, 2000: 118; Sissom, 2000b: 498; Soleglad and Sissom, 2001: fig. 40; Volschenk et al., 2001: 161; Soleglad and Fet, 2003a: 6, figs. 8, 10; Soleglad and Fet, 2003b: 8, 76; Prendini and Wheeler, 2005: 454 (table 5), 469 (figs. 12, 13); Graham and Fet, 2006: 7; Volschenk and Prendini, 2008: 236 (table 1); Kamenz and Prendini, 2008: 10 (table 2), 44.

TYPE MATERIAL: **Mexico:** *Oaxaca:* Municipio de San Miguel: Holotype: 1 ♀ (AMNH), 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. Paratypes: 1 juv. ♂ (AMNH), same data as holotype; 1 ♂ (AMNH), Sótano Li Nita [18°08'51"N 96°47'56"W, -812 m], San Agustín, 5 km SE Huautla de Jiménez, B. Steele and S. Zeman, 1980 Río Iglesia Expedition, 29.III.1980; 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 and M. McEachern, 23.V. 1978; 1 ♀ (MNHN), Cueva de Escorpión [18°06'23"N 96°47'53"W], San Miguel Dolina, 5 km SE Huautla de Jiménez, R. Jameson and P. Mothes, I.1978.

DIAGNOSIS: As for subfamily.

DESCRIPTION: The following redescription supplements Francke's (1982a) original description. It is based on the holotype, three paratypes, and six additional specimens. Only two adult males and five adult females are known (table 2).

Color: Adult (fig. 13), carapace, pedipalp femur, tergites, metasomal segments, and telson, Amber (36) with darker carinae; pedipalp patella and chela, Kingfisher Rufous (240) to Mahogany Red (132B), fingers slightly darker; chelicerae, legs, and sternites, Buff (24); pectines, Chamois (123D); cheliceral teeth, aculeus dark. Subadult (fig. 14), Sulphur Yellow (57) to Cream (54); aculeus and telotarsal ungues dark, Chestnut (32).

Chelicerae: Manus, dorsal and ventral surfaces smooth; dorsal surface with two microsetae; ventral surface with short brush-like macrosetae becoming longer on fixed finger. Fixed finger with four teeth (distal, subdistal, median and basal); median and basal teeth not fused into bicuspid; distal tooth largest, subdistal and median teeth equal, smaller, basal tooth smallest. Movable finger, internal distal and external distal teeth opposable, internal distal tooth completely overlapping external distal tooth in dorsal view; dorsal margin with five teeth (internal distal, two subdistal, median and basal; fig. 5A), internal distal tooth largest, subdistal and median teeth equal, smaller, basal tooth smallest; ventral surface with serrula, extending less than half length of finger, completely covered by long, dense macrosetae.

Carapace: Length slightly greater than anterior width (table 6). Anterior margin sublinear, without median projection (epistome); with 6–8 microsetae (fig. 6A, B). Posterior margin concave; asetose. Median and lateral ocelli absent. Median longitudinal sulcus obsolete; posterolateral sulci shallow; posterior transverse sulcus deep. Surface acarinate, with scattered subspiniform granules.

Pedipalps: Femur dorsoexternal, dorsointernal, ventrointernal, ventroexternal carinae distinct, comprising discontinuous rounded to spiniform granules (fig. 16A); ventroexternal carina less developed, comprising fewer granules, of similar dimensions. Dorsal surface smooth, with few granules medially; external surface granular; ventral surface

with few granules proximally and small row of granules distally; internal surface smooth. Patella dorsoexternal, dorsointernal, ventroexternal, and ventrointernal carinae distinct, granular; internomedian carina comprising well-developed granular row; externomedian carinae obsolete (fig. 16B–D). Dorsal surface slightly concave and smooth except for two small granular areas surrounding trichobothria d_2 and i ; external surface with several large granules, close to trichobothria; ventral surface smooth. Chela long, with relatively large, swollen manus (fig. 15). Dorsomedian, dorsal secondary, digital, ventroexternal, ventromedian and ventrointernal carinae distinct, similar, each comprising row of granules; external secondary carina distinct but weaker, comprising fewer, smaller granules; internomedian and dorsointernal carinae comprising few isolated granules between ventromedian and dorsomedian carinae. Manus, intercarinal surfaces smooth; internal surface with prominent, isolated granule near movable finger condyle and row of prominent, isolated granules from base of movable finger to base of fixed finger; fixed finger smooth. Fixed and movable fingers, median denticle row comprising six (occasionally five) and seven (occasionally six) oblique primary subrows, respectively (fig. 9A, B); internal denticles smaller than external denticles; fixed finger, terminal denticle considerably larger than preceding denticles, hooklike, fingertips interlocking unevenly when closed.

Trichobothria: Femur with three trichobothria (fig. 16A): one external (e), one dorsal (d), one internal (i). Patella with 26 or 27 trichobothria (fig. 16B–D), eight accessory (et_{a1} , et_{a2} , est_a , em_3 , em_{a1} , em_{a2} , esb_{a1} , esb_{a2}): three ventral (v_1 – v_3); 21 (rarely 19 or 20) external (et_1 – et_3 , et_{a1} , et_{a2} , est , est_a , em_1 – em_3 , em_{a1} , em_{a2} , esb_1 , esb_2 , esb_{a1} , esb_{a2} , eb_1 – eb_5); two dorsal (d_1 , d_2); one internal (i). Chela with 29 trichobothria (fig. 15), three accessory (V_a , em , Em , V_a): 18 on manus, five ventral (V_1 – V_4 , V_a), 11 external (Et_1 – Et_5 , Est , Esb , Em , Eb_1 – Eb_3), two dorsal (Db , Dt); 11 on fixed finger, five external (et , est , em , esb , eb), four dorsal (dt , dst , dsb , db), two internal (it , ib). All trichobothrial areolae small, similar in diameter, trichobothrial setae similar in length (none “petite”).

Legs: Femur and patella elongated, similar in length. Femur laterally compressed; unicarinate; dorsal and ventral surfaces separated by row of distinct granules; surfaces with few macrosetae. Patella less compressed than femur; dorsal surface smooth; ventral edge granular; surfaces sparsely setose. Basitarsi prolateral, retrolateral and proventral surfaces with macrosetae, similar in number on I–III, fewer on IV; I–IV, each with large prolateral pedal spur (fig. 10A–D); I and II, proventral surface without spinules. Telotarsi, dorsomedian lobe with one large microseta; ventral surface without spinules and with at least 10 ventrosubmedian pairs of thin, acuminate macrosetae; ungues well developed, curved, equal in length; dactyl large, prominent.

Tergites: Pretergites, surfaces smooth. Posttergites I–V, surfaces smooth; VI and VII, surfaces with scattered granules posteriorly; VII, lateral margins with small spiniform granules in distal three-quarters, large sparse granules medially; I–VI, acarinate; VII, dorsosubmedian carinae vestigial, reduced to few posterior granules, dorsolateral carinae distinct, complete (fig. 13A).

Sternum: Posterior width greater than length (fig. 7A); apex rounded; lateral margins converging anteriorly; lateral lobes flat; posterior depression shallow. Surface with two macrosetae and several microsetae.

Genital operculum: Sclerites (δ) completely divided; genital papillae protruding distinctly beyond posterior edges. Sclerites (♀) fused, but loosely connected by membrane along entire length of suture (fig. 7A). Surfaces covered by microsetae.

Pectines: Pectinal plate, surface with several macrosetae. Lamella comprising four segments (fig. 7A); surfaces with four macrosetae and several microsetae. Tooth count, 5/5–6 (δ), 5/5 (♀); teeth elongated, similar in dimensions; proximal and distal teeth slightly larger; surfaces covered with microsetae.

Sternites: Anterior and posterior margins straight (posterior margin of sternite III concave in one female; fig. 13B), with few macrosetae; III and IV, surfaces almost smooth, lateral and posterior margins with very small granules; V and VI, surfaces with few granules; VII, surfaces with more granules, especially in distal half, and with pair of

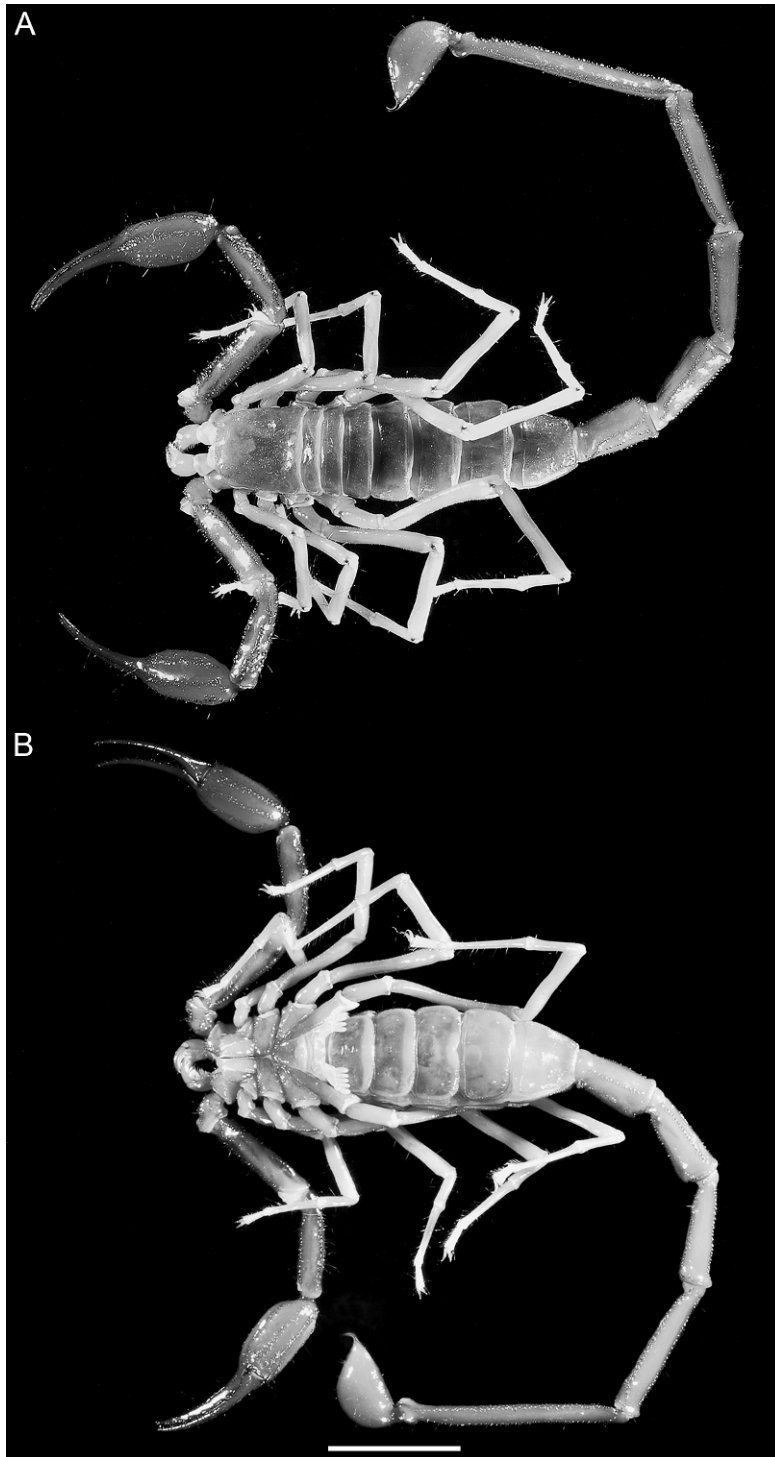


Fig. 13. *Alacran tartarus* Francke, 1982, ♀ (AMNH), habitus. A. Dorsal aspect. B. Ventral aspect. Scale = 1 cm.

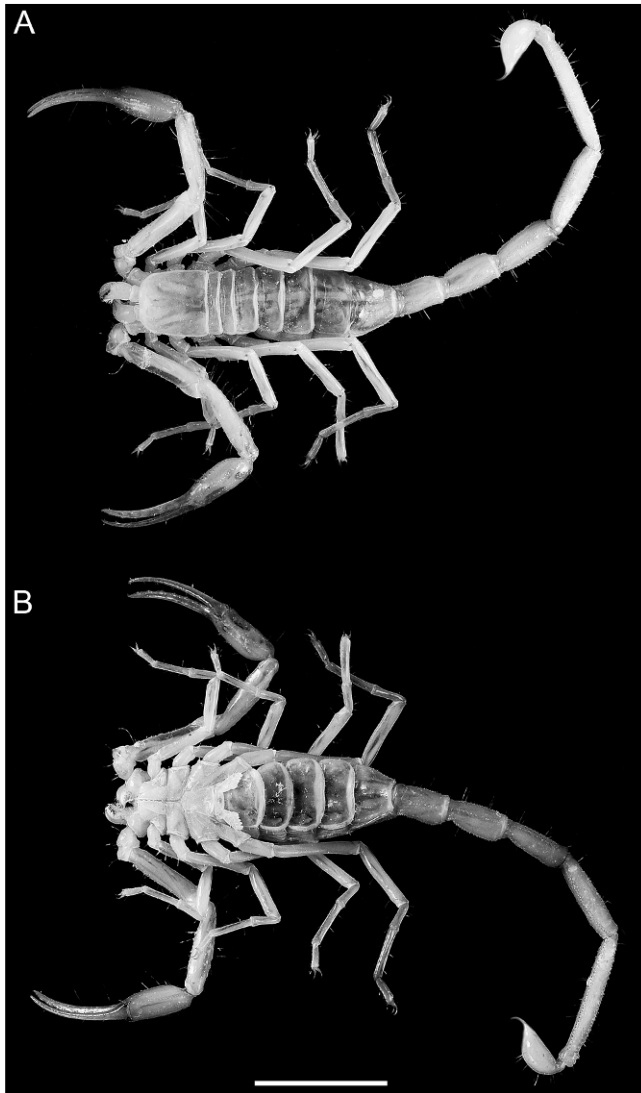


Fig. 14. *Alacran tartarus* Francke, 1982, juv. ♂ paratype (AMNH), habitus. **A.** Dorsal aspect. **B.** Ventral aspect. Scale = 1 cm.

weakly developed ventrolateral carinae. Respiratory spiracles (stigmata) small, round, situated posterolaterally (fig. 7A).

Metasoma: Segments elongated, length greater than width (fig. 11), progressively increasing in length, decreasing in width (table 6); segment V longer than carapace. Dorsosubmedian carinae, segments I–IV, distinct, granular, distal granules not noticeably larger than preceding granules; V, absent. Dorsolateral carinae, segments I–III,

obsolete, composed of sparsely distributed granules; IV, absent; V, distinct, granular. Median lateral carinae, segments I and II, distinct, granular, incomplete; III–V, absent. Ventrolateral carinae, segments I–V, distinct, granular, complete. Ventrosubmedian carinae, segments I–IV, and ventromedian carina, segment V, absent. Anal arch smooth dorsally, granular and setose ventrally. Intercarinal surfaces smooth except dorsal surfaces, segments IV and V, sparsely granular.



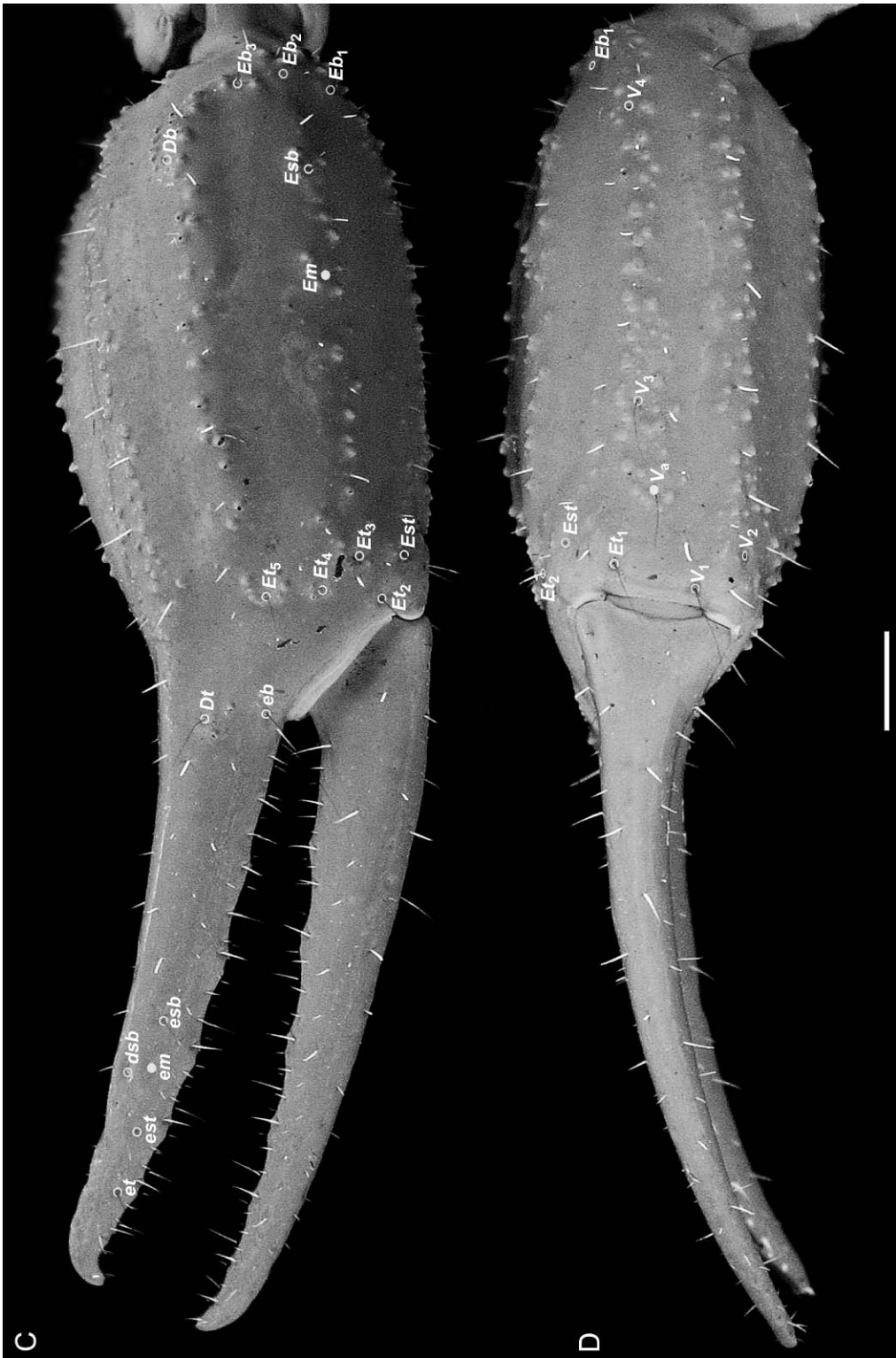


Fig. 15. *Alacran tartarus* Francke, 1982, sinistral pedipalp chela showing carinae and distribution of trichobothria. A. Paratype ♂ (AMNH). B-D. ♀ (WDS). A, C. External aspect. B. Dorsal aspect. D. Ventral aspect. Scales = 1 mm.

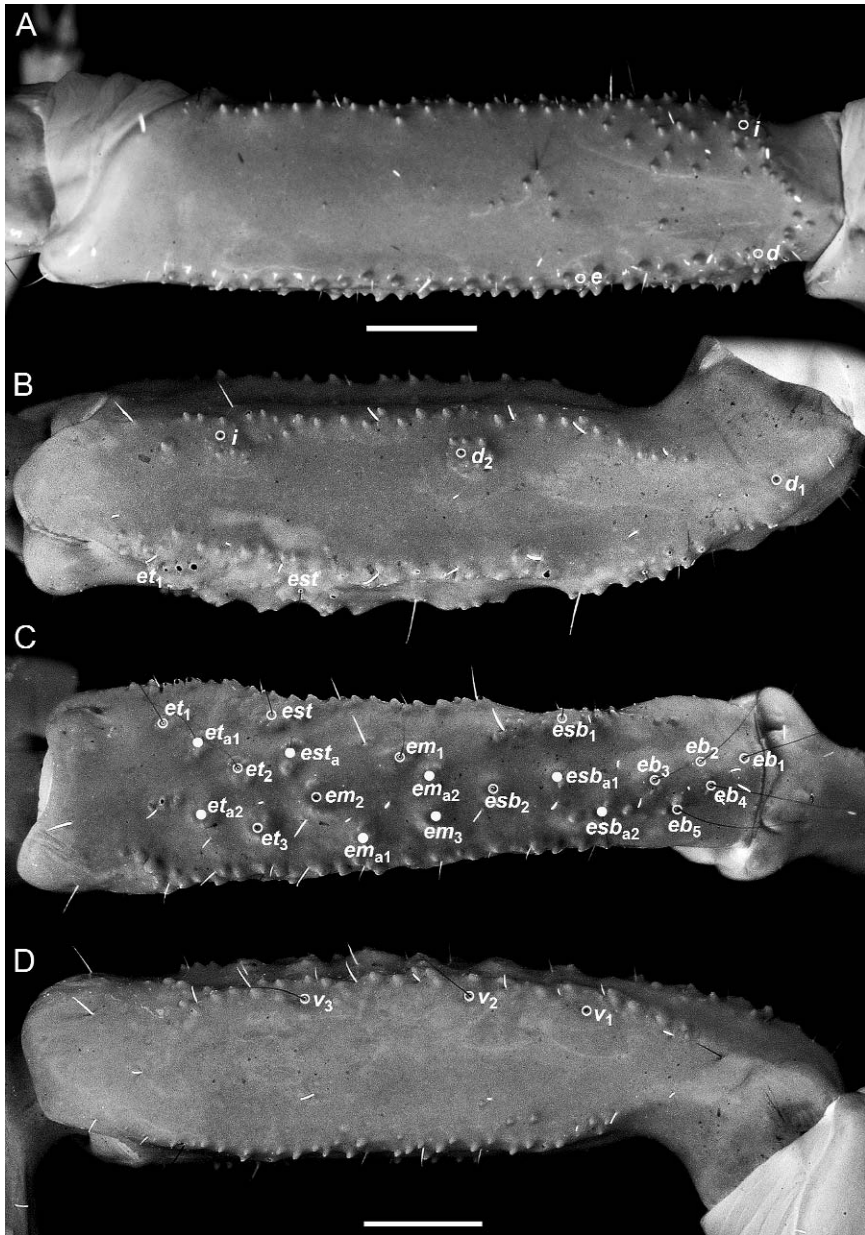


Fig. 16. *Alacran tartarus* Francke, 1982, ♀ (WDS), sinistral pedipalp femur (A) and patella (B–D) showing carinae and distribution of trichobothria. A, B. Dorsal aspect. C. External aspect. D. Ventral aspect. Scales = 1 mm.

Lateral and ventral intercarinal surfaces with few microsetae, increasing in number from segments I–V.

Telson: Vesicle globose, especially in adults, slightly compressed laterally; anterodorsal lateral lobes absent (fig. 11); surface

smooth with few, small granules along anterodorsal margin; few short macrosetae anteriorly; short microsetae ventrally and near base of aculeus. Aculeus very short, arising abruptly from vesicle, slightly curved.

Hemispermatothore: Lamelliform, basal portion narrow; capsular region with large, sclerotized lobe; spiniform processes absent. See Francke (1982a: 58) for illustrations.

Ontogenetic variation: Subadults and juveniles (fig. 14) differ from adults (fig. 13) as follows. Coloration of subadult and juvenile paler than adult: yellowish cream with aculeus, extremity of leg ungues, pedipalp chela denticle rows and cheliceral teeth brownish. Carapace, anterior margin with well-developed median projection (epistome) in juvenile, weakly developed to absent in adult. Pedipalp and metasomal carination largely absent in juvenile, weakly developed in subadult, well developed in adult. Surface granulation less developed in subadult and juvenile. Telson of subadult and juvenile more setose, less globose (ratio of vesicle height : length 150% in juvenile, 100–122% in subadult, 76–112% in adult), with longer aculeus (table 6).

Sexual dimorphism: Adult male similar to adult female in most respects, except for slightly more pronounced carination and granulation (fig. 6A, B), completely divided genital operculum, presence of genital papillae and slightly larger pectinal teeth.

Geographical variation: Little variation among specimens from the Sistema Huautla.

REMARKS: The female paratype was listed by Francke (1982a: 55) as deposited in the author's collection and by Fet and Sissom (2000) as deposited in the AMNH collection. The paratype is actually deposited in the MNHN.

A large, sinistral pedipalp chela, collected together with the holotype of *Stygochactas granulatus* from Sótano de Poncho in the neighboring state of Veracruz, is conspecific with the latter species and not with *Alacran tartarus*, with which it was compared by Sissom and Cokendolpher (1998: 289). See remarks to *S. granulatus* for details.

DISTRIBUTION: Specimens of *A. tartarus* have been collected from four caves of the Sistema Huautla (figs. 1A, 3C–F) in the state of Oaxaca, southeastern Mexico (Cueva de Escorpión, Sótano Agua de Carrizo, Sótano Li Nita, Sótano de San Agustín).

ECOLOGY: As for genus.

ADDITIONAL MATERIAL: **Mexico**: *Oaxaca*: Municipio de San Miguel: 2 ♀ (WDS), Sótano

de San Agustín [18°06'23"N 96°47'53"W, –720 m] Section, Sistema Huautla, A.G. Grubbs, J.H. Smith and F. Holliday, V.1985; 1 juv. ♀ (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 ♀ (AMNH), Sótano Li Nita [18°08'51"N 96°47'56"W], –916 m, San Agustín, 5 km SE Huautla de Jiménez, M. Minton, L. Wilk and R. Simmons, 1.IV.1981; 1 ♂ (AMNH), leg (AMCC [LP 3499]), Cueva de Escorpión, 18°06'23"N 96°47'53"W, 1561 m, A. Gluesenkamp, P. Sprouse and C. Savvas, 18.IX.2004.

Alacran sp.
(Fig. 1A)

REMARKS: A single female specimen recently collected in Te Cimutaá Cave (fig. 1A) may be an undescribed species. The specimen has a different number of primary subrows in the median denticle row of the pedipalp chela fingers, a proportionally shorter metasoma, and is less granular, with slightly weaker carinae, than specimens of *A. tartarus* from the Sistema Huautla.

MATERIAL EXAMINED: **Mexico**: *Oaxaca*: Municipio de Valle Nacional: 1 ♀ (IBU-NAM), leg (AMCC [LP 8571]), Te Cimutaá Cave, 17°54'19"N 96°22'39"W, 944 m, P. Bryant, 25.IV.2008.

TYPHLOCHACTINAE Mitchell, 1971

Typhlochactinae Mitchell, 1971: 135; type genus *Typhlochactas* Mitchell, 1971.

Typhlochactini: Francke, 1982a: 51, 59–61, fig. 26; Francke, 1986: 5; Sissom, 1988: 365; Sissom and Cokendolpher, 1998: 285.

DIAGNOSIS: Typhlochactinae, the sister group of Alacraninae (fig. 4), may be separated from the latter on the basis of the following combination of characters. Size usually small to very small, total length (adult) less than 25 mm. Cheliceral fixed finger, median and basal teeth usually not fused into a bicuspid; movable finger with three, four, or five dorsal teeth (none, one, or two subdistal teeth). Carapace, anterior margin, median projection (epistome) usually present; median longitudinal sulcus well developed. Pedipalp femur dorsoexternal, dorsointernal, and ventrointernal carinae,

TABLE 6
Meristic data for *Alacran tartarus* Francke, 1982
 Measurements (mm) follow Francke et al. (2009). Abbreviations as follows: AMNH = American Museum of Natural History, New York; MNHN = Muséum National d'Histoire Naturelle, Paris; WDS = W. David Sissom Private Collection, Canyon, TX

Specimen type	<i>Alacran tartarus</i>												
	Paratype		Holotype		Paratype		♀		Paratype				
sex	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀			
collection	AMNH	AMNH	AMNH	AMNH	MNHN	RS 7439	AMNH	WDS	WDS	AMNH	AMNH	AMNH	AMNH
Carapace													
anterior width	4.8	4.2	4.2	4.2	4.9		5.0	5.5	4.3	1.9	4.4	4.4	0.9
posterior width	5.4	5.3	5.8	5.8	5.8		6.2	6.8	6.1	2.5	4.9	4.9	1.4
length	4.9	4.7	5.1	5.1	5.2		5.5	6.3	5.5	2.5	5.1	5.1	1.2
Chela													
maximum width	2.8	3.0	3.0	3.0	2.9		3.4	3.6	3.3	1.1	1.0	1.0	0.5
maximum height	3.2	3.3	3.2	3.2	3.6		3.8	4.2	3.9	1.2	1.1	1.1	0.5
length ¹	12.1	12.3	12.7	12.7	12.5		14.6	14.1	13.5	5.8	5.7	5.7	2.9
length ventroexternal carina	5.0	5.1	5.1	5.1	5.9		6.6	5.6	5.0	2.5	2.1	2.1	1.1
length of movable finger	7.8	7.3	7.6	7.6	7.8		8.3	8.6	8.5	3.7	3.7	3.7	1.8
Patella													
maximum width	1.5	1.4	1.6	1.6	1.5		2.1	1.9	2.0	0.7	0.8	0.8	0.4
maximum height	1.5	1.7	1.8	1.8	1.8		2.2	2.0	2.1	0.8	0.8	0.8	0.4
length	6.1	6.5	6.9	6.9	7.4		7.1	6.9	7.4	3.3	3.4	3.4	1.6
<i>e</i> trichobothria (left/right)	21/21	21/21	21/21	21/21	21/21		21/20	21/21	21/19	21/21	21/21	21/21	20/21
Femur													
maximum width	1.6	1.6	1.7	1.7	1.8		1.7	2.1	1.9	0.7	0.7	0.7	0.4
maximum height	0.8	0.9	1.0	1.0	1.0		0.9	1.0	1.1	0.7	0.5	0.5	0.3
length	6.5	6.9	7.4	7.4	7.4		7.5	7.4	8.3	3.2	3.3	3.3	1.6
Pedipalp													
total length (incl. trochanter)	26.3	26.9	27.9	27.9	28.8		31.1	30.4	31.0	13.5	13.2	13.2	6.7
Mesosoma													
total length (tergites)	13.0	12.5	15.5	15.5	16.0		17.3	17.9	18.4	6.7	7.6	7.6	3.9
Sternite VII													
width	4.1	4.3	4.5	4.5	4.9		5.1	6.0	4.9	2.1	2.2	2.2	1.2
length	3.3	3.2	3.4	3.4	3.3		4.2	4.6	4.5	1.7	1.7	1.7	0.6
Metasoma I													
maximum width	2.6	2.3	2.4	2.4	2.4		2.6	3.1	2.7	1.2	1.2	1.2	0.6
maximum height	2.4	2.1	2.4	2.4	2.2		2.4	2.7	2.4	1.0	1.0	1.0	0.6
length	4.4	4.9	5.1	5.1	4.8		4.8	4.1	4.8	1.8	1.6	1.6	0.8

TABLE 6
(Continued)

Specimen type	<i>Alacran tartarus</i>												
	Paratype		Holotype		Paratype		♀		♂		♀		
	AMNH	AMNH	AMNH	AMNH	MNHN	RS 7439	AMNH	AMNH	♀	♂	♀	♀	
sex													
collection													
Metasoma II													
maximum width	2.4	2.3	2.4	2.4	2.4	2.4	2.6	2.7	2.7	2.7	2.7	2.7	2.7
maximum height	2.1	2.1	2.1	2.1	2.0	2.0	2.2	2.4	2.2	2.2	2.2	2.2	2.2
length	5.2	5.2	6.0	6.0	5.7	5.7	6.5	6.5	6.5	6.5	5.7	5.7	5.7
Metasoma III													
maximum width	2.3	2.1	2.4	2.4	2.4	2.4	2.5	2.4	2.4	2.4	2.6	2.6	2.6
maximum height	2.1	2.1	2.1	2.1	2.0	2.0	2.0	2.2	2.2	2.2	2.0	2.2	2.2
length	6.2	6.5	6.7	6.7	6.6	6.6	7.2	8.4	8.4	8.4	7.2	6.9	2.3
Metasoma IV													
maximum width	1.9	1.7	1.9	1.9	1.9	1.9	2.2	2.0	2.0	2.2	2.2	2.2	2.2
maximum height	1.9	2.0	1.4	1.4	1.7	1.7	1.9	2.0	2.0	1.7	1.7	1.7	0.8
length	8.4	8.5	8.6	8.6	9.3	9.3	9.5	11.7	11.7	9.7	3.4	3.4	3.4
Metasoma V													
maximum width	1.7	1.5	1.6	1.6	1.6	1.6	1.8	1.7	1.7	1.6	1.6	1.6	0.8
maximum height	1.4	1.9	1.2	1.2	1.2	1.2	1.5	1.6	1.6	1.3	0.6	0.6	0.6
length	12.6	12.2	13.3	13.3	13.1	13.1	14.4	16.5	16.5	15.0	4.9	4.9	4.7
Telson													
maximum width	2.9	2.7	2.8	2.8	2.9	2.9	3.3	3.7	3.7	3.4	0.9	0.9	1.0
maximum height	3.0	2.7	2.5	2.5	3.2	3.2	3.3	3.5	3.5	3.4	0.8	0.9	0.9
aculeus length	0.9	0.8	0.8	0.8	0.9	0.9	1.0	0.8	0.8	1.0	— ³	0.6	0.2
total length	6.5	5.9	6.1	6.1	6.3	6.3	6.9	7.8	7.8	7.0	1.7	2.6	1.1
Metasoma													
total length ²	43.3	43.2	45.8	45.8	45.8	45.8	49.3	55.0	55.0	49.1	16.6	13.5	7.2
Total length													
pro-+meso-+metasoma	61.2	60.6	66.4	66.4	67.0	67.0	72.1	79.2	79.2	73.0	25.8	25.5	20.7
Pectines													
total length	2.1	2.4	2.5	2.5	2.4	2.4	2.1	2.4	2.4	2.2	0.8	0.7	0.5
length along dentate margin	1.8	1.5	1.5	1.5	1.3	1.3	1.7	1.8	1.8	1.6	0.6	0.5	0.4
tooth count (left/right)	5/6	5/5	5/5	5/5	5/5	5/5	5/5	5/5	5/5	5/5	5/5	5/5	5/5

¹Measured from base of condyle to tip of fixed finger.

²Sum of metasomal segments I–V and telson.

³Aculeus broken.

patella dorsoexternal, externomedian, ventroexternal, and ventrointernal carinae, and chela external secondary, ventroexternal and ventrointernal carinae, usually absent or obsolete. Pedipalp chela, fixed and movable fingers, median denticle row comprising 4–7 and 5–7 oblique primary subrows, respectively; internal denticles larger than external denticles. Pedipalp patella with 19 (rarely 20) trichobothria, three situated on dorsal surface, 14 (rarely 15), including one (rarely two) accessory trichobothria, on external surface, and two on ventral surface. Chela with 26 trichobothria, 10 situated on fixed finger and 16 situated on manus. Twelve (rarely 13) trichobothria with areolae noticeably smaller and setae noticeably shorter than the others (“petite”): five (rarely six) on patella (d_1 , d_2 , et_2 , esb_2 , eb_2 , v_3), seven on chela (Db , Esb , Et_4 , Et_5 , V_1 , db , esb). Leg basitarsi often without prolateral pedal spurs, retrolateral surfaces with short row of tiny spinules distally; telotarsi each with 3–8 subspiniform macrosetae in paired ventrosulmedian rows, usually without ventromedian row of spinules. Sternite VII, ventrolateral carinae absent. Metasomal segments I–IV, dorsosulmedian and ventrolateral carinae usually absent or obsolete; segment V, dorsolateral carinae and, usually, ventrolateral carinae absent or obsolete. Telson (adult) vesicle unmodified to globose; aculeus short to moderate in length.

INCLUDED TAXA: Three genera: *Sotanochoactas* Francke, 1986, monotypic; *Stygochoactas*, new genus, monotypic; *Typhlochoactas* Mitchell, 1971, with six species (table 2).

DISTRIBUTION: Endemic to Mexico. Recorded from five states: Oaxaca, Queretaro, San Luis Potosí, Tamaulipas, Veracruz (fig. 1B).

ECOLOGY: *Sotanochoactas*, *Stygochoactas*, and three species of *Typhlochoactas* are troglotic (hypogean). The other three species of *Typhlochoactas*, *T. mitchelli*, *T. sissomi*, and *T. sylvestris*, are humicolous (endogean) (Mitchell and Peck, 1977; Sissom, 1988; Francke et al., 2009; table 2). The three endogean species are also markedly troglomorphic, however. It is possible that they may inhabit caves, on occasion. A similar ecology was described for *Belisarius xambeui*, a troglomorphic scorpion from the Pyrenees of France and Spain, and

other cave-adapted arthropods, e.g., beetles and crickets (Auber, 1959; Peck and Thayer, 2003; Sbordonni et al., 2004), which have been collected in leaf litter and also in caves.

Sotanochoactas Francke, 1986

Sotanochoactas Francke, 1986: 5, 8; type species *Typhlochoactas elliotti* Mitchell, 1971 [= *Sotanochoactas elliotti* (Mitchell, 1971)].

Sotanochoactas: Lourenço and Francke, 1985: 4 (nomen nudum); Sissom, 1988: 365; 1990: 109, 113; Polis, 1990: 253; Stockwell, 1992: 410, 412–414, 419, figs. 10, 34; Kovářík, 1998: 142; Sissom and Cokendolpher, 1998: 285; Beutelspacher Baigts, 2000: 6, 13–16, 18, 20, 48, 53, 57, 151, fig. 11B, C, graph 1, tables 1, 2; Lourenço, 2000: 25; Lourenço and Sissom, 2000: 118; Sissom, 2000b: 498; Lourenço, 2001: 4; Soleglad and Sissom, 2001: 40; Soleglad and Fet, 2003a: 7, 16–17, 32, fig. 12; 2003b: 36, 72, 74, 82, 106–109, 141, 162, tab. 9; Fet et al., 2004: 197; Prendini and Wheeler, 2005: 454, 458, 460, 468, 470, 476, tab. 9, 10, figs. 18, 19; Fet and Soleglad, 2005: 12; Sissom and Hendrixson, 2005: 130; Dupré, 2007: 10; Francke and Savary, 2006: 29; Graham and Fet, 2006: 2; Volschenk and Prendini, 2008: 249.

DIAGNOSIS: *Sotanochoactas* is the sister taxon of a monophyletic group comprising *Stygochoactas* and *Typhlochoactas* (fig. 4), from which it may be separated on the basis of the following combination of characters. Size small, total length (adult) less than 25 mm. Cheliceral fixed finger with four teeth (subdistal present); median and basal teeth not fused into a bicuspid; movable finger with four dorsal teeth (one subdistal present). Carapace, anterior margin, median projection (epistome) present. Pedipalps greatly elongated, chela fingers twice as long as manus. Pedipalp femur, ventroexternal carina, and patella, internomedian carina, distinct. Pedipalp chela, dorsal secondary, digital, ventroexternal, ventromedian, and ventrointernal carinae absent or obsolete. Chela fixed and movable fingers, median denticle rows comprising six and five oblique primary subrows, respectively; basal primary subrows considerably longer than other subrows; terminal denticle of fixed finger slightly larger than preceding denticles, fingertips interlocking evenly when closed. Patella trichobothrium v_1 situated distal to trichobothrium esb_1 . Chela fixed finger,

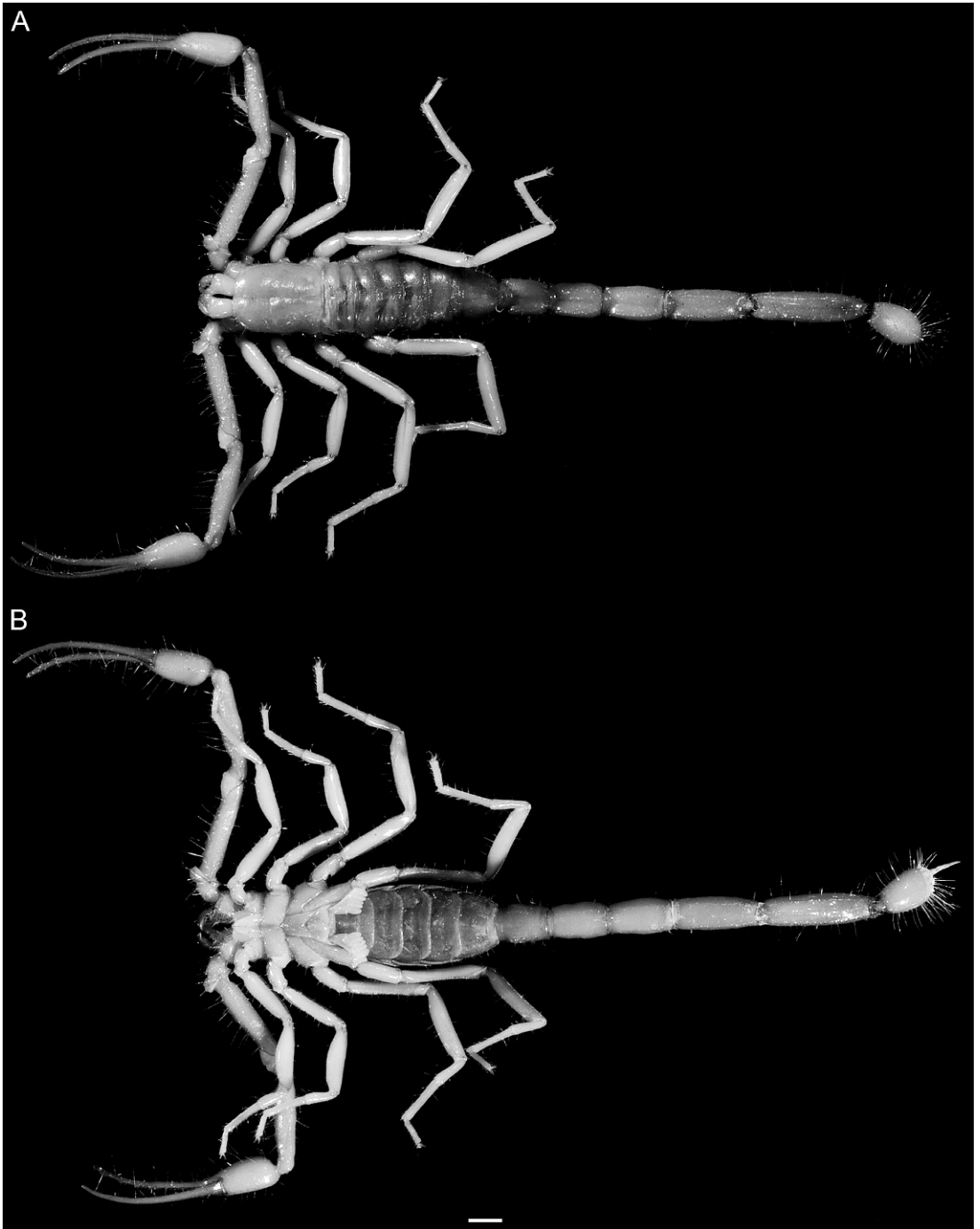


Fig. 17. *Sotanochoactas elliotti* (Mitchell, 1971), paratype ♂ (WDS), habitus. **A.** Dorsal aspect. **B.** Ventral aspect. Scale = 1 mm.



Fig. 18. *Sotanochactas elliotti* (Mitchell, 1971), paratype ♂ (WDS), sinistral pedipalp chela showing carinae and distribution of trichobothria. A. Dorsal aspect. B. External aspect. C. Ventral aspect. Scale = 0.5 mm.

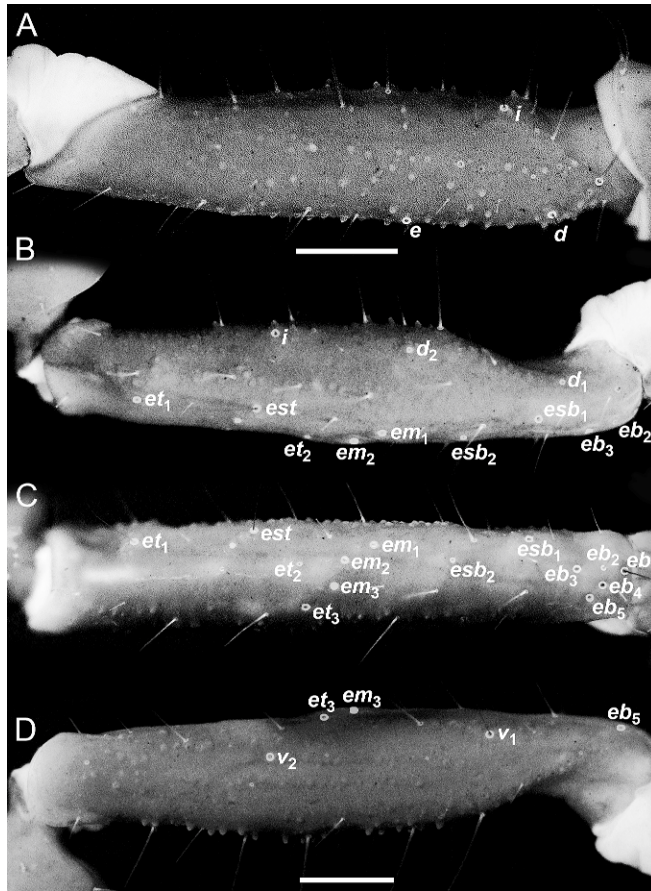


Fig. 19. *Sotanochoactas elliotti* (Mitchell, 1971), paratype ♂ (WDS), sinistral pedipalp femur (A) and patella (B–D) showing carinae and distribution of trichobothria. A, B. Dorsal aspect. C. External aspect. D. Ventral aspect. Scales = 0.5 mm.

external trichobothria situated in distal half of finger, trichobothrium *eb* situated midway on finger; trichobothrium *it* situated midway along finger; trichobothrium *ib* situated midway in proximal third of finger. Legs without prolateral pedal spurs. Basitarsi I and II, proventral surfaces with short row of closely aligned spinules subdistally. Telotarsi, ventral surface without ventromedian row of spinules. Sclerites of genital operculum (♀) fused, but loosely connected by membrane along entire length of suture. Tergite VII, dorsolateral carinae distinct, complete. Mesosomal segments I–IV, dorsosubmedian carinae distinct; I–III, dorsolateral carinae distinct; I, median lateral carinae obsolete, incomplete; I–V, ventrolateral carinae obso-

lete (I) to distinct (II–V); V, ventromedian carina obsolete.

INCLUDED TAXA: Monotypic genus: *Sotanochoactas elliotti* (Mitchell, 1971).

DISTRIBUTION: Endemic to Mexico. Recorded from San Luis Potosí.

Sotanochoactas elliotti (Mitchell, 1971)
(Figs. 1B, 2C–F, 4, 5B, 6C, 7B, 9C, 9D,
10E–H, 12A, 17–19; table 7)

Typhlochoactas elliotti Mitchell, 1971: 135–147, figs. 1–17, 26, 27, table 1.

Typhlochoactas elliotti: Reddell and Mitchell, 1971: 144, fig. 1; Reddell, 1973: 33, 37; Reddell and Elliott, 1973: 171; González-Sponga, 1974: 56; Sologlad, 1976: 253; Mitchell and Peck, 1977: 159, 164, 167, 168; Lourenço, 1981: 660; Red-

TABLE 7
Meristic data for *Sotanochactas elliotti* (Mitchell, 1971), *Stygochactas granulosa* (Sissom and Cokendolpher, 1998) and *Typhlochactas sissomi* Francke et al., 2009

Measurements (mm) follow Francke et al. (2009). Abbreviations as follows: AMNH = American Museum of Natural History, New York; IBUNAM = Instituto de Biología, Universidad Nacional Autónoma de México, Mexico City; MNHN = Muséum National d'Histoire Naturelle, Paris; WDS = W. David Sissom Private Collection, Canyon, TX

Specimen type	<i>Sotanochactas elliotti</i>		<i>Stygochactas granulosa</i>		<i>Typhlochactas sissomi</i>	
	Paratype ♂ WDS	Holotype subad. ♂ AMNH	Paratype juv. ♀ MNHN RS 5376	Holotype juv. ♂ AMNH	Holotype subad. ♂ IBUNAM	
Carapace						
anterior width	1.8	1.2	0.7	1.6	2.1	
posterior width	2.1	1.8	1.1	2.0	2.8	
length	2.6	2.0	1.7	1.8	2.9	
Chela						
maximum width	0.9	0.7	0.4	0.8	1.8	
maximum height	1.0	0.6	0.4	1.0	1.6	
length ¹	5.4	3.7	1.9	4.2	4.8	
length ventroexternal carina	1.0	0.9	0.7	1.5	2.1	
length of movable finger	4.1	2.3	1.1	2.7	2.7	
Patella						
maximum width	0.6	0.5	0.3	0.6	1.0	
maximum height	0.5	0.4	0.3	0.5	1.0	
length	3.2	2.1	1.3	2.3	2.5	
<i>e</i> trichobothria (left/right)	14/14	14/14	14/14	14/14	14/14	
Femur						
maximum width	0.6	0.4	0.3	0.6	0.9	
maximum height	0.4	0.4	0.3	0.5	1.0	
length	2.9	2.0	0.7	2.2	2.5	
Pedipalp						
total length (incl. trochanter)	12.0	8.2	4.2	9.3	10.8	
Mesosoma						
total length (tergites)	5.2	4.5	2.4	4.6	6.9	
Sternite VII						
width	1.9	1.4	-	1.7	2.6	
length	1.0	0.8	-	1.0	1.6	
Metasoma I						
maximum width	1.1	0.7	0.5	0.9	1.7	
maximum height	1.0	0.7	0.4	0.7	1.3	
length	1.3	0.8	0.3	0.9	1.2	

TABLE 7
(Continued)

Specimen	Satanochactas elliotti		Stygochactas granulosis		Typhlochactas sissomi	
	Paratype ♂	Holotype subad. ♂	Paratype juv. ♀	Holotype juv. ♂	Holotype subad. ♂	Holotype subad. ♂
sex	♂	♂	♀	♂	♂	♂
collection	WDS	AMNH	MNHN RS 5376	AMNH	IBUNAM	IBUNAM
Metasoma II						
maximum width	1.0	0.6	0.4	0.7	1.5	1.5
maximum height	1.0	0.6	0.4	0.7	1.3	1.3
length	1.6	0.9	0.5	1.1	1.5	1.5
Metasoma III						
maximum width	1.0	0.6	0.4	0.7	1.5	1.5
maximum height	0.9	0.6	0.4	0.7	1.3	1.3
length	1.8	1.0	0.5	1.2	1.6	1.6
Metasoma IV						
maximum width	0.9	0.6	0.4	0.7	1.5	1.5
maximum height	0.9	0.6	0.4	0.7	1.3	1.3
length	2.4	1.4	0.7	1.6	1.7	1.7
Metasoma V						
maximum width	0.9	0.6	0.4	0.7	1.5	1.5
maximum height	0.9	0.6	0.4	0.7	1.3	1.3
length	3.4	2.0	1.0	2.4	3.1	3.1
Telson						
maximum width	1.0	0.7	0.5	1.0	1.7	1.7
maximum height	1.1	0.7	0.4	0.8	1.5	1.5
aculeus length	0.7	0.6	0.4	0.6	0.8	0.8
total length	2.5	2.0	1.0	2.5	3.5	3.5
Metasoma						
total length ²	14.7	8.0	4.1	9.9	12.6	12.6
Total length						
pro-+meso-+metasoma	22.5	14.5	8.1	16.3	22.4	22.4
Pectines						
total length	0.9	0.7	0.6	0.8	1.1	1.1
length along dentate margin	0.6	0.5	0.3	0.7	0.9	0.9
tooth count (left/right)	5/5	4/4	5/5	5/4	5/5	5/5

¹Measured from base of condyle to tip of fixed finger.²Sum of metasomal segments I–V and telson.

dell, 1981: 36, 115, fig. 17; Francke, 1982a: 51, 59, 60, figs. 18–21, 26, 28, 33; 1986: 5, 8; Sissom, 1988: 365; Sissom and Cokendolpher, 1998: 285; Lourenço and Sissom, 2000: 118.

Typlochaectas ellioti: Díaz Najera, 1975: 3, 30.

Sotanochaectas ellioti: Lourenço and Francke, 1985: 5 (table 1); Armas, 1994: 21; Kovařík, 1998: 142; Beutelspacher Baigts, 2000: 18, 53, 54, 145, 151, map 22.

Sotanochaectas ellioti: Francke, 1986: 7, 8, figs. 11–13; Polis, 1990: 253 (fig. 6.4); Lourenço, 1994: 182, 183; Sissom, 2000b: 498; Soleglad and Sissom, 2001: 40, fig. 41; Volschenk et al., 2001: 161; Soleglad and Fet, 2003a: fig. 12; 2003b: 30, 32, 76; Vignoli and Kovařík, 2003: 131; Özkan and Karaer, 2004: 57; Prendini and Wheeler, 2005: table 5; Volschenk and Prendini, 2008: 236 (table 1).

Typlochaectas ellioti: Beutelspacher Baigts, 2000: 20, 53.

TYPE MATERIAL: **Mexico:** *San Luis Potosí:* Municipio de Ciudad Valles: Holotype: 1 subad. ♂ (AMNH), 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. Paratypes: 1 juv. ♀ (MNHN RS 5376), same locality, W.R. Elliott, 27.III.1970; 1 ♂ (WDS), same locality, R.W. Mitchell, 4.VII.1970.

DIAGNOSIS: As for genus.

DESCRIPTION: Mitchell (1971: 144) listed a holotype and two paratypes: a possible immature female (MNHN), marked with a questionmark, and another specimen, alive when the paper was published and the sex of which was given as undetermined, but which was, in fact, an adult male. Mitchell's (1971) description was based on the subadult male holotype. Francke (1982a) subsequently illustrated the hemispermaphore of the adult male paratype. We present the first description of the adult male (fig. 17), supplementing Mitchell's (1971) original description of the subadult male and Francke's (1982a) description of the hemispermaphore.

Color: Mitchell (1971) described the living specimens as almost transparent and lacking pigmentation. Coloration of preserved specimens as follows (fig. 17). Holotype, uniformly Cinnamon (123A). Paratype ♂ (WDS), chelicerae, carapace and pedipalps, Chamois (123D); mesosoma and metasoma, Clay (123B); legs, Cream (54); telson similar

to but slightly darker than legs; cheliceral teeth, pedipalp finger denticle rows, leg unguis and dactyl, and aculeus, reddish.

Chelicerae: Manus, dorsal and ventral surfaces smooth; dorsal surface with several microsetae, two larger microsetae situated near base of fixed finger; movable finger, dorsal surface with six microsetae. Fixed finger, dorsal margin with four teeth (distal, subdistal, median, and basal; fig. 5B); median and basal teeth not fused into bicuspid; distal tooth largest, subdistal and median teeth equal, smaller, basal tooth smallest. Movable finger, internal distal and external distal teeth opposable, internal distal tooth completely overlapping external distal tooth in dorsal view; dorsal margin with four teeth (internal distal, subdistal, median, and basal), internal distal tooth largest, subdistal and median teeth equal, smaller, basal tooth smallest; ventral surface with long serrula, extending distal three-quarters of finger, tines increasing in size distally, covered by dense brush of macrosetae.

Carapace: Length considerably greater than anterior width (table 7). Anterior margin weakly convex, with small median projection (epistome) (fig. 6C). Posterior margin convex; asetose. Median and lateral ocelli absent. Median longitudinal sulcus well developed; posterolateral sulci obsolete; posterior transverse sulcus deep. Surface acarinate, uniformly finely granular, especially along median longitudinal sulcus. Surface and margins with several microsetae.

Pedipalps: Pedipalps greatly elongated, slender (figs. 18, 19). Femur, ventroexternal carina distinct, granular, other carinae obsolete (fig. 19A). Dorsal surface with scattered granules on proximal three-quarters, becoming smooth distally; external and internal surfaces smooth; ventral surface granular proximally, becoming smooth distally. Dorsal, external, and internal surfaces each with several long microsetae; ventral surface asetose. Patella, dorsointernal carina distinct, granular; dorsoexternal, ventroexternal, and ventrointernal carinae obsolete; internomedian carina comprising row of granules; externomedian carinae absent (fig. 19B–D). Dorsal and external surfaces smooth; internal surface with scattered granules and long microsetae. Chela fingers very elongated,

movable finger longer than carapace, more than twice length along ventroexternal carina (table 7); manus width greater than or equal to height. Dorsal secondary, digital, external secondary, and ventrointernal carinae absent; ventroexternal and ventromedian carinae obsolete; other carinae absent (fig. 18). Chela manus, intercarinal surfaces smooth except for few small round granules on dorsal surface near base of fixed finger; internal surface with few granules except for prominent, isolated granule near movable finger condyle; fixed finger smooth. Manus and fingers, internal surfaces with several microsetae, often associated with median denticle row. Fixed finger, median denticle row comprising six oblique primary subrows, basal subrow very long (fig. 9C); internal denticles larger than external denticles, large internal denticle present between terminal and subterminal subrows, other four internal denticles smaller; terminal denticle of fixed finger slightly larger than preceding denticles, fingertips interlocking evenly when closed. Movable finger, median denticle row comprising five oblique primary subrows, basal subrow very long (fig. 9D).

Trichobothria: Femur with three trichobothria (fig. 19A): one external (*e*), one dorsal (*d*), one internal (*i*). Patella with 19 trichobothria (fig. 19B–D), five petite (*d*₁, *d*₂, *et*₂, *esb*₂, *eb*₂), one accessory (*em*₃): two ventral (*v*₁, *v*₂); 14 external (*et*₁–*et*₃, *est*, *em*₁–*em*₃, *esb*₁, *esb*₂, *eb*₁–*eb*₅); two dorsal (*d*₁, *d*₂); one internal (*i*). Chela with 26 trichobothria (fig. 18), seven petite (*V*₁, *Et*₄, *Et*₅, *Esb*, *Db*, *esb*, *db*): 16 on manus, four ventral (*V*₁–*V*₄), 10 external (*Et*₁–*Et*₅, *Est*, *Esb*, *Eb*₁–*Eb*₃), two dorsal (*Db*, *Dt*); 10 on fixed finger, four external (*et*, *est*, *esb*, *eb*), four dorsal (*dt*, *dst*, *d**sb*, *db*), two internal (*it*, *ib*).

Legs: All segments smooth except for femur ventral surface, covered by stout granules increasing in size and density from legs I–IV. Dorsal and ventral surfaces with few short microsetae; basitarsi sparsely setose, setae more numerous on legs I and II. Basitarsi I–IV without prolateral pedal spurs (fig. 10E–H); I and II, proventral surface with short subdistal row of closely aligned spinules. Telotarsi, dorsomedian lobe with one large microseta; ventral surface without spinules, and with six submedian pairs of

subspiniform macrosetae; unguis well developed, curved, equal in length; dactyl four times shorter than unguis.

Tergites: Pretergites, surfaces smooth. Posttergites with few microsetae, especially on posterior and lateral margins, granulation and setation increasing posteriorly; I–VI acarinate, surfaces finely granular; VII with small depression posteromedially, lateral and dorsolateral surfaces granular, more pronounced than on preceding tergites, dorso-submedian carinae vestigial, reduced to few posterior granules, dorsolateral carinae distinct, complete (fig. 17A).

Sternum: Length greater than posterior width (fig. 7B); apex rounded; lateral margins converging anteriorly; lateral lobes flat; posterior depression shallow. Surface with eight macrosetae and several scattered microsetae.

Genital operculum: Sclerites (♂) completely divided; genital papillae protruding distinctly beyond posterior edges (fig. 7B). Sclerites (♀) fused, but loosely connected by membrane along entire length of suture.

Pectines: Pectinal plate, surface with two macrosetae situated mediolaterally. Lamella comprising three segments (fig. 7B), demarcated by very faint sutures; surfaces with few setae. Tooth count, 4–5/4–5; teeth elongated; proximal and distal teeth slightly larger.

Sternites: Posterior margin III, slightly concave (holotype) or sublinear, of other sternites convex. Surfaces acarinate (fig. 17B), smooth; VI and VII, lateral margins with small granules; VII, surface and posterior margin with microsetae. Respiratory spiracles (stigmata) small, round, situated posterolaterally.

Metasoma: Segments elongated, length greater than width (fig. 12A), progressively increasing in length, decreasing in width (table 7); segment V equal to or longer than carapace. Dorsosubmedian carinae, segments I–IV, distinct, granular, distal granules not noticeably larger than preceding granules; V, absent. Dorsolateral carinae, segment I, obsolete, granular, complete; II and III, obsolete, granular, incomplete; IV, absent; V, obsolete, granular. Median lateral carinae, segment I, distinct, granular, incomplete; II–V, absent. Ventrolateral carinae, segment I, obsolete, granular; II–V, distinct, composed

of small, stout granules, complete. Ventro-submedian carinae, segments I–IV, absent. Ventromedian carina, segment V, distinct, granular in anterior half of segment, becoming obsolete, sparsely granular posteriorly. Dorsal intercarinal surfaces, segments I–IV, slightly concave; V, convex. Intercarinal surfaces smooth except segment I, with few large granules. Dorsolateral carinae and lateral intercarinal surfaces with long microsetae; ventral intercarinal surfaces with at least three paired macrosetae.

Telson: Vesicle elongated, width equal to height (table 7), flattened dorsally, rounded ventrally; anterodorsal lateral lobes absent (fig. 12A); surface smooth, almost entirely covered in long macrosetae, except medially on dorsal surface. Aculeus long, moderately sclerotized, gently curved.

Hemispermatothore: Lamelliform; broad trunk, with long narrow prominence, originating in capsular region, bearing small, strongly sclerotized lobe; spiniform processes absent. See Francke (1982a: 58) for illustrations.

Ontogenetic variation: Subadult and juvenile paratypes completely whitish, unguis and cheliceral teeth only slightly darker at extremities, aculeus light reddish. Pedipalp and metasomal carinae less pronounced; all surfaces smooth.

Sexual dimorphism: Adult female unknown. Males exhibit completely divided genital operculum and genital papillae.

Geographical variation: All specimens from same locality.

REMARKS: The juvenile ♀ paratype (MNHN) is damaged. The metasoma is broken, and the left pedipalp, legs I, II, and IV, are lost.

DISTRIBUTION: Known only from the type locality, El Sótano de Yerbaniz, a vertical cave in the Sierra de El Abra karstic region, San Luis Potosí, central Mexico (figs. 1B, 2C–F).

ECOLOGY: According to the original description, the holotype and one paratype of this troglobitic species were collected within 1 or 2 m of one another in a small, wet limestone tunnel about 75 m below the cave entrance (Mitchell, 1971). No data were provided for the third specimen, except that it was collected in the same cave. This species is considered the most troglomorphic mem-

ber of the family, on account of the pronounced attenuation of its pedipalps (Francke, 1982a).

Stygochactas, new genus

Type species *Typhlochactas granulosus* Sissom and Cokendolpher, 1998 [= *Stygochactas granulosus* (Sissom and Cokendolpher, 1998)].

DIAGNOSIS: *Stygochactas* is the sister taxon of *Typhlochactas* (fig. 4). It may be separated from *Typhlochactas* and *Sotamo-chactas* on the basis of the following combination of characters. Size moderate to large, total length of adult estimated (from single pedipalp chela) to be 60–70 mm. Cheliceral fixed finger with four teeth (subdistal present); median and basal teeth fused into a bicuspid. Cheliceral movable finger with four dorsal teeth (one subdistal present). Carapace, anterior margin, median projection (epistome) obsolete. Pedipalps moderately elongated, chela fingers slightly longer than manus. Pedipalp femur, ventroexternal carina and patella, internomedian carina absent. Pedipalp chela, dorsal secondary, digital, ventroexternal, ventromedian, and ventrointernal carinae distinct. Chela fixed and movable fingers, median denticle rows of each comprising seven oblique primary subrows; basal primary subrows similar in length to other subrows; terminal denticle of fixed finger considerably larger than preceding denticles, hooklike, fingertips interlocking unevenly when closed. Patella trichobothrium v_1 situated level with trichobothrium esb_1 . Chela fixed finger, external trichobothria distributed across entire length of finger, with trichobothrium eb situated near base of finger; trichobothria it and ib situated near base of finger. Legs without prolateral pedal spurs. Basitarsi I and II, proventral surfaces without short row of closely aligned spinules subdistally. Telotarsi, ventral surface, with curved proximal row spinules; without ventromedian row of spinules. Tergite VII, dorsolateral carinae absent or vestigial. Metasomal segments I–IV, dorsosubmedian carinae obsolete; I–III, dorsolateral carinae distinct; I, median lateral carinae absent; I–V, ventrolateral carinae absent or obsolete; V, ventromedian carina absent.

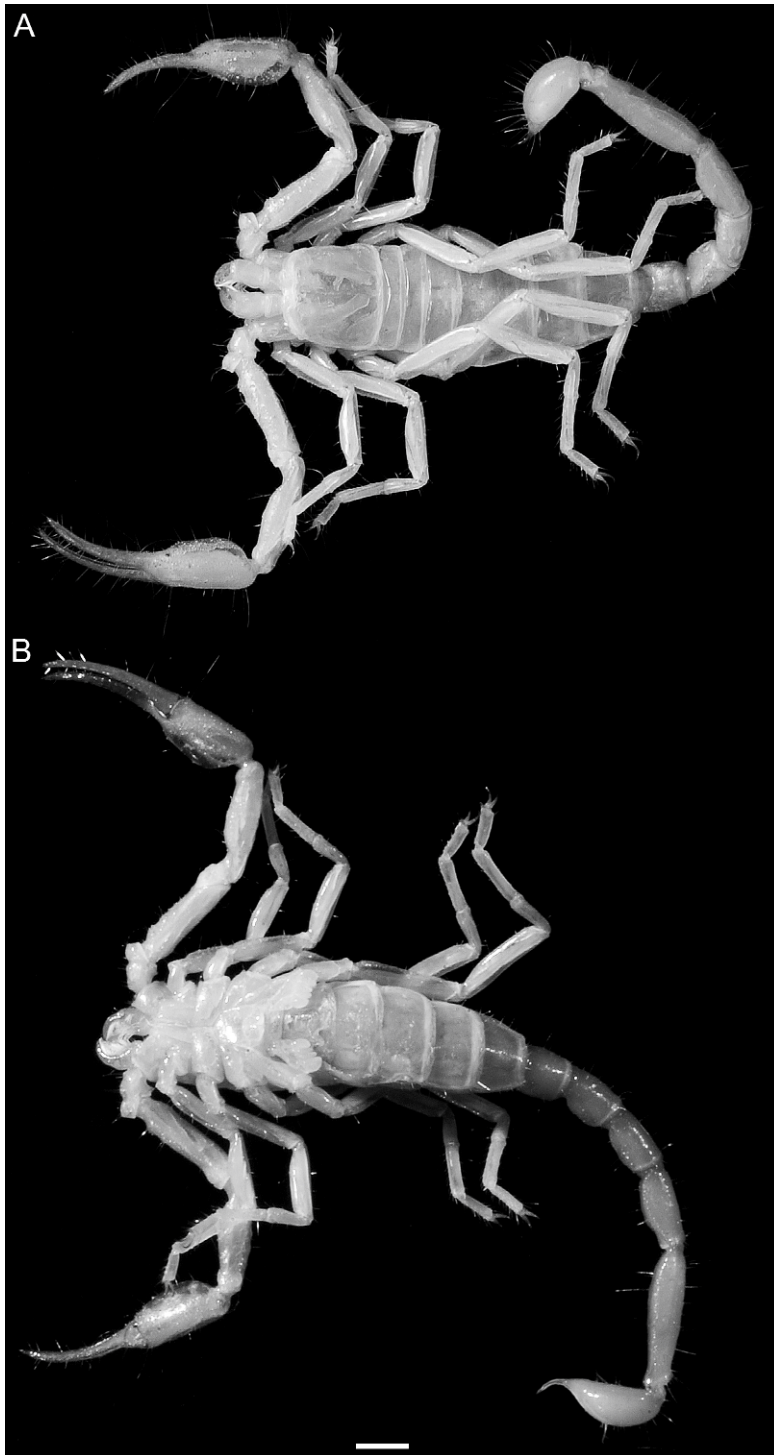


Fig. 20. *Stygochactas granulatus* (Sissom and Cokendolpher, 1998), juv. ♂ holotype (AMNH), habitus. **A.** Dorsal aspect. **B.** Ventral aspect. Scale = 1 mm.

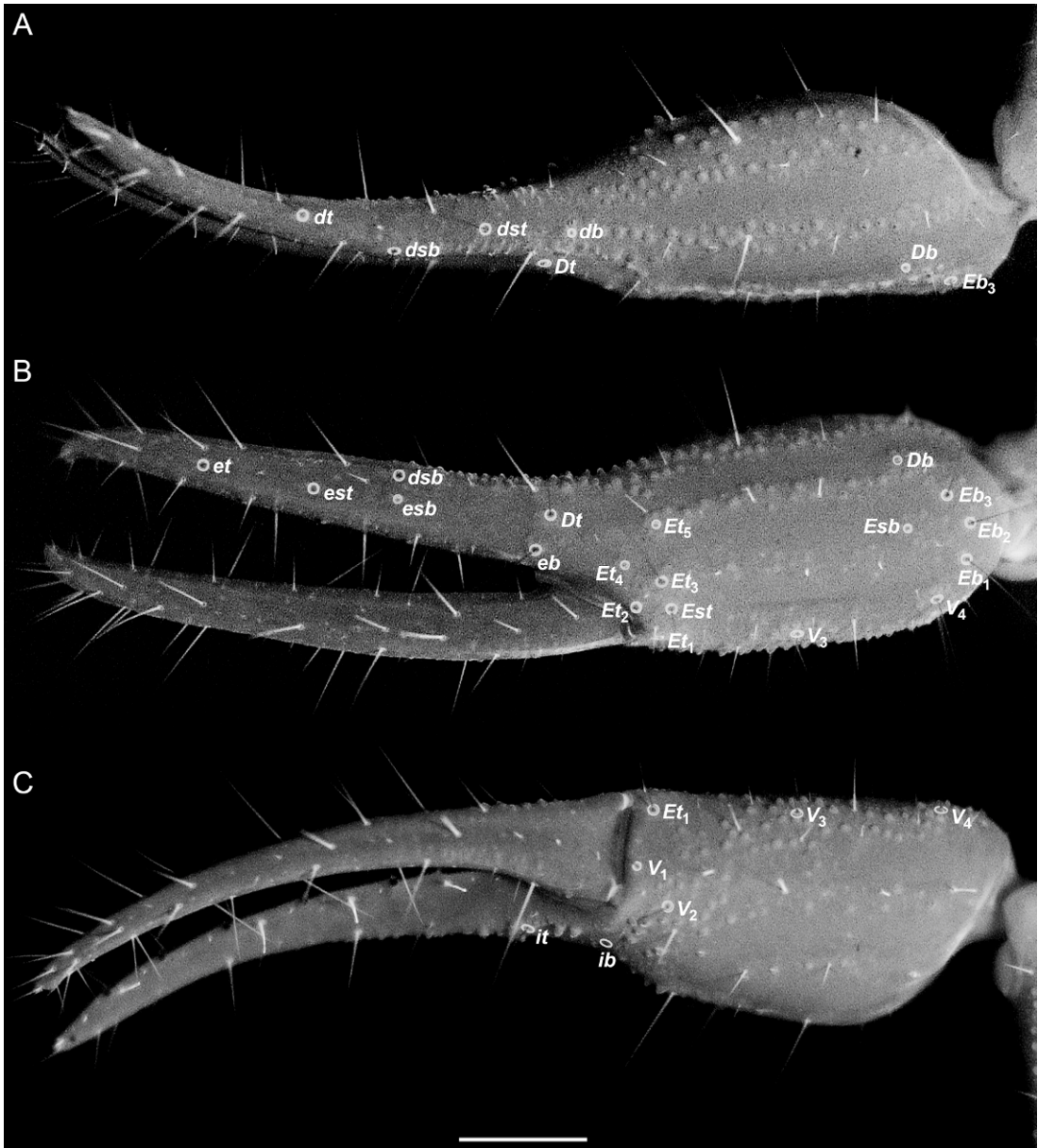


Fig. 21. *Stygochactas granulatus* (Sissom and Cokendolpher, 1998), juv. ♂ holotype (AMNH), sinistral pedipalp chela showing carinae and distribution of trichobothria. **A.** Dorsal aspect. **B.** External aspect. **C.** Ventral aspect. Scale = 0.5 mm.

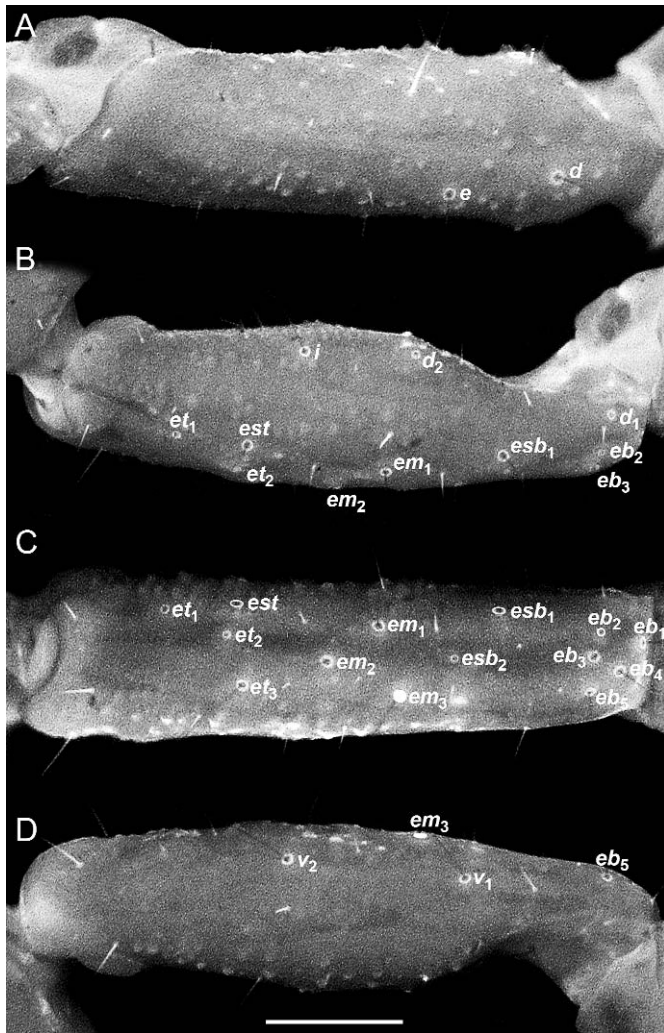


Fig. 22. *Stygochactas granulosis* (Sissom and Cokendolpher, 1998), juv. ♂ holotype (AMNH), sinistral pedipalp femur (A) and patella (B–D) showing carinae and distribution of trichobothria. A, B. Dorsal aspect. C. External aspect. D. Ventral aspect. Scales = 0.5 mm.

INCLUDED TAXA: Monotypic genus: *Stygochactas granulosis* (Sissom and Cokendolpher, 1998).

DISTRIBUTION: Endemic to Mexico. Recorded from Veracruz.

Stygochactas granulosis

(Sissom and Cokendolpher, 1998)

(Figs. 1B, 4, 5C, 6D, 8A, 9E, 9F, 10I–L, 12B, 20–22; table 7)

Typhlochactas granulosis Sissom and Cokendolpher, 1998: 285–290, table 1, figs. 1–11.

Typhlochactas granulosis: Sissom, 2000b: 499; Sogleglad and Fet, 2003a: fig. 13; 2003b: 30, 162; Vignoli and Kovařík, 2003: 131; Volschenk and Prendini, 2008: 236 (table 1).

TYPE MATERIAL: **Mexico:** Veracruz: Municipio Tlaquilpa: Holotype: 1 juv. ♂ (AMNH), Sótano de Poncho [18°37'N 97°07'W, –73 m], P. Sprouse, 22.III.1995.

DIAGNOSIS: As for genus.

DESCRIPTION: The following redescription supplements the original description of the holotype (fig. 20) by Sissom and Cokendolpher (1998).

Color: Chelicerae, carapace, legs, tergites, sternites, metasoma uniformly Cream (54); pedipalp chela Buff Yellow (53). Cheliceral teeth paler; pedipalp chela manus and denticle rows of fingers darker; unguis similar in color to telotarsi, but slightly darker distally (fig. 20).

Chelicerae: Manus, dorsal and ventral surfaces smooth; dorsal surface with four microsetae situated near base of fixed finger; movable finger with few microsetae. Fixed finger, dorsal margin with four teeth (distal, subdistal, median, and basal; fig. 5C); distal tooth largest, median and basal teeth equal, fused into bicuspid. Movable finger, internal distal and external distal teeth opposable, internal distal tooth completely overlapping external distal tooth in dorsal view; dorsal margin with four teeth (internal distal, subdistal, median, and basal), internal distal tooth largest, subdistal and median teeth equal, smaller, basal tooth smallest; ventral surface with serrula along distal half of finger, comprising relatively large tines, partially covered by dense brush of macrosetae.

Carapace: Length similar to anterior width (table 7). Anterior margin sublinear, with small median projection (epistome) and six macrosetae (fig. 6D). Posterior margin sublinear; asetose. Median and lateral ocelli absent. Median longitudinal sulcus present, shallow; posterolateral sulci shallow; posterior transverse sulcus deep. Surface acarinate, uniformly finely granular, especially on posterolateral surfaces. Surface and margins with several microsetae.

Pedipalps: Pedipalps moderately elongated (figs. 21, 22). Femur, dorsoexternal, dorsointernal, ventrointernal, ventroexternal carinae obsolete, granular (fig. 22A). Dorsal, external, and internal surfaces with scattered granules; ventral surfaces smooth. Patella dorsoexternal carina distinct, granular; dorsoexternal, ventroexternal, and ventrointernal carinae obsolete; internomedian carina absent or vestigial, comprising at most one or two granules besides dorsal process; externomedian carinae absent (fig. 22B–D). Intercarinal surfaces less granular than femur; dorsal surfaces smooth; external surfaces with few larger granules distally; internal surface uniformly finely granular, with few

larger granules proximally; ventral surfaces smooth. Chela manus slightly swollen, fingers longer than manus (fig. 21). Dorsal secondary, digital, ventroexternal, ventromedian, and ventrointernal carinae distinct, composed of similar, rounded granules; external secondary carina obsolete; other carinae absent. Manus, intercarinal surfaces smooth; internal surface with prominent, isolated granule near movable finger condyle and pair of prominent, isolated granules situated close together at base of fixed finger; fixed finger, proximal half granular dorsally. Manus and fingers covered by macrosetae; several extremely long macrosetae situated terminally on fingers. Fixed finger, median denticle row comprising seven oblique primary subrows of denticles, similar in length except for basal subrow, which is shorter (fig. 9E); internal denticles larger than external denticles; terminal denticle of fixed finger considerably larger than preceding denticles, hooklike, fingertips interlocking unevenly when closed. Movable finger, median denticle row comprising seven oblique primary subrows of denticles, terminal and proximal subrows shortest (fig. 9F); terminal denticle enlarged.

Trichobothria: Femur with three trichobothria (fig. 22A): one external (*e*), one dorsal (*d*), one internal (*i*). Patella with 19 trichobothria (fig. 22B–D), five petite (*d*₁, *d*₂, *e*₂, *esb*₂, *eb*₂), one accessory (*em*₃): two ventral (*v*₁, *v*₂); 14 external (*et*₁–*et*₃, *est*, *em*₁–*em*₃, *esb*₁, *esb*₂, *eb*₁–*eb*₅); two dorsal (*d*₁, *d*₂); one internal (*i*). Chela with 26 trichobothria (fig. 21), seven petite (*V*₁, *Et*₄, *Et*₅, *Esb*, *Db*, *esb*, *db*): 16 on manus, four ventral (*V*₁–*V*₄), 10 external (*Et*₁–*Et*₅, *Est*, *Esb*, *Eb*₁–*Eb*₃), two dorsal (*Db*, *Dt*); 10 on fixed finger, four external (*et*, *est*, *esb*, *eb*), four dorsal (*dt*, *dst*, *dsb*, *db*), two internal (*it*, *ib*).

Legs: Femur and patella II–IV, ventral surfaces, sparsely granular; basitarsi each with two rows of long macrosetae. Basitarsi I–IV without prolateral pedal spurs; I and II, proventral surface without spinules. Telotarsi, dorsomedian lobe with one microseta; ventral surface with curved row of spinules, proximally, and four or five submedian pairs of subspiniform macrosetae (fig. 10I–L); unguis long, curved, equal in length; dactyl short, robust.

Tergites: Pretergites, surfaces smooth. Posttergites, surfaces densely and finely granular, more so on VII, with scattered microsetae and pair of macrosetae submedially on posterior margins; I–VI, acarinate, VII, dorsosubmedian and dorsolateral carinae vestigial, reduced to few posterior granules (fig. 20A).

Sternum: Posterior width greater than length (fig. 8A); apex slightly rounded; lateral margins converging anteriorly; lateral lobes flat; posterior depression shallow. Surface with two pairs of macrosetae and several microsetae.

Genital operculum: Sclerites completely divided, strongly rounded posteriorly, each with single macroseta situated medially; genital papillae protruding distinctly beyond posterior edges (fig. 8A).

Pectines: Pectinal plate, surface with pair of macrosetae. Lamella comprising three segments (fig. 8A), demarcated by very faint sutures; surfaces with several macrosetae and numerous microsetae. Tooth count: 5/4; distal tooth larger, broader.

Sternites: Surfaces and margins smooth, acarinate (fig. 20B), with scattered microsetae; VII with several macrosetae. Respiratory spiracles (stigmata) small, round, situated posterolaterally.

Metasoma: Segments elongated, length greater than width (fig. 12B), progressively increasing in length, decreasing in width (table 7); segment V much longer than carapace. Dorsosubmedian carinae, segments I–IV, obsolete, granular, distal granules not noticeably larger than preceding granules (fig. 12B); V, absent. Dorsolateral and ventrolateral carinae, segment V, obsolete, granular, complete. Dorsolateral, median lateral, ventrolateral and ventrosubmedian carinae, segments I–IV, and ventromedian carina, segment V, absent. Dorsal intercarinal surfaces, segments I–IV, slightly concave; V, convex. Dorsal and ventral intercarinal surfaces sparsely granular, especially posteriorly; lateral intercarinal surfaces smooth. All segments with several macrosetae, especially on ventral surfaces.

Telson: Vesicle broad, elongated, flattened dorsally, rounded ventrally; anterodorsal lateral lobes absent (fig. 12B); surface smooth, with scattered long macrosetae.

Aculeus short, weakly curved, arising gradually from vesicle.

Hemispermatothore: Adult male unknown.

Ontogenetic variation: The granulation and sclerotization of the chela are more pronounced in the adult than the juvenile.

Sexual dimorphism: Female unknown.

Geographical variation: Single complete specimen.

REMARKS: The movable finger of the dextral pedipalp chela of the holotype is detached. A large, sinistral pedipalp chela, also without a movable finger, was collected together with the holotype and placed in the same vial. According to Sissom and Cokendolpher (1998: 289) this chela “structurally resembles the chela of *Alacran tartarus* Francke, 1982, known only from deep caves of the Sistema Huautla, Oaxaca ... but until more material becomes available it will not be possible to draw comparisons with the Oaxacan specimens.” We compared the damaged chela with the types of *A. tartarus* and the holotype of *S. granulosus* and observed that, aside from its larger size, more pronounced granulation and sclerotization (all consistent with sexual maturity), the chela was otherwise identical to that of the holotype of *S. granulosus*. The proximal half of the fixed finger was granular dorsally, the median denticle row comprised seven oblique primary subrows, the basal subrow being the shortest, and there were six internal denticles. The chelal carination, though more pronounced, was consistent with the holotype of *S. granulosus*. Except for three trichobothria, which could not be observed due to damage to the specimen (V_1 , Et_1 , ib), the following 23 trichobothria were observed in the same positions as in the holotype of *S. granulosus* (fig. 18): 14 on manus, three ventral (V_3 – V_4), nine external (Et_2 – Et_5 , Est , Esb , Eb_1 – Eb_3), two dorsal (Db , Dt); nine on fixed finger, four external (et , est , esb , eb), four dorsal (dt , dst , dsb , db), one internal (it). Six of these trichobothria were petite, based on the smaller diameter of their areolae: Et_4 , Et_5 , Esb , Db , esb , db . The presence of seven primary subrows on the median denticle row of the fixed finger, six petite trichobothria, the absence of three accessory trichobothria, and other differences in trichobothrial posi-

tions rule out the possibility that the chela is conspecific with *A. tartarus*, or indeed that it is congeneric. Based on the overwhelming similarity of the chela to that of the holotype of *S. granulatus*, together with their collection from nearby one another in the same cave, we conclude that they are conspecific, that the chela belongs to an adult of the species and that the holotype is a juvenile. The discovery is significant because the length of the chela (at least 11 mm, as the tip of the finger is missing) is comparable to that of *A. tartarus* (12–14 mm), implying that the adult of *S. granulatus* may be similar in size (adult *A. tartarus* measure 60–70 mm in length), and hence that this would represent the second large-bodied species in the family, albeit from a much shallower cave (–73 m). The finding also calls into question whether some species of *Typhlochoactas*, known only from single specimens and/or females (notably *T. cavicola* and *T. reddelli*), are adult and, if not, what size the adults might reach. In this regard, it is noteworthy that the second-largest typhlochoactine specimen known, the holotype of *T. sissomi*, is subadult. Its total length is 0.3 mm greater than the adult male holotype of *T. rhodesi* and 0.9 mm greater than the adult male paratype of *S. elliotti* (tables 4, 5).

DISTRIBUTION: Known only from the type locality, Sótano de Poncho (Veracruz, México) (fig. 1B).

ECOLOGY: This troglobitic species was taken from a vertical cave, 95 m long and 73 m deep, with a small entrance (Sissom and Cokendolpher, 1998). The holotype was collected on the talus slope at the base of the entrance drop and the single pedipalp chela collected nearby.

ADDITIONAL MATERIAL: **Mexico:** Veracruz: Municipio Tlaquilpa: 1 ad., pedipalp chela only (AMNH), Sótano de Poncho [18°37'N 97°07'W, –73 m], P. Sprouse, 22.III.1995.

Typhlochoactas Mitchell, 1971

Typhlochoactas Mitchell, 1971: 238; type species by subsequent designation (Mitchell, 1971: 238)
Typhlochoactas rhodesi Mitchell, 1968.

Typhlochoactas: Mitchell, 1968: 753–756, 771–774; 1971: 135, 138, 147 (part); Vachon, 1974: 914, 923; Soleglad, 1976: 253, 254; Mitchell and Peck, 1977: 159, 162, 164, 165, 167 (part; revised diagnosis); Francke, 1978: 44; Reddell, 1981:

115, 175; Francke, 1982a: 51–53, 57, 59–61; 1982b: 36; 1985: 14, 16, 20; 1986: 5, 8; Locket, 1986: 101, 111, 112; Sissom, 1988: 365, 370; 1990: 109, 114; Polis, 1990: 253; Nenilin and Fet, 1992: 10, 28; Stockwell, 1992: 410, 412–414, 419, figs. 3, 28, 30, 33, 35; Armas, 1994: 18, 19; Locket, 1995: 191; Kovařík, 1998: 142; Sissom and Cokendolpher, 1998: 285, 286; Beutelspacher Baigts, 2000: 6, 13–16, 18, 20, 48, 51, 53, 57, 151, fig. 11A, graph 1, tables 1, 2; Lourenço, 2000: 25; Lourenço and Sissom, 2000: 118; Sissom, 2000b: 498; Lourenço, 2001: 4; Soleglad and Sissom, 2001: 68, 69; Morrone et al., 2002: 93; Soleglad and Fet, 2003a: 7, 16, 17, 32, fig. 12; 2003b: 36, 67, 72, 74, 82, 106–109, 141, 162, fig. 116, tables 3, 4, 9; Fet et al., 2004: 197; Rojas-Runjaic, 2004: 245; Prendini and Wheeler, 2005: 454, 458, 460, 463, 468, 470, 477, 478, tables 3, 4, 5, 9, 10, figs. 18, 19; Fet and Soleglad, 2005: 12; Sissom and Hendrixson, 2005: 123, 130; Dupré, 2006: 11; Francke and Savary, 2006: 29; Graham and Fet, 2006: 2; Volschenk and Prendini, 2008: 249; Botero-Trujillo and Francke, 2009: 2.

Typhlochoactas: Díaz Najera, 1975: 3; Dupré, 2007: 11.

DIAGNOSIS: *Typhlochoactas* is the sister taxon of *Stygochoactas* (fig. 4). Species of *Typhlochoactas* may be separated from *Stygochoactas* and *Sotanochoactas* on the basis of the following combination of characters. Size small to very small, total length (adult) less than 25 mm. Cheliceral fixed finger with three or four teeth, basal teeth usually not fused into a bicuspid. Cheliceral movable finger with three, four, or (usually) five dorsal teeth (none, one, or two subdistal teeth). Carapace, anterior margin, median projection (epistome) usually present. Pedipalps not elongated, chela fingers similar in length to chela manus. Pedipalp femur, ventroexternal carina, patella, internomedial carina, and chela, dorsal secondary, digital, ventroexternal, ventromedian, and ventrointernal carinae, absent or obsolete. Chela fixed and movable fingers, median denticle row comprising 4–6 and 5–7 oblique primary subrows, respectively; basal primary subrows of fixed finger similar in length to other subrows. Patella trichobothrium v_1 situated level with or proximal to trichobothrium *esb*₁. Chela fixed finger, external trichobothria distributed across entire length of finger, with trichobothrium *eb* situated near base of finger; trichobothria *it* and *ib* situated near base of finger. Legs usually with prolateral pedal

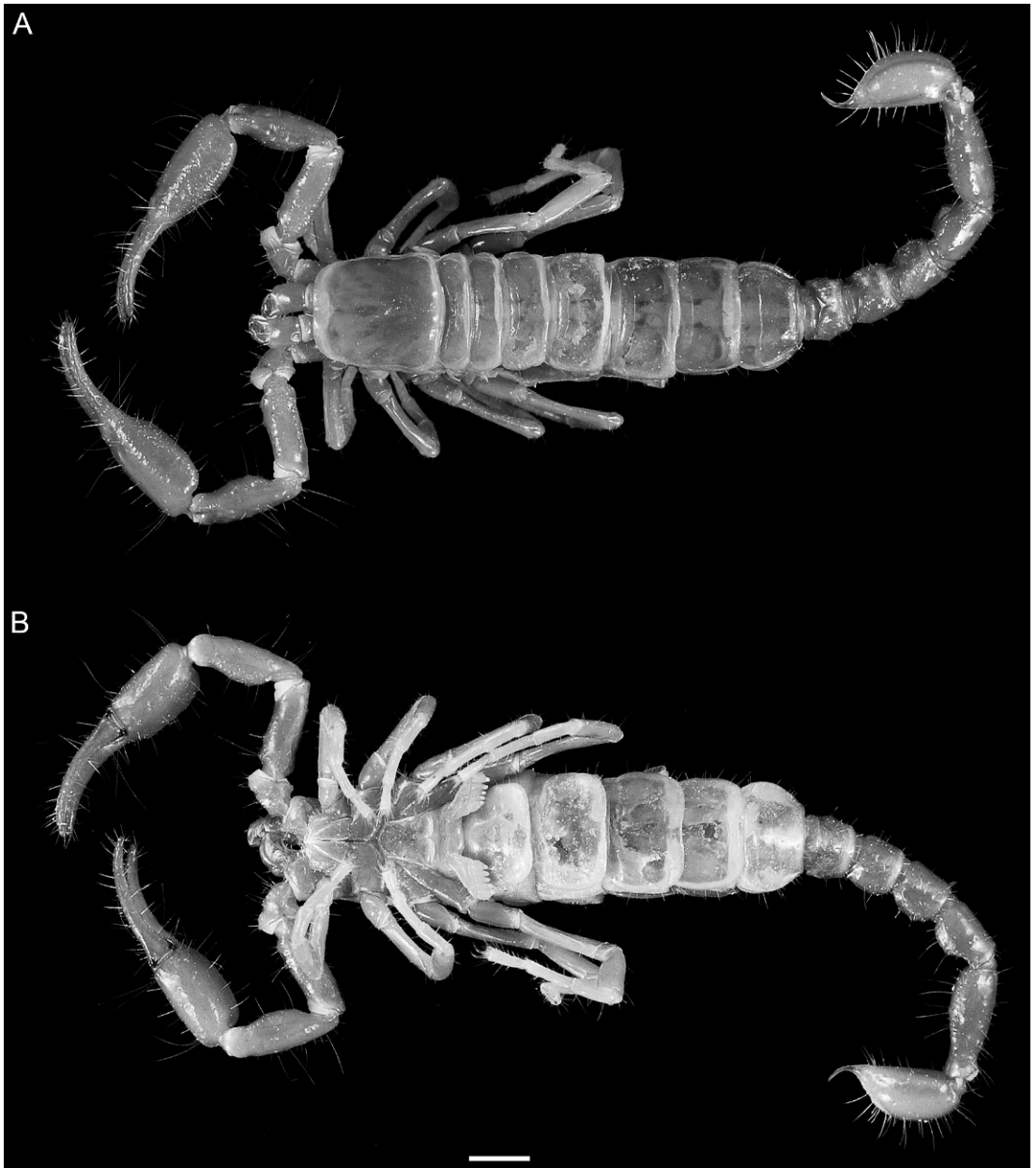


Fig. 23. *Typhlochaetas cavicola* Francke, 1986, holotype ♀ (AMNH), habitus. **A.** Dorsal aspect. **B.** Ventral aspect. Scale = 1 mm.

spurs. Basitarsi I and II, proventral surfaces usually with short row of closely aligned spinules subdistally. Telotarsi, ventral surface, usually with curved proximal row spinules and without ventromedian row of spinules. Tergite VII, dorsolateral carinae absent or

vestigial. Metasomal segments I–IV, dorso-submedian carinae obsolete; I–III, dorsolateral carinae absent or obsolete; I, median lateral carinae absent; I–V, ventrolateral carinae absent or obsolete; V, ventromedian carina absent.

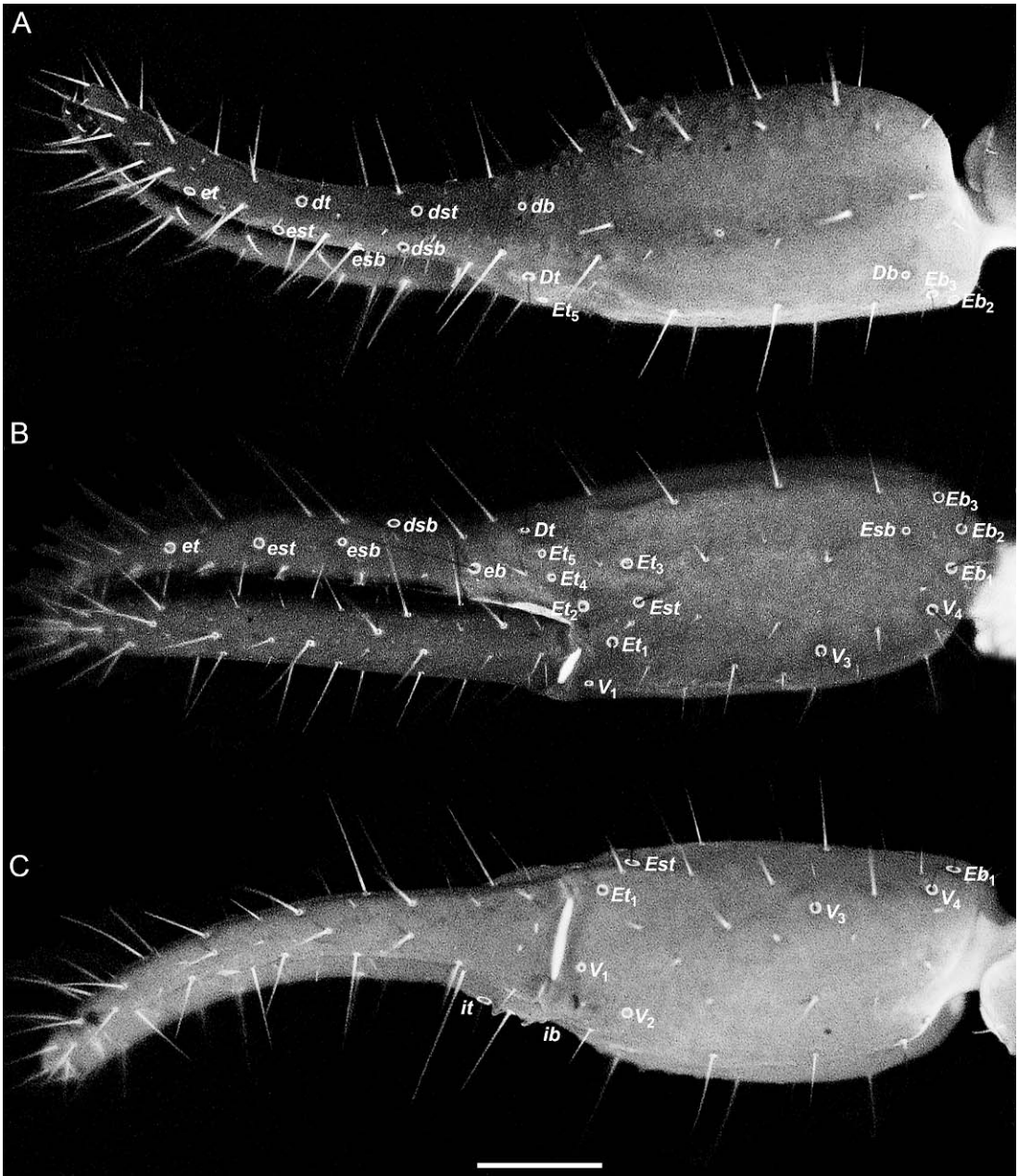


Fig. 24. *Typhlochactas cavicola* Francke, 1986, holotype ♀ (AMNH), sinistral pedipalp chela showing carinae and distribution of trichobothria. **A.** Dorsal aspect. **B.** External aspect. **C.** Ventral aspect. Scale = 0.5 mm.

INCLUDED TAXA: Six species: *Typhlochactas cavicola* Francke, 1986; *Typhlochactas mitchelli* Sissom, 1988; *Typhlochactas reddelli* Mitchell, 1968; *Typhlochactas rhodesi* Mitchell, 1968; *Typhlochactas sissomi* Francke et

al., 2009; *Typhlochactas sylvestris* Mitchell and Peck, 1977.

DISTRIBUTION: Endemic to Mexico. Recorded from four states: Oaxaca, Queretaro, Tamaulipas, Veracruz.

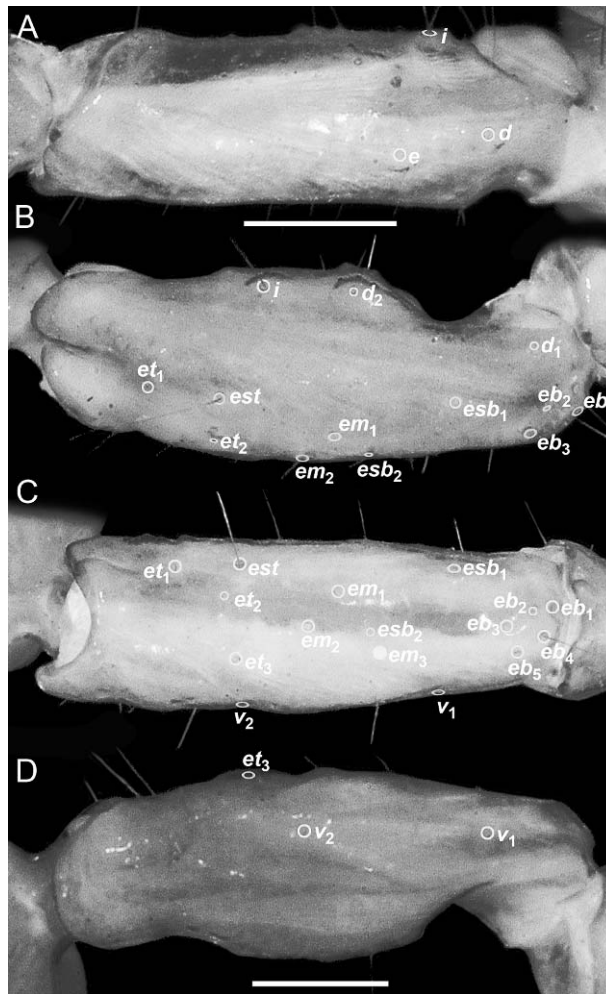


Fig. 25. *Typhlochactas cavicola* Francke, 1986, holotype ♀ (AMNH), sinistral pedipalp femur (A) and patella (B–D) showing carinae and distribution of trichobothria. A, B. Dorsal aspect. C. External aspect. D. Ventral aspect. Scales = 0.5 mm.

Typhlochactas cavicola Francke, 1986
(Figs. 1B, 4, 5D, 8C, 9G,
9H, 12C, 23–25; table 8)

Typhlochactas cavicola Francke, 1986: 5–9, figs. 1–10, 17–19, table 1.

Typhlochactas cavicola: Sissom, 1988: 365; Armas, 1994: 21; Lourenço, 1994: 182, 183; Kovařík, 1998: 142. Sissom and Cokendolpher, 1998: 285, 287 (table 1); Beutelspacher Baigts, 2000: 18, 20, 52, 54, 147, 151, map 22; Sissom, 2000b: 499; Volschenk et al., 2001: 161; Soleglad and Fet, 2003a: 7; 2003b: 30, 32, 76; Vignoli and Kovařík, 2003: 131; Sissom and Hendrixson,

2005: 127, table 6.2; Volschenk and Prendini, 2008: 236 (table 1).

TYPE MATERIAL: **Mexico:** *Tamaulipas:* Municipio de Guemez: Holotype: 1 ♀ (AMNH), Cueva del Vandalismo [23°51'54"N 99°26'45"W], ca. 2600 m, 1 km SE Rancho Nuevo, D. Honea, 15.III.1982.

DIAGNOSIS: *Typhlochactas cavicola* is most closely related to *T. rhodesi* (fig. 4). It may be separated from *T. rhodesi* and all other *Typhlochactas* species by the following combination of characters. Cheliceral fixed finger with four teeth (subdistal present); median

TABLE 8
Meristic data for *Typhlochactas cavicola* Francke, 1986, *Typhlochactas reddelli* Mitchell, 1968, and *Typhlochactas rhodesi* Mitchell, 1968
 Measurements (mm) follow Francke et al. (2009). Abbreviations as follows: AMNH = American Museum of Natural History, New York; IBUNAM = Instituto de Biología, Universidad Nacional Autónoma de México, Mexico City; MNHN = Muséum National d'Histoire Naturelle, Paris

Specimen type	<i>Typhlochactas cavicola</i>			<i>Typhlochactas reddelli</i>			<i>Typhlochactas rhodesi</i>		
	Holotype ♀ AMNH	Holotype ♀ AMNH	juv. ♂ IBUNAM	juv. ♀ IBUNAM	juv. ♀ IBUNAM	juv. ♀ IBUNAM	Holotype ♀ AMNH	Paratype ♀ MNHN RS 4760	Paratype subad. ♀ AMNH
Carapace									
anterior width	1.6	1.2	—	—	—	—	2.0	0.9	0.7
posterior width	2.0	1.9	—	—	—	—	2.8	1.0	1.0
length	2.1	2.2	1.5	1.9	1.3	—	2.7	1.0	0.9
Chela									
maximum width	1.0	1.1	—	—	—	—	1.3	0.4	0.4
maximum height	1.0	1.2	—	—	—	—	1.5	0.4	0.4
length ¹	3.8	3.9	—	—	—	—	5.3	1.9	1.8
length ventroexternal carina	1.6	1.7	—	—	—	—	2.5	0.9	0.6
length of movable finger	2.2	2.3	—	—	—	—	3.1	0.9	0.8
Patella									
maximum width	0.7	0.8	—	—	—	—	0.9	0.4	0.5
maximum height	0.7	0.7	—	—	—	—	0.9	0.3	0.3
length	1.9	2.2	—	—	—	—	2.5	1.1	1.0
<i>e</i> trichobothria (left/right)	14/14	14/14	14/14	14/14	14/14	—	14/14	14/14	14/14
Femur									
maximum width	0.5	0.6	—	—	—	—	0.8	0.4	0.3
maximum height	0.5	0.6	—	—	—	—	0.6	0.3	0.3
length	1.8	1.9	—	—	—	—	2.3	1.5	0.8
Pedipalp									
total length (incl. trochanter)	8.2	6.7	—	—	—	—	10.7	ca. 5.0	3.9
Mesosoma									
total length (tergites)	5.4	5.0	—	—	—	—	7.8	—	2.5
Sternite VII									
width	1.8	1.6	—	—	—	—	2.1	—	0.8
length	1.0	0.8	—	—	—	—	1.0	—	0.4
Metasoma I									
maximum width	1.1	1.1	—	—	—	—	1.4	—	0.5
maximum height	0.8	0.8	—	—	—	—	1.1	—	0.4
length	0.7	0.8	—	—	—	—	1.1	—	0.4

TABLE 8
(Continued)

Specimen type	<i>Typhlochactas cavicola</i>			<i>Typhlochactas reddelli</i>			<i>Typhlochactas rhodesi</i>		
	Holotype ♀ AMNH	Holotype ♀ AMNH	Holotype ♀ IBUNAM	juv. ♂ IBUNAM	juv. ♀ IBUNAM	juv. ♀ IBUNAM	Holotype ♀ AMNH	Paratype ♀ MNHN RS 4760	Paratype subad. ♀ AMNH
Metasoma II									
maximum width	1.0	1.0	1.0	—	—	—	1.2	—	0.4
maximum height	0.8	0.7	—	—	—	—	1.1	—	0.4
length	0.8	0.9	—	—	—	—	1.2	—	0.4
Metasoma III									
maximum width	0.9	0.9	—	—	—	—	1.2	—	0.4
maximum height	0.8	0.7	—	—	—	—	1.0	—	0.4
length	1.0	0.9	—	—	—	—	1.4	—	0.5
Metasoma IV									
maximum width	0.9	0.9	—	—	—	—	1.1	—	0.4
maximum height	0.8	0.7	—	—	—	—	1.0	—	0.4
length	1.2	1.4	—	—	—	—	1.7	—	0.5
Metasoma V									
maximum width	0.9	0.9	—	—	—	—	1.1	—	0.4
maximum height	0.8	0.7	—	—	—	—	1.0	—	0.4
length	2.0	2.3	—	—	—	—	2.8	—	1.0
Telson									
maximum width	1.0	1.0	—	—	—	—	1.4	—	0.5
maximum height	0.9	0.8	—	—	—	—	1.3	—	0.4
aculeus length	0.5	0.6	—	—	—	—	0.6	0.3	0.3
total length	2.4	2.2	—	—	—	—	3.1	—	1.0
Metasoma									
total length ²	8.2	8.6	—	—	—	—	11.5	—	3.8
Total length									
pro-+meso-+metasoma	15.7	15.8	—	—	—	—	22.1	ca. 5.6	7.4
Pectines									
total length	1.2	0.8	—	—	—	—	0.8	—	0.4
length along dentate margin	1.0	0.7	—	—	—	—	0.7	—	0.3
tooth count (left/right)	5/5	5/5	5/5	5/5	5/5	5/5	5/5	—	5/5

¹Measured from base of condyle to tip of fixed finger.

²Sum of metasomal segments I–V and telson.

and basal teeth not fused into bicusp. Cheliceral movable finger with four dorsal teeth (one subdistal present). Carapace, anterior margin, median projection (epistome) absent. Pedipalp chela fixed and movable fingers, median denticle row comprising six and five oblique primary subrows, respectively; basal primary subrow of movable finger considerably longer than other subrows; terminal denticle of fixed finger slightly larger than preceding denticles, fingertips interlocking evenly when closed. Legs without prolateral pedal spurs. Telotarsi without ventromedian row of spinules. Sclerites of genital operculum (♀) mostly fused, but loosely connected by membrane along entire length of suture, posterior edges free.

DESCRIPTION: The following description supplements the original description by Francke (1986).

Color: Carapace, pedipalps, legs, tergites, and metasoma, Raw Sienna (136). Pedipalp chela fingers darker; cheliceral teeth, unguis paler than aculeus (fig. 23).

Chelicerae: Manus, dorsal and ventral surfaces smooth; dorsal surface with three microsetae situated near base of fixed finger; movable finger with two larger microsetae and one smaller microseta. Fixed finger, dorsal margin with four teeth (distal, subdistal, median, and basal; fig. 5D); median and basal teeth not fused into bicusp; distal tooth largest, subdistal and median teeth equal, smaller, basal tooth smallest. Movable finger, internal distal and external distal teeth opposable, internal distal tooth completely overlapping external distal tooth in dorsal view; dorsal margin with four teeth (internal distal, subdistal, median, and basal), internal distal tooth largest, subdistal and median teeth equal, smaller, basal tooth smallest; ventral surface with well-developed serrula, covered in part by dense brush of macrosetae.

Carapace: Length slightly greater than anterior width (table 8). Anterior margin sublinear, without median projection (epistome); asetose (fig. 23A). Posterior margin sublinear; asetose. Median and lateral ocelli absent. Median longitudinal, posterolateral and posterior transverse sulci shallow. Surface smooth, acarinate, with few microsetae.

Pedipalps: Femur, dorsoexternal, ventroexternal, and ventrointernal carinae obsolete, comprising a few small scattered granules, decreasing in number distally; dorsointernal carina absent. Dorsal and external surfaces smooth, with several short setae (fig. 25A); internal surface with few granules proximally. Patella, ventrointernal carina obsolete, granular; other carinae absent (fig. 25B–D). Intercarinal surfaces less granular than femur, with several short setae. Chela relatively large, longer than carapace (table 8). Manus acarinate (fig. 24); manus and fingers, surfaces mostly smooth, with several long setae; dorsal, external, and internal surfaces with small scattered granules; internal surface additionally with pair of prominent, isolated granules situated close together at base of fixed finger. Fixed finger, median denticle row comprising six oblique primary subrows (fig. 9G); internal denticles larger than external denticles; terminal denticle small, equal to internal denticle, fingertips interlocking evenly when closed. Movable finger, median denticle row comprising five oblique primary subrows of denticles, basal primary subrow considerably longer than other subrows (fig. 9H); terminal denticle small.

Trichobothria: Femur with three trichobothria (fig. 25A): one external (*e*), one dorsal (*d*), one internal (*i*). Patella with 19 trichobothria (fig. 25B–D), five petite (*d*₁, *d*₂, *et*₂, *esb*₂, *eb*₂), one accessory (*em*₃): two ventral (*v*₁, *v*₂); 14 external (*et*₁–*et*₃, *est*, *em*₁–*em*₃, *esb*₁, *esb*₂, *eb*₁–*eb*₅); two dorsal (*d*₁, *d*₂); one internal (*i*). Chela with 26 trichobothria (fig. 24), seven petite (*V*₁, *Et*₄, *Et*₅, *Esb*, *Db*, *esb*, *db*): 16 on manus, four ventral (*V*₁–*V*₄), 10 external (*Et*₁–*Et*₅, *Est*, *Esb*, *Eb*₁–*Eb*₃), two dorsal (*Db*, *Dt*); 10 on fixed finger, four external (*et*, *est*, *esb*, *eb*), four dorsal (*dt*, *dst*, *dsb*, *db*), two internal (*it*, *ib*).

Legs: All segments smooth, setose, especially telotarsi. Basitarsi I–IV without prolateral pedal spurs; I and II, proventral surface with short subdistal row of closely aligned spinules. Telotarsi, dorsomedian lobe with one microseta; ventral surface with curved row of spinules, proximally, and four or five submedian pairs of subspiniform macrosetae; unguis well developed, curved, equal in length; dactyl long, prominent.

Tergites: Surfaces I–VI, smooth, acarinate; VII, mostly smooth, posterolateral surfaces granular, dorsosubmedian carinae vestigial, reduced to few posterior granules, dorsolateral carinae absent (fig. 23A). Lateral and posterior margins setose.

Sternum: Posterior width slightly greater than length (fig. 8C); apex rounded; lateral margins converging anteriorly; lateral lobes flat; posterior depression moderate. Surfaces with few macrosetae.

Genital operculum: Sclerites mostly fused, but loosely connected by membrane along entire length of suture, posterior edges free (fig. 8C); suboval, each with pair of macrosetae and several microsetae on margin.

Pectines: Pectinal plate, surface with pair of macrosetae. Lamella comprising three segments (fig. 8C); surfaces with several macrosetae and microsetae. Tooth count, 5/5; teeth equal to subequal, except for distal tooth, larger, pointed.

Sternites: Surfaces smooth, acarinate (fig. 23B); surfaces and margins with several microsetae. Respiratory spiracles (stigmata) small, round, situated posterolaterally.

Metasoma: Segments elongated, progressively increasing in length, decreasing in width (fig. 12C), I and II width greater than length, III–V length greater than width (table 8). Dorsosubmedian carinae, segments I–IV, obsolete, granular, distal granules not noticeably larger than preceding granules (fig. 12C). Dorsolateral carinae, segment V, obsolete, granular. Dorsolateral, median lateral, and ventrosubmedian carinae, segments I–IV, ventrolateral carinae, segments I–V, and ventromedian carina, segment V, absent. Dorsal intercarinal surfaces, segments I–V, slightly concave, uniformly finely granular; other surfaces smooth. All segments setose.

Telson: Vesicle broad, elongated, flattened dorsally, rounded ventrally; anterodorsal lateral lobes absent (fig. 12C); surface smooth, setae distributed uniformly across ventral surface. Aculeus short, slightly curved, arising gradually from vesicle.

Hemispermatorphore: Male unknown.

Ontogenetic variation: It is unclear whether the holotype female is adult.

Sexual dimorphism: Male unknown.

Geographical variation: Single specimen.

REMARKS: Francke (1986: 5, 6) described the holotype as a male and stated that the genital opercula were “without membranous connection,” but noted that genital papillae “could not be detected.” We confirmed the absence of genital papillae but observed that the genital opercula are mostly fused, being loosely connected by a membrane along the entire length of the suture, although the posterior edges are free. These observations, together with the shape of the pectinal teeth, lead us to conclude that the holotype is female. Males of all other typhlochactid species display genital papillae and divided genital opercula.

DISTRIBUTION: Known only from the type locality, Cueva del Vandalismo, in the Sistema Purificación karstic region, northwest of Ciudad Victoria, Tamaulipas (central-eastern Mexico) (fig. 1B).

ECOLOGY: No additional data are available for the cave from which this troglobitic species was collected.

Typhlochactas mitchelli Sissom, 1988
(Figs. 1B, 4, 5E, 8B, 9I, 9J, 12D, 26–28)

Typhlochactas mitchelli Sissom, 1988: 365–371, figs. 1–14, table 1.

Typhlochactas mitchelli: Kovařík, 1998: 142; Sissom and Cokendolpher, 1998: 285, 287 (table 1); Beutelspacher Baigts, 2000: 20, 52, 54, 151, map 22; Sissom, 2000b: 499; Volschenk et al., 2001: 161; Soleglad and Sissom, 2001: 40, fig. 39; Soleglad and Fet, 2001: 31; 2003a: fig. 11; 2003b: 28, 30, 32, 76; Volschenk and Prendini, 2008: 236 (table 1), 249, 250; Botero-Trujillo and Francke, 2009: 2.

Typhlochactas mitchelli: Beutelspacher Baigts, 2000: 143.

TYPE MATERIAL: **Mexico**: *Oaxaca*: Municipio de San José Tenango: Holotype: 1 ♂ (AMNH), Cerro Ocote [18°08'57.5"N 96°43'59.1"W], 5 mi. S San José de Tenango, A. Grubbs, A. Cressler and P. Smith, IV.1987. Paratypes: 1 ♂, 1 subad. ♀ (AMNH), same data.

DIAGNOSIS: *Typhlochactas mitchelli* is most closely related to *T. sylvestris* (fig. 4). It may be separated from *T. sylvestris* and all other *Typhlochactas* species by the following combination of characters. Cheliceral fixed finger with three teeth (subdistal absent); median and basal teeth not fused into bicusps.

Cheliceral movable finger with three dorsal teeth (subdistal teeth absent). Carapace, anterior margin with well-developed median projection (epistome). Pedipalp chela fixed and movable fingers, median denticle row comprising four or five and five or six oblique primary subrows, respectively; basal primary subrow of movable finger similar in length to other subrows; terminal denticle of fixed finger slightly larger than preceding denticles, fingertips interlocking evenly when closed. Legs with prolateral pedal spurs. Telotarsi with ventromedian row of spinules. Sclerites of genital operculum (♀) fused, but loosely connected by membrane along entire length of suture.

DESCRIPTION: The following description supplements the original description by Sissom (1988).

Color: Holotype and paratype ♂, pedipalp femur, patella, and mesosoma, Yellow Ocher (123C); pedipalp chela and telson, Robin Rufous (340); metasoma, Brick Red (132A). Subadult ♀ paratype, uniformly Buff (124).

Chelicerae: Manus, dorsal and ventral surfaces smooth; dorsal surface with three microsetae near base of fixed finger; movable finger with single microseta. Fixed finger, dorsal margin with three teeth (distal, median and basal; fig. 5E); median and basal teeth equal, not fused into bicuspid, considerably smaller than distal tooth. Movable finger, internal distal and external distal teeth not opposable, internal distal tooth at most partially overlapping external distal tooth in dorsal view; dorsal margin with three teeth (internal distal, median, and basal), internal distal tooth largest, median smallest; ventral surface with serrula extending two-thirds of finger, covered in part by dense brush of macrosetae.

Carapace: Length greater than anterior width (table 9). Anterior margin sublinear, with small median projection (epistome); asetose (fig. 26A). Posterior margin weakly concave medially; asetose. Median and lateral ocelli absent. Median longitudinal, posterolateral, and posterior transverse sulci shallow. Surface smooth to finely granular, acarinate, with scattered microsetae.

Pedipalps: Femur, ventroexternal carina obsolete, granular, dorsoexternal carina vestigial, restricted to proximal third; other

carinae absent; intercarinal surfaces moderately granular (fig. 28A). Patella acarinate; intercarinal surfaces moderately granular (fig. 28B–D). Chela stout, with broad, rounded manus (fig. 27); fingers short, slightly longer than manus (table 9). Manus acarinate; dorsointernal and, to a lesser extent, dorsoexternal surfaces, markedly granular distally; fixed and movable fingers, proximal surfaces, markedly granular, without denticle rows. Fixed finger, median denticle row comprising four or five oblique primary subrows, restricted to distal two-thirds of finger (fig. 9I); internal denticles larger than external denticles; terminal denticle small, slightly larger than preceding denticles, fingertips interlocking evenly when closed. Movable finger, median denticle row comprising five or six oblique primary subrows, restricted to distal two-thirds of finger (Fig. 9J); basal primary subrow short, similar in length to distal subrow; terminal denticle small.

Trichobothria: Femur with three trichobothria (fig. 28A): one external (*e*), one dorsal (*d*), one internal (*i*). Patella with 19 trichobothria (fig. 28B–D), five petite (*d*₁, *d*₂, *et*₂, *esb*₂, *eb*₂), one accessory (*em*₃): two ventral (*v*₁, *v*₂); 14 external (*et*₁–*et*₃, *est*, *em*₁–*em*₃, *esb*₁, *esb*₂, *eb*₁–*eb*₅); two dorsal (*d*₁, *d*₂); one internal (*i*). Chela with 26 trichobothria (fig. 27), seven petite (*V*₁, *Et*₄, *Et*₅, *Esb*, *Db*, *esb*, *db*): 16 on manus, four ventral (*V*₁–*V*₄), 10 external (*Et*₁–*Et*₅, *Est*, *Esb*, *Eb*₁–*Eb*₃), two dorsal (*Db*, *Dt*); 10 on fixed finger, four external (*et*, *est*, *esb*, *eb*), four dorsal (*dt*, *dst*, *dsb*, *db*), two internal (*it*, *ib*).

Legs: All segments setose; basitarsi, ventral surface with three or four pairs of macrosetae. Basitarsi I–IV with prolateral pedal spurs; I and II, proventral surface with short subdistal row of closely aligned spinules. Telotarsi, dorsomedian lobe with one microseta; ventral surface with curved row of spinules, proximally, and straight ventromedian row of spinules, flanked by three or four submedian pairs of subspiniform macrosetae; unguis moderately developed, equal in length; dactyl short, robust.

Tergites: Surfaces acarinate; I–V, smooth, VI and VII sparsely, coarsely granular (fig. 26A). Surfaces and margins with sparse microsetae.

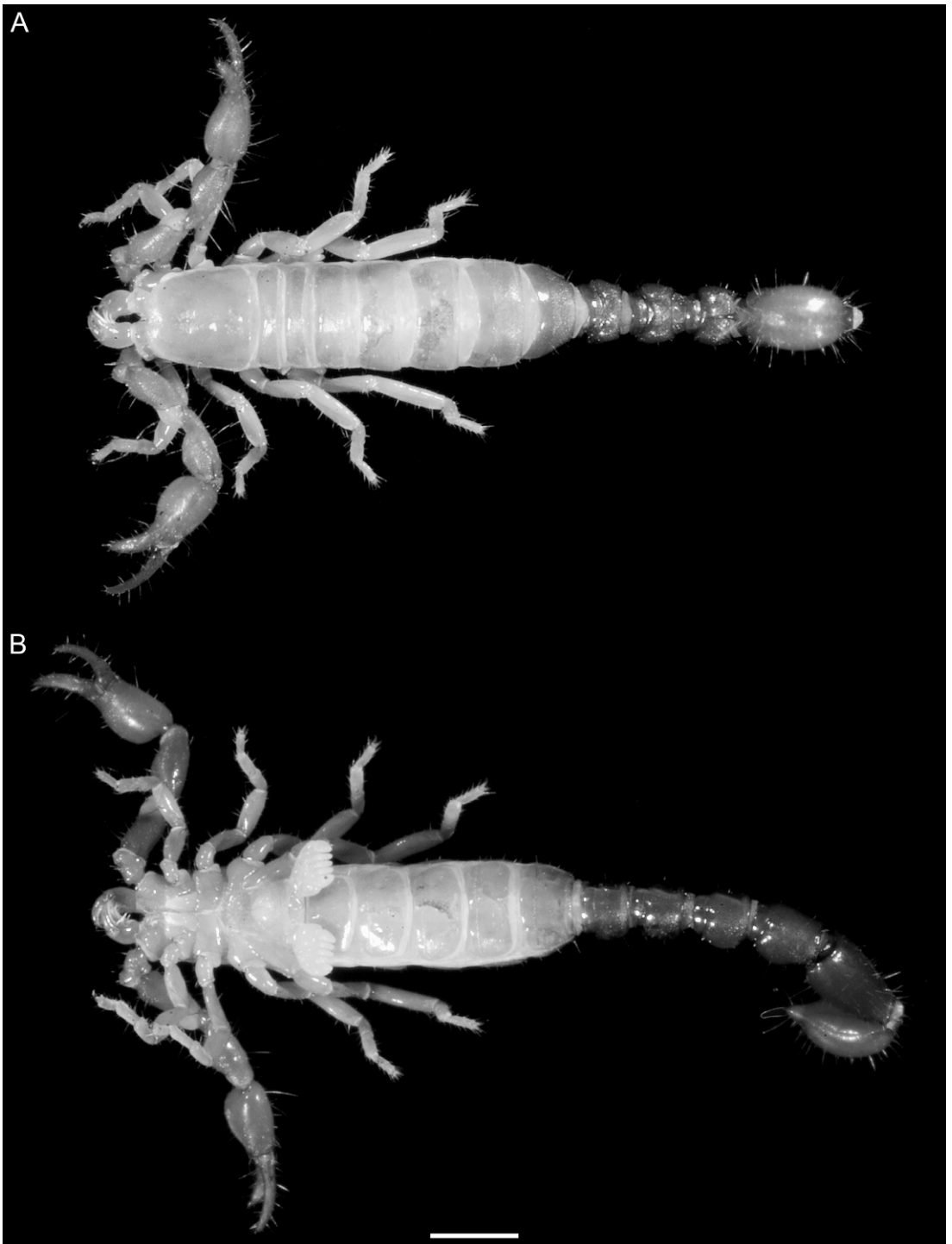


Fig. 26. *Typhlochactas mitchelli* Sissom, 1988, holotype ♂ (AMNH), habitus. A. Dorsal aspect. B. Ventral aspect. Scale = 1 mm.

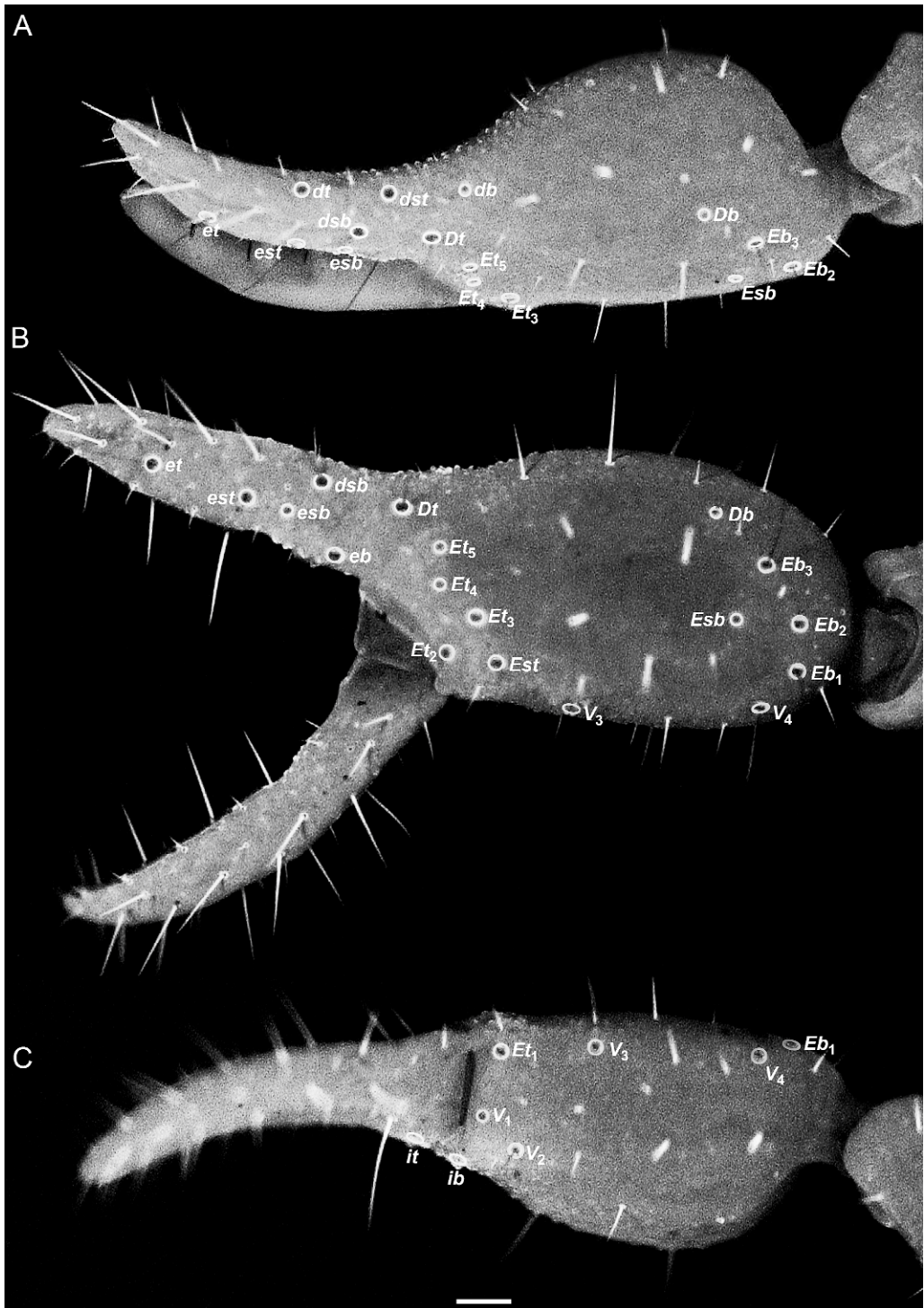


Fig. 27. *Typhlochactas mitchelli* Sissom, 1988, holotype ♂ (AMNH), sinistral pedipalp chela showing carinae and distribution of trichobothria. **A.** Dorsal aspect. **B.** External aspect. **C.** Ventral aspect. Scale = 0.1 mm.

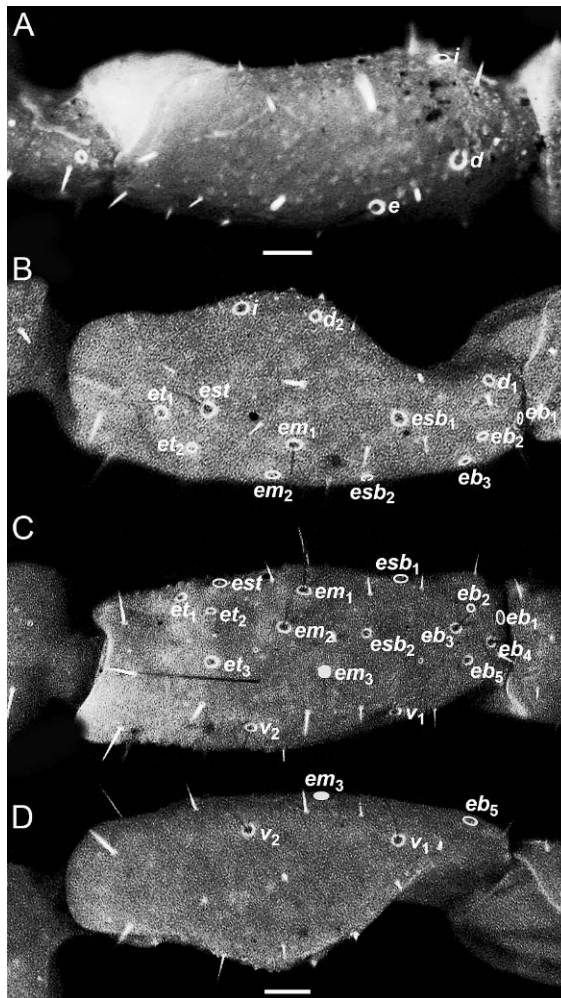


Fig. 28. *Typhlochactas mitchelli* Sissom, 1988, holotype ♂ (AMNH), sinistral pedipalp femur (A) and patella (B–D) showing carinae and distribution of trichobothria. A, B. Dorsal aspect. C. External aspect. D. Ventral aspect. Scales = 0.1 mm.

Sternum: Posterior width greater than length (fig. 8B); apex slightly rounded; lateral margins subparallel; lateral lobes flat; posterior depression very shallow. Surface with approximately 10 microsetae.

Genital operculum: Sclerites (♂) suboval, completely divided; genital papillae large, protruding distinctly beyond posterior edges (fig. 8B). Sclerites (♀) fused, but loosely connected by membrane along entire length of suture. Surfaces with few microsetae.

Pectines: Pectinal plate, surface with several microsetae. Lamella comprising five segments (fig. 8B); surfaces covered with

microsetae. Tooth count, 5/5; teeth similar in shape and size, except for distal tooth, slightly enlarged, lobate.

Sternites: Surfaces acarinate, smooth, sparsely setose (fig. 26B). Respiratory spiracles (stigmata) small, round, situated posterolaterally.

Metasoma: Metasoma stout, segments I–III width greater than length, IV and V length greater than width (fig. 12D), progressively increasing in length, decreasing in width (table 9); segment V longer than carapace. Dorsosubmedian carinae, segments I–IV, obsolete, distal granules not noticeably

TABLE 9

Meristic data for *Typhlochactas mitchelli* Sissom, 1988, and *Typhlochactas sylvestris* Mitchell and Peck, 1977
 Measurements (mm) follow Francke et al. (2009). Abbreviations as follows: AMNH = American Museum of Natural History, New York

Specimen	<i>Typhlochactas mitchelli</i>			<i>Typhlochactas sylvestris</i>
	Holotype	Paratype	Paratype subad. ♀	Holotype ♀
type				
sex	♂	♂	subad. ♀	♀
collection	AMNH	AMNH	AMNH	AMNH
Carapace				
anterior width	0.8	0.8	0.5	0.8
posterior width	1.1	1.0	0.8	1.1
length	1.0	0.9	0.8	1.0
Chela				
maximum width	0.5	0.5	0.3	0.5
maximum height	0.5	0.5	0.4	0.6
length ¹	1.6	1.6	1.3	1.8
length ventroexternal carina	0.7	0.6	0.4	0.8
length of movable finger	0.8	0.9	0.7	0.9
Patella				
maximum width	0.4	0.4	0.3	0.4
maximum height	0.4	0.4	0.3	0.4
length	0.9	0.9	0.7	1.0
<i>e</i> trichobothria (left/right)	14/14	14/14	14/14	14/15
Femur				
maximum width	0.3	0.3	0.3	0.3
maximum height	0.3	0.3	0.3	0.4
length	0.8	0.8	0.7	0.8
Pedipalp				
total length (incl. trochanter)	3.7	3.7	3.0	3.9
Mesosoma				
total length (tergites)	2.8	2.6	2.7	2.8
Sternite VII				
width	0.9	0.9	0.9	1.0
length	0.5	0.5	0.5	0.6
Metasoma I				
maximum width	0.6	0.6	0.5	0.6
maximum height	0.5	0.5	0.5	0.5
length	0.5	0.5	0.4	0.4
Metasoma II				
maximum width	0.7	0.6	0.5	0.6
maximum height	0.5	0.5	0.5	0.5
length	0.5	0.5	0.4	0.4
Metasoma III				
maximum width	0.7	0.6	0.6	0.6
maximum height	0.5	0.5	0.5	0.5
length	0.6	0.5	0.5	0.5
Metasoma IV				
maximum width	0.7	0.6	0.6	0.6
maximum height	0.5	0.5	0.5	0.5
length	0.8	0.7	0.6	0.6
Metasoma V				
maximum width	0.7	0.6	0.6	0.6
maximum height	0.5	0.5	0.5	0.5
length	1.4	1.3	1.3	1.1
Telson				
maximum width	0.7	0.6	0.6	0.7

TABLE 9
(Continued)

Specimen type	<i>Typhlochactas mitchelli</i>			<i>Typhlochactas sylvestris</i>
	Holotype	Paratype	Paratype subad. ♀	Holotype
sex	♂	♂		♀
collection	AMNH	AMNH	AMNH	AMNH
maximum height	0.6	0.6	0.5	0.5
aculeus length	0.3	0.2	0.4	0.3
total length	1.5	1.4	1.4	1.4
Metasoma				
total length ²	5.4	5.0	4.6	4.7
Total length				
pro-+meso-+metasoma	9.2	8.6	8.1	8.6
Pectines				
total length	0.5	0.6	0.4	0.4
length along dentate margin	0.5	0.5	0.4	0.3
tooth count (left/right)	5/5	5/5	5/5	5/5

¹Measured from base of condyle to tip of fixed finger.

²Sum of metasomal segments I–V and telson.

larger than preceding granules (fig. 12D). Dorsolateral carinae, segment V, obsolete. Dorsolateral, median lateral and ventrosulmedian carinae, segments I–IV, ventrolateral carinae, segments I–V, and ventromedian carina, segment V, absent. Dorsal intercarinal surfaces, segments I–V, slightly concave. Segments I–IV, dorsolateral surfaces coarsely granular, other intercarinal surfaces smooth; segment V entirely granular except posteroverentrally. Surfaces of all segments with short microsetae; V additionally with several longer macrosetae.

Telson: Vesicle globose, wider than segments II–V (table 9), flattened to slightly concave dorsally, rounded ventrally; anterodorsal lateral lobes absent (fig. 12D); lateral and ventral surfaces granular, with several long and short setae posteriorly. Aculeus short, moderately curved, arising abruptly from vesicle.

Hemispermatothore: Unknown (neither adult male specimens dissected).

Ontogenetic variation: Paler, cream coloration and less elongated, more rounded telson of subadult female attributed to ontogenetic rather than sexual variation. Subadult female retains vestigial subrows of denticles extending to near base of

chela fixed and movable fingers (i.e., five subrows on fixed finger, six on movable finger) and there are no internal denticles on fourth row of fixed finger or fifth row of movable finger. These observations suggest a reduction in number of subrows in the adult occurs at the final instar (Sissom, 1988) or else that it is a sexually dimorphic character.

Sexual dimorphism: Males exhibit more pronounced granulation, completely divided genital operculum and genital papillae.

Geographical variation: All specimens from same locality.

REMARKS: *Typhlochactas mitchelli* and *T. sylvestris* are the smallest species of the family and among the smallest known scorpions. Adults measure less than 10 mm in total length (table 9).

DISTRIBUTION: Known only from the type locality, Cerro Ocote, near San José de Tenango, Oaxaca, Mexico (fig. 1B). This locality is part of the same mountain range (Sistema Montañoso Poblano Oaxaqueño) in which *T. sylvestris* was collected.

ECOLOGY: This endogean (humicolous) species was hand-collected from the surfaces of small stones 1 to 2 feet below the surface, in crevices and alongside rock faces excavat-

ed from beneath leaf litter, wood debris, roots, small stones and slight amounts of soil, in a montane forest (A.G. Grubbs, personal commun.). This habitat is very similar to that of *Belisarius xambeui*, an endogean scorpion from the Pyrenees of France and Spain, often found under stones deeply embedded in forest litter (Auber, 1959).

Typhlochactas reddelli Mitchell, 1968
(Figs. 1B, 2A, 2B, 4, 5F, 9K, 9L, 12E, 29–31; table 8)

Typhlochactas reddelli Mitchell, 1968: 753, 762–772, 774–776, figs. 22–41, table 1.

Typhlochactas reddelli: Reddell, 1971a: 26; 1971b: 217; Mitchell, 1971: 135, 138, 143, 145, 146, figs. 21–23, 25, 27; Reddell, 1973: 32, 37; Vachon, 1974: figs. 167, 199–210; Soleglad, 1976: 254; Mitchell and Peck, 1977: 159, 162, 164, 167, 168; Reddell, 1981: 45, 115, fig. 17; Francke, 1982a: 59, 60, figs. 26, 30, 35; Lourenço and Francke, 1985: 3, 5 (table 1); Francke, 1986: 5, 7, 8, figs. 20–22; Sissom, 1988: 365; Armas, 1994: 18, 21; Lourenço, 1994: 182, 183; Sissom and Cokendolpher, 1998: 285–287 (table 1); Sissom, 2000b: 499; Soleglad and Fet, 2003b: 30, 76; Lourenço et al., 2004: 1152, 1153; Prendini and Wheeler, 2005: figs. 18–23; Lourenço and Goodman, 2008: 667; Volschenk and Prendini, 2008: 236 (table 1), 249.

Typhlochactas reddelli: González-Sponga, 1974: 56.

Typhlochactas reddelli: Díaz Najera, 1975: 4, 33.

Typhlochactas reddelli: Lourenço, 1981: 660; Kovařík, 1998: 142; Beutelspacher Baigts, 2000: 18, 20, 52, 54, 147, 151, map 22.

TYPE MATERIAL: **Mexico:** *Veracruz:* Municipio de Tlilapan: Holotype: 1 ♀ (AMNH), 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 and T.R. Evans, 4.VIII.1967.

DIAGNOSIS: *Typhlochactas reddelli* is most closely related to the monophyletic group comprising *T. mitchelli* and *T. sylvestris* (fig. 4). It may be separated from these and other *Typhlochactas* species by means of the following combination of characters. Cheliceral fixed finger with four teeth (subdistal present); median and basal teeth fused into a bicusp. Cheliceral movable finger with five dorsal teeth (two subdistals present). Carapace, anterior margin with well-developed median projection (epistome). Pedipalp chela fixed and movable fingers, median denticle row comprising six

and seven primary subrows, respectively; basal primary subrow of movable finger similar in length to other subrows; terminal denticle of fixed finger considerably larger than preceding denticles, hooklike, fingertips interlocking unevenly when closed. Legs with prolateral pedal spurs. Telotarsi without ventromedian row of spinules. Sclerites of genital operculum (♀) fused, but loosely connected by membrane along entire length of suture.

DESCRIPTION: The following description of the holotype (fig. 29) supplements the original description by Mitchell (1968) and additional data provided by Mitchell (1971) and Francke (1982a, 1986).

Color: Carapace, pedipalp femur and patella, legs, tergites, sternites, metasoma, and telson, Yellow Ocher (123C); pedipalp chela, Pratt's Rufous (140). Aculeus and denticle rows of pedipalp fingers darker.

Chelicerae: Manus, dorsal and ventral surfaces smooth; dorsal surface with two microsetae situated near base of fixed finger; movable finger, dorsal surface with two microsetae. Fixed finger, dorsal margin with four teeth (distal, subdistal, median, and basal; fig. 5F); distal tooth largest, median and basal teeth equal, fused into bicusp. Movable finger, internal distal and external distal teeth opposable, internal distal tooth completely overlapping external distal tooth in dorsal view; dorsal margin with five closely aligned teeth (internal distal, two subdistal, median, and basal) situated on slightly convex ridge, internal distal tooth largest, median tooth slightly larger than subdistal and basal teeth (all similar in dimensions); ventral surface with serrula covering almost entire length of finger, comprising long tines, all equal in length, partially covered by dense brush of macrosetae.

Carapace: Length greater than anterior width (table 8). Anterior margin weakly concave, with small median projection (epistome) and few microsetae (fig. 29A). Posterior margin weakly convex; asetose. Median and lateral ocelli absent. Median longitudinal, posterolateral and posterior transverse sulci shallow. Surface acarinate, smooth, with few microsetae.

Pedipalps: Femur, ventroexternal carina obsolete, granular; other carinae absent



Fig. 29. *Typhlochactas reddelli* Mitchell, 1968, holotype ♀ (AMNH), habitus. **A.** Dorsal aspect. **B.** Ventral aspect. Scale = 1 mm.

(fig. 31A). Intercarinal surfaces mostly smooth, with few small granules proximally, and covered with microsetae. Patella longer than femur (table 8); acarinate, with three granules on ventrointernal margin (fig. 31B–

D). Intercarinal surfaces covered with microsetae. Chela stout, fingers relatively short, slightly longer than manus (table 8). Manus acarinate (fig. 30); surfaces mostly smooth; dorsal and ventral surfaces with few granules

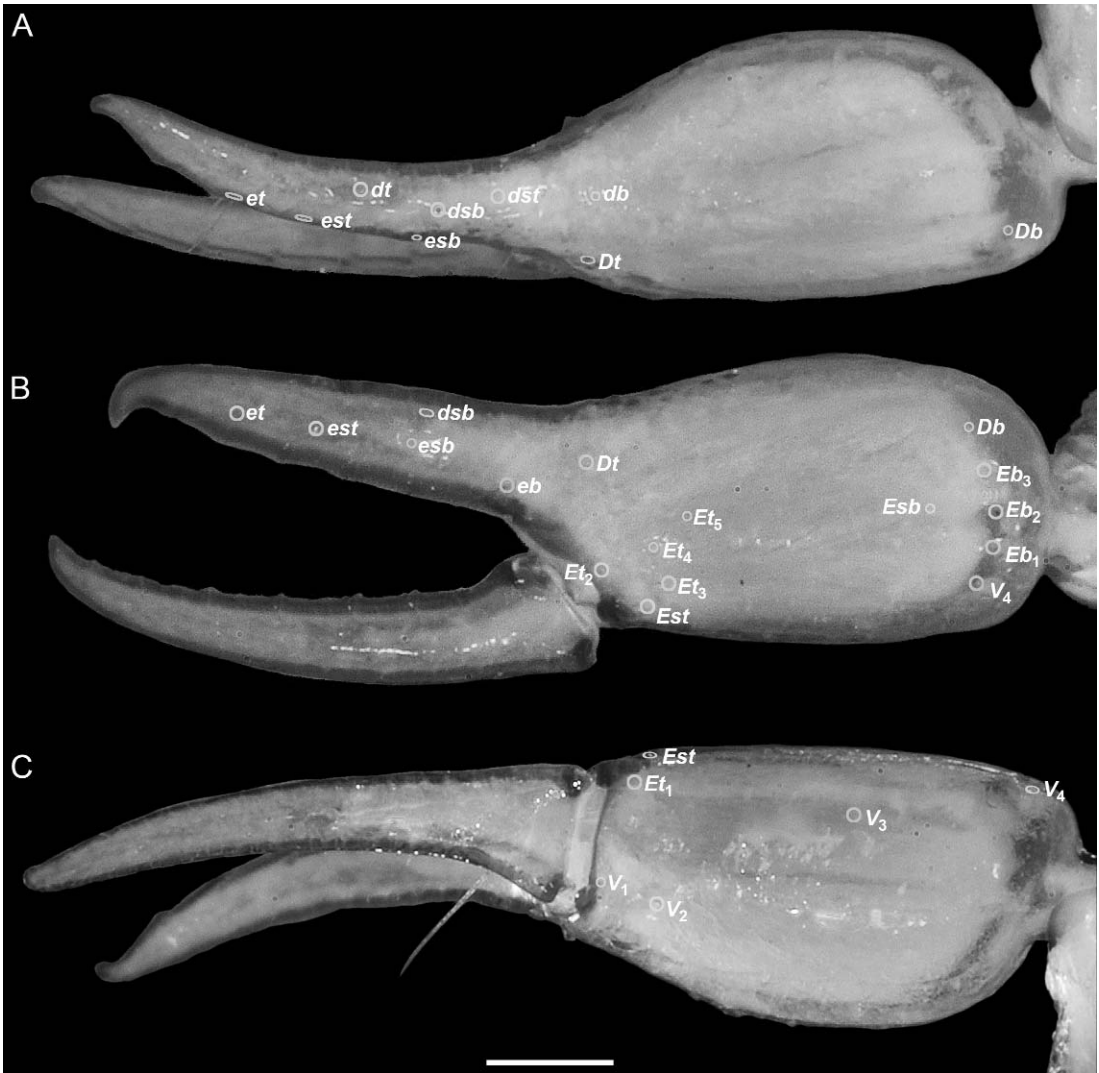


Fig. 30. *Typhlochactas reddelli* Mitchell, 1968, holotype ♀ (AMNH), sinistral pedipalp chela showing carinae and distribution of trichobothria. **A.** Dorsal aspect. **B.** External aspect. **C.** Ventral aspect. Scale = 0.5 mm.

distally; internal surface with pair of prominent, isolated granules situated close together at base of fixed finger; fingers, internal and external surfaces setose. Fixed finger, median denticle row comprising six oblique primary subrows, terminal subrow shorter, third subrow longer than other subrows (fig. 9K); internal denticles larger than external denticles; terminal denticle considerably larger than preceding denticles, hooklike, fingertips interlocking unevenly when closed. Movable

finger, median denticle row comprising seven oblique primary subrows, terminal subrow shorter, basal subrow slightly longer than other subrows (fig. 9L); terminal denticle smaller than on fixed finger.

Trichobothria: Femur with three trichobothria (fig. 31A): one external (*e*), one dorsal (*d*), one internal (*i*). Patella with 19 trichobothria (fig. 31B–D), five petite (*d*₁, *d*₂, *et*₂, *esb*₂, *eb*₂), one accessory (*em*₃): two ventral (*v*₁, *v*₂); 14 external (*et*₁–*et*₃, *est*, *em*₁–*em*₃, *esb*₁, *esb*₂,

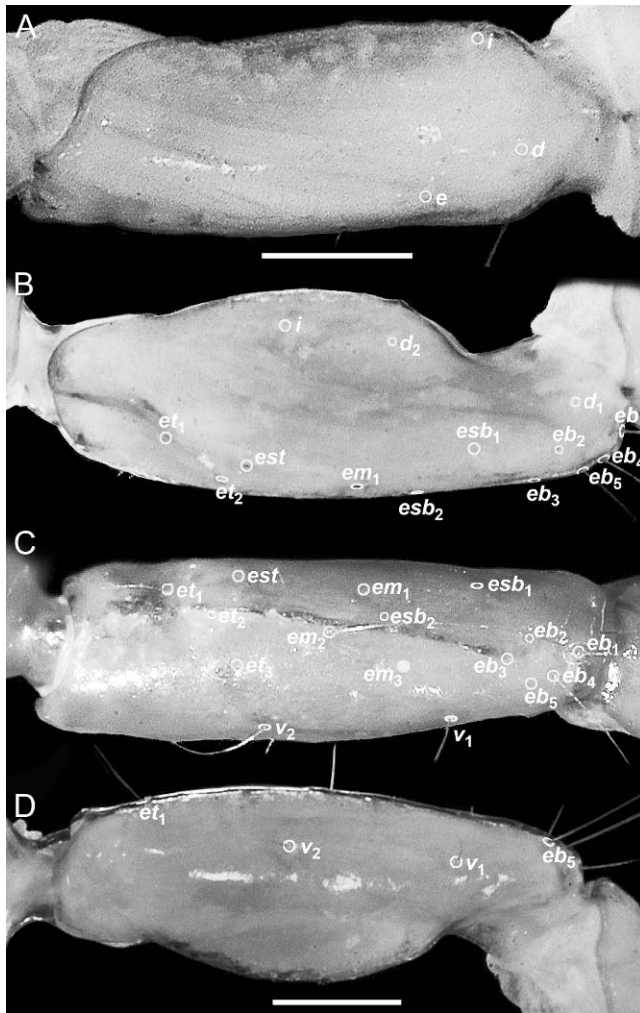


Fig. 31. *Typhlochactas reddelli* Mitchell, 1968, holotype ♀ (AMNH), sinistral pedipalp femur (A) and patella (B–D) showing carinae and distribution of trichobothria. A, B. Dorsal aspect. C. External aspect. D. Ventral aspect. Scales = 0.5 mm.

eb_1 – eb_5); two dorsal (d_1 , d_2); one internal (i). Chela with 26 trichobothria (fig. 30), seven petite (V_1 , Et_4 , Et_5 , Esb , Db , esb , db): 16 on manus, four ventral (V_1 – V_4), 10 external (Et_1 – Et_5 , Est , Esb , Eb_1 – Eb_3), two dorsal (Db , Dt); 10 on fixed finger, four external (et , est , esb , eb), four dorsal (dt , dst , dsb , db), two internal (it , ib).

Legs: All segments smooth, setose, especially femora and telotarsi. Basitarsi I and II, proventral surface with short subdistal row of closely aligned spinules; I–IV with prolateral pedal spurs. Telotarsi, dorsomedian lobe

with one microseta; ventral surface without spinules, and with four or five ventrosubmedian pairs of subspiniiform macrosetae; ungues long, well developed, curved, equal in length; dactyl short, slightly curved.

Tergites: Surfaces I–VI, smooth, acarinate; VII, mostly smooth, granular posterolaterally, dorsosubmedian carinae vestigial, reduced to few posterior granules, dorsolateral carinae absent (fig. 29A). Lateral and posterior margins with microsetae.

Sternum: Posterior width greater than length; apex rounded; lateral margins sub-

parallel; lateral lobes flat; posterior depression shallow. Surface sparsely covered with microsetae.

Genital operculum: Sclerites (♂) completely divided; genital papillae protruding distinctly beyond posterior edges of opercula. Sclerites (♀) fused, but loosely connected by membrane along entire length of suture.

Pectines: Pectinal plate, surface with two macrosetae situated mediolaterally. Lamella comprising three segments, demarcated by faint sutures; surfaces covered with microsetae. Tooth count, 5/5; teeth oval; proximal and distal teeth slightly larger.

Sternites: Surfaces acarinate, smooth (fig. 29B). Surfaces and margins with few, scattered setae. Respiratory spiracles (stigmata) small, round, situated posterolaterally.

Metasoma: Segments elongated, progressively increasing in length, decreasing in width (table 8), I and II width greater than length, III width equal to length, IV and V length greater than width. Dorsosubmedian carinae, segments I–IV, obsolete, composed of few stout granules, distal granules not noticeably larger than preceding granules. Dorsolateral carinae, segment V, obsolete, complete. Ventrolateral carinae, segment V, obsolete, complete, comprising spiniform granules increasing in size posteriorly. Dorsolateral, median lateral, ventrolateral, and ventrosubmedian carinae, segments I–IV, and ventromedian carina, segment V, absent. Dorsal intercarinal surfaces, segments I–V, slightly concave, smooth. All segments setose, especially on ventral and lateral surfaces. Anal arch with macro- and microsetae and few granules ventrolaterally.

Telson: Vesicle globose, shorter than metasomal segment V (table 8), flattened dorsally, rounded ventrally; anterodorsal lateral lobes absent; surfaces mostly smooth, with scattered granules near base of aculeus; ventral surface with scattered long and short macrosetae, increasing in number posteriorly. Aculeus short, weakly curved, arising gradually from vesicle (fig. 12E).

Hemispermaphore: Adult male unknown.

Ontogenetic variation: Juveniles paler in coloration.

Sexual dimorphism: Adult male unknown. Juvenile male exhibits completely divided genital operculum and genital papillae.

Geographical variation: All specimens from same locality.

REMARKS: The holotype is severely damaged (fig. 29): the mesosoma is broken, the metasoma broken in two places, and dextral leg II is disarticulated.

DISTRIBUTION: Known only from the type locality, La Cueva del Ojo de Agua de Tlilapan, in the karstic region of Orizaba, Veracruz (eastern Mexico) (figs. 1B, 2A, 2B).

ECOLOGY: The cave in which this troglotic species was collected, comprises two large horizontal rooms and a wide entrance (Mitchell, 1968; Reddell, 1981). According to the original description (Mitchell, 1968), the holotype was collected in the first bat room, approximately 30 m from the cave entrance immediately after a low, narrow passage separating it from the entrance room. The specimen was found beneath a stone on guano, although not near the main guano deposits. Subsequently collected specimens were also taken from under stones.

ADDITIONAL MATERIAL: **Mexico**: *Veracruz*: Municipio de Tlilapan: 1 juv. ♀ (IBUNAM), Cueva Ojo de Agua, Tlilapan, R. Sanchez, 8.II.1990; 1 juv. ♂ (IBUNAM), same locality, I. Vazquez, 30.III.1990, under rock; 1 juv. ♀ (IBUNAM), same locality, I. Vazquez, 30.III.1990, under rock, dark zone.

Typhlochactas rhodesi Mitchell, 1968
(Figs. 1B, 3A, 3B, 4, 5G, 7C, 9M, 9N, 12F, 32–34; table 8)

Typhlochactas rhodesi Mitchell, 1968: 753, 756–762, 771, 772, 774–777, figs. 1–21, 41, table 1, pl.

Typhlochactas rhodesi: Mitchell, 1971: 135, 138, 143, 145, 146, figs. 18–20, 24, 27; Delamare Deboutteville, 1971: 49; Reddell, 1971: 3, 27; Reddell and Mitchell, 1971: 181, 184, fig. 9; Reddell, 1973, 32, 37; Reddell and Elliott, 1973: 181; González-Sponga, 1974: 56; Soleglad, 1976: 253; Mitchell and Peck, 1977: 159, 164, 165, 167, 168; Lourenço, 1981: 660; Reddell, 1981: 37, 115, fig. 17; Francke, 1982a: 59, 60, figs. 26, 29, 34; Lourenço and Francke, 1985: 3, 5 (table 1); Francke, 1986: 5–8, figs. 14–16; Sissom, 1988: 365; Armas, 1994: 18, 21; Lourenço, 1994: 182, 183; Kovařík, 1998: 142; Sissom and Cokendolpher, 1998: 285–287 (table 1); Beutelspacher Baigts, 2000: 18, 20, 51, 52, 54, 147, 151, map 22; Sissom, 2000b: 499; Volschenk et al., 2001: 161; Soleglad and Fet, 2003b: 30, 76; Vignoli and Kovařík, 2003: 131; Lourenço et al., 2004:



Fig. 32. *Typhlochactas rhodesi* Mitchell, 1968, holotype ♀ (AMNH), habitus. **A.** Dorsal aspect. **B.** Ventral aspect. Scale = 1 mm.

1152, 1153; Sissom and Hendrixson, 2005: 123, 127, table 6.2; Lourenço and Goodman, 2008: 667; Volschenk and Prendini, 2008: 236 (table 1), 249.

Typhlochactas rhodesi: Díaz Najera, 1975: 4, 32.

TYPE MATERIAL: **Mexico:** *Tamaulipas:* Municipio de Gómez Farias: Holotype: 1 ♀ (AMNH), La Cueva de la Mina, Sierra de Guatemala [23°06'06"N 99°12'56"W], 1600 m, R.W. and R. Mitchell, K. Pittard, D. Falls, and V. Colvin, 24.III.1967. Paratypes: 1 subad. ♀ (AMNH), same locality, R.W. Mitchell, F. Abernethy and W. Rhodes, 29–30.VIII.1966; 1 ♀ (MNHN RS 4760), same locality, R.W. Mitchell, F. Abernethy and W. Rhodes, 29.VIII.1967.

DIAGNOSIS: *Typhlochactas rhodesi* is most closely related to *T. cavicola* (fig. 4). It may be separated from *T. cavicola* and all other *Typhlochactas* species by the following combination of characters. Cheliceral fixed finger with four teeth (subdistal present); median and basal teeth not fused into bicusp. Cheliceral movable finger with five dorsal teeth (two subdistals present). Carapace, anterior margin with well-developed median projection (epistome). Pedipalp chela fixed and movable fingers, median denticle row of each comprising six oblique primary subrows; basal primary subrow of movable finger considerably longer than other subrows; terminal denticle of fixed finger slightly

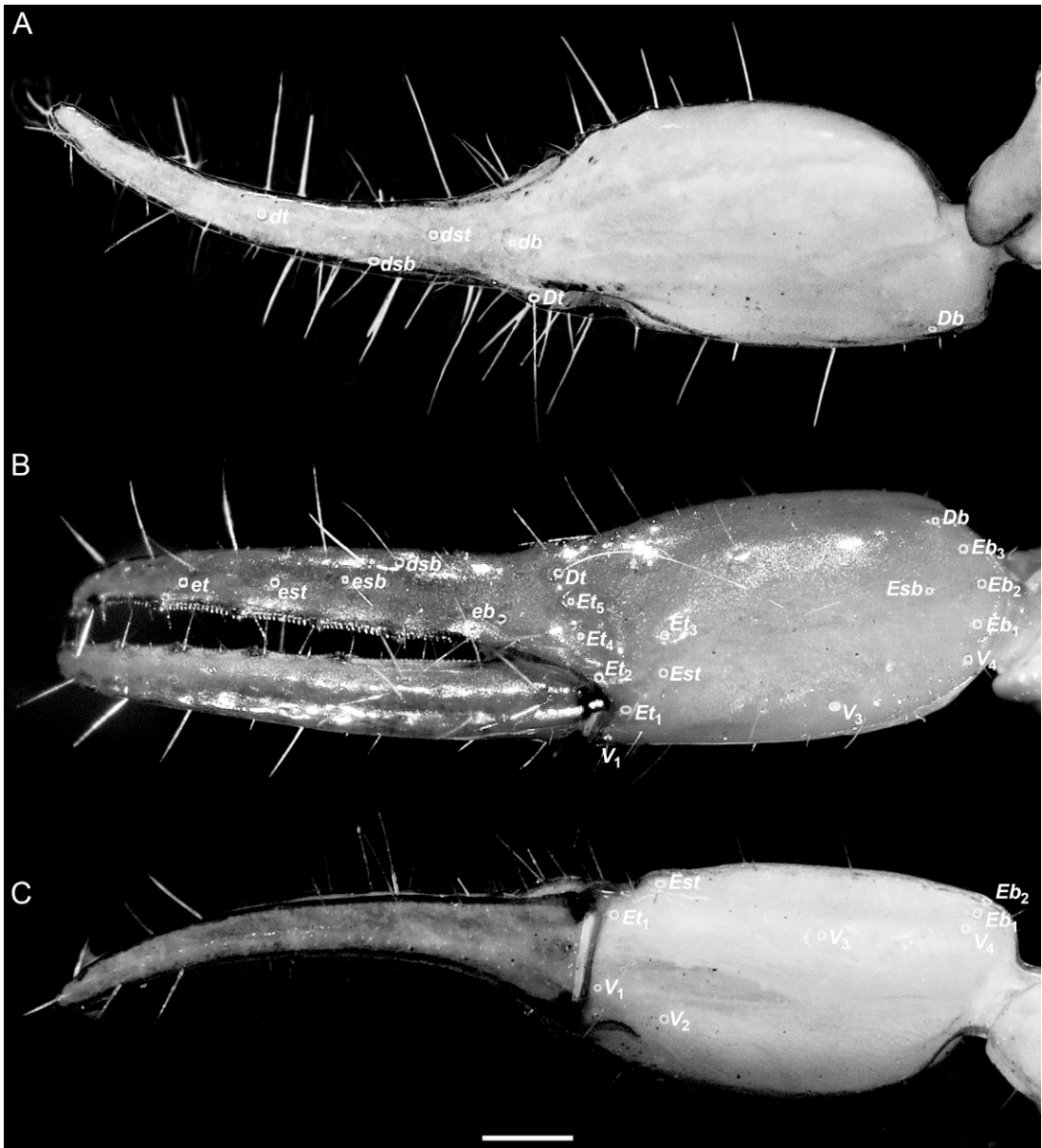


Fig. 33. *Typhlochactas rhodesi* Mitchell, 1968, holotype ♀ (AMNH), sinistral pedipalp chela showing carinae and distribution of trichobothria. A. Dorsal aspect. B. External aspect. C. Ventral aspect. Scale = 0.5 mm.

larger than preceding denticles, fingertips interlocking evenly when closed. Legs without prolateral pedal spurs. Telotarsi without ventromedian row of spinules. Sclerites of genital operculum (♀) fused, but loosely connected by membrane along entire length of suture.

DESCRIPTION: The following description supplements the original description of Mitchell (1968) and additional data provided by Mitchell (1971) and Francke (1982a, 1986).

Color: Carapace, pedipalp femur and patella, legs, tergites, sternites, metasoma,

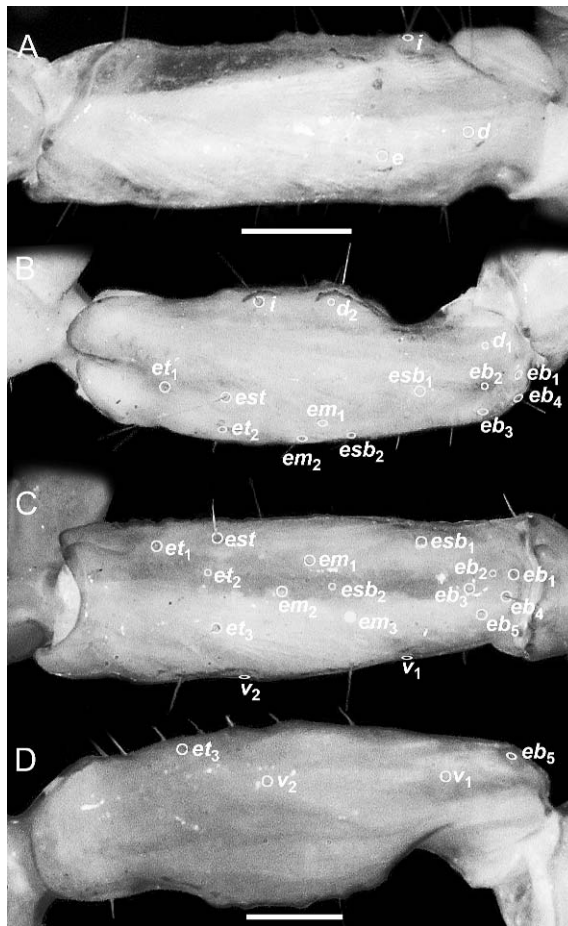


Fig. 34. *Typhlochactes rhodesi* Mitchell, 1968, holotype ♀ (AMNH), sinistral pedipalp femur (A) and patella (B–D) showing carinae and distribution of trichobothria. A, B. Dorsal aspect. C. External aspect. D. Ventral aspect. Scales = 0.5 mm.

and telson, Yellow Ocher (123C); pedipalp chela, Pratt's Rufous (140). Aculeus and denticle rows of pedipalp fingers darker. Larger paratype (AMNH) uniformly Buff Yellow (53); smaller paratype (MNHN) paler, except for aculeus and pedipalp finger denticles, Chamois (123D).

Chelicerae: Manus, dorsal and ventral surfaces smooth; dorsal surface with three microsetae situated near base of fixed finger; movable finger, dorsal surface with six microsetae. Fixed finger, dorsal margin with four teeth (distal, subdistal, median, and basal; fig. 5G); median and basal teeth not fused into bicuspid; distal tooth largest, sub-

distal and median teeth equal, smaller, basal tooth smallest. Movable finger, internal distal and external distal teeth opposable, internal distal tooth completely overlapping external distal tooth in dorsal view; dorsal margin with five closely aligned teeth (internal distal, two subdistal, median, and basal), first subdistal, second subdistal and median teeth progressively increasing in size, basal tooth equal to second subdistal tooth; ventral surface with well-developed serrula, extending half length of finger; macrosetae on proximal third of finger only, not covering serrula.

Carapace: Length slightly greater than anterior width (table 8). Anterior margin

sublinear to weakly convex, with small median projection (epistome) and few microsetae (fig. 32A). Posterior margin sublinear to weakly convex; asetose. Median and lateral ocelli absent. Median longitudinal and posterolateral sulci shallow; posterior transverse sulcus deep. Surface acarinate, smooth except for posterolateral margins, which are weakly granular, with scattered microsetae.

Pedipalps: Femur, dorsoexternal and ventroexternal carinae obsolete, granular; dorsointernal and ventrointernal carinae absent (fig. 34A). Dorsal and ventral surfaces mostly smooth; external and internal surfaces with scattered granules proximally; all surfaces, especially external surfaces, setose. Patella dorsoexternal carina distinct, granular; dorsointernal and ventrointernal carinae obsolete; other carinae absent. Dorsal and external surfaces less granular than femur, mostly smooth except for small granules concentrated around trichobothria (figs. 34B–D); ventral and internal surfaces with small, scattered granules; ventral surface asetose. Chela longer than carapace, relatively stout, manus length greater than width (table 8); movable finger slightly longer than manus. Manus acarinate (fig. 33); internal surface with depression near base of movable finger; manus and fingers, surfaces mostly smooth with scattered setae; dorsal, external, and internal surfaces with small, scattered granules distally near base of fingers; internal surface additionally with pair of prominent, isolated granules situated close together at base of fixed finger; ventroexternal surface with small group of granules proximally. Fixed finger, median denticle row comprising six oblique primary subrows, terminal subrow shorter, basal subrow slightly longer than other subrows (fig. 9M); internal denticles larger than external denticles; terminal denticle small, equal to internal denticle, fingertips interlocking evenly when closed. Movable finger, median denticle row comprising six oblique primary subrows, terminal subrow shorter, basal subrow considerably longer than other subrows (fig. 9N); terminal denticle small.

Trichobothria: Femur with three trichobothria (fig. 34A): one external (*e*), one dorsal (*d*), one internal (*i*). Patella with 19 trichobothria (fig. 34B–D), five petite (*d*₁, *d*₂, *et*₂, *esb*₂, *eb*₂), one accessory (*em*₃): two ventral (*v*₁, *v*₂); 14 external (*et*₁–*et*₃, *est*, *em*₁–*em*₃, *esb*₁, *esb*₂, *eb*₁–*eb*₅); two dorsal (*d*₁, *d*₂); one internal (*i*). Chela with 26 trichobothria (Fig. 33), seven petite (*V*₁, *Et*₄, *Et*₅, *Esb*, *Db*, *esb*, *db*): 16 on manus, four ventral (*V*₁–*V*₄), 10 external (*Et*₁–*Et*₅, *Est*, *Esb*, *Eb*₁–*Eb*₃), two dorsal (*Db*, *Dt*); 10 on fixed finger, four external (*et*, *est*, *esb*, *eb*), four dorsal (*dt*, *dst*, *dsb*, *db*), two internal (*it*, *ib*).

Legs: All surfaces with scattered microsetae; basitarsi with fewer setae than telotarsi. Basitarsi I–IV without prolateral pedal spurs; I and II, proventral surfaces with short subdistal row of closely aligned spinules. Telotarsi, dorsomedian lobe with one microseta; ventral surface with curved row of spinules, proximally, and six or seven submedian pairs of subspiniiform macrosetae; ungues long, equal in length; dactyl short, slightly curved.

Tergites: Surfaces acarinate; I–VI, uniformly smooth; VII, mostly smooth, with few small granules posterolaterally (fig. 32A). Posteromedian surfaces with paired setae; lateral and posterior margins, especially of tergites V and VI, with microsetae.

Sternum: Posterior width equal to length (fig. 7C); apex rounded; lateral margins converging anteriorly; lateral lobes flat; posterior depression shallow. Surface with four macrosetae anteromedially and two macrosetae posterolaterally.

Genital operculum: Sclerites fused, but loosely connected by membrane along entire length of suture; anterior margins rounded (fig. 7C); microsetae situated close to median suture and posterior margins.

Pectines: Pectinal plate, surface with two macrosetae situated mediolaterally. Lamella comprising four segments (fig. 7C); surfaces covered in microsetae, larger along margins. Tooth count, 5/5; teeth oval; proximal and distal teeth slightly larger.

Sternites: Surfaces acarinate, smooth (fig. 32B). Surfaces and margins setose. Respiratory spiracles (stigmata) small, round, situated posterolaterally.

Metasoma: Segments elongated, progressively increasing in length, decreasing in width (fig. 12F), segment I width greater than length, II width equal to length, III–V

length greater than width (table 8); segment V slightly shorter than carapace. Dorsosubmedian carinae, segments I–IV, obsolete, granular, distal granules not noticeably larger than preceding granules (fig. 12F). Dorsolateral carinae, segment V, obsolete, granular, present only in anterior part of segment. Dorsolateral, median lateral and ventrosubmedian carinae, segments I–IV, ventrolateral carinae, segments I–V, and ventromedian carina, segment V, absent. Dorsal intercarinal surfaces, segments I–V, slightly concave, uniformly, finely granular; other surfaces smooth. Lateral and ventral surfaces of all segments with several macrosetae.

Telson: Vesicle globose, flattened dorsally, rounded ventrally; anterodorsal lateral lobes absent (fig. 12F); surfaces smooth; ventral surface with several long and short setae. Aculeus short, slightly curved, arising gradually from vesicle.

Hemispermatothore: Male unknown.

Ontogenetic variation: Subadult similar to adults in general proportions but lacks depression and granules on pedipalp chela internal surface.

Geographical variation: All specimens from same locality.

Sexual dimorphism: Male unknown.

REMARKS: The label with the holotype indicates a different collecting date, “29.III.1967,” to that listed in the original description (Mitchell, 1968: 762), “24.III.1967.” The specimen listed as “depository unknown” by Sissom (2000b: 499) is deposited at the AMNH. The specimen at the MNHN is damaged (probably by dehydration): the sinistral pedipalp is lost, telson dislocated, mesosoma opened and metasoma broken.

DISTRIBUTION: Known only from the type locality, La Cueva de la Mina, in the Sierra de Guatemala, Tamaulipas, Mexico (figs. 1B, 3A, 3B), a karstic region characterized by many vertical caves ranging from a few meters to more than 100 m in depth (Mitchell, 1968; Reddell, 1981).

ECOLOGY: The holotype and paratypes of this troglobitic species were taken in a small room, about 50 m from the entrance to the cave, floored by a dark soil that apparently entered through small cracks in the overburden (Mitchell, 1968).

Typhlochactas sissomi Francke et al., 2009 (Figs. 1B, 4, 5H, 9O, 9P, 35–37; table 7)

Typhlochactas sissomi Francke et al., 2009: 5–11, figs. 1–7, table 2.

Typhlochactas sissomi: Botero-Trujillo and Francke, 2009: 2

TYPE MATERIAL: **Mexico:** *Queretaro:* Municipio de Jalpan: Holotype: 1 subadult ♂ (IBUNAM T-0308), leg (AMCC [LP 2949]), Cañada de La Joya, 21°27'23"N 99°08'26"W, 1944 m, H. Montañón and A. Valdez, 12.vi.2004, rock-rolling.

DIAGNOSIS: *Typhlochactas sissomi* is the sister taxon of a monophyletic group comprising all other species of *Typhlochactas*, from which it may be separated on the basis of the following combination of characters. Cheliceral fixed finger with four teeth (subdistal present); median and basal teeth not fused into bicusp. Cheliceral movable finger with five dorsal teeth (two subdistals present). Carapace, anterior margin with well-developed median projection (epistome). Pedipalp chela fixed and movable fingers, median denticle row of each comprising six oblique primary subrows; basal primary subrow of movable finger longer than other subrows; terminal denticle of fixed finger slightly larger than preceding denticles, fingertips interlocking evenly when closed. Legs with prolateral pedal spurs. Telotarsi without ventromedian row of spinules.

DESCRIPTION: The following description of the holotype (fig. 33) supplements the original description by Francke et al. (2009).

Color: Cheliceral manus, Cream (54), teeth Amber (36). Carapace, pedipalps, tergites, and metasoma, Buff Yellow (53). Coxosternal region, legs, sternites, and telson vesicle, Cream (54). Telson aculeus, Raw Sienna (136).

Chelicerae: Manus, dorsal and ventral surfaces smooth; dorsal surface with few microsetae. Fixed finger, dorsal margin with four teeth (distal, subdistal, median and basal; fig. 5H); median and basal teeth equal, not fused into bicusp. Movable finger, internal distal and external distal teeth opposable, internal distal tooth completely overlapping external distal tooth in dorsal view; dorsal margin with five teeth (internal distal, two subdistal, median and basal),

internal distal tooth largest; ventral surface with prominent serrula, partially covered by dense brush of macrosetae.

Carapace: Length greater than anterior width (table 7). Anterior margin sublinear, with small median projection (epistome); asetose (fig. 35A). Posterior margin weakly convex; asetose. Median and lateral ocelli absent. Median longitudinal, posterolateral, and posterior transverse sulci present, shallow. Surface smooth, shiny, acarinate, with scattered microsetae.

Pedipalps: Femur, dorsoexternal, dorsointernal, ventrointernal, ventroexternal carinae obsolete, granular (fig. 37A). Dorsal and internal surfaces sparsely and coarsely granular; ventral and external surfaces smooth. Patella dorsointernal carina distinct, coarsely granular; dorsoexternal, ventroexternal, and ventrointernal carinae obsolete, costate; internomedian carina comprising only a basal granule; other carinae absent or obsolete (fig. 37B–D). Chela manus broad (fig. 36). Dorsomedian, dorsal secondary, and ventroexternal carinae obsolete, granular; other carinae absent. Manus, intercarinal surfaces smooth proximally, becoming moderately granular medially; internal surface with pair of prominent, isolated granules situated close together at base of fixed finger; fingers smooth. Fixed finger, median denticle row comprising six oblique primary subrows, terminal subrow short, comprising one or two denticles, other subrows similar in length (fig. 9O); terminal denticle of fixed finger similar to preceding denticles, fingertips interlocking evenly when closed. Movable finger, median denticle row comprising six oblique primary subrows, terminal row short, comprising one or two denticles, basal subrow longer than other subrows (fig. 9P).

Trichobothria: Femur with three trichobothria (fig. 37A): one external (*e*), one dorsal (*d*), one internal (*i*). Patella with 19 trichobothria (fig. 37B–D), five petite ($d_1, d_2, et_2, esb_2, eb_2$), one accessory (em_3): two ventral (v_1, v_2); 14 external ($et_1-et_3, est, em_1-em_3, esb_1, esb_2, eb_1-eb_5$); two dorsal (d_1, d_2); one internal (*i*). Chela with 26 trichobothria (fig. 36), seven petite ($V_1, Et_4, Et_5, Esb, Db, esb, db$): 16 on manus, four ventral (V_1-V_4), 10 external ($Et_1-Et_5, Est, Esb, Eb_1-Eb_3$), two dorsal (Db, Dt); 10 on fixed finger, four external

(*et, est, esb, eb*), four dorsal (*dt, dst, dsb, db*), two internal (*it, ib*).

Legs: All surfaces covered with scattered microsetae; basitarsi with fewer setae than telotarsi. Basitarsi I–IV without prolateral pedal spurs; I and II, proventral surfaces with short subdistal row of closely aligned spinules. Telotarsi, ventral surface with curved row of spinules, proximally, and 6–8 submedian pairs of subspiniform macrosetae; unguis moderately long, equal in length; dactyl moderately developed, slightly curved.

Tergites: Surfaces I–VI smooth, shiny, acarinate (fig. 35A); VII coarsely granular in posterior half, dorsosubmedian and dorsolateral carinae vestigial, reduced to few posterior granules.

Sternum: Posterior width greater than length; apex rounded; lateral margins converging anteriorly; lateral lobes flat; posterior depression shallow. Surface smooth, asetose.

Genital operculum: Sclerites completely divided; genital papillae protruding distinctly beyond posterior edges. Surfaces smooth, shiny, asetose.

Pectines: Pectinal plate, surface with pair of macrosetae. Lamella comprising three segments. Tooth count, 5/5; teeth oval; proximal and distal teeth slightly larger.

Sternites: Surfaces acarinate. Surfaces and margins smooth, shiny, with scattered microsetae. Respiratory spiracles (stigmata) small, round, situated posterolaterally.

Metasoma: Segments stout, progressively increasing in length, decreasing in width (fig. 35B), segment I width greater than length, II width equal to length, III–V length greater than width (table 7). Dorsosubmedian carinae, segments I–IV, obsolete, coarsely and sparsely granular, distal granules not noticeably larger than preceding granules; V, absent. Dorsolateral carinae, segments I–IV, absent to obsolete, smooth; V, obsolete, granular. Median lateral carinae, segments I–V, absent. Ventrolateral carinae, segment I, absent; II–IV, obsolete, smooth; V, obsolete, granular. Ventrosubmedian carinae, segments I–IV, and ventromedian carina, segment V, absent. Dorsal intercarinal surfaces, segments I–V, slightly concave. All segments, intercarinal surfaces smooth, shiny, with scattered macrosetae.



Fig. 35. *Typhlochactas sissomi* Francke et al., 2009, subadult ♂ holotype (IBUNAM), habitus. **A.** Dorsal aspect. **B.** Ventral aspect. Scale = 1 mm.

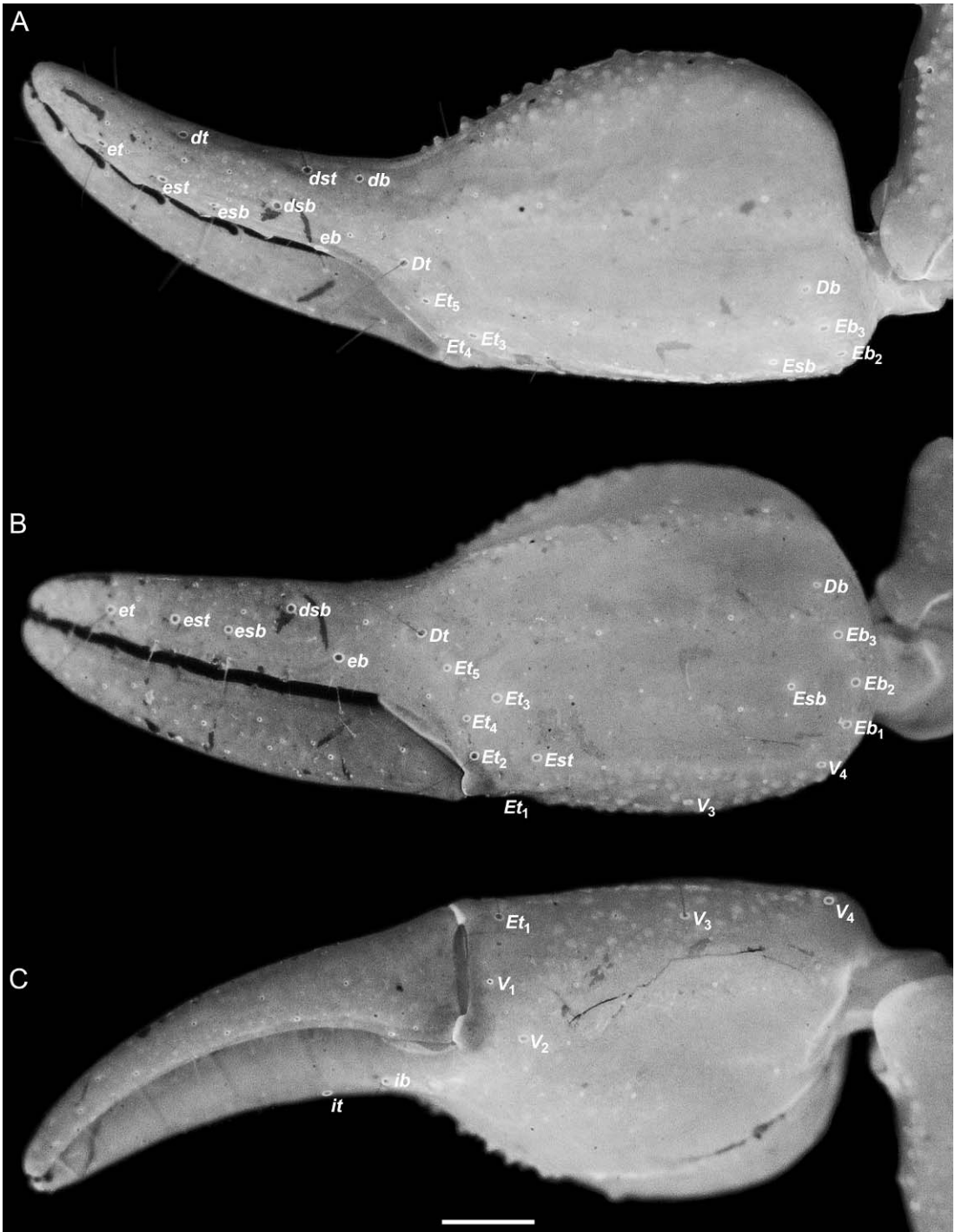


Fig. 36. *Typhlochactas sissomi* Francke et al., 2009, subadult ♂ holotype (IBUNAM), sinistral pedipalp chela showing carinae and distribution of trichobothria. A. Dorsal aspect. B. External aspect. C. Ventral aspect. Scale = 0.5 mm.

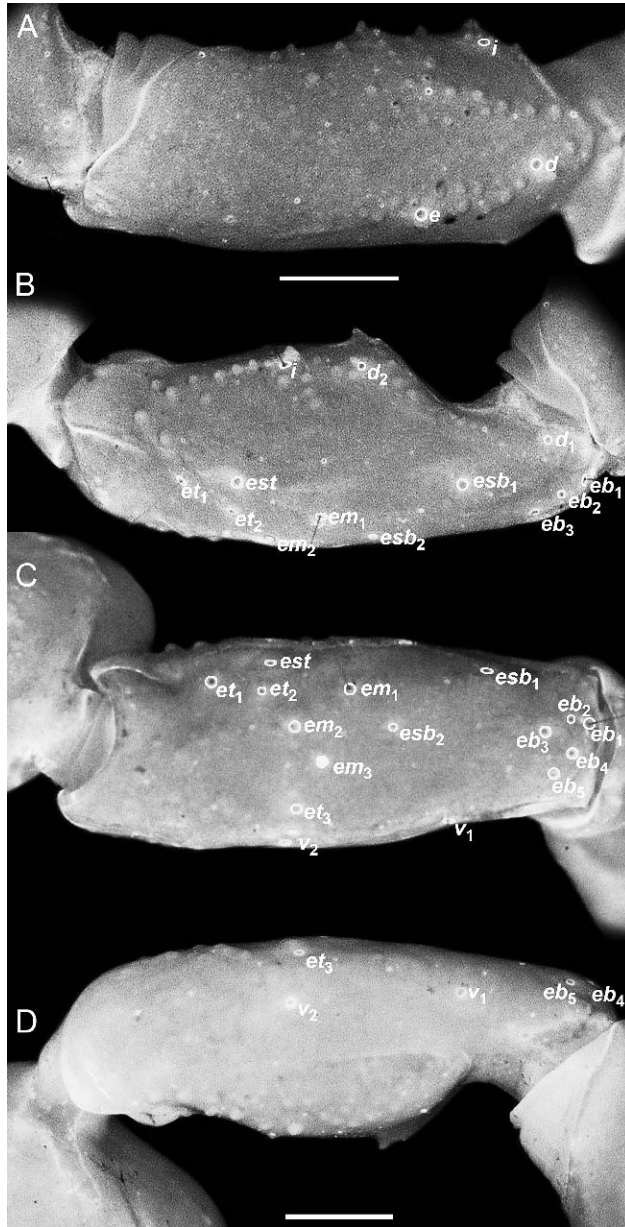


Fig. 37. *Typhlochactas sissomi* Francke et al., 2009, subadult ♂ holotype (IBUNAM), sinistral pedipalp femur (A) and patella (B–D) showing carinae and distribution of trichobothria. A, B. Dorsal aspect. C. External aspect. D. Ventral aspect. Scales = 0.5 mm.

Telson: Vesicle globose, flattened to slightly concave dorsally, rounded ventrally; anterodorsal lateral lobes absent (fig. 35B); surface smooth, with sparse setae ventrally and posteriorly. Aculeus short, sharply curved, arising abruptly from vesicle.

Hemispermatothore: Adult male unknown.

Ontogenetic variation: Adult unknown.

Geographical variation: Single specimen.

Sexual dimorphism: Female unknown.

REMARKS: The metasoma of the holotype is separated from the body at the articulation

of segments I and II, the left pedipalp chela is crushed, and the posterior margin of the carapace is slightly damaged. Left leg I was removed and retained at the AMCC for DNA isolation, amplification, and sequencing.

DISTRIBUTION: Known only from the type locality in Queretaro (central Mexico) (fig. 1B).

ECOLOGY: This troglomorphic species was taken from under a stone in a mesophilous forest (Francke et al., 2009). The fact that it was not collected inside a cave, taken together with its similar habitus to the two endogean species, *T. mitchelli* and *T. sylvestris*, suggests that it may also be endogean.

Typhlochactas sylvestris

Mitchell and Peck, 1977

(Figs. 1B, 4, 5I, 8D, 9Q, 9R, 12G, 38–40; table 9)

Typhlochactas sylvestris Mitchell and Peck, 1977: 159–164, 166–168, figs. 1–14, table 1.

Typhlochactas sylvestris: Lourenço, 1981: 659; Reddell, 1981: 115; Francke, 1982a: 53, 59, 60, figs. 26, 31, 36; 1986: 5, 7, 8, figs. 23–25; Sissom, 1988: 365, 370, 371; Kovařík, 1998: 142; Sissom and Cokendolpher, 1998: 285, 287 (table 1); Beutelspacher Baigts, 2000: 20, 52, 54, 143, 151, map 22; Sissom, 2000b: 500; Soleglad and Fet, 2003b: 30, 76; Prendini and Wheeler, 2005: 468–470, figs. 22, 23, table 9; Volschenk and Prendini, 2008: 236 (table 1), 249, 250; Botero-Trujillo and Francke, 2009: 2.

TYPE MATERIAL: **Mexico:** *Oaxaca:* Municipio de Valle Nacional. Holotype: 1 ♀ (AMNH), 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.

DIAGNOSIS: *Typhlochactas sylvestris* is most closely related to *T. mitchelli* (fig. 4). It may be separated from *T. mitchelli* and all other *Typhlochactas* species by the following combination of characters. Cheliceral fixed finger with three teeth (subdistal absent); median and basal teeth not fused into bicusp. Cheliceral movable finger with four dorsal teeth (one subdistal present). Carapace, anterior margin with well-developed median projection (epistome). Pedipalp chela fixed and movable fingers, median denticle row comprising five and six oblique primary

subrows, respectively; basal primary subrow of movable finger similar in length to other subrows; terminal denticle of fixed finger slightly larger than preceding denticles, fingertips interlocking evenly when closed. Legs with prolateral pedal spurs. Telotarsi with ventromedian row of spinules. Sclerites of genital operculum (♀) completely fused, no suture evident.

DESCRIPTION: The following description of the holotype (fig. 38) supplements the original description by Mitchell and Peck (1977) and supplementary data provided by Francke (1982a, 1986).

Color: Holotype uniformly Kingfisher Rufous (240).

Chelicerae: Manus, dorsal and ventral surfaces smooth; dorsal surface with few microsetae, one on movable finger. Fixed finger, dorsal margin with three teeth (distal, median and basal; fig. 5I); median and basal teeth equal, not fused into bicusp, considerably smaller than distal tooth. Movable finger, internal distal and external distal teeth not opposable, internal distal tooth at most partially overlapping external distal tooth in dorsal view; dorsal margin of dextral chelicera with four teeth (internal distal, subdistal, median and basal), of sinistral chelicera with three teeth (basal tooth absent), subdistal, median and basal teeth very small, equal, situated very close together, forming a compound tooth, three-quarters along finger, internal distal tooth considerably larger; ventral surface with long serrula occupying four-fifths of finger, covered in part by dense brush of macrosetae.

Carapace: Length greater than anterior width (table 9). Anterior margin sublinear, with small median projection (epistome); asetose (fig. 38A). Posterior margin weakly concave medially; asetose. Median and lateral ocelli absent. Median longitudinal, posterolateral, and posterior transverse sulci shallow. Surface smooth, acarinate, with scattered microsetae.

Pedipalps: Femur, ventroexternal carina obsolete, granular; other carinae absent (fig. 40A). Dorsal and internal surfaces with few granules and short, sparse setae. Patella acarinate (fig. 40B–D); all surfaces smooth. Chela stout, with broad, rounded manus and short fingers (table 9). Manus acarinate

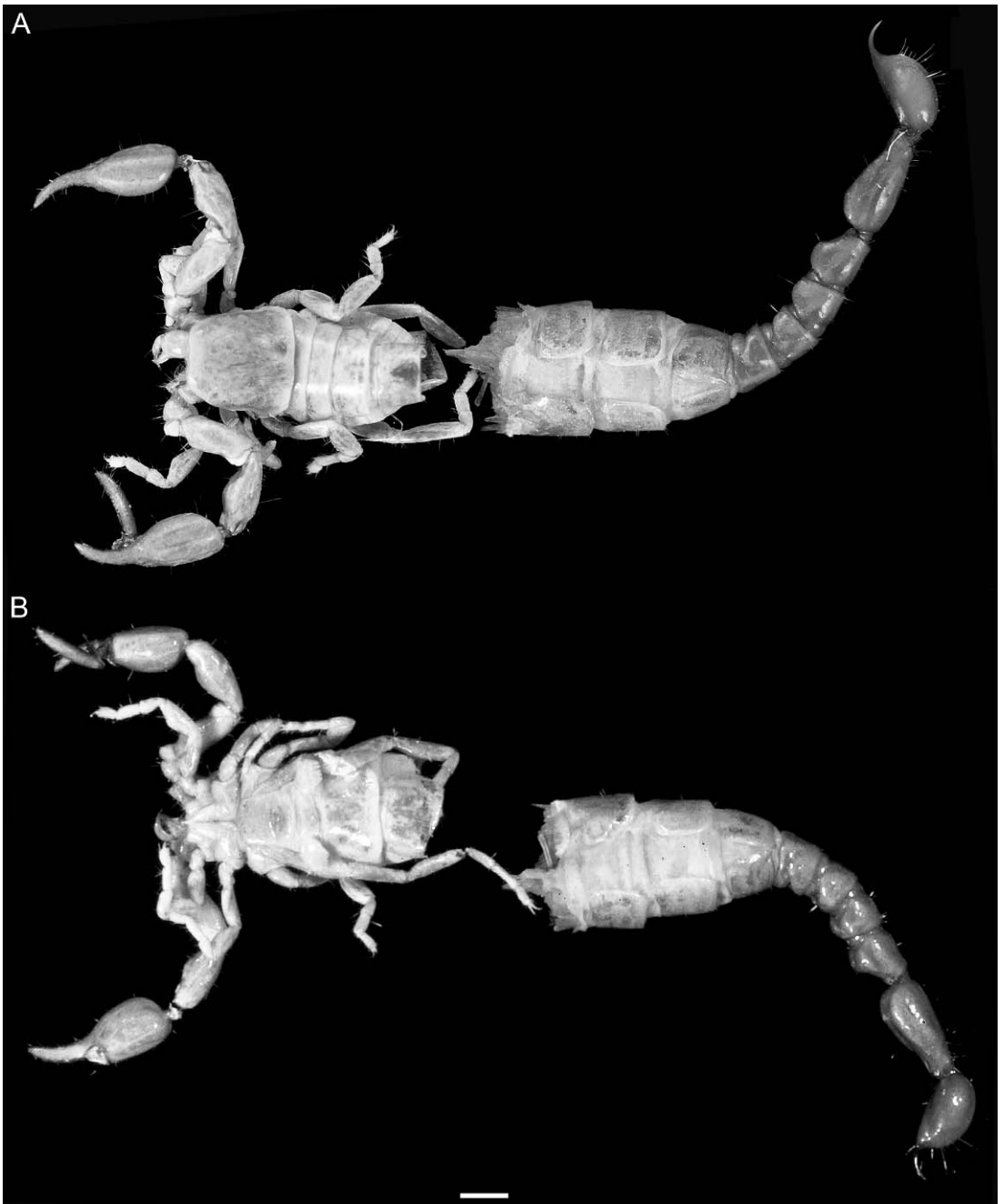


Fig. 38. *Typhlochactas sylvestris* Mitchell and Peck, 1977, holotype ♀ (AMNH), habitus. **A.** Dorsal aspect. **B.** Ventral aspect. Scale = 1 mm.

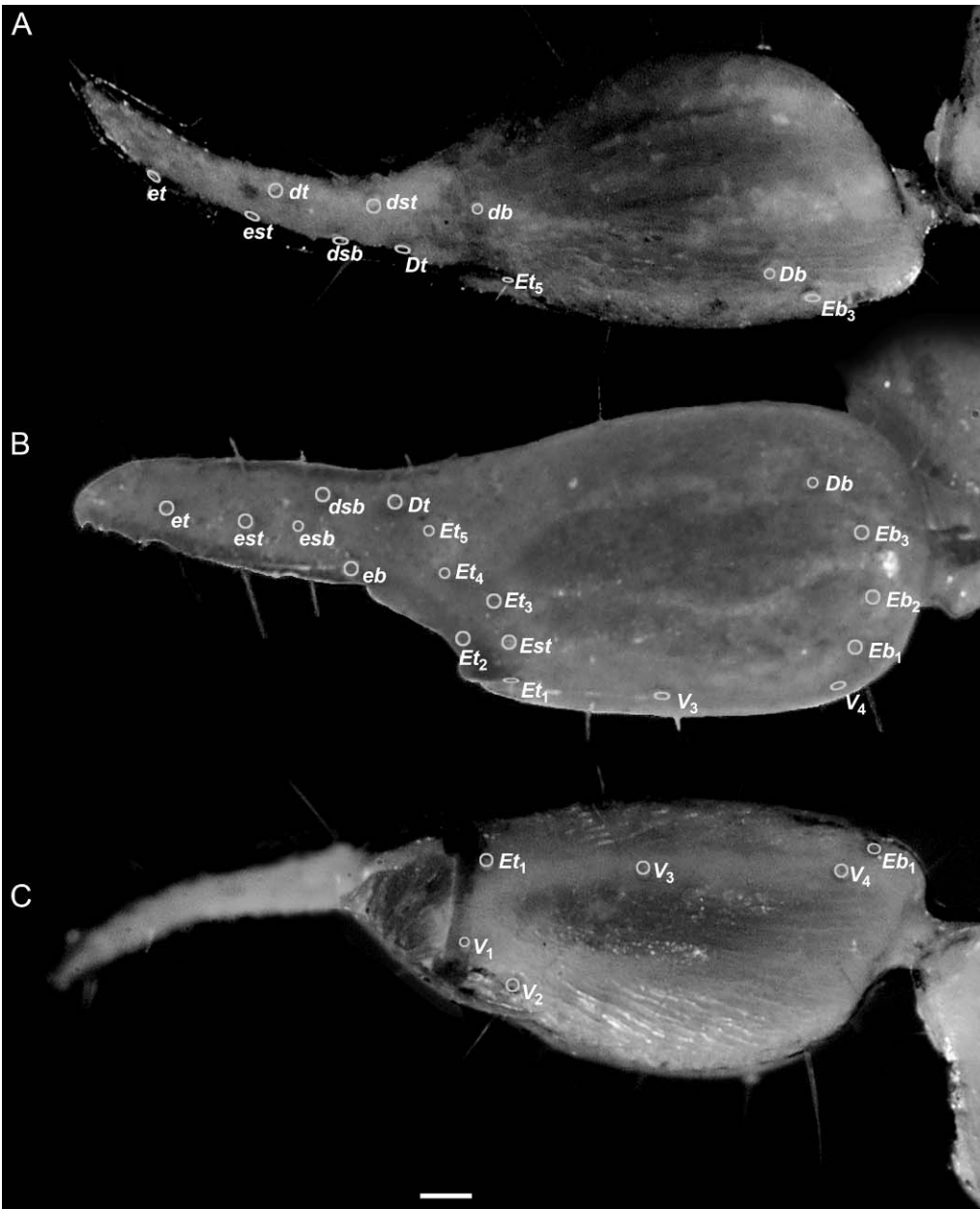


Fig. 39. *Typhlochactas sylvestris* Mitchell and Peck, 1977, holotype ♀ (AMNH), sinistral pedipalp chela showing carinae and distribution of trichobothria. **A.** Dorsal aspect. **B.** External aspect. **C.** Ventral aspect. Scale = 0.1 mm.

(fig. 39); surfaces of manus, fixed and movable fingers smooth, with short microsetae. Fixed finger, median denticle row comprising five oblique primary subrows, similar in length (fig. 9Q); terminal denticle small, slightly larger than preceding denticles, fin-

gertips interlocking evenly when closed. Movable finger, median denticle row comprising six oblique primary subrows; all subrows similar in length, but terminal and basal subrows slightly shorter (fig. 9R); terminal denticle small.

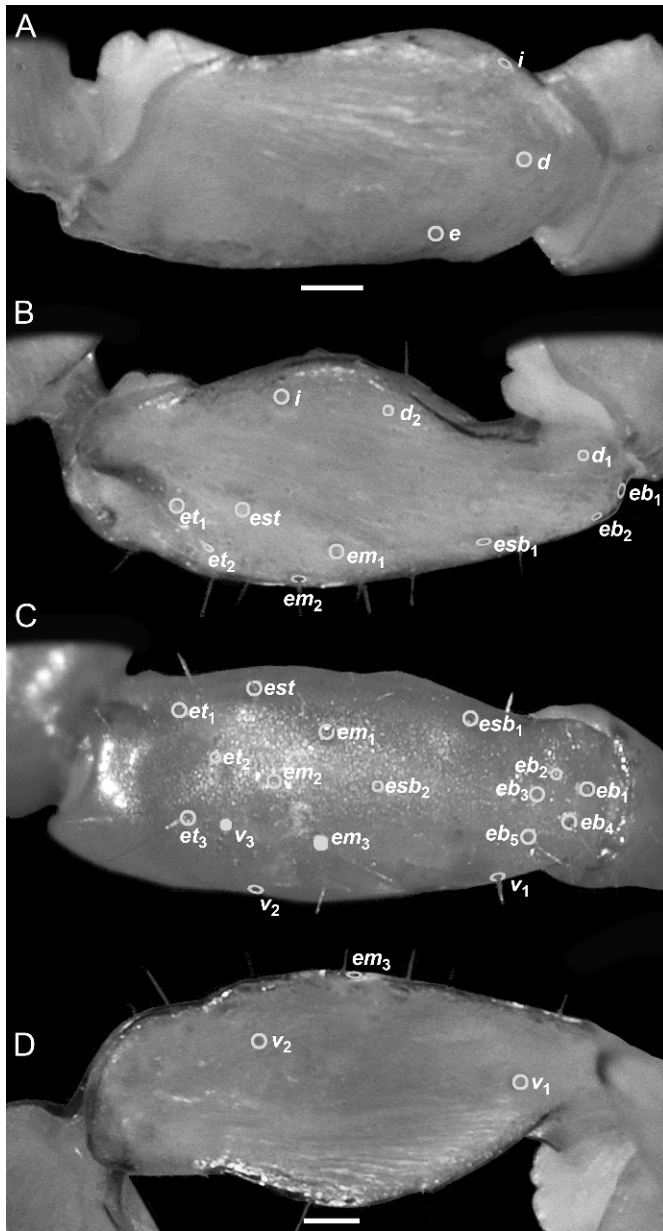


Fig. 40. *Typhlochactas sylvestris* Mitchell and Peck, 1977, holotype ♀ (AMNH), sinistral pedipalp femur (A) and patella (B–D) showing carinae and distribution of trichobothria. A, B. Dorsal aspect. C. External aspect. D. Ventral aspect. Scales = 0.1 mm.

Trichobothria: Femur with three trichobothria (fig. 40A): one external (*e*), one dorsal (*d*), one internal (*i*). Patella with 19 or 20 trichobothria (fig. 40B–D), six petite (*d*₁, *d*₂, *e*₂, *esb*₂, *eb*₂, *v*₃), two accessory (*em*₃, *v*₃ dextral only); two ventral (*v*₁, *v*₂); 14 (sinis-

tral) or 15 (dextral) external (*et*₁–*et*₃, *est*, *em*₁–*em*₃, *esb*₁, *esb*₂, *eb*₁–*eb*₅, *v*₃ dextral only); two dorsal (*d*₁, *d*₂); one internal (*i*). Chela with 26 trichobothria (fig. 39), seven petite (*V*₁, *Et*₄, *Et*₅, *Esb*, *Db*, *esb*, *db*): 16 on manus, four ventral (*V*₁–*V*₄), 10 external (*Et*₁–*Et*₅,

Est, Esb, Eb₁–Eb₃), two dorsal (*Db, Dt*); 10 on fixed finger, four external (*et, est, esb, eb*), four dorsal (*dt, dst, dsb, db*), two internal (*it, ib*). The designations of *et₃* and *v₃* used in this paper follow the fourth interpretation proposed by Prendini and Wheeler (2005: 470), according to which these trichobothria correspond, respectively, to Mitchell and Peck's (1977, 163: fig. 12) *et₃* and *sn*, rather than the third interpretation, favored by Prendini and Wheeler (2005: 469, figs. 22, 23).

Legs: All surfaces setose. Basitarsi I–IV with prolateral pedal spurs; I and II, proventral surfaces with short subdistal row of closely aligned spinules. Telotarsi, dorsomedian lobe with one microseta; ventral surface with curved row of spinules, proximally, and straight ventromedian row of spinules, flanked by three or four submedian pairs of subspiniform macrosetae; unguis short, equal in length, weakly curved; dactyl short, robust.

Tergites: Surfaces acarinate. Surfaces and margins smooth, with few microsetae (fig. 38A).

Sternum: Posterior width greater than length; apex rounded (fig. 8D); lateral margins subparallel; lateral lobes flat; posterior depression very shallow. Surface with eight macrosetae.

Genital operculum: Sclerites completely fused, no suture evident (fig. 8D); anterior margin slightly concave; posterior margin convex. Surfaces almost asetose.

Pectines: Pectinal plate, surface with two macrosetae situated mediolaterally. Lamella comprising five segments (fig. 8D). Tooth count, 5/5; teeth pointed; proximal and distal teeth slightly larger.

Sternites: Surfaces acarinate (fig. 38B). Surfaces and margins smooth, with scattered microsetae. Respiratory spiracles (stigmata) small, round, situated posterolaterally.

Metasoma: Metasoma stout, segments progressively increasing in length, decreasing in width (fig. 12G), I–III width greater than length, IV width equal to length, V length greater than width (table 9). Dorsosubmedian carinae, segments I–IV, obsolete, granular, distal granules not noticeably larger than preceding granules. Dorsolateral carinae, segment V, obsolete, comprising few granules in posterior part of segment. Dor-

solateral, median lateral and ventrosubmedian carinae, segments I–IV, ventrolateral carinae, segments I–V, and ventromedian carina, segment V, absent. Dorsal intercarinal surfaces, segments I–V, slightly concave. Intercarinal surfaces smooth, shiny, setose.

Telson: Vesicle globose, flattened to slightly concave dorsally, rounded ventrally; anterodorsal lateral lobes absent (fig. 12G); surface smooth, with several long and short setae posteriorly. Aculeus short, sharply curved, arising abruptly from vesicle.

Hemispermaphore: Male unknown.

Ontogenetic variation: Juvenile and subadult unknown.

Geographical variation: Single specimen.

Sexual dimorphism: Male unknown.

REMARKS: Mitchell and Peck (1977) listed the Museum of Texas Tech University as depository. The specimen has since been transferred to the AMNH (Sissom, 2000b). The holotype is severely damaged (fig. 38): the mesosoma is broken and the dextral chelicera, movable finger of the sinistral pedipalp chela, and part of sinistral leg IV are lost.

DISTRIBUTION: Known only from the type locality, a mixed-species cloud forest with a dominant oak component, in the Sistema Montañoso Poblano Oaxaqueño, Oaxaca (southern Mexico) (fig. 1B).

ECOLOGY: This endogean (humicolous) species was extracted, using metal "Tulgren" Berlese funnels, from 271 of forest litter collected and pooled from two sites at the type locality. For more details, see Mitchell and Peck (1977).

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APPENDIX 1

List of 196 characters for nine taxa in the family Typhlochactidae Mitchell, 1971 and three outgroup taxa, from Prendini et al. (2009). Fifty-four characters, indicated by †, were deactivated in all analyses. Character 196 was optimized on the phylogeny *a posteriori*. Characters from previous analyses that correspond partially or entirely to those in 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 (2003b), 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 ventrodiscal 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 (δ): 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 (δ): 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 (δ): 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 (δ): 5 (0); 6 (1); 7 (2); unknown (?). [S&F03.5/103]
173. †Pectinal teeth, number (δ): 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 (δ): 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 posterior 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, posterior width: broader than (0); similar to (1).
195. Telson vesicle, anterodorsal lateral lobes: present (0); absent (1).
- Habitat**
196. †Ecomorphotype: epigeal (0); endogean (1); hypogean (2).