Systematics of the Relictual Asian Scorpion Family Pseudochactidae Gromov, 1998, with a Review of Cavernicolous, Troglobitic, and Troglomorphic Scorpions

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SYSTEMATICS OF THE RELICTUAL ASIAN SCORPION FAMILY PSEUDOCHACTIDAE GROMOV, 1998, WITH A REVIEW OF CAVERNICOLOUS, TROGLOBITIC, AND TROGLOMORPHIC SCORPIONS

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ABSTRACT

The first integrative systematic revision of the relictual Asian scorpion family Pseudochactidae Gromov, 1998, making use of an unprecedented collection of material acquired during several expeditions to most of the type localities, is presented. The subfamilies, genera and species of Pseudochactidae are revised based on a phylogenetic analysis of 140 morphological characters and 8608 nucleotide base pairs of concatenated DNA sequence from two nuclear and three mitochondrial gene loci, and a multivariate statistical analysis of 22 ratios and 8 counts for 60 specimens. Three subfamilies, four genera and six species are recognized in the family. Troglokhammouaninae, subfam. nov., is created to restore the monophyly of the nominotypical subfamily Pseudochactinae Gromov, 1998. *Aemngvantom*, gen. nov., is created to accommodate *Aemngvantom lao* (Lourenço, 2012), comb. nov., and *Aemngvantom thamnongpaseuam* gen. et sp. nov. Four new synonyms are presented: *Troglokhammouanus louisanneorum* Lourenço, 2017 = *Troglokhammouanus steineri* Lourenço, 2007, syn. nov.; *Vietbocap thienduongensis* Lourenço and Pham, 2012 = *Vietbocap canhi* Lourenço and Pham, 2010, syn. nov.; *Vietbocap aurantiacus* Lourenço et al., 2018 = *V. canhi*, syn. nov.; *Vietbocap quinquemilia* Lourenço et al., 2018 = *V. canhi*, syn. nov. Revised diagnoses of the subfamilies, genera and species, with comparative images, a key and distribution maps are provided, along with a summary of available data on ecology and conservation status, where applicable. Among the Southeast Asian pseudochactids, all of which appear to be obligately cavernicolous, the three species of Vietbocapinae Lourenço, 2012, are highly troglomorphic whereas the sole species of Troglokhammouaninae is barely so. Applying recently revised definitions of the Schiner-Racovitza system for the classification of subterranean organisms, only Vietbocapinae can be considered troglobitic. The global diversity of cavernicolous, troglomorphic and troglobitic scorpions is similarly revisited and a key to ecological classification of cavernicolous and troglomorphic scorpions presented. The world totals of troglomorphic vs. troglobitic scorpions are currently 58 vs. 28 species, in 29 vs. 17 genera and 15 vs. 13 families, respectively.

INTRODUCTION

Pseudochactas ovchinnikovi Gromov, 1998, a small, nondescript brownish scorpion (fig. 1) from a remote, mountainous region of southeastern Uzbekistan and southwestern Tajikistan, Central Asia (fig. 2), was arguably the most remarkable scorpion discovered in the previous century. As noted in the original description (Gromov, 1998), several characters of this species suggested a close phylogenetic relationship to the largest and most widely distributed scorpion family, Buthidae C.L. Koch, 1837, whereas other characters suggested a closer relationship to the so-called nonbuthid scorpion families, especially the family Chaerilidae Pocock, 1893, from South and Southeast Asia, the phylogenetic position of which was also unclear at the time (Lamoral, 1980; Stockwell, 1989; Sissom, 1990; Prendini, 2000; Soleglad and Fet, 2001, 2003a; Coddington et al., 2004). Besides a mixture of characters

shared with buthid and nonbuthid scorpions, Gromov (1998) noted several characters of *P. ovchinnikovi* that were unique among Recent (extant) scorpions, among the most important being the trichobothrial pattern of its pedipalps, which could not be accommodated in any of the three "fundamental" (orthobothriotaxic) patterns first defined by Vachon (1974) and so influential in scorpion systematics since. The unique combination of characters that *P. ovchinnikovi* shared with Buthidae, on the one hand, and the nonbuthid families, on the other, led Gromov (1998) to place it close to the common ancestor of all these families, i.e., to the common ancestor of all the Recent scorpions, and create a monotypic family, Pseudochactidae Gromov, 1998, to accommodate it.

Subsequent authors reassessed the morphology of *P. ovchinnikovi* and offered three alternative hypotheses concerning its phylogenetic position (Coddington et al., 2004; Prendini et
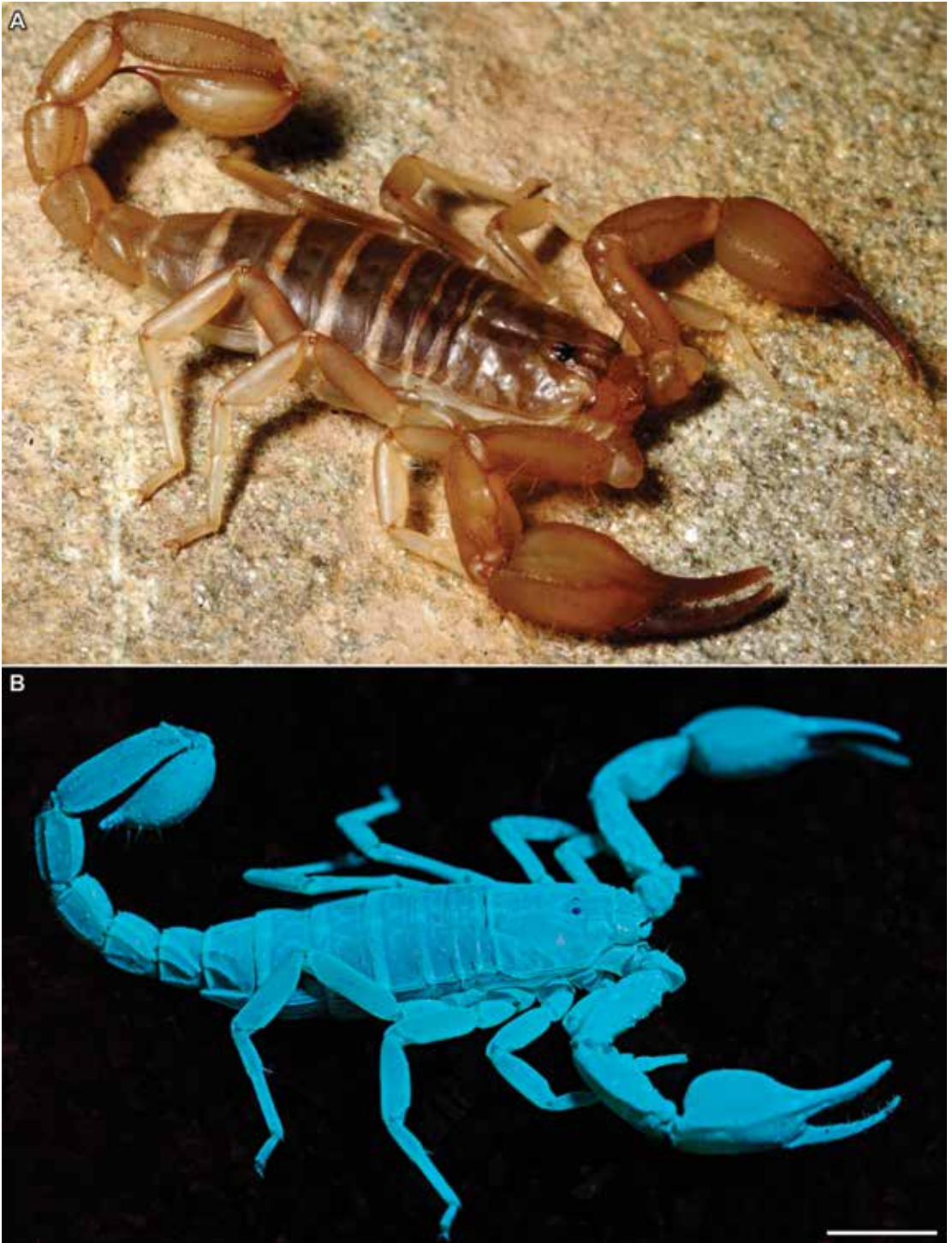
FIGURE 1. *Pseudochactas ovchinnikovi* Gromov, 1998, adult ♀ (AMNH), Babatag, habitus in life: **A.** natural light, **B.** ultraviolet light. Scale bar = 3 mm.
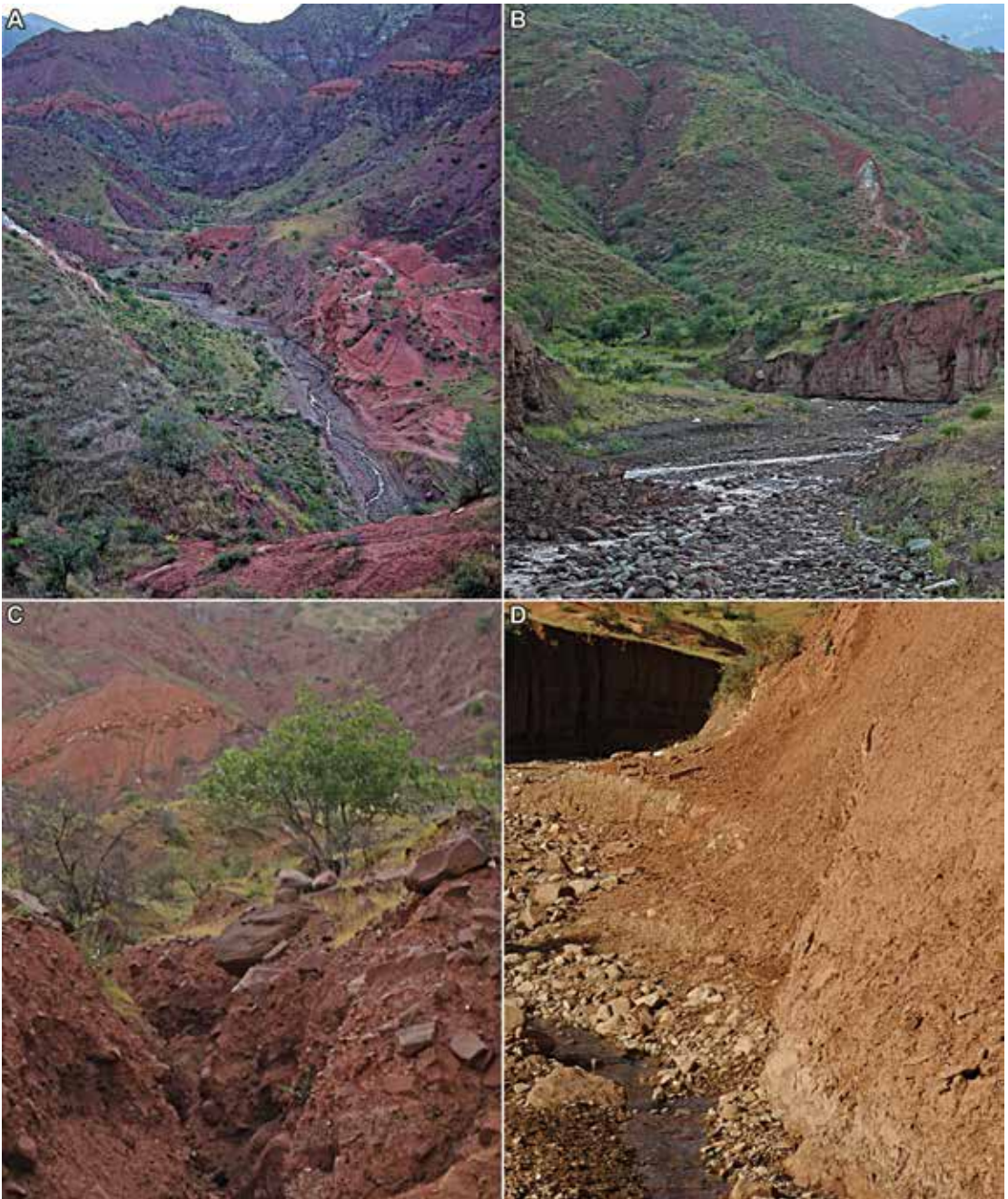
FIGURE 2. Dikhana Canyon, Babatag Mountains, Surkhandarya Area, Uzbekistan, collection locality and habitat of *Pseudochactas ovchinnikovi* Gromov, 1998: **A.** aerial view of canyon, **B.** canyon, facing upstream, **C.** gully in canyon, where several *P. ovchinnikovi* were collected, **D.** microhabitat, *P. ovchinnikovi* were observed sitting and walking on mud walls, close to stream at night.

al., 2006): (1) sister to all Recent (extant) scorpions; (2) sister to Buthidae; (3) sister to Chaerilidae. According to Fet (2000), the trichobothrial pattern of *P. ovchinnikovi* suggested a relationship to the most plesiomorphic Buthidae or to Chaerilidae, whereas Lourenço (2000a) placed *P. ovchinnikovi* in a newly elevated superfamily, Chaeriloidea Pocock, 1893, implying it was sister to Chaerilidae. Soleglad and Fet (2001) set out to quantitatively determine the phylogenetic position of *P. ovchinnikovi* based on a reassessment of its trichobothria. Gromov's (1998) designations of the individual trichobothria of *P. ovchinnikovi* were amended, the definition of its trichobothrial pattern formalized and named "Type D," and a cladistic analysis of the four orthobothriotaxic patterns of scorpions presented, on which basis *P. ovchinnikovi* was placed sister to Buthidae. The analysis by Soleglad and Fet (2001) was restricted to trichobothrial characters, the primary homology assessment of which is contentious (Lamoral, 1979; Francke and Soleglad, 1981; Francke, 1982; Sissom, 1990; Prendini, 2000; Prendini and Wheeler, 2005; Prendini et al., 2010), whereas other sources of evidence were ignored (Coddington et al., 2004), and rooted on a hypothetical outgroup, with consequent problems for determining character polarity (Prendini, 2001a; Prendini and Wheeler, 2005).

Soleglad and Fet (2003b) subsequently presented a quantitative assessment of the sternum of *P. ovchinnikovi* as part of a survey of sternal morphology across all scorpions that demonstrated similarities among the sterna of *P. ovchinnikovi*, Buthidae, and Chaerilidae, formally designated "Type 1" sterna. Soleglad and Fet (2003b) concluded that the sternum of *P. ovchinnikovi* is the most plesiomorphic of any Recent scorpion, showing a close affinity with that of the Carboniferous, *Palaeopisthacanthus* Petrunkevitch, 1913. Soleglad and Fet (2003a) followed up with further putative affinities between *P. ovchinnikovi* and *Palaeopisthacanthus*, and a new cladistic analysis of the higher phylogeny of Recent scorpions, based on trichobothria and other morphological characters, which placed *P. ovchinnikovi* sister to all Recent scorpions, supporting the original suggestion of Gromov (1998). Besides incorporating problematic data from the earlier analysis (Soleglad and Fet, 2001), other problems with Soleglad and Fet's (2003a) analysis were pointed out by Prendini and Wheeler (2005). Nevertheless, Fet et al. (2004) republished Soleglad and Fet's (2003a) diagnosis of *P. ovchinnikovi* and maintained their opinion that *P. ovchinnikovi* is the basal sister group of all Recent scorpions.

Prendini et al. (2006) presented an illustrated reassessment of the morphology of *P. ovchinnikovi*, based on a large series of material, which included the first descriptions of the male hemispermatophore, female overiuterus, and pectinal peg sensillae, and a reinterpretation of the trichobothrial pattern, in which additional petite trichobothria, previously overlooked, were identified. Several misconceptions regarding other character systems, e.g., pedipalpal and metasomal carinae, were also clarified. Although the aim was not to determine the phylogenetic position of *Pseudochactas*, Prendini et al. (2006) concluded that the evidence suggested a sister-group relationship with Buthidae or a monophyletic group comprising Buthidae and the Cretaceous *Archaeobuthus* Lourenço, 2001 and its relatives.

In the years that followed, two new genera, *Troglokhammouanus* Lourenço, 2007, and *Vietbocap* Lourenço and Pham, 2010, and seven new species of Pseudochactidae, were described from the Southeast Asian countries of Laos and Vietnam (Lourenço, 2007a, 2012a, 2017a; Lourenço

FIGURE 3. Tham Xe Bang Fai [Xe Bang Fai River Cave] (or Tham Khoun Xe), near Boualapha, Khammouane Province, Laos, type locality and habitat of *Troglokhammouanus steineri* Lourenço, 2007: **A.** Xe Bang Fai River, outside cave, **B–D.** cave entrance from outside (**B, C**) and inside (**D**), **E–H.** moist, mud banks of river inside cave (**E**), with mud cracks (**F**) and detritus (**G, H**) microhabitats of *T. steineri*.
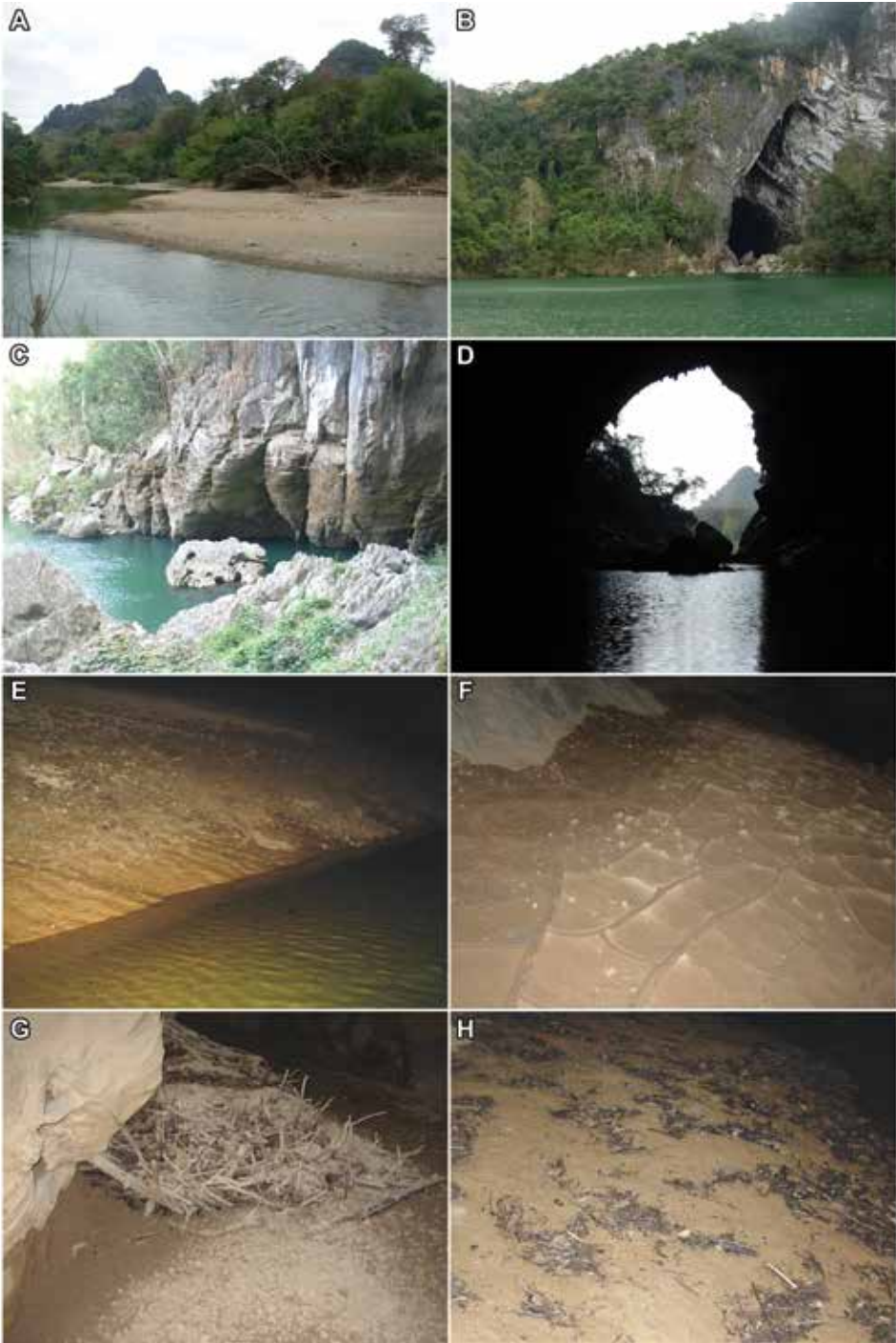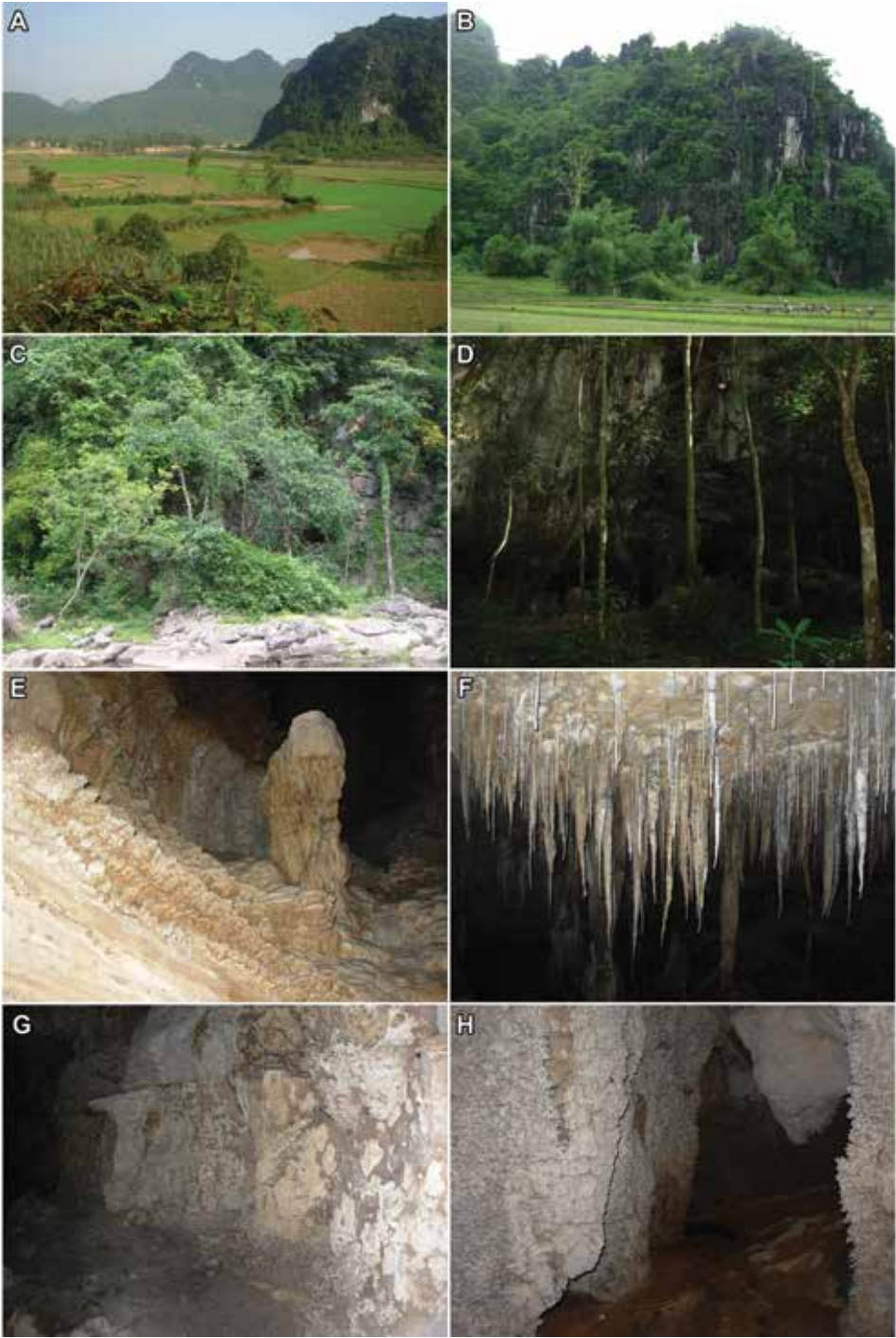
and Pham, 2010, 2012; Lourenço et al., 2018), along with a second species of *Pseudochactas* from Afghanistan (Soleglad et al., 2012), vastly extending the known distribution of the family (figs. 3–7) and suggesting a Pangean origin for the family. Unlike the two Central Asian species of *Pseudochactas*, all Southeast Asian species are hypogean and five are eyeless, depigmented troglobites. Three were described from a single cave, ca. 2.5 km away from a fourth (Lourenço and Pham, 2010, 2012; Lourenço et al., 2018), raising questions about their validity. Additionally, recent phylogenomic analyses of transcriptomes placed two of the Southeast Asian species sister to an exemplar species of Chaerilidae (Sharma et al., 2015a, 2015b), confirming the Chaeriloidea hypothesis (Lourenço, 2000a), and suggesting Pseudochactidae diverged from Chaerilidae ca. 329 Ma (Sharma et al., 2018).

Despite these advances, no attempt has yet been made to compare the morphology of Central and Southeast Asian pseudochactids, or test species limits and phylogenetic relationships within the family. The present contribution provides the first integrative systematic revision of Pseudochactidae, making use of an unprecedented collection of material acquired during several expeditions to most of the type localities. The subfamilies, genera, and species of this relictual family are revised based on a phylogenetic analysis of 140 morphological characters and 8608 nucleotide base pairs (bp) of concatenated DNA sequence from two nuclear and three mitochondrial gene loci, and a multivariate statistical analysis of 22 ratios and 8 counts for 60 specimens. Three subfamilies, four genera and six species are recognized (table 1). Troglokhammouaninae, subfam. nov., is created to restore the monophyly of the nominotypical subfamily Pseu-

dochactinae Gromov, 1998. *Aemngvantom*, gen. nov., is created to accommodate *Aemngvantom lao* (Lourenço, 2012), comb. nov., and *Aemngvantom thamnongpaseuam* gen. et sp. nov. Four new synonyms are presented: *Troglokhammouanus louisanneorum* Lourenço, 2017 = *Troglokhammouanus steineri* Lourenço, 2007, syn. nov.; *Vietbocap thienduongensis* Lourenço and Pham, 2012 = *Vietbocap canhi* Lourenço and Pham, 2010, syn. nov.; *Vietbocap aurantiacus* Lourenço et al., 2018 = *V. canhi*, syn. nov.; *Vietbocap quinquemilia* Lourenço et al., 2018 = *V. canhi*, syn. nov. Revised diagnoses of the subfamilies, genera and species, with comparative images, a key, and distribution maps are provided, along with a summary of available data on ecology and conservation status, where applicable.

Among the Southeast Asian pseudochactids, all of which appear to be obligately cavernicolous, the three species of Vietbocapinae Lourenço, 2012, are highly troglomorphic whereas the sole species of Troglokhammouaninae is barely so. Applying recently revised definitions of the Schiner-Racovitza system for the classification of subterranean organisms (Trajano, 2012; Trajano and Carvalho, 2017; Mammola, 2019), only Vietbocapinae can be considered troglobitic. The global diversity of cavernicolous, troglomorphic and troglobitic scorpions is similarly revisited and a key to ecological classification of cavernicolous and troglomorphic scorpions presented.

REVIEW OF CAVERNICOLOUS, TROGLOBITIC, AND TROGLOMORPHIC SCORPIONS

Schiner-Racovitza System: Ecological classification of subterranean organisms (cavernicoles sensu lato) is integral for understanding

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FIGURE 4. Type localities and habitats of *Vietbocap* Lourenço and Pham, 2010 in Quảng Bình Province, Vietnam (**A, E**) and *Aemngvantom*, gen. nov., in Khammouane Province, Laos (**B–D, F–H**): **A, E.** Tiên Sơn, near Sơn Trạch: karst landscape viewed from cave entrance (**A**) and microhabitat of *Vietbocap canhi* Lourenço and Pham, 2010, inside cave (**E**). **B, C, F.** Tham Nong Pa Seuam, near Thakhek: karst landscape in vicinity (**B**), cave entrance (**C**) and microhabitat of *Aemngvantom thamnongpaseuam*, gen. et sp. nov., inside cave (pillar room) (**F**). **D, G, H.** Tham Nam Lot (Lod), near Ban Naden: cave entrance (**D**) and microhabitat of *Aemngvantom lao* (Lourenço, 2012), comb. nov., inside cave (**G, H**).
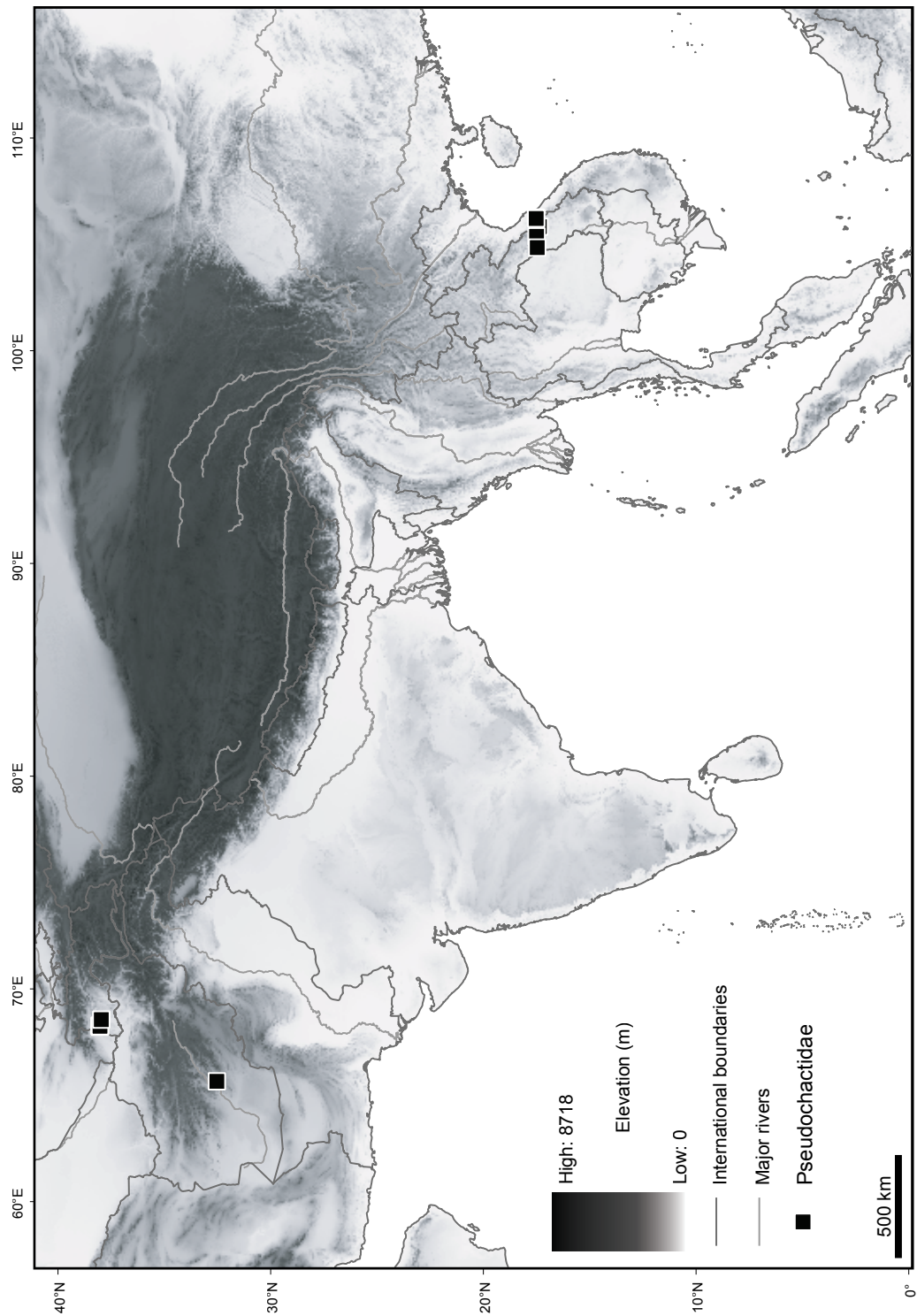
FIGURE 5. Distribution of Pseudochactidae Gromov, 1998 in Asia (squares).

TABLE 1

**Currently Recognized Subfamilies, Genera, Species, and Synonyms in
the Relictual Asian Scorpion Family Pseudochactidae Gromov, 1998**

Pseudochactinae Gromov, 1998
Type genus: *Pseudochactas* Gromov, 1998
 Pseudochactas Gromov, 1998
 Type species: *Pseudochactas ovchinnikovi* Gromov, 1998
  Pseudochactas mischi Soleglad et al., 2012
  Pseudochactas ovchinnikovi Gromov, 1998

Troglokhammouaninae, subfam. nov.
Type genus: *Troglokhammouanus* Lourenço, 2007
 Troglokhammouanus Lourenço, 2007
 Type species: *Troglokhammouanus steineri* Lourenço, 2007
  Troglokhammouanus steineri Lourenço, 2007
   = *Troglokhammouanus louisanneorum* Lourenço, 2017, syn. nov.

Vietbocapinae Lourenço, 2012
Type genus: *Vietbocap* Lourenço and Pham, 2010
 Aemngvantom, gen. nov.
 Type species: *Aemngvantom lao* (Lourenço, 2012), comb. nov.
  Aemngvantom lao (Lourenço, 2012), comb. nov.
  Aemngvantom thamnongpaseuam, gen. et sp. nov.
 Vietbocap Lourenço and Pham, 2010
 Type species: *Vietbocap canhi* Lourenço and Pham, 2010
  Vietbocap canhi Lourenço and Pham, 2010
   = *Vietbocap thienduongensis* Lourenço and Pham, 2012, syn. nov.
   = *Vietbocap aurantiacus* Lourenço et al., 2018, syn. nov.
   = *Vietbocap quinquemilia* Lourenço et al., 2018, syn. nov.

and conserving the biodiversity of fragile and often threatened cavernicolous habitats and the unique biota they contain (Sket, 2008; Trajano, 2012; Trajano and Carvalho, 2017; Mammola, 2019). The traditional and widely used Schiner-Racovitza system of classification (Schiner, 1854; Racovitza, 1907) comprises three categories: troglobites, troglophiles, and trogloxenes. Troglobites, or troglobionts, have traditionally been defined as organisms that are restricted to deep cave environments (Howarth, 1982, 1983; Humphreys, 2000) and exhibit pronounced troglomorphies or troglomorphisms (Christiansen, 1962, 2012), specific ecomorphological adapta-tions to subterranean habitats that include the loss (or reduction) of eyes and pigmentation, attenuation of the appendages, and thinning of the cuticle (Poulson, 1963; Hamilton-Smith, 1967; Barr, 1968a; Howarth, 1982, 1983, 1993; Barr and Holsinger, 1985; Holsinger, 1988; Humphreys, 2000). The evolution of troglomorphies has been attributed to the unusual characteristics of subterranean environments, including extremely stable temperature, very high humidity, absolute and continuous darkness, and limited energy (food) availability (Barr, 1968a; Poulson and White, 1969; Howarth, 1982, 1983, 1993; Parzefall, 1985), which select for the loss of

characters that are both unnecessary and costly to produce or maintain (e.g., eyes, pigmentation, thickened cuticle), and the accentuation of characters that assist in resource location or compensate for putatively "unnecessary" characters that have been lost (e.g., attenuated appendages, reduced metabolic rate).

Whereas troglobites are considered obligately cavernicolous, troglophiles and trogloxenes are facultatively cavernicolous and typically lack pronounced troglomorphies, consistent with the ability to survive on the surface, even if they have never been observed above ground. Troglophiles and trogloxenes differ in the extent of their reliance on the subterranean environment, with troglophiles able to complete their life cycles in either the hypogean (subterranean) or the epigean (surface) environment, and at least theoretically capable of forming populations in both habitats, whereas trogloxenes are regularly found in the subterranean habitat, but unable to complete their entire life cycles therein (Sket, 2008; Mammola, 2019). The paleoclimatic model implies isolation of troglophilic populations in subterranean refugia due to contraction of epigean populations, as a consequence of climatic changes that render surface habitats unsuitable for their continued survival (Barr, 1968b; Bryson et al., 2014). In times of cyclic or alternating phases of contrasting climate, the original, suitable environmental conditions may be restored during favorable climatic phases, allowing previously epigean species that survived temporarily in subterranean refugia, to recolonize the surface, and so on. In some cases, such populations may even coexist with congeneric troglobites that evolved during earlier, and more protracted vicariance events (Trajano and Carvalho, 2017).

Although the Schiner-Racovitza system has been employed for over a century, problems with its application, especially when attempting to classify cavernicolous taxa based on either the habitat or the presence of troglomorphies, resulted in a succession of critiques, emendations, and proposals (e.g., Christiansen, 1962; Poulson, 1963; Vandel, 1964; Barr, 1967, 1968b;

Thinès and Tercafs, 1972; Holsinger and Culver, 1988; Sket, 2008; Trajano, 2012). Trajano (2012) and Trajano and Carvalho (2017) reviewed the history of the Schiner-Racovitza system, redefined it conceptually in terms of source and sink populations, and recognized four categories:

> 1. troglobites (or troglobionts), corresponding to exclusively subterranean source populations (sink populations may be found in surface habitats);
> 2. troglophiles, including source populations in both hypogean and epigean habitats, with individuals regularly commuting between these habitats, promoting the introgression of genes selected under epigean regimes into subterranean populations (and vice versa) = eutroglophiles sensu Sket (2008), essentially epigean species able to establish more or less permanent subterranean populations;
> 3. trogloxenes, instances of source populations in epigean habitats, but using subterranean resources (so-called obligatory trogloxenes, all individuals are dependent on both surface and subterranean resources) = subtroglophiles sensu Sket (2008), which need to utilize the surface environment for at least one vital function (e.g., reproduction or feeding); and
> 4. accidentals, organisms introduced into caves by mishap or entering in search of a mild climate; they may survive temporarily, but the inability to orient themselves and find food leads to their eventual demise = trogloxenes sensu Sket (2008).

Whereas troglobites, troglophiles, and trogloxenes are each adapted, in their own way, to subterranean life, accidentals are not evolutionary units responding to subterranean selection, hence they are excluded from the Schiner-Racovitza system (Trajano, 2012; Trajano and Carvalho, 2017).

Trajano and Carvalho (2017) provided criteria for classifying cavernicolous species into the Schiner-Racovitza categories. As these authors

emphasized, prior knowledge of the taxonomic group and a combination of evidence from ecology, morphology, and phylogeny, are often required to make a determination.

Geographical isolation in subterranean habitats is the primary criterion distinguishing troglobites from troglophiles and trogloxenes. However, it is impossible to prove epigean absence, therefore, in practice, species known only from caves are usually considered troglobites if there is evidence of morphological differentiation, i.e., troglomorphies such as reduction of visual structures and reduction or absence of pigmentation (Prendini, 2001b; Prendini et al., 2010). The evolution of troglomorphies implies time in isolation resulting in genetic and morphological divergence from epigean relatives, consistent with allopatric speciation (Trajano and Carvalho, 2017). Endogean taxa are particularly problematic for classification according to the Schiner-Racovitza system, however, because many are troglomorphic and may disperse via soil between subterranean habitats. Therefore, morphology and habitat must both be considered when classifying taxa.

Species known only from caves but lacking pronounced troglomorphies should be considered troglophiles a priori, unless ecological data suggest otherwise, e.g., when the epigean habitat is unsuitable for survival (Trajano and Carvalho, 2017). Species recorded in both hypogean and epigean habitats may be considered troglophiles or trogloxenes, the distinction between them ecological, not evolutionary, and driven by factors such as the availability of food, moisture, or shelter. Troglophiles are usually more common, all age/size classes occurring throughout the cave, often far from the surface entrance, and can be found throughout the year, implying a self-sustained source population in the subterranean habitat. Troglophiles may exhibit limited troglomorphism, suggesting incipient geographical and genetic isolation from closely related epigean species.

Trogloxenes, in contrast, are typically found close to cave entrances, allowing them to move easily between epigean and hypogean habitats and are also abundant outside caves (Trajano and Carvalho, 2017). Their epigean distribution is usually associated with rocky areas, as observed in *Pseudouroctonus reddelli* (Gertsch and Soleglad, 1972), a common trogloxene from Texas (Reddell, 1981; Bryson et al., 2014). Many trogloxenes also use caves seasonally and are therefore absent from hypogean habitats during part of the year. Trogloxenes are unlikely to exhibit troglomorphies because source populations are epigean. Whereas trogloxenes are typically found in the vicinity of caves or in karstic areas more broadly, singletons of widespread epigean species recorded inside caves, but otherwise common in areas that would not be considered karstic, are assumed to be accidental.

Troglobitic and Troglomorphic Scorpions: Most scorpions are lapidicolous or lithophilous (Prendini, 2001b) and copious reports document species collected from under stones or in rock crevices outside or inside the entrances of caves. Despite the affinity of scorpions for rocky habitats, however, only a small number of scorpion species appear to be restricted to the subterranean environment and/or present troglomorphies. Consistent with other subterranean taxa, scorpions from cavernicolous environments often exhibit troglomorphies, particularly reduction or loss of the median and/or lateral ocelli, reduction or loss of pigmentation and sclerotization, attenuation of the appendages, loss of the tibial and pedal spurs, and enlargement of the telson vesicle, thought to be associated with enlargement of the venom glands for maximizing prey capture efficiency in a resource-limited environment (Prendini, 2001b; Volschenk et al., 2001; Volschenk and Prendini, 2008). Traditionally, troglomorphies were considered present in troglobitic scorpions but absent in troglophilous scorpions, even those never recorded outside caves (e.g., Reddell, 1981; Sissom and Reddell, 2009). However, an increasing number of markedly troglomorphic scorpions taken from endogean habitats, such as leaf litter, rather than hypogean
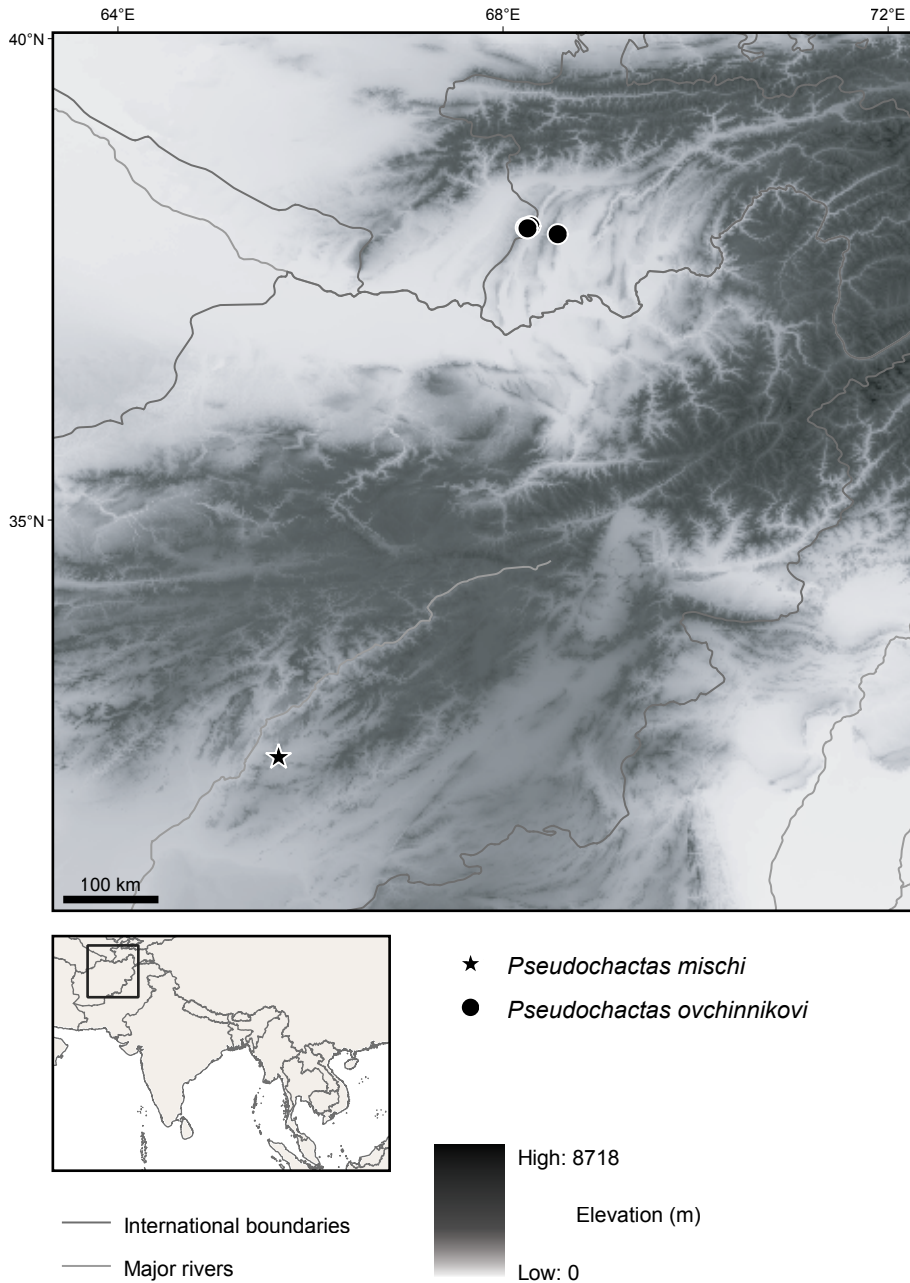
FIGURE 6. Distribution of Pseudochactidae Gromov, 1998 in Central Asia: known localities of *Pseudochactas ovchinnikovi* Gromov, 1998 (circles) in Uzbekistan and Tajikistan; Bolakh, Afghanistan, type locality of *Pseudochactas mischi* Soleglad et al., 2012 (star). Contour interval, 500 m.
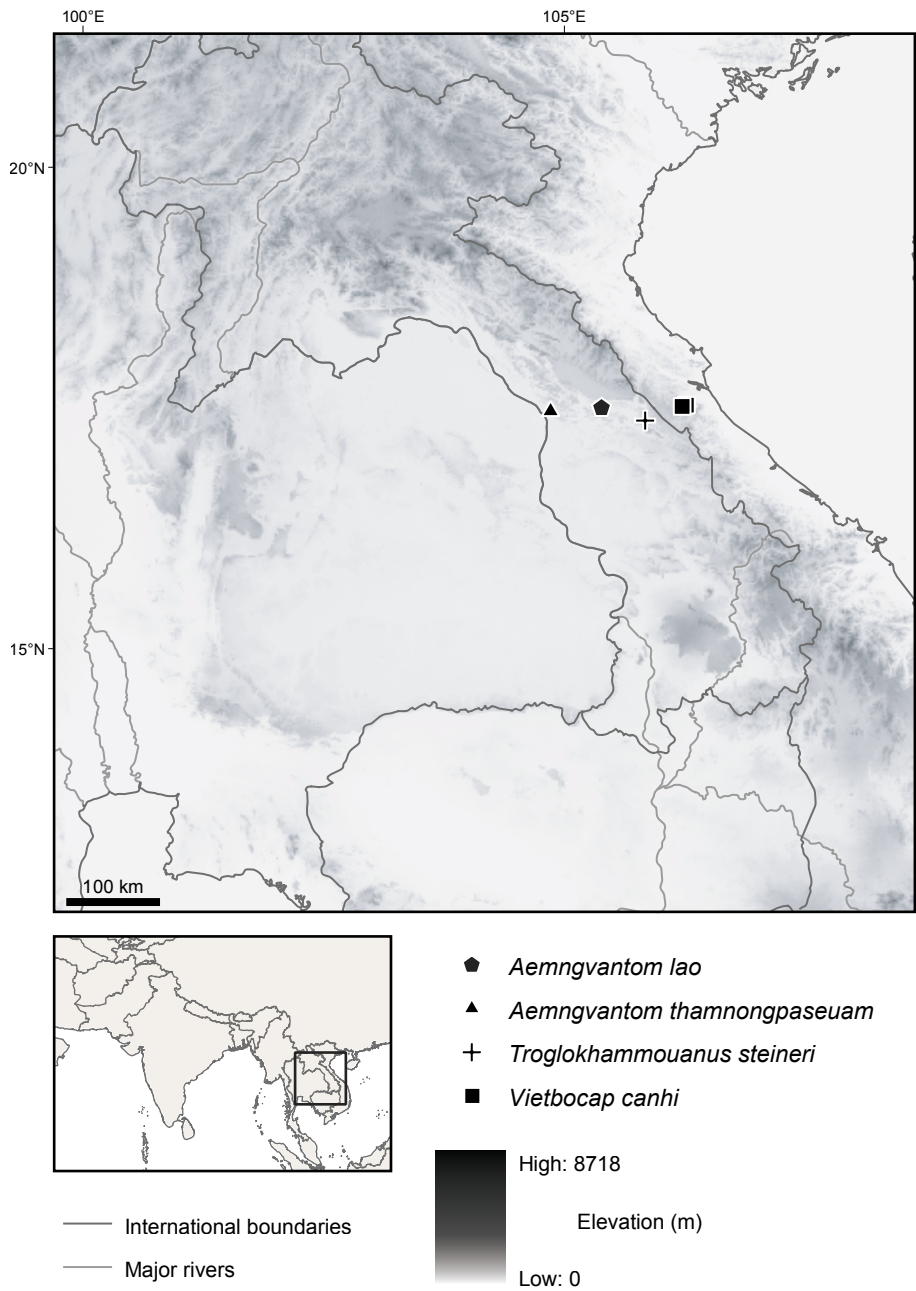
FIGURE 7. Distribution of Pseudochactidae Gromov, 1998 in Southeast Asia: cross, Xe Bang Fai River Cave (Tham Khoun Xe), Laos, type locality of *Troglokhammouanus steineri* Lourenço, 2007; squares, known localities of *Vietbocap canhi* Lourenço and Pham, 2010, in Vietnam: type locality, Tiên Sơn, and Thiên Đường (Paradise Cave), type locality of *Vietbocap aurantiacus* Lourenço et al., 2018, syn. nov., *Vietbocap quinquemilia* Lourenço et al., 2018, syn. nov., and *Vietbocap thienduongensis* Lourenço and Pham, 2012, syn. nov.); pentagon, Tham Nam Lot (Lod), Laos: type locality of *Aemngvantom lao* (Lourenço, 2012), comb. nov., and *Troglokhammouanus louisanneorum* Lourenço, 2017, syn. nov.; triangle, Tham Nong Pa Seuam, Laos, type locality of *Aemngvantom thamnongpaseuam*, gen. et sp. nov.

habitats (caves), led Volschenk and Prendini (2008) to make a distinction between scorpions that are cavernicolous and scorpions that are troglomorphic, and to restrict the definition of troglobitic scorpions to species that are both restricted to cavernicolous (hypogean) habitats and exhibit pronounced troglomorphies. For example, *Belisarius xambeui* Simon, 1879, endemic to the Pyrenees of France and Spain, is eyeless and partially depigmented, with a weakly sclerotized cuticle, and an enlarged telson vesicle. This species inhabits limestone caves and leaf litter in montane forests (Jeannel and Racovitza, 1912, 1914, 1918; Jeannel, 1926; Auber, 1959; Emerit et al., 1996). *Typhlochactas mitchelli* Sissom, 1988, *Typhlochactas sissomi* Francke et al., 2009, and *Typhlochactas sylvestris* Mitchell and Peck, 1977, endogean species collected from leaf litter or under stones in the montane forests of central and southeastern Mexico (Mitchell and Peck, 1977; Sissom, 1988; Francke et al., 2009), are eyeless, completely depigmented, and weakly sclerotized. These endogean species of *Typhlochactas* Mitchell, 1971 resemble their hypogean counterparts, known from caves in eastern Mexico (Mitchell, 1968, 1971; Francke, 1982, 1986; Sissom and Cokendolpher, 1998; Vignoli and Prendini, 2009). The genus *Troglotayosicus* Lourenço, 1981 comprises five species, all without median ocelli and some partially depigmented, from the forests of Colombia and Ecuador (Lourenço, 1981; Botero-Trujillo and Francke, 2009; Botero-Trujillo et al., 2012, 2017; Sánchez-Vialas et al., 2020), only one of which, *Troglotayosicus vachoni* Lourenço, 1981, was collected inside a cave, all others having been taken from leaf litter. *Chaerilus telnovi* Lourenço, 2009, which is partially depigmented, lacks median ocelli, and has reduced lateral ocelli, was also found in the leaf litter, in a karstic region on the Indonesian island of Halmahera. The Venezuelan species, *Broteochactas trezzii* Vignoli and Kovařík, 2003, also partially depigmented and with reduced median ocelli, was collected under a stone inside Sima Aonda, a long narrow gorge, ca. 50 m deep, the remains of a cave, the ceiling

of which collapsed (Forti, 1994; Mecchia and Piccini, 1999). These species demonstrate that the presence of troglomorphies does not necessarily predict the occurrence in cavernicolous habitats. Similarly, several scorpion species, never recorded outside caves, do not possess pronounced troglomorphies or lack troglomorphies altogether, e.g., *Chaerilus pathom* Lourenço and Pham, 2014, *Chaerilus spinatus* Lourenço and Duhem, 2010, *Troglokhammouanus steineri*, and *Troglorhopalurus lacrau* (Lourenço and Pinto-da-Rocha, 1997). Either these species are troglophiles that only recently became isolated in cavernicolous habitats and have not yet evolved troglomorphies, or they are trogloxenes for which epigean records are presently absent. Some cave records, such as *Reddyanus deharvengi* (Lourenço and Duhem, 2010), are presumed to be accidental based on morphology and/or the biology of congeners. Other cases of scorpions reported from caves and/or deemed to be troglobitic, which fail to meet one or both the above-mentioned criteria, i.e., they are neither restricted to cavernicolous habitats nor exhibit pronounced troglomorphies, were provided by Volschenk and Prendini (2008), who concluded that only 21 species, in 14 genera and nine families, worldwide, meet both criteria and can be considered unequivocally troglobitic.

Many new troglomorphic scorpion taxa, including the Southeast Asian pseudochactids covered in the present contribution, have been discovered in the decade since Volschenk and Prendini (2008). It is therefore appropriate to revisit the global diversity of subterranean scorpions, and to reassess the taxa recorded from caves, and identified as troglobites, troglophiles, and trogloxenes by previous authors, in light of conceptual advances to the Schiner-Racovitza system described above (Trajano, 2012; Trajano and Carvalho, 2017; Mammola, 2019). For example, among the Southeast Asian pseudochactids, all of which appear to be obligately cavernicolous, based on the data available, the three species of Vietbocapinae are highly troglomorphic

whereas the sole species of Troglokhammouani-nae is barely so, leading to the conclusion that only the Vietbocapinae can be considered troglobitic. In applying the categories above (Trajano, 2012; Trajano and Carvalho, 2017), as implemented in the key below, numerous records of otherwise epigean scorpion species, lacking troglomorphies, from caves were omitted unless one or more authors suggested such species were potentially adapted or restricted to caves, in which case they were evaluated according to the categories and criteria. Also omitted from consideration are various presently undescribed species, restricted to subterranean environments and/or troglomorphic, from Australia, Ecuador, Mexico, the United States, and Venezuela (e.g., Reddell, 1981, 1982; Pate, 1997; Moulds and Bannik, 2012; Ochoa and Rojas-Runjaic, 2019). Based on application of the criteria, the world totals of troglomorphic vs. troglobitic scorpions are currently 58 vs. 28 species, in 29 vs. 17 genera and 15 vs. 13 families, respectively (table 2; appendix 1). Mexico presently has 38%, or 18 species, of the world's 47 troglomorphic cavernicolous scorpions, followed by Laos and the United States, with 6% (3 species) each.

Key to Ecological Classification of
Cavernicolous and Troglomorphic Scorpions

1. Never collected inside a cave 2
– Collected inside a cave ....3 (hypogean)
2. Troglomorphies absent (e.g., ocelli and pigmentation unmodified) ....epigean
– Troglomorphies present (e.g., loss or reduction of ocelli and pigmentation) ....endogean
3. Only ever collected inside a cave 4
– Collected inside and outside a cave 6
4. Troglomorphies pronounced (especially loss or reduction of ocelli and pigmentation)..troglobite
– Troglomorphies absent or weakly developed..5
5. Collected near or far from cave entrance, throughout the year; no closely related species known outside caves..............troglophile

– Collected seasonally, usually near cave entrance; closely related species abundant outside caves ....trogloxene
6. Collected inside a cave but also collected far from caves; troglomorphies absent .... accidental
– Collected inside a cave (usually near entrance) and also abundant outside cave entrances; troglomorphies absent or weakly developed....................................... trogloxene

MATERIAL AND METHODS

FIELD COLLECTIONS: Scorpions personally collected by the authors were located during the day or night using portable ultraviolet (UV) lamps, comprising a pair of mercury-vapor tubes attached to a chromium parabolic reflector and powered by a rechargeable 7 amp/hr, 12 V battery, or UV light-emitting diode (LED) flashlights, and captured with forceps. Material collected was preserved and injected with 95% ethanol. Portable Garmin™ GPS II Plus and etrex 30 devices were used for recording the geographical coordinates (WGS84 datum) of collection localities in the field.

MATERIAL REPOSITORIES: Type and nontype material is deposited in the following collections: Alexander V. Gromov private collection (AGPC), Almaty, Kazakhstan; American Museum of Natural History (AMNH), New York; František Kovařík Private Collection (FKPC), Prague, Czech Republic; Institute of Ecology and Biological Resources (IEBR), Vietnamese Academy of Sciences, Hanoi; Muséum National d'Histoire Naturelle (MNHN), Paris, France; Phong Nha-Kẻ Bàng National Park (PNKB), Bố Trạch, Vietnam; Victor Fet Private Collection (VFPC), Huntington, West Virginia; Zoological Museum, Moscow State University (ZMMSU), Moscow, Russia. Tissue samples are stored at -150° C in the Ambrose Monell Cryocollection for Molecular and Microbial Research (AMCC) at the AMNH.

MICROSCOPY AND IMAGING: Specimens were examined, and measurements and other meristic data recorded with Nikon SMZ1500 and Leica

TABLE 2

Species Counts and Percentages of Troglomorphic, Endogean, and Hypogean (Cavernicolous) Scorpions according to the Schiner-Racovitza Categories

Family	Troglomorphic	Endogean	Hypogean (Cavernicolous)		
			Troglobite	Troglophile	Trogloxene
Akravidae Levy, 2007	1 (1.7%)		1 (3.6%)		
Belisariidae Lourenço, 1998	3 (5.2%)	2 (14.3%)	1 (3.6%)	1 (5.9%)	
Buthidae C.L. Koch, 1837	5 (8.6%)		1 (3.6%)	4 (23.6%)	3 (16.7%)
Chactidae Pocock, 1893	1 (1.7%)	1 (7.1%)		1 (5.9%)	
Chaerilidae Pocock, 1893	6 (10.3%)	1 (7.1%)	4 (14.3%)	3 (17.6%)	
Diplocentridae Karsch, 1880	5 (8.6%)	2 (14.3%)	3 (10.7%)		1 (5.6%)
Euscorpiidae Laurie, 1896	5 (8.6%)		1 (3.6%)	1 (5.9%)	3 (16.7%)
Hormuridae Laurie, 1896	1 (1.7%)		1 (3.6%)		
Iuridae Thorell, 1876	1 (1.7%)				2 (11.1%)
Pseudochactidae Gromov, 1998	4 (6.9%)		3 (10.7%)	1 (5.9%)	
Scorpiopidae Latreille, 1802	2 (3.4%)		2 (7.1%)		4 (22.2%)
Troglotayosicidae Lourenço, 1998	5 (8.6%)	4 (28.6%)	1 (3.6%)		
Typhlochactidae Mitchell, 1971	11 (18.9%)	3 (21.4%)	8 (28.6%)		
Urodacidae Pocock, 1893	1 (1.7%)		1 (3.6%)		
Vaejovidae Thorell, 1876	7 (12.1%)	1 (7.1%)	1 (3.6%)	6 (35.3%)	5 (27.8%)
Total	58	14	28	17	18

MZ16 stereo dissecting microscopes. Photographs were taken in visible light as well as under long-wave UV light using a Microptics™ ML-1000 digital photomicrography system.

Morphology: Sexual maturity of males and females was assessed based on total length, coloration, sclerotization, granulation, and carination of the tegument (including the presence of a pale, raised, triangular surface on the posteroventral margin of mesosomal sternite V, more pronounced in the adult male), confirmed in a subsample of individuals by observation of testicular tubules or paraxial organs in males and mating plugs or ovariuterine tubules in females. Although the immature stages are not always significantly smaller in total length, the tegument is typically paler, less sclerotized, with less surface granulation, if any, and less pronounced carinae. A pale, raised, triangular surface is absent from the posteroventral margin of mesosomal sternite V in immatures.

The key and diagnoses are based on characters of the external morphology considered informative among Pseudochactidae. Morphological terminology mostly follows Prendini et al. (2006), who introduced new characters concerning carapacial sutures and trichobothrial homology, among others, setting the standard that was subsequently adopted, practically verbatim, by Lourenço (2007a, 2012a, 2017a), Lourenço and Pham (2010, 2012) and Lourenço et al. (2018) and, with minor variations, by Soleglad et al. (2012). The terminology applied by Prendini et al. (2006) is updated for the lateral ocelli, following Loria and Prendini (2014), and for the pectines, the male hemispermatophore, and the carinae and intercarinal surfaces of the pedipalps, in accordance with ongoing research on scorpion systematics and morphology by the first author.

Based on comparisons with the trichobothrial patterns of buthid scorpions, particularly those that deviate from Type A orthobothriotaxy, Prendini et

al. (2006) concluded that the Type D trichobothrial pattern of Pseudochactidae is homologous, fundamentally, with that of Buthidae. More similarities (i.e., potentially synapomorphic or symplesiomorphic trichobothria) than differences between the two patterns were identified, even if Soleglad and Fet's (2001) interpretation was adopted. Prendini et al. (2006) proposed a reinterpretation of the trichobothrial pattern of Pseudochactidae that is more similar to the buthid pattern than either the interpretations of Gromov (1998) or Soleglad and Fet (2001). This reinterpretation, also applied in the present contribution, is only one of several possible reinterpretations for particular trichobothria, however. Other interpretations imply even more potential similarities with Buthidae. Despite recent phylogenetic reconstructions which place Pseudochactidae sister to Chaerilidae, the Type D pattern of Pseudochactidae shares few similarities with the Type B pattern of Chaerilidae, which may be more derived.

A morphological data matrix, comprising 140 characters (appendices 2, 3) scored for 25 terminals (including two outgroups) and incorporating characters from previously published matrices by Lamoral (1980), Stockwell (1989), Prendini (2000), Soleglad and Sissom (2001), Soleglad and Fet (2001), Soleglad and Fet (2003a), and Prendini (2004), augmented by observations in Prendini et al. (2006) was prepared using WinClada ver. 1.00.08 (Nixon, 2002), and deposited in Morphobank (http://morphobank.org/permalink/P3916). Characters scored in the matrix included a variety of traits capturing the morphological diversity within Pseudochactidae, most pertaining to the adult stage: coloration and infuscation, 4 (2.9%); chelicerae, 5 (3.6%); carapace, 24 (17.1%); pedipalps, 60 (42.9%); coxosternum, 4 (2.9%); legs, 5 (3.6%); genital operculum, 1 (0.7%); male and female reproductive anatomy, 4 (2.9%); pectines, 12 (8.6%); tergites, 1 (0.7%); sternites, 3 (2.1%); metasoma, 11 (7.9%); telson, 6 (4.3%). The breakdown of morphological characters by character system is as follows: trichobothria, 36 (25.7%); surface macrosculpture, 35 (25%); shape and size, 14 (10%); pectines, 12 (8.6%); surface topogra-

phy, 7 (5%); ocelli, 7 (5%); pedipalp finger dentition, 6 (4.3%); cheliceral dentition, 5 (3.6%); genitalia, 5 (3.6%); leg setation and spination, 5 (3.6%); color patterns, 4 (2.9%); sutures, 2 (1.4%); respiratory spiracles (stigmata), 1 (0.7%); venom glands, 1 (0.7%). Thirty-four (24%) multistate characters were treated as unordered/nonadditive (Fitch, 1971) to avoid a priori character state transformations, and 58 (41%) characters were uninformative.

MORPHOMETRICS AND MULTIVARIATE STATISTICAL ANALYSIS: Sixty measurements (mm) and 10 counts, following Prendini et al. (2006), were recorded for 53 specimens (tables 6–10), to which corresponding data from the literature (table 3) were added for another 11 specimens, including the types of all described species except *P. ovchinnikovi*, for a total of 64 specimens (n = 20 males and n = 44 females). Morphometric ratios, expressed as mean and range, are provided separately for males and females. Nonmetric multidimensional scaling (NMDS) was conducted on 22 ratios and 8 counts for 60 specimens (n = 20 males and n = 40 females; three female *P. ovchinnikovi* and one female *T. steineri* were omitted due to incomplete measurements), each sex analyzed separately (appendices 4–7; fig. 8), using the programs "vegan" (Oksanen et al., 2020) and "ggplot2" (Wickham, 2016) in R version 4.0.0 (R Core Team, 2020).

DNA SEQUENCING AND GENETIC DISTANCES: Two loci in the nuclear genome, the region comprising the 18S rDNA and the Internal Transcribed Spacer 2 (18S-ITS2) and 28S rDNA (28S), and three loci in the mitochondrial genome, 12S rDNA (12S), 16S rDNA (16S), and cytochrome *c* oxidase subunit I (COI) were Sanger dideoxy sequenced using an ABI Prism 3730 XL DNA Sequencer (Perkin-Elmer, Melville, NY) at the AMNH Sackler Institute of Comparative Genomics. Double-stranded sequences were edited and assembled into consensus sequences using Sequencher ver. 5.4.6 (Gene Codes Corporation, Ann Arbor, MI), and deposited in GenBank (https://www.ncbi.nlm.nih.gov/genbank) (appendix 8).

TABLE 3

Measurements (mm) and Counts for Type and Nontype Specimens of Five Species of the Relictual Asian Scorpion Family Pseudochactidae Gromov, 1998, from Lourenço (2007a, 2012a, 2017a), Lourenço and Pham (2010, 2012), Lourenço et al. (2018), and Soleglad et al. (2012)

Species		P. ovchinnikovi		P. mischi	T. steineri		A. lao			V. canhi		V. aurantiacus	V. quinquemilia	
Synonym						T. louisanneorum				V. thienduongensis				
Type				Holo.	Holo.	Holo.	Holo.	Holo.	Para.	Holo.		Holo.	Holo.	Para.
Sex		♀	♀	subad. ♀	♀	♀	juv. ♀	juv. ♂	juv. ♀	subad. ♂	subad. ♀	♀	juv. ♂	juv. ♀
Total	length	27.3	30.0	18.0	39.1	38.3	23.4	22.4	21.3	27.3	23.9	35.8	25.4	20.2
Carapace	length	3.8	3.9	2.7	5.3	6.6	3.2	2.9	2.8	3.6	3.0	4.5	3.2	2.5
	anterior width	–	–	–	3.0	3.1	2.2	2.0	1.8	2.2	2.0	2.7	2.0	1.8
	posterior width	–	–	–	5.4	5.2	3.1	3.2	2.9	3.5	3.2	4.8	3.3	2.7
Pedipalp	total length	13.3	13.9	9.1	19.5	19.9	14.6	14.5	12.1	17.1	15.0	22.1	15.6	11.7
Femur	length	3.5	3.6	2.3	5.1	5.4	3.8	3.8	3.1	4.5	4.0	6.0	4.1	2.9
	width	1.1	1.2	0.8	2.0	2.2	0.9	0.9	0.7	0.9	1.0	1.3	1.0	0.8
Patella	length	3.4	3.5	2.4	5.5	5.4	4.1	3.6	3.2	4.3	3.8	5.5	4.0	3.1
	width	1.4	1.4	1.0	2.1	2.2	0.9	1.1	0.9	1.2	1.2	1.6	1.1	0.9
Chela	length	6.5	6.8	4.4	8.9	9.1	6.7	7.1	5.8	8.3	7.5	10.6	7.5	5.7
Manus	length	3.2	3.3	2.3	–	–	–	–	–	–	–	–	–	–
	width	2.1	2.1	1.5	3.3	3.5	1.2	1.2	1.0	1.3	1.2	1.7	1.2	1.0
	height	2.3	2.3	1.6	2.6	2.8	1.1	1.0	0.9	1.2	1.2	1.6	1.1	0.9
Fixed finger	length	2.9	2.9	1.7	–	–	–	–	–	–	–	–	–	–
	denticle rows (l/r)	–	–	7/7	7/7	7/7	10/11	8/8	8/8	7/7	–	7/7	7/7	7/7
Mov. finger	length	3.8	4.0	2.4	5.1	5.0	4.4	4.2	3.9	4.6	4.4	6.3	4.4	3.4
	denticle rows (l/r)	–	–	7/7	8/8	7/7	10/11	8/8	8/8	7/7	–	7/7	7/7	7/7
Sternum	length	1.6	1.7	1.1	–	–	–	–	–	–	1.2	2.1	1.4	1.1
	posterior width	1.4	1.5	1.1	–	–	–	–	–	–	1.2	1.8	1.2	1.0
Pectines	marginal lamellae	–	–	3/3	3/3	3/3	3/4	3/4	–	3/4	3/4	3/4	3/3	3/3
	median lamellae	–	–	9/8	13/14	13/14	7/8	8/9	7/7	7/8	6/7	7/8	7/8	7/8
	tooth count (l/r)	–/11	10/10	10/9	14/14	14/14	13/13	9/9	7/7	8/8	7/7	7/7	8/8	7/7
Mesosoma	total length	7.9	10.0	4.6	11.2	9.3	4.9	5.5	6.4	6.7	5.5	8.4	7.4	6.1

TABLE 3 *continued*

Species		P. ovchinnikovi		P. mischi	T. steineri		A. lao			V. thienduongensis	V. canhi	V. aurantiacus	V. quinquemilia	
Synonym						T. louisanneorum								
Type				Holo.	Holo.	Holo.	Holo.	Holo.	Para.	Holo.		Holo.	Holo.	Para.
Sex		♀	♀	subad. ♀	♀	♀	juv. ♀	juv. ♂	juv. ♀	subad. ♂	subad. ♂	♀	juv. ♂	juv. ♀
Metasoma	total length	11.2	11.4	10.7	22.6	23.3	15.3	14.0	12.1	17.0	15.4	22.9	14.8	11.6
Metasoma I	length	1.4	1.4	1.0	2.0	1.9	1.4	1.2	1.0	1.4	1.2	1.9	1.2	1.0
	width	1.9	1.9	1.5	2.9	2.9	1.4	1.4	1.2	1.6	1.5	2.2	1.6	1.2
Metasoma II	length	1.7	1.7	1.1	2.2	2.3	1.5	1.4	1.2	1.7	1.4	2.2	1.4	1.2
	width	1.6	1.7	1.4	2.6	2.5	1.3	1.3	1.0	1.4	1.2	1.9	1.4	1.0
Metasoma III	length	1.8	1.8	1.2	2.5	2.6	1.6	1.5	1.4	2.0	1.7	2.5	1.6	1.3
	width	1.6	1.6	1.4	2.5	2.5	1.3	1.2	0.9	1.4	1.1	1.8	1.3	0.9
Metasoma IV	length	2.1	2.2	1.5	3.1	3.4	2.2	2.1	1.7	2.3	2.2	3.2	2.1	1.6
	width	1.6	1.6	1.3	2.3	2.3	1.2	1.1	0.8	1.3	1.1	1.7	1.2	0.8
Metasoma V	length	4.2	4.2	2.8	5.9	6.3	4.1	3.9	3.2	4.8	4.3	6.3	4.2	3.2
	width	1.5	1.5	1.3	2.3	2.4	1.3	1.1	0.8	1.3	1.0	1.6	1.2	0.8
	height	–	–	–	2.1	2.1	1.1	0.9	0.8	1.2	1.0	1.4	1.1	0.8
Telson	total length	4.4	4.7	3.1	6.9	6.8	4.5	3.9	3.6	4.8	4.6	6.8	4.3	3.3
Vesicle	length	3.2	3.3	2.1	4.9	4.8	3.4	2.4	2.2	3.6	–	–	–	–
	width	1.9	1.8	1.4	2.6	2.5	1.4	1.3	1.0	1.6	1.4	2.2	1.4	1.1
	height	1.6	1.6	1.1	2.3	2.1	1.2	1.2	0.9	1.4	1.2	1.9	1.2	0.9
Aculeus	length	1.2	1.4	1.1	2.0	2.0	1.1	1.5	1.4	1.2	–	–	–	–

TABLE 4

**Counts of Median Denticle Subrows on Fingers of Pedipalp Chela in Species of the
Relictual Asian Scorpion Family Pseudochactidae Gromov, 1998**

	Fixed Finger				
	6	7	8	10	n (fingers)
Pseudochactas mischi		2			2
Pseudochactas ovchinnikovi		108			108
Troglokhammouanus steineri	7	136			143
Aemngvantom lao				66	66
Aemngvantom thamnongpaseuam				2	2
Vietbocap canhi		22	46		68

	Movable Finger				
	6	7	8	10	n (fingers)
Pseudochactas mischi		2			2
Pseudochactas ovchinnikovi		107			107
Troglokhammouanus steineri	1	26	114		141
Aemngvantom lao				64	64
Aemngvantom thamnongpaseuam				2	2
Vietbocap canhi		22	46		68

Sequence length was calculated using the script "gc_calculator.py" in Biopython (Cock et al., 2009). Mean nucleotide composition, the number of variable positions, and the number of parsimony informative sites were calculated for each locus and the concatenated dataset in MEGA v. 10.1.7 (Kumar et al., 2018; Stecher et al., 2020). MEGA was also used to calculate mean uncorrected pairwise genetic distances (*p*-distances) of all loci within and between the species of Pseudochactidae (Kumar et al., 2018; Stecher et al., 2020). Sequences of the COI locus were length invariant, comprising 1078 nucleotide bp in all terminals (table 11; appendix 9). Complete sequences of the 18S locus varied from 1760–1762 bp with a mode of 1760 bp (complete 18S-ITS2 sequences of Pseudochactidae varied from 3384–3926 bp), of the 28S locus, from 2088–2193 bp with a mode of 2188 bp, the 12S locus, from 337–344 bp with a mode of 341 bp, and the 16S locus, from 475–483 bp with a mode of 483 bp.

DNA Sequence Alignment: DNA sequence alignment was performed with MAFFT ver. 7.429 (Katoh et al., 2002; Katoh and Standley, 2013) on the CIPRES Science Gateway (https://www.phylo.org; Miller et al., 2010). All loci except COI were aligned using the Q-INS-i alignment strategy, which considers the secondary structure of RNA; COI was aligned using the G-INS-i alignment strategy. The aligned sequences were concatenated to produce a matrix of 8608 bp. The concatenated alignment contained 2245 variable sites and 1259 parsimony-informative sites. Considered as a percentage of the alignment length of each locus, the numbers of variable positions and parsimony-informative sites were highest for 12S (variable, 58%; parsimony informative, 41%), followed by 16S (49%, 34%), COI (36%, 30%), 18S-ITS (22%, 10%) and 28S (19%, 8%). As expected for a protein-coding gene, the third codon position of the COI was the most informative, containing 27% and 24% of the variable and parsimony-informative sites in the locus, followed by the first codon position, containing 7% and 5%, respectively.

TABLE 5

**Counts of Pectinal Median Lamellae and Teeth in Species of the
Relictual Asian Scorpion Family Pseudochactidae Gromov, 1998**

		Pectinal Median Lamellae												
		5	6	7	8	9	10	11	12	13	14	15	16	*n* (pectines)
Pseudochactas mischi	♀			1	1									2
Pseudochactas ovchinnikovi	♂				3	25	26							54
	♀				25	27								52
Troglokhammouanus steineri	♂									6	39	42	5	92
	♀								53	113	23	1		190
Aemngvantom lao	♂							1	8	16	9			34
	♀							1	23	4				28
Aemngvantom thamnongpaseuam	♀							1	1					2
Vietbocap canhi	♂			7	7	1								15
	♀	2	6	25	1									34

		Pectinal Teeth												
		6	7	8	9	10	11	12	13	14	15	16	17	*n* (pectines)
Pseudochactas mischi	♀				1	1								2
Pseudochactas ovchinnikovi	♂					4	24	26						54
	♀					27	28							55
Troglokhammouanus steineri	♂									7	41	40	6	94
	♀								48	118	23	1		190
Aemngvantom lao	♂							1	8	16	9			34
	♀							1	24	5				30
Aemngvantom thamnongpaseuam	♀								2					2
Vietbocap canhi	♂			9	8	1								18
	♀		4	15	25	2								46

PHYLOGENETIC ANALYSIS: The morphological character matrix and the concatenated dataset of aligned nuclear and mitochondrial DNA sequences (hereafter, "the molecular dataset") were analyzed simultaneously using maximum likelihood (ML), Bayesian inference (BI), and parsimony with equal weighting and implied weighting (Goloboff, 1993), applying five values for the concavity constant, k, ranging from strong to mild (k = 1, 3, 10, 60, 100). The morphological and molecular datasets were also analyzed separately using parsimony with equal weighting and implied weighting with k = 1, 3, 10, 60, 100, and the molecular dataset was analyzed separately using ML and BI. Parsimony analyses were performed using TNT ver. 1.1 (Goloboff et al., 2003, 2008), with a script from Dimitrov et al. (2012, 2013) modified by Santibáñez-López et al. (2014a), which includes tree drifting, mixed sectorial search, and tree fusing for the tree search. Gaps were treated as missing data and uninformative characters deactivated. A jackknife analysis was performed to evaluate nodal support using another script modified from Dimitrov et al. (2012). A bootstrap analysis was performed for comparison

with 1000 pseudoreplicates. The ML analysis was conducted using RAxMLHPC ver. 8.2.12 on CIPRES (Stamatakis, 2006, 2014). The dataset was partitioned by loci, a MULTIGAMMA model was implemented, and, in one run, an ascertainment bias was applied to the Mk model (Lewis, 2001) for the morphological partition. A rapid bootstrap analysis with 1000 replicates (Stamatakis, 2014) was used to search for the ML tree. Twenty-four nucleotide substitution models were tested for each locus using JModelTest2 ver. 2.1.6 (Guindon and Gascuel, 2003; Darriba et al., 2012) on CIPRES. Models were selected using the Akaike Information Criterion (table 11) and a gamma distribution assumed for the morphological dataset (Lewis, 2001). Using these models, BI was conducted in MrBayes ver. 3.2.7a (Ronquist and Huelsenbeck, 2003) on CIPRES with unlinked parameters for all partitions. The analysis was terminated after 25 million generations when the standard deviation of the split frequencies was below 0.01.

Mapping: Distribution maps were produced using QGIS version 3.14 (http://www.qgis.org), by superimposing locality records and borders, coastlines, and rivers from Natural Earth (https://www.naturalearthdata.com) on the global multiresolution terrain elevation data (GTMTED2010; https://www.usgs.gov/core-science-systems/eros/coastal-changes-and-impacts/gmted2010).

Conservation Status: The number of known locality records, extent of the distributional range, occurrence inside or outside protected areas, and prevailing land uses that might be construed as threats to the future survival of pseudochactids, were used to assess its conservation status and assign an appropriate category from the IUCN Red List (IUCN, 2001).

RESULTS AND DISCUSSION

Multivariate Statistical Analysis: Nonmetric multidimensional scaling (NMDS) of morphometric data falsified the hypotheses that *T. louisanneorum* is distinct from *T. steineri* and that *V. aurantiacus*, *V. quinquemilia*, and *V. thien-*

duongensis are distinct from *V. canhi*. The NMDS score for the female holotype of *T. louiseanneorum* (-0.10, 0.03) was similar to that for the female holotype of *T. steineri* (-0.09, 0.01) and both holotypes clustered together with other nontype females of *T. steineri* from the type locality (fig. 8B). Similarly, the NMDS scores were similar for the subadult male holotype of *V. thienduongensis* (0.09, 0.07), the juvenile male holotype of *V. quinquemilia* (0.07, 0.08), and the juvenile male holotype of *V. canhi* (0.08, 0.05), all of which clustered together with other immature males of *V. canhi* from the type locality (fig. 8A), and the scores were similar for the female holotype of *V. aurantiacus* (0.08, -0.07), the juvenile female paratype of *V. quinquemilia* (0.07, -0.07), and the juvenile female paratype of *V. canhi* (0.10, -0.05), all of which clustered together with other nontype females of *V. canhi* from the type locality (fig. 8B).

Phylogenetic Analysis: Separate and simultaneous analysis of the morphological and molecular datasets using parsimony, ML and BI were largely congruent, with high bootstrap and posterior probability values across all analyses. Two major clades were consistently recovered, corresponding to the species from Central and Southeast Asia. Within the Central Asian clade, i.e., *Pseudochactas*, *P. ovchinnikovi* was consistently monophyletic. Within the Southeast Asian clade, *Troglokhammouanus* was consistently recovered as the monophyletic sister group of a monophyletic Vietbocapinae, within which the species from Laos, accommodated within *Aemngvantom*, formed a monophyletic sister group to the Vietnamese *Vietbocap*. Species for which more than one individual was sequenced, i.e., *A. lao*, *P. ovchinnikovi*, *T. steineri*, and *V. canhi*, were consistently monophyletic. The three specimens of *V. canhi* from Tiên Sơn Cave and the six specimens collected from Thiên Đường Cave were also reciprocally monophyletic. The preferred hypothesis for the phylogeny of Pseudochactidae, with unambiguous morphological synapomorphies optimized, is presented (fig. 9). A more detailed explanation of the methods and results of the phylogenetic analyses will be published elsewhere.
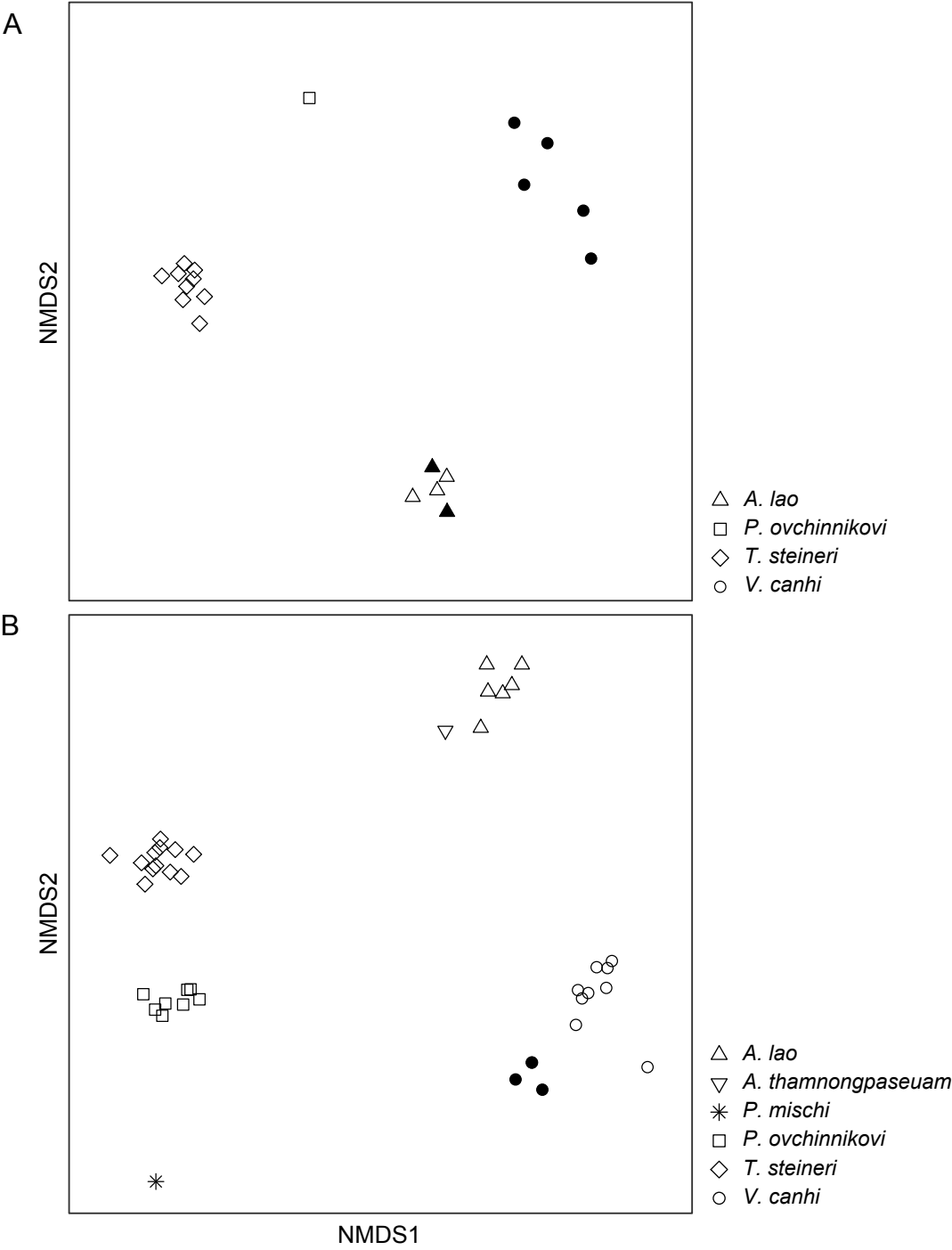
FIGURE 8. Nonmetric multidimensional scaling (NMDS) plots for males (**A**) and females (**B**) of all species in the scorpion family Pseudochactidae Gromov, 1998, based on 22 morphometric ratios and 8 counts, for 60 specimens (49 adults, seven subadults and four juveniles). Each symbol represents an individual, empty (white) symbols represent adults, solid (black) symbols represent immatures.

TABLE 6

Measurements (mm) and Counts of Adult Male and Female Specimens of *Pseudochactas ovchinnikovi* Gromov, 1998 (Pseudochactidae Gromov, 1998), deposited in the American Museum of Natural History, New York

Species			*Pseudochactas ovchinnikovi*								
Sex		♂	♀								
Total	length	19.4	32.0	30.5	30.1	29.7	–	25.2	24.9	24.0	22.6
Carapace	length	2.3	3.7	3.9	3.8	3.8	3.5	3.3	3.2	3.0	2.9
	ant. marg. to oc. tubercle	0.5	1.0	1.1	1.0	1.1	1.0	1.1	0.9	0.8	0.8
	ant. marg. to circumoc. sut.	1.0	1.8	1.8	1.8	1.8	1.6	1.7	1.5	1.4	1.3
	anterior width	1.4	2.1	2.2	2.1	2.2	2.0	1.9	1.8	1.8	1.6
	posterior width	2.3	3.7	3.7	3.6	3.5	3.4	3.1	3.1	3.1	2.9
Pedipalp	total length	10.2	16.8	16.5	15.7	16.6	15.1	14.1	13.3	12.9	12.1
Trochanter	length	1.0	1.9	1.8	1.7	2.0	1.6	1.7	1.6	1.4	1.4
Femur	length	2.4	3.8	3.8	3.6	3.8	3.5	3.2	3.2	3.0	2.8
	width	0.8	1.3	1.3	1.2	1.2	1.2	1.1	1.1	1.0	1.0
	height	0.7	1.2	1.1	1.0	1.2	1.0	0.9	0.9	0.8	0.8
Patella	length	2.3	3.7	3.6	3.5	3.6	3.2	3.0	2.9	2.9	2.7
	width	1.0	1.8	1.8	1.6	1.7	1.5	1.4	1.3	1.3	1.3
	height	0.9	1.4	1.4	1.2	1.3	1.1	1.0	1.0	1.0	1.0
Chela	length	4.5	7.4	7.3	6.9	7.2	6.8	6.2	5.7	5.6	5.2
Manus	length	2.0	3.3	3.4	3.2	3.3	3.1	2.8	2.7	2.6	2.4
	width	1.4	2.5	2.7	2.3	2.6	2.3	2.0	1.9	1.9	1.7
	height	1.2	2.0	2.1	1.9	1.9	1.8	1.6	1.5	1.5	1.5
Fixed finger	length	2.5	4.1	3.9	3.7	3.9	3.7	3.4	3.0	3.0	2.8
	denticle rows (l/r)	7/7	7/7	7/7	7/7	7/7	7/7	7/7	7/7	7/7	7/7
Movable finger	length	2.5	3.8	4.0	3.6	3.8	3.6	3.3	3.1	2.9	2.9
	denticle rows (l/r)	7/7	7/7	7/–	7/7	7/7	7/7	7/7	7/7	7/7	7/7
Sternum	length	1.1	1.8	1.7	1.6	1.8	1.6	1.5	1.4	1.3	1.3
	anterior length	0.6	0.9	0.9	0.9	0.9	0.8	0.8	0.7	0.7	0.7
	anterior width	0.9	1.4	1.4	1.3	1.4	1.3	1.2	1.2	1.1	1.1
	posterior width	1.1	1.6	1.6	1.5	1.5	1.4	1.2	1.3	1.3	1.1
Leg coxa II	length	1.1	1.6	1.7	1.6	1.7	1.5	1.4	1.4	1.4	1.3
Leg coxa III	length	1.1	1.6	1.7	1.6	1.7	1.6	1.4	1.4	1.5	1.3
Leg coxa IV	length	1.6	2.7	2.9	2.7	2.8	2.6	2.4	2.3	2.3	2.1
Pectines	total length	1.7	2.2	2.0	2.0	2.2	1.9	1.8	1.7	1.7	1.5
	length dent. marg.	1.5	2.0	1.6	1.7	1.7	1.6	1.4	1.3	1.4	1.2
	marginal lamellae (l/r)	3/3	3/3	3/3	3/3	3/3	3/3	3/3	3/3	3/3	3/3
	median lamellae (l/r)	10/9	10/9	10/10	9/10	10/9	10/9	9/10	10/9	10/9	10/9
	tooth count (l/r)	11/10	11/10	11/11	10/11	11/10	11/10	10/11	11/10	11/10	11/10

TABLE 6 *continued*

Species		♂	*Pseudochactas ovchinnikovi* ♀								
Mesosoma	total length	5.7	10.0	9.6	10.1	9.0	8.6	8.0	7.8	8.2	7.6
Sternite VII	length	1.2	2.2	1.9	1.7	1.9	1.7	1.6	1.5	1.5	1.5
	width	2.0	3.5	3.4	3.0	3.4	3.0	2.7	2.6	2.6	2.4
Metasoma	total length	11.4	18.3	17.0	16.3	16.9	>15.1	13.9	13.9	12.8	12.1
Metasoma I	length	1.1	1.7	1.4	1.2	1.3	1.3	1.3	1.2	1.0	1.1
	width	1.3	2.2	2.2	2.0	2.2	1.9	1.8	1.7	1.7	1.6
	height	1.1	1.8	1.7	1.6	1.6	1.5	1.5	1.3	1.3	1.3
Metasoma II	length	1.2	1.9	1.8	1.6	1.7	1.6	1.4	1.4	1.2	1.3
	width	1.2	1.9	1.9	1.8	1.9	1.7	1.6	1.5	1.5	1.4
	height	1.1	1.7	1.7	1.5	1.6	1.4	1.4	1.3	1.3	1.2
Metasoma III	length	1.3	2.2	2.0	1.9	2.0	1.9	1.5	1.6	1.5	1.4
	width	1.2	1.9	1.9	1.7	1.9	1.7	1.5	1.5	1.4	1.3
	height	1.0	1.6	1.7	1.5	1.7	1.4	1.3	1.3	1.3	1.2
Metasoma IV	length	1.7	2.7	2.5	2.4	2.5	2.3	2.0	2.0	1.8	1.7
	width	1.1	1.8	1.9	1.7	1.7	1.5	1.5	1.4	1.4	1.3
	height	1.0	1.5	1.6	1.4	1.4	1.3	1.2	1.2	1.2	1.1
Metasoma V	length	3.0	4.6	4.3	4.2	4.3	4.0	3.5	3.6	3.4	3.1
	width	1.1	1.8	1.9	1.6	1.6	1.5	1.4	1.4	1.3	1.2
	height	1.0	1.4	1.5	1.4	1.4	1.3	1.2	1.2	1.2	1.0
Telson	total length	3.2	5.2	5.0	5.0	5.1	>4.03	4.2	4.1	3.9	3.5
Vesicle	length	2.1	3.6	3.5	3.4	3.5	3.3	3.0	2.8	2.7	2.3
	width	1.2	2.0	2.1	1.9	2.0	1.8	1.5	1.6	1.5	1.3
	height	1.1	1.8	1.9	1.6	1.9	1.7	1.4	1.5	1.3	1.1
Aculeus	length	0.7	1.5	1.5	1.4	1.5	–	1.2	1.2	1.1	1.1

GENETIC DIVERGENCE: Uncorrected pairwise genetic distances (*p*-distances) within species were low across all loci, compared to *p*-distances between species (table 12): 12S (0%–3%), 16S (0%–2%), COI (0%–4%), 28S (0%–0.08%) and 18S-ITS2 (0%–0.02%). The *p*-distances between species were higher for the mitochondrial loci, with greatest variation in 12S (6%–28%), followed by 16S (6%–23%), and COI (9%–18%), than for the nuclear loci, in which the distances were higher for 18S-ITS2 (0.8%–4%) than for 28S (0.2%–3%). Low *p*-distances both within and among the samples of *V. canhi* from two Vietnamese caves, Tiên Sơn and Động Thiên Đường, consistent with panmixis, falsified the hypothesis that the two caves harbor four species, i.e., that *V. aurantiacus*, *V. quinquemilia*, and *V. thienduongensis*, are distinct from *V. canhi*.

SYSTEMATICS

Family Pseudochactidae Gromov, 1998

Figures 1–43, tables 1–10

Pseudochactidae Gromov, 1998: 1003, type genus: *Pseudochactas* Gromov, 1998; Fet, 2000: 426; Lourenço, 2000a: 24, 32; 2001: 5; Soleglad and Fet, 2001: 1, 7–9, 10–16, 18, 20–22, 24–26, 35, 38, figs. 2–9, 12, 13, B-1, table 6, appendices B, C; 2003a: 1, 5, 9, 10, 12, 25, 28–30,

figs. 3, 44, table 1; 2003b: 1, 2, 4, 5, 8, 11, 17, 18, 30, 31, 33, 34, 53, 67, 69–71, 74–77, 84, 87–89, 92, 104, 120, 121, 135, 139–146, 148, 150–153, 170, 174, figs. 114, B-1, B-2, B-3, E-1, tables 9, 11, appendices A, B, E; Fet et al., 2003: 2, 3, table 1; Coddington et al., 2004: 309, 310, fig. 18.5; Fet and Soleglad, 2005: 2, 12, table 2; Prendini and Wheeler, 2005: 448, 460, 463–465, 473, 482, 491–494, tables 2, 8, 10; Fet et al., 2006: 269; Graham and Fet, 2006: 1, 2, 11; Prendini et al., 2006: 211, 213, 218–220, 225, 226, 234, 238, 243, tables 2–4, 6, 7; Kovařík et al., 2007: 206; Lourenço, 2007a: 770, 771, 774; 2007b: 1, 5; Lourenço and Goodman, 2008: 667; Soleglad and Fet, 2008: 71; Volschenk et al., 2008: 656, 659, 670; Vignoli and Prendini, 2009: 3, table 1; Lourenço and Pham, 2010: 1, 2, 6, 12; Botero-Trujillo and Noriega, 2011: 41; Fet et al., 2011a: 15; Prendini, 2011: 117; Lourenço, 2012a: 232, 233, 236, 237, appendix A; 2012b: 732, 733, table 1; Lourenço and Pham, 2012: 80, 84, fig. 4; Soleglad et al., 2012: 89, 95, 96; Steiner, 2013: 417, table 1; Yang et al., 2013: 1; Loria and Prendini, 2014: 3, 5, 7, 11, 12, 18, 20, 21, 24, tables 1–4, fig. 3; Lourenço, 2014: 31, 36–38, 45, map 4; Lourenço and Pham, 2014a: 536; Beron, 2015: 172; Sharma et al., 2015a: 351; 2015b: 1, 3–6, 8, 9, table 1, figs. 1, 2b, 4; Lourenço, 2017a: 19; Pham et al., 2017: 133, 134; Beron, 2018: 834; Deharveng and Bedos, 2018: 121; Kovařík et al., 2018: 10; Loria and Prendini, 2018: 186, table 2; Lourenço et al., 2018: 264, 265, 272; Francke, 2019: 32; Howard et al., 2019: 74, 75; Santibáñez-López et al., 2019a: 26, 29, tables 3, 4.

Diagnosis: Pseudochactidae may be separated from all other scorpion families by means of the following combination of characters: carapace with distinct circumocular sutures; pedipalps with Type D trichobothrial pattern; telotarsi of legs I–IV each with pair of ventrosubmedian rows of spinules; Type 1, pentagonal sternum; lamelliform hemispermatophore; metasomal segment V with ventrosubmedian carinae complete.

Pseudochactidae may be separated from Buthidae and Chaerilidae as follows. Whereas basal teeth are absent from the dorsal margin of the cheliceral movable finger in Pseudochactidae, one or two basal teeth are present in Chaerilidae and Buthidae, respectively. A serrula, present on the ventral margin of the cheliceral movable finger in Pseudochactidae, is absent in the other families. Anterosubmedial depressions of the carapace, situated medial to the lateral ocelli, are well developed in Pseudochactidae (figs. 10–12), vestigial in Chaerilidae, and absent in Buthidae. Circumocular sutures of the carapace, present in Pseudochactidae (figs. 10–12), are absent in the other families. Mediolateral major (MLMa) ocelli, absent in Pseudochactidae, are present in the other families. The retrodorsal carina of the pedipalp femur is present and distinct in Pseudochactidae (figs. 23, 28, 34, 38, 42), but often absent or obsolete in the other families. Pedipalp femur trichobothria d_1 and d_6, petite in Pseudochactidae (figs. 23, 28, 34, 38, 42), are full size in the other families, whereas d_4, full size in Pseudochactidae, is petite in Chaerilidae and absent in Buthidae; d_3 and d_4 are situated in the same axis, such that d_3–d_4 is parallel to the retrodorsal carina in Pseudochactidae, d_4 is retrolateral to d_3 such that d_3–d_4 is directed toward the retrodorsal carina (α configuration) in Chaerilidae and some Buthidae, or d_4 is prolateral to d_3 such that d_3–d_4 is directed away from the retrodorsal carina (β configuration) in some Buthidae. The dorsomedian, retromedian, and ventromedian carinae of the pedipalp patella, absent in Pseudochactidae (figs. 23, 28, 34, 38, 42), are present in the other families. Pedipalp patella trichobothium em_1, absent in Pseudochactidae (figs. 23, 28, 34, 38, 42), is present in the other families and est, petite in Pseudochactidae, is full size in the other families. Pedipalp chela trichobothrium it_1 (it situated at the base of the fixed finger) and petite trichobothrium ib_2, present in Pseudochactidae (figs. 24, 25, 29, 30, 35, 36, 39, 43), are absent in the other families, whereas trichobothria est, et, and V_1, absent in Pseudochactidae, are present in the other families. A pair of ventrosubmedian rows

FIGURE 9. Phylogeny of the scorpion family Pseudochactidae Gromov, 1998, obtained by simultaneous phylogenetic analysis of 140 morphological characters and 8608 aligned DNA nucleotides from three mitochondrial and two nuclear gene loci. Maximum likelihood tree with unambiguous morphological synapomorphies optimized. Black circles indicate uniquely derived apomorphic states, white circles parallel derivations of apomorphic states. Numbers above circles indicate characters, numbers below indicate states (appendix 1).

TABLE 7

Measurements (mm) and Counts of Adult Male Specimens of *Troglokhammouanus steineri* Lourenço, 2007 (Pseudochactidae Gromov, 1998), deposited in the American Museum of Natural History, New York

Species		*Troglokhammouanus steineri*								
Sex		♂								
Total	length	34.6	30.5	31.0	31.2	36.4	34.2	31.6	32.1	28.4
Carapace	length	4.8	4.1	4.2	4.2	5.0	4.8	4.2	4.3	4.0
	ant. marg. to oc. tubercle	1.5	1.1	1.3	1.4	1.6	1.8	1.5	1.4	1.3
	ant. marg. to circumoc.	2.6	1.9	2.2	2.1	2.5	2.5	2.1	2.2	1.9
	anterior width	2.6	1.8	2.2	2.1	2.5	2.6	2.2	2.4	1.9
	posterior width	4.5	3.7	3.7	3.7	4.5	4.5	3.8	3.7	3.7
Pedipalp	total length	19.8	16.6	16.8	17.0	19.8	19.7	16.4	17.8	15.9
Trochanter	length	2.1	1.8	1.7	1.8	1.9	2.0	1.6	2.1	1.7
Femur	length	4.7	3.9	4.1	4.1	4.7	4.8	4.0	4.2	3.7
	width	1.6	1.1	1.3	1.3	1.5	1.6	1.2	1.4	1.2
	height	1.2	0.8	1.1	0.9	1.1	1.1	0.9	0.9	1.0
Patella	length	4.7	4.0	4.1	4.1	4.7	4.8	3.8	4.2	3.8
	width	1.7	1.2	1.6	1.6	1.9	1.8	1.5	1.6	1.5
	height	1.8	1.3	1.4	1.4	1.8	1.7	1.4	1.5	1.4
Chela	length	8.4	7.0	7.0	7.1	8.5	8.1	7.0	7.3	6.6
Manus	length	4.1	3.3	3.3	3.4	4.4	4.1	3.5	3.5	3.1
	width	3.6	2.8	2.8	2.9	3.6	3.5	2.9	3.2	2.9
	height	2.7	2.2	2.2	2.2	2.9	2.6	2.3	2.5	2.4
Fixed finger	length	4.3	3.7	3.7	3.7	4.1	4.1	3.5	3.8	3.5
	denticle rows (l/r)	7/7	7/7	7/7	7/7	7/7	7/7	7/7	7/7	7/7
Movable finger	length	4.8	3.8	4.1	3.8	5.0	4.7	3.8	4.2	3.6
	denticle rows (l/r)	8/8	8/8	8/–	8/8	8/8	8/8	8/8	8/8	8/7
Sternum	length	1.8	1.5	1.8	1.7	1.9	1.8	1.6	1.5	1.4
	anterior length	0.4	0.2	0.5	0.5	0.4	0.5	0.3	0.4	0.3
	anterior width	1.4	1.1	1.4	1.3	1.5	1.4	1.2	1.3	1.2
	posterior width	1.7	1.4	1.6	1.4	1.6	1.5	1.4	1.4	1.4
Leg coxa II	length	1.9	1.4	1.6	1.6	2.0	1.8	1.5	1.7	1.6
Leg coxa III	length	2.3	1.6	1.9	1.8	2.3	2.2	1.8	1.9	1.7
Leg coxa IV	length	3.6	2.8	3.2	3.1	3.7	3.6	2.9	3.1	2.6
Pectines	total length	4.1	3.2	3.3	3.4	4.1	3.6	3.3	3.3	3.0
	length dent. marg.	3.8	3.1	3.3	3.3	3.9	3.6	3.1	3.3	2.9
	marginal lamellae (l/r)	3/3	3/3	3/3	3/3	3/3	3/3	3/3	3/3	3/3
	median lamellae (l/r)	15/15	15/15	14/15	14/14	15/14	13/14	14/14	13/14	14/14
	tooth count (l/r)	16/15	16/16	15/16	15/15	16/15	14/15	15/15	14/15	15/15

TABLE 7 *continued*

Species		*Troglokhammouanus steineri*								
Sex		♂								
Mesosoma	total length	9.9	9.0	9.4	9.2	11.6	9.5	10.1	9.1	8.2
Sternite VII	length	2.1	1.8	1.8	1.5	2.2	1.8	1.7	1.7	1.7
	width	3.5	2.8	2.9	2.8	3.5	3.4	2.9	3.2	2.7
Metasoma	total length	20.0	17.3	17.3	17.9	19.8	19.9	17.3	18.7	16.2
Metasoma I	length	1.8	1.6	1.6	1.7	1.9	1.8	1.6	1.8	1.5
	width	2.2	1.9	2.1	2.2	2.4	2.3	2.1	2.1	2.0
	height	2.0	1.6	1.8	1.8	2.2	2.2	1.8	1.9	1.8
Metasoma II	length	2.4	1.9	2.0	1.9	2.2	2.2	2.0	2.1	1.8
	width	2.2	1.8	2.0	1.9	2.4	2.3	2.0	2.1	1.9
	height	1.9	1.5	1.8	1.7	2.1	1.9	1.8	1.8	1.7
Metasoma III	length	2.6	2.1	2.2	2.4	2.4	2.3	2.1	2.4	2.0
	width	2.2	1.7	1.9	1.8	2.4	2.2	1.9	2.1	1.8
	height	1.8	1.5	1.8	1.6	2.0	1.8	1.7	1.8	1.6
Metasoma IV	length	3.3	2.8	3.0	3.0	3.3	3.2	2.8	2.9	2.6
	width	2.1	1.7	1.9	1.8	2.3	2.2	1.9	1.9	1.7
	height	1.8	1.5	1.7	1.6	2.0	1.8	1.6	1.7	1.6
Metasoma V	length	6.1	5.3	5.2	5.5	5.5	5.9	5.1	5.5	4.8
	width	2.1	1.7	1.8	1.8	2.1	2.0	1.8	1.9	1.7
	height	1.8	1.4	1.6	1.5	1.8	1.7	1.6	1.6	1.4
Telson	total length	6.5	5.8	5.7	5.8	6.9	6.9	5.8	6.4	5.5
Vesicle	length	4.7	4.5	4.3	4.4	5.4	5.4	4.4	5.0	4.3
	width	2.2	1.8	1.9	1.9	2.1	2.2	2.0	2.0	1.7
	height	2.1	1.5	1.6	1.6	2.0	2.0	1.7	1.6	1.5
Aculeus	length	1.8	1.3	1.3	1.4	1.5	1.4	1.4	1.4	1.2

of spinules are present on the telotarsi of legs I–IV in Pseudochactidae (fig. 15) whereas a single ventromedian row is present in the other families. Proventral and retroventral rows of (socketed) macrosetae, absent on the telotarsi of legs I–IV in Pseudochactidae (fig. 15), are present in the other families. The ventrosubmedian carinae of metasomal segment V are complete in Pseudochactidae (figs. 20, 21), partial or absent in Buthidae, and absent in Chaerilidae.

Pseudochactidae may be further separated from Chaerilidae as follows. The median and basal teeth of the cheliceral fixed finger are fused into a bicuspid in Pseudochactidae but separate in Chaerilidae.

A lateral eyespot is absent on the carapace in Pseudochactidae (figs. 10–12) but present in Chaerilidae. The prodorsal carina of the pedipalp femur is complete in Pseudochactidae (figs. 23, 28, 34, 38, 42) but partial in Chaerilidae. Pedipalp femur trichobothria i_2 and d_5, and petite trichobothria i_4 and d_2, present in Pseudochactidae (figs. 23, 28, 34, 38, 42), are absent in Chaerilidae, whereas trichobothrium e_4, absent in Pseudochactidae, is present in Chaerilidae. The dorsal prolateral carina of the pedipalp patella, absent in Pseudochactidae (figs. 23, 28, 34, 38, 42), is present in Chaerilidae. A pair of spiniform granules proximally on the dorsoventral projection of the patella prolateral surface

TABLE 8

Measurements (mm) and Counts of Adult Female Specimens of *Troglokhammouanus steineri* Lourenço, 2007 (Pseudochactidae Gromov, 1998), deposited in the American Museum of Natural History, New York

Species		*Troglokhammouanus steineri*										
Sex		♀										
Total	length	37.6	39.0	35.8	39.5	39.3	35.9	39.3	38.0	39.0	39.1	41.3
Carapace	length	5.1	5.3	5.0	5.4	5.3	4.9	5.3	5.3	5.4	5.3	5.6
	ant. marg. to oc. tuber.	1.5	1.7	1.7	1.8	1.8	1.6	1.8	1.7	1.8	1.8	1.9
	ant. marg. to circumoc.	2.5	2.6	2.5	2.8	2.6	2.4	2.7	2.6	2.6	2.6	2.8
	anterior width	2.8	2.4	2.3	2.8	2.6	2.2	2.9	2.6	2.8	2.9	2.9
	posterior width	5.2	5.2	4.6	5.0	5.1	4.5	5.2	5.3	5.1	4.9	5.6
Pedipalp	total length	20.8	21.9	19.5	20.6	20.9	19.1	21.9	20.7	21.3	21.1	21.8
Trochanter	length	2.2	2.8	1.8	2.1	2.2	2.1	2.8	2.2	2.7	2.6	2.4
Femur	length	4.8	5.1	4.6	4.7	4.9	4.5	5.0	4.8	4.9	4.9	5.1
	width	1.8	1.8	1.6	1.6	1.7	1.4	1.9	1.8	1.9	1.7	1.7
	height	1.2	1.1	1.1	1.2	1.2	1.1	1.2	1.2	1.2	1.1	1.2
Patella	length	4.9	5.2	4.8	5.1	5.2	4.7	5.3	5.0	5.1	5.1	5.3
	width	2.0	2.0	1.8	2.1	2.0	1.8	2.0	2.0	2.0	2.0	2.1
	height	1.8	1.8	1.7	1.8	1.9	1.6	1.9	1.8	1.8	1.8	1.9
Chela	length	8.9	8.9	8.3	8.7	8.6	7.9	8.8	8.7	8.6	8.6	9.0
Manus	length	3.9	4.4	3.7	4.1	4.1	3.6	4.2	4.0	4.1	4.1	4.3
	width	3.3	3.2	3.0	3.2	3.3	2.7	3.3	3.1	3.3	3.2	3.5
	height	2.5	2.7	2.4	2.7	2.6	2.3	2.6	2.5	2.6	2.5	2.8
Fixed finger	length	4.9	4.5	4.6	4.6	4.5	4.3	4.6	4.7	4.5	4.5	4.7
	denticle rows (l/r)	7/6	7/7	7/7	7/7	7/6	7/7	7/7	7/7	7/7	7/7	7/7
Movable finger	length	4.9	5.1	4.9	5.0	4.9	4.8	5.2	5.0	5.1	4.9	5.1
	denticle rows (l/r)	8/7	8/8	8/8	7/7	7/7	8/8	8/8	8/8	8/8	8/7	7/7
Sternum	length	2.1	1.9	1.9	2.1	2.0	2.0	2.2	2.1	2.0	2.1	2.0
	anterior length	0.7	0.6	0.5	0.5	0.5	0.6	0.5	0.6	0.4	0.5	0.6
	anterior width	1.5	1.7	1.5	1.6	1.7	1.5	1.8	1.6	1.7	1.6	1.7
	posterior width	1.7	1.9	1.6	1.9	1.8	1.7	1.8	1.8	1.8	1.9	1.8
Leg coxa II	length	2.2	2.0	1.9	2.1	2.1	1.8	2.1	2.0	2.0	2.0	2.1
Leg coxa III	length	2.5	2.3	2.4	2.3	2.3	2.0	2.3	2.5	2.3	2.2	2.5
Leg coxa IV	length	3.6	3.6	3.5	3.7	3.8	3.4	3.8	3.7	3.8	3.6	4.0
Pectines	total length	3.2	3.4	3.1	3.3	3.4	2.9	3.4	3.5	3.3	3.2	3.6
	length dent. marg.	2.8	2.7	2.8	2.8	2.8	2.5	2.8	3.0	2.7	2.9	3.0
	marginal lamellae (l/r)	3/3	3/3	3/3	3/3	3/3	3/3	3/3	3/3	3/3	3/3	3/3
	median lamellae (l/r)	13/12	13/13	13/13	12/13	13/13	12/13	14/14	13/13	12/12	13/14	13/13
	tooth count (l/r)	14/13	15/14	14/14	13/14	14/14	13/14	15/15	14/14	13/13	14/15	15/14

TABLE 8 *continued*

Species		*Troglokhammouanus steineri*										
Sex		♀										
Mesosoma	total length	11.7	12.5	11.3	12.6	12.5	11.9	12.5	12.4	12.5	12.4	13.1
Sternite VII	length	2.4	2.2	2.2	2.5	2.2	2.3	2.4	2.3	2.1	2.5	2.4
	width	3.8	4.0	3.6	4.1	4.1	3.6	4.0	4.0	3.9	3.9	4.1
Metasoma	total length	20.7	21.2	19.5	21.5	21.5	19.2	21.4	20.4	21.1	21.3	22.6
Metasoma I	length	1.8	2.0	1.8	2.1	2.2	1.8	2.0	1.9	1.9	2.0	2.0
	width	2.8	2.6	2.4	2.6	2.8	2.3	2.6	2.8	2.6	2.7	2.7
	height	2.1	2.3	2.2	2.2	2.5	2.0	2.2	2.1	2.3	2.2	2.3
Metasoma II	length	2.4	2.4	2.1	2.6	2.6	2.1	2.4	2.3	2.2	2.4	2.5
	width	2.5	2.4	2.3	2.5	2.6	2.2	2.5	2.6	2.5	2.6	2.7
	height	2.1	2.1	1.9	2.1	2.2	1.9	2.1	2.1	2.1	2.1	2.2
Metasoma III	length	2.5	2.7	2.5	2.6	2.8	2.4	2.6	2.6	2.5	2.7	2.9
	width	2.5	2.4	2.2	2.5	2.5	2.1	2.4	2.5	2.5	2.4	2.5
	height	2.1	2.1	1.9	2.1	2.1	1.9	2.0	1.9	2.0	2.1	2.1
Metasoma IV	length	3.6	3.4	3.1	3.2	3.6	3.2	3.3	3.3	3.6	3.5	3.7
	width	2.3	2.3	2.1	2.3	2.5	2.1	2.3	2.4	2.3	2.4	2.5
	height	1.9	2.0	1.8	2.0	2.1	1.8	2.0	1.9	2.0	1.9	2.1
Metasoma V	length	6.2	6.3	5.9	6.6	6.4	5.7	6.4	6.0	6.4	6.6	6.7
	width	2.2	2.2	–	2.2	2.4	2.0	2.3	2.3	2.3	2.3	2.5
	height	1.9	2.0	–	2.0	2.0	1.7	2.0	1.8	2.0	1.9	2.0
Telson	total length	6.8	7.2	6.7	7.1	6.9	6.4	7.4	6.9	7.0	6.9	7.6
Vesicle	length	4.7	5.6	5.2	5.7	5.4	4.8	5.7	5.5	5.4	5.5	5.9
	width	2.2	2.5	2.2	2.6	2.6	2.2	2.5	2.4	2.3	2.4	2.4
	height	2.1	2.0	1.9	2.0	2.1	1.9	2.1	1.9	2.0	2.1	2.1
Aculeus	length	2.2	1.6	1.5	1.5	1.5	1.6	1.7	1.5	1.7	1.4	1.6

(dorsal and ventral "patellar spurs" situated proximally on dorsal and ventral prolateral carinae, respectively), present in Pseudochactidae (figs. 23, 28, 34, 38, 42), are absent in Chaerilidae. Pedipalp patella trichobothium d_3, present in Pseudochactidae (figs. 23, 28, 34, 38, 42), is absent in Chaerilidae, whereas trichobothria i_2, v_1, v_2 and v_3, absent in Pseudochactidae, are present in Chaerilidae. Pedipalp chela trichobothria Est_1 (*Est* situated distal on the chela manus) and V_2, present in Pseudochactidae (figs. 24, 25, 29, 30, 35, 36, 39, 43), are absent in Chaerilidae, whereas trichobothria it_2 (*it* situated in the proximal third of the fixed finger) and Est_2 (*Est* situated proximal to the movable fin-

ger condyle), absent in Pseudochactidae, are present in Chaerilidae; and trichobothrium Eb_3 is petite in Pseudochactidae but full size in Chaerilidae. The distal margins of the maxillary lobes (coxapophyses) of leg I are unmodified in Pseudochactidae (figs. 22, 26, 27, 32, 33, 37, 40, 41) but distinctly expanded (spatulate or dilate) in Chaerilidae. A basal lobe is present on the hemispermatophore in Pseudochactidae but absent in Chaerilidae. Three marginal lamellae are present in the pectines of Pseudochactidae (figs. 13, 14) whereas two are present, due to fusion of the proximal and medial marginal lamellae, in Chaerilidae, and the marginal and median lamellae are separate, with a longitudi-
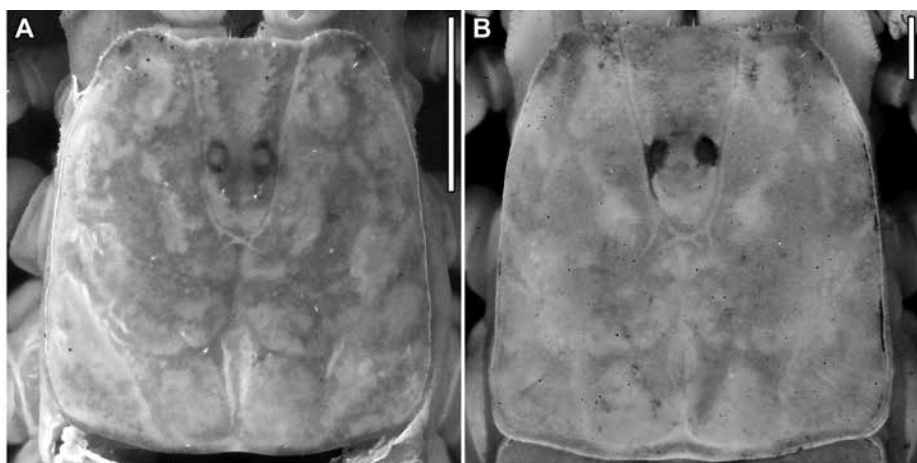
FIGURE 10. *Pseudochactas ovchinnikovi* Gromov, 1998, **A.** ♂, **B.** ♀ (AMNH), Babatag, Uzbekistan, carapace, dorsal aspect. Scale bars = 1 mm.

nal suture present between them, in Pseudochactidae but fused, without a longitudinal suture between them, in Chaerilidae.

Pseudochactidae may be further separated from the buthid subfamily Buthinae C.L. Koch, 1837 as follows. The ventral surface of the cheliceral fixed finger bears four or five small denticles (ventral accessory denticles) in Pseudochactidae but two major teeth in Buthinae. The ventral margin of the cheliceral movable finger bears four or five ventral accessory denticles, appearing to be crenulate, in Pseudochactidae but two large, subequal median teeth in Buthinae. The anterosubmedial lyriform carinae of the carapace are absent or obsolete, granular in Pseudochactidae (figs. 10–12), but pronounced and costate-granular in many Buthinae. The anterolateral major (ALMa), anterodorsal minor (ADMi) and posterodorsal minor (PDMi) ocelli, absent in Pseudochactidae (figs. 10–12), are present in Buthinae. Pedipalp femur petite trichobothrium i_3, absent in Pseudochactidae (figs. 23, 28, 34, 38, 42), is present in Buthinae whereas trichobothrium e_3, present in Pseudochactidae, is absent in Buthinae; trichobothrium d_1 is proximal to trichobothria i_{1-4} in Pseudochactidae but aligned with or distal to i_{1-4} in Buthinae; trichobothrium d_3 is full size in Pseudochactidae but petite in Buthinae. Pedipalp patella trichobothium d_4 and petite trichobothrium

d_5, absent in Pseudochactidae (figs. 23, 28, 34, 38, 42), are present in Buthinae. Pedipalp chela trichobothrium ib_1, present in Pseudochactidae (figs. 24, 25, 29, 30, 35, 36, 39, 43), is absent in Buthinae whereas trichobothrium it_3 (*it* situated distally on the fixed finger), petite trichobothrium Et_4, and petite trichobothrium esb_1 (*esb* situated in the proximal quarter of the fixed finger, between the second and third most proximal retrolateral denticles of the median denticle row), absent in Pseudochactidae, are present in Buthinae. The sternum is pentagonal in Pseudochactidae (figs. 13, 14) but subtriangular in Buthinae. The genital papillae of the male, conspicuously visible along the entire length of the opercula in Pseudochactidae (figs. 13, 14), are inconspicuous in Buthinae. Accessory glands are absent from the paraxial organ in Pseudochactidae but present in Buthinae. A *pars recta* is absent on the hemispermatophore in Pseudochactidae (fig. 31) but present in Buthinae. The reticulate mesh of tubules in the ovariuterine net creates six "cells" in Pseudochactidae but eight in Buthinae. The median lamellae of the pectines are separate, and similar in number to the pectinal teeth in Pseudochactidae (figs. 13, 14), but variously fused, and many fewer in number than the pectinal teeth, in Buthinae. The sockets of the pectinal peg sensillae are smooth in Pseudochactidae but papillate in Buthinae. The
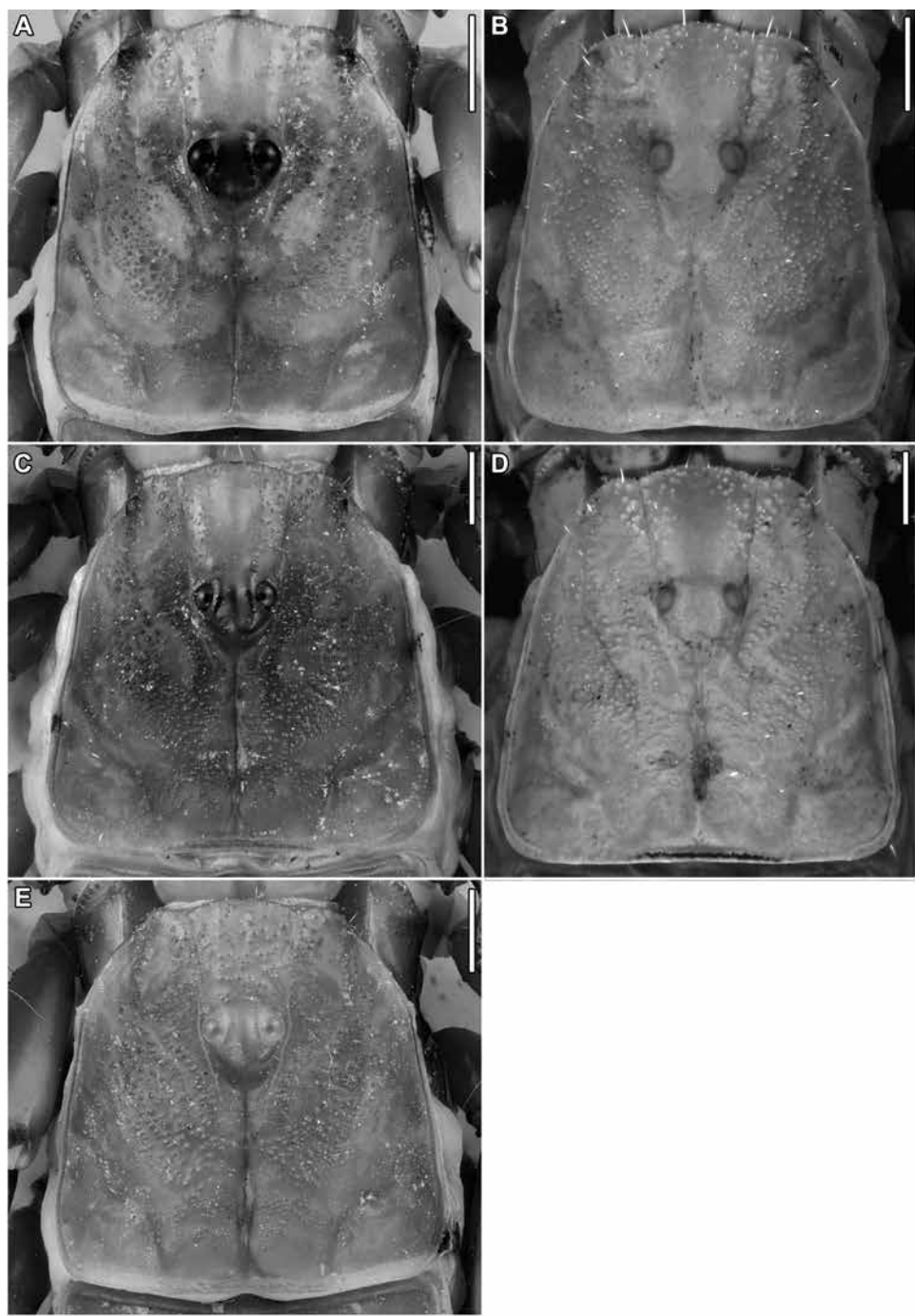
FIGURE 11. *Troglokhammouanus steineri* Lourenço, 2007, **A, B.** ♂, **C–E.** ♀♀ (AMNH), Tham Xe Bang Fai, Laos, carapace, dorsal aspect, with pigmented (**A, C**) or depigmented (**E**) ocelli (UV fluorescence images in **B, D**). Scale bars = 1 mm.

FIGURE 12. Pseudochactidae Gromov, 1998, carapace, dorsal aspect. **A, C.** *Aemngvantom lao* (Lourenço, 2012), comb. nov., **A.** ♂, **C.** ♀ (AMNH), Tham Nam Lot (Lod), Laos. **B, D, F.** *Vietbocap canhi* Lourenço and Pham, 2010, **B.** subadult ♂, **D.** ♀ (AMNH), Tiên Sơn, Vietnam, **F.** ♀ (AMNH), Thiên Đường, Vietnam. **E.** *Aemngvantom thamnongpaseuam*, gen. et sp. nov., holotype ♀ (AMNH), Tham Nong Pa Seuam, Laos. Scale bars = 1 mm.

respiratory spiracles (stigmata) of sternites III–VI are small and circular or oval in Pseudochactidae (figs. 13, 14) but long and slitlike in Buthinae. The ventrosubmedian carinae of metasomal segment I are absent or obsolete in Pseudochactidae (figs. 20, 21) but distinct in many Buthinae. The epithelial walls of the venom glands in the telson vesicle are simple and unfolded in Pseudochactidae but complex and folded in Buthinae. The aculeus is short and shallowly curved in Pseudochactidae (figs. 18, 19) but long and deeply curved in Buthinae.

INCLUDED TAXA: As redefined in the present contribution, Pseudochactidae comprises four genera and six species, accommodated in three subfamilies (table 1): Pseudochactinae Gromov, 1998; Troglokhammouaninae, subfam. nov.; Vietbocapinae Lourenço, 2012.

DISTRIBUTION: The family is endemic to Asia and presently recorded in five countries: Afghanistan, Laos, Tajikistan, Uzbekistan, Vietnam (fig. 5).

ECOLOGY: Both species of Pseudochactinae are epigean, occurring above ground (fig. 2), whereas the four species of Troglokhammouaninae and Vietbocapinae are hypogean, occurring below ground, in caves (figs. 3, 4).

Key to the Subfamilies, Genera, and Species
of Pseudochactidae Gromov, 1998

1. Tegument usually partially infuscate; carapace median and lateral ocelli present (figs. 10, 11); circumocular sutures complete, connected or disconnected posteriorly; pedipalps relatively robust, chela manus prolateral ventral carina complete, fixed and movable fingers (adult ♂) sinuous, sexually dimorphic (figs. 24, 25, 29, 30); legs III and IV, tibial spurs present (fig. 15A, B); telson vesicle lateral and ventral surfaces with granular carinae, subaculear tubercle obsolete (very small bump evident) (fig. 18) .... 2 (Pseudochactinae, Troglokhammouaninae)

– Tegument immaculate; carapace median and lateral ocelli absent (fig. 12); circumocular sutures partial (disconnected); pedipalps gracile, chela manus prolateral ventral carina

absent or obsolete, fixed and movable fingers (adult ♂) sublinear, similar to adult ♀ (figs. 35, 36, 39, 43); legs III and IV, tibial spurs absent (fig. 15C, D); telson vesicle lateral surfaces smooth, ventral surfaces smooth or with sparsely granular (obsolete) carinae, subaculear tubercle absent (fig. 19)................ ....4 (Vietbocapinae)

2. Tegument brown; carapace anteromedian margin convex (procurved), protruding, posterolateral margins gently curved (fig. 11); circumocular sutures disconnected posteriorly; carapace and posttergites I–VI, surfaces granular; pedipalp patella prolateral surface, dorsoventral projection ("anterior process") moderate (fig. 28E, G); pedipalp chela manus dorsomedian, dorsal secondary and subdigital carinae vestigial, retromedian and ventromedian carinae partial, secondary accessory and retroventral carinae incompletely fused, slight disjunction evident in proximal third (figs. 29, 30); legs I–IV basitarsi and telotarsi, spinules long (fig. 15B); sternum ventral surface shallowly concave, lateral margins recurved medially (fig. 13B, D); pectines with 12–16 median lamellae and 13–17 teeth (tables 3, 5, 7, 8); metasomal segments I–IV, dorsosubmedian and dorsolateral carinae, posterior granules markedly larger than preceding granules and spiniform (fig. 16C, D); segments III and IV, median lateral carinae complete (fig. 18C, D); telson vesicle elongate (fig. 20C, D) ....*Troglokhammouanus steineri*

– Tegument yellowish; carapace anteromedian margin sublinear, recessed, posterolateral margins angular, slanting (fig. 10); circumocular sutures connected posteriorly; carapace and posttergites I–VI, surfaces smooth or nearly so; pedipalp patella prolateral surface, dorsoventral projection ("anterior process") pronounced (fig. 23E, G); pedipalp chela manus dorsomedian, dorsal secondary, subdigital and retromedian carinae absent, ventromedian carina vestigial, secondary accessory and retroventral carinae entirely

fused (figs. 24, 25); legs I–IV basitarsi and telotarsi, spinules short (fig. 15A); sternum ventral surface flat/planar, lateral margins sublinear (fig. 13A, C); pectines with 8–12 median lamellae and 9–13 teeth (tables 3, 5, 6); metasomal segments I–IV, dorsosubmedian and dorsolateral carinae, posterior granules similar to preceding granules (fig. 16A, B); segments III and IV, median lateral carinae partial, becoming obsolete anteriorly on III, vestigial or absent on IV (fig. 18A, B); telson vesicle globose (fig. 20A, B) ....3 (*Pseudochactas*)

3. Carapace, tergites, and legs yellowish, immaculate; pedipalp patella retrodorsal carina costate; pectines with 8 or 9 median lamellae and 9 or 10 teeth (tables 3, 5); metasomal segments, median lateral carinae complete on segment II, partial on V ....*Pseudochactas mischi*

– Carapace, tergites, and legs brownish, infuscate; pedipalp patella retrodorsal carina costate granular (fig. 23E, F); pectines with 9–12 median lamellae and 10–13 teeth (tables 3, 5, 6); metasomal segments, median lateral carinae partial, becoming obsolete anteriorly on II, absent or obsolete on V (fig. 18A, B) ....*Pseudochactas ovchinnikovi*

4. Carapace median ocular tubercle (demarcated by posterior margin of circumocular sulci) situated medially (fig. 12B, D, F); circumocular triangle parallel sided (U-shape), median ocular curvatures absent; anterolateral surfaces mostly smooth, sparsely granular near anterior carapace margin; posteromedian margin sublinear to shallowly convex (procurved); pedipalp chela manus elongate, prolateral dorsal carina (♂) absent or obsolete (fig. 43); fixed and movable fingers, median denticle rows comprising seven or eight subrows (tables 3, 4, 10); trichobothrium Et_1 situated distally on manus, aligned with or proximal to movable finger condyle, esb_2 in proximal third of fixed finger, between first and second most proximal retrolateral denticles of median

denticle row (fig. 43B); pectines with 5–8 median lamellae and 6–10 teeth (tables 3, 5, 10); metasomal segments, median lateral carinae complete on I, partial, becoming obsolete anteriorly on II (fig. 19D, E) ....*Vietbocap canhi*

– Carapace median ocular tubercle (demarcated by posterior margin of circumocular sulci) situated anteromedially (fig. 12A, C, E); circumocular triangle subtriangular (broad V-shape), median ocular curvatures present; anterolateral surfaces mostly granular; posteromedian margin shallowly concave (recurved); pedipalp chela manus globose, prolateral dorsal carina (♂) complete (figs. 35, 36, 39); fixed and movable fingers, median denticle rows usually comprising 10 subrows (tables 3, 4, 9, 10); trichobothrium Et_1 situated on fixed finger, slightly distal to movable finger condyle, esb_2 situated approximately midway on fixed finger, between second and third most proximal retrolateral denticles of median denticle row (figs. 35B, 36B, 39B); pectines with 11–14 lamellae and 12–15 teeth (tables 3, 5, 9, 10); metasomal segments I and II, median lateral carinae complete (fig. 19A–C) ....5 (*Aemngvantom*)

5. Carapace mediolateral and posteromedian surfaces granular (fig. 12A, C); posttergites I–VI, surfaces smooth or nearly so; pedipalp segments proportionally longer and narrower and metasomal segments proportionally longer and broader (figs. 17A, B, 19A, B, 21A, B, 34–36; table 9); metasomal segments II–IV, ventrosubmedian carinae, distinct (fig. 21A, B); segment V, dorsolateral and ventromedian carinae distinct, median lateral carinae complete (figs. 17A, B, 21A, B) .... *Aemngvantom lao*

– Carapace mediolateral and posteromedian surfaces smooth (fig. 12E); posttergites I–VI, surfaces granular; pedipalp segments proportionally shorter and broader and metasomal segments proportionally shorter and narrower (figs. 17C, 19C, 21C, 38, 39; table

10); metasomal segments II–IV, ventrosubmedian carinae, absent or obsolete (fig. 21C); segment V, dorsolateral carinae obsolete, median lateral and ventromedian carinae absent or obsolete (figs. 17C, 21C) .... *Aemngvantom thamnongpaseuam*

Subfamily Pseudochactinae Gromov, 1998

Figures 1, 2, 5, 6, 8–10, 13A, C, 15A, 16A, B, 18A, B, 20A, B, 22–25, tables 2–6

Pseudochactidae Gromov, 1998, type genus: *Pseudochactas* Gromov, 1998.

Diagnosis: Pseudochactinae may be separated from the other two subfamilies of Pseudochactidae as follows. The anteromedian margin of the carapace is recessed (posterior to the anterolateral margins) and sublinear in Pseudochactinae (fig. 10) but protruding (anterior to the anterolateral margins) in the other subfamilies, convex (procurved) in Troglokhammouaninae (fig. 11) and shallowly concave (recurved) in Vietbocapinae (fig. 12). The posterolateral margins of the carapace are angular and slanting in Pseudochactinae (fig. 10) but gently curved in the other subfamilies (figs. 11, 12). The circumocular sutures of the carapace are complete and connected posteriorly in Pseudochactinae (fig. 10), complete but disconnected posteriorly in Troglokhammouaninae (fig. 11), and partial (disconnected) in Vietbocapinae (fig. 12). The dorsoventral projection ("anterior process") on the prolateral surface of the pedipalp patella is pronounced in Pseudochactinae (fig. 23E, G) but moderately developed in the other subfamilies (figs. 28, 34, 38, 42). The secondary accessory and retroventral carinae of the pedipalp chela manus are entirely fused in Pseudochactinae (figs. 24C, 25C) but incompletely fused, with a slight disjunction evident in the proximal third, in the other subfamilies (figs. 29, 30, 35, 36, 39, 43). The ventral surface of the sternum is flat/planar in Pseudochactinae (fig. 13A, C)

but shallowly concave in the other subfamilies (figs. 13B, D, 14). The spinules of the basitarsi and telotarsi of legs I–IV are short in Pseudochactinae (fig. 15A) but long in the other subfamilies (fig. 15B–D). The peg sensillae of the pectinal teeth are relatively short, stout, flattened and truncate distally, with laterodistal processes in Pseudochactinae but long, cylindrical, tubular or bottle shaped, and rounded distally, without laterodistal processes in the other subfamilies. The telson vesicle is globose in Pseudochactinae (fig. 20A, B) but elongate in the other subfamilies (figs. 20C, D, 21).

Pseudochactinae may be further separated from Troglokhammouaninae as follows. The base coloration of the tegument is yellow in Pseudochactinae but brown in Troglokhammouaninae. The dorsomedian, dorsal secondary, subdigital, and retromedian carinae of the pedipalp chela manus are absent, and the ventromedian carina vestigial, in Pseudochactinae (figs. 24, 25), whereas the dorsomedian, dorsal secondary and subdigital carinae are vestigial, and the retromedian and ventromedian carinae partial in Troglokhammouaninae (figs. 29, 30). The lateral margins of the sternum are sublinear in Pseudochactinae (fig. 13A, C) but recurved medially in Troglokhammouaninae (fig. 13B, D). The pectines possess 8–12 median lamellae and 9–13 teeth in Pseudochactinae (tables 3, 5, 6) but 12–16 median lamellae and 13–17 teeth in Troglokhammouaninae (tables 3, 5, 7, 8). The posterior granules of the dorsosubmedian and dorsolateral carinae of metasomal segments I–IV are similar in size and shape to the preceding granules in Pseudochactinae (fig. 16A, B) but markedly larger than the preceding granules and spiniform in Troglokhammouaninae (fig. 16C, D). The median lateral carinae are partial, becoming obsolete anteriorly on metasomal segment III, and vestigial or absent on IV in Pseudochactinae (fig. 18A, B) but complete on III and IV in Troglokhammouaninae (fig. 18C, D).

Pseudochactinae may be further separated from Vietbocapinae as follows. The tegument is infuscate (e.g., on the carapace, tergites, and
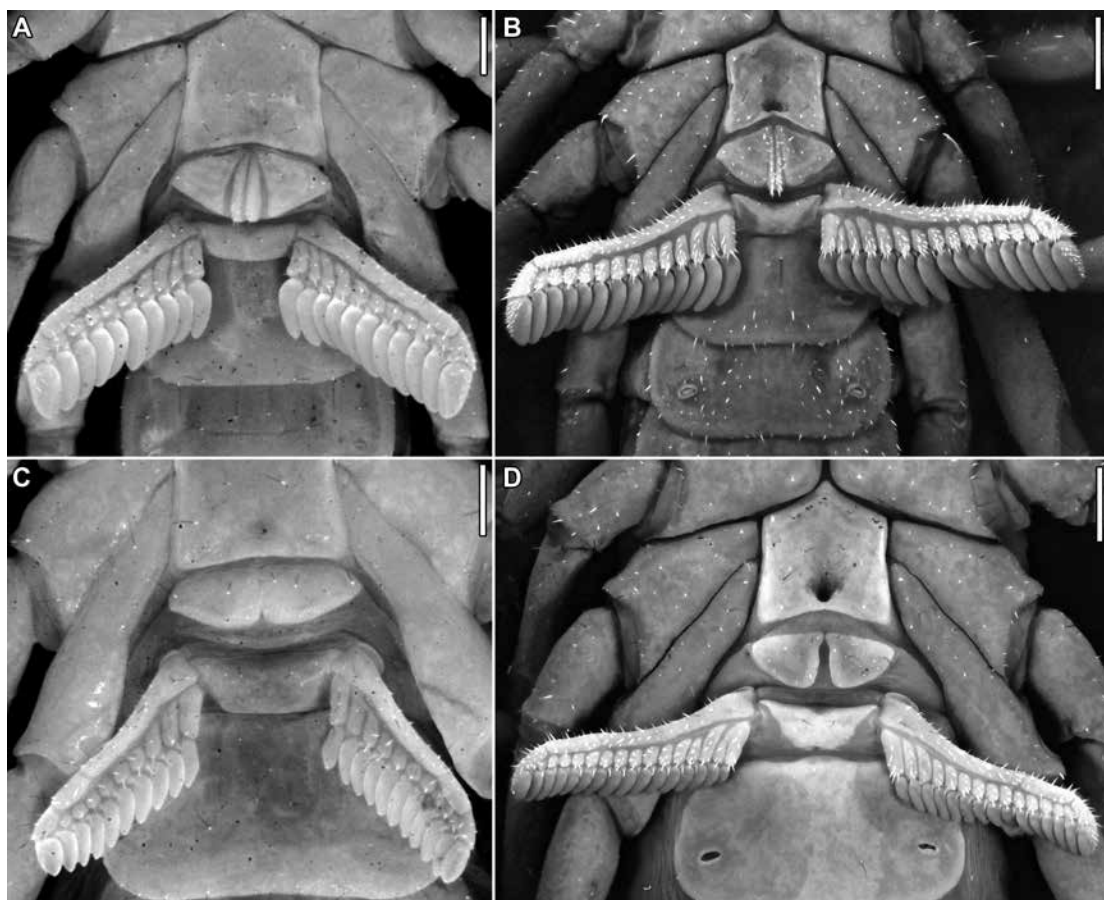
FIGURE 13. Pseudochactidae Gromov, 1998, sternum, genital operculum and pectines, ventral aspect. **A, C.** *Pseudochactas ovchinnikovi* Gromov, 1998, **A.** ♂, **C.** ♀ (AMNH), Babatag, Uzbekistan. **B, D.** *Troglokhammouanus steineri* Lourenço, 2007, **B.** ♂, **D.** ♀ (AMNH), Tham Xe Bang Fai, Laos. Scale bars = 1 mm.

legs) in Pseudochactinae but immaculate in Vietbocapinae. The median and lateral ocelli are present in Pseudochactinae (fig. 10) but absent in Vietbocapinae (fig. 12). The pedipalps are relatively robust, with the chela fingers of the adult male sinuous and sexually dimorphic in Pseudochactinae (figs. 24, 25), whereas the pedipalps are gracile, with the fingers of the adult male sublinear, and similar to the adult female in Vietbocapinae (figs. 35, 36). The prolateral ventral carina of the pedipalp chela manus is complete in Pseudochactinae (figs. 24D, 25D) but absent or obsolete in Vietbocapinae (figs. 35D, 36D, 39D, 43D).

Tibial spurs are present on legs III and IV in Pseudochactinae (fig. 15A) but absent in Vietbocapinae (fig. 15C, D). The lateral and ventral surfaces of the telson vesicle possess granular carinae in Pseudochactinae (figs. 18A, B, 20A, B) whereas the lateral surfaces are smooth, and the ventral surfaces smooth or with sparsely granular (obsolete) carinae in Vietbocapinae (figs. 19, 21). The subaculear tubercle is obsolete (evident as a very small bump) in Pseudochactinae but absent in Vietbocapinae.

INCLUDED TAXA: One genus comprising two species (table 1): *Pseudochactas* Gromov, 1998.
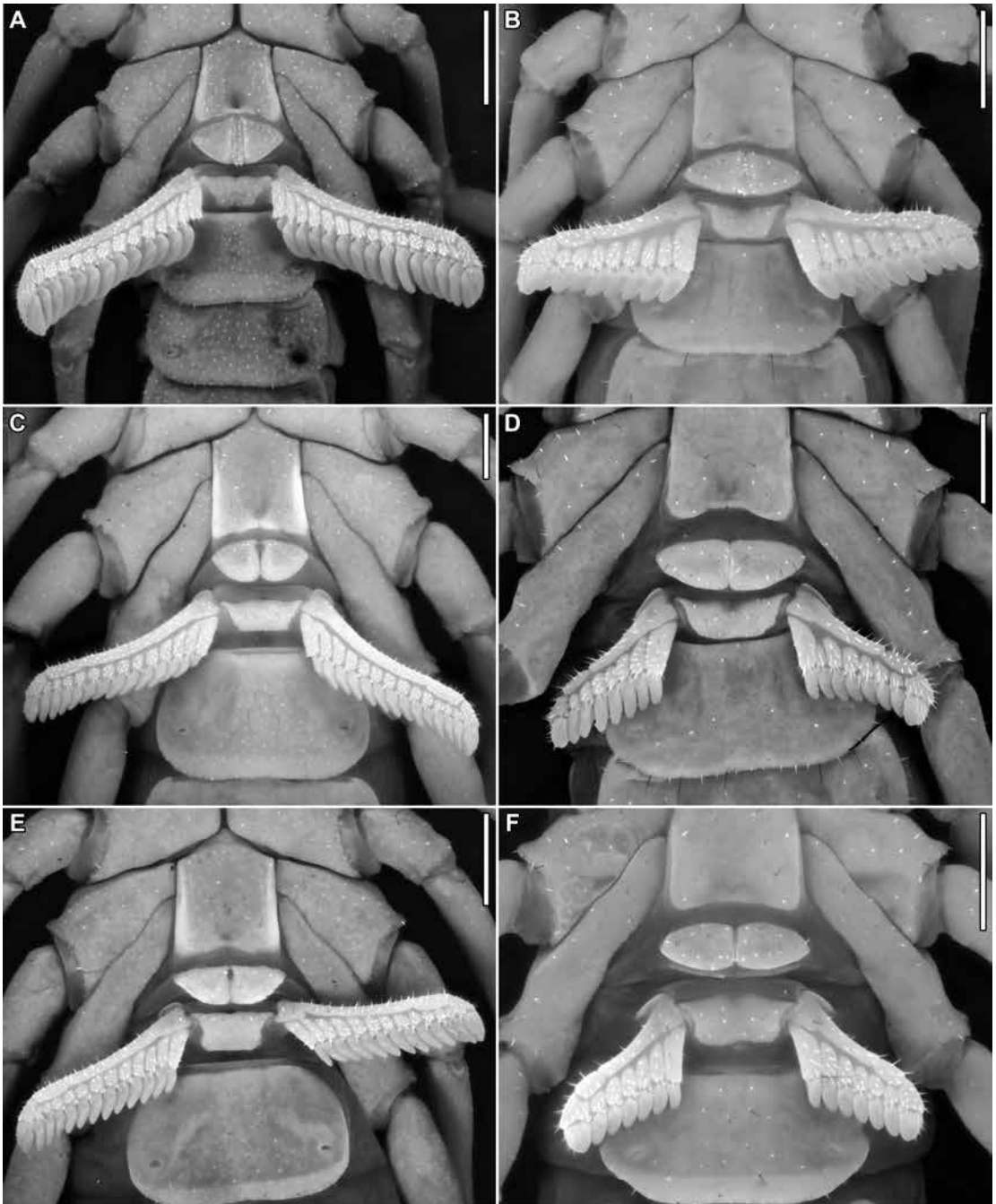
FIGURE 14. Pseudochactidae Gromov, 1998, sternum, genital operculum and pectines, ventral aspect. **A, C.** *Aemngvantom lao* (Lourenço, 2012), comb. nov., **A.** ♂, **C.** ♀ (AMNH), Tham Nam Lot (Lod), Laos. **B, D, F.** *Vietbocap canhi* Lourenço and Pham, 2010, **B.** subadult ♂, **D.** ♀ (AMNH), Tiên Sơn, Vietnam, **F.** ♀ (AMNH), Thiên Đường, Vietnam. **E.** *Aemngvantom thamnongpaseuam*, gen. et sp. nov., holotype ♀ (AMNH), Tham Nong Pa Seuam, Laos. Scale bars = 1 mm.

DISTRIBUTION: Endemic to Central Asia and presently recorded from the countries of Afghanistan, Tajikistan, and Uzbekistan (fig. 6).

ECOLOGY: Both species of Pseudochactinae are epigean, occurring above ground (fig. 2).

Pseudochactas Gromov, 1998

Figures 1, 2, 5, 6, 8–10, 13A, C, 15A, 16A, B, 18A, B, 20A, B, 22–25, tables 2–6

Pseudochactas Gromov, 1998: 1003, type species by monotypy: *Pseudochactas ovchinnikovi* Gromov, 1998; Fet, 2000: 426; Lourenço, 2000a: 24, 32, fig. 6; 2001: 5; Soleglad and Fet, 2001: 1–4, 8, 12, 13, 19, 21, 22, 24, 28, 34, appendix B; 2003a: i, 8, 11–13, 18–20, 29, 30, 32–35, 53, 54, 60, 65–69, 72, 75–79, 88, 89, 121, 122, 135, 139, 143–146, 148, 150–155, 174, figs. 1, 4, 10–12, 41, 49, 57, 64, 92, 108, 115, B-1, B-2, B-3, tables 3, 4, 9, appendices A–C; 2003b: 5, 8, 9, 12, 18–20, 22, 24, 26, figs. 2, 3, 14; Fet et al., 2003: 2, 3, 5, 10, fig. 1, table 1, appendix; 2005: 4, 5, 9, 19–25, 27, figs. 1, 2, 23–25, table 2; Fet and Soleglad, 2005: 27, table 2; Prendini and Wheeler, 2005: 451, 454, 459–462, 470, 474, 482, tables 3, 5, 10; Fet et al., 2006: 272; Graham and Fet, 2006: 2, 11; Prendini et al., 2006: 211, 213, 216, 217, 219, 220, 222, 224–227, 229, 234, 235, 237–243, tables 1, 3, 4, 6, 7, figs. 8–10; Kovařík, et al., 2007: 207; Lourenço, 2007a: 771, 774; Volschenk et al., 2008: 651, 661, 663; Lourenço and Pham, 2010: 2; Loria and Prendini, 2014: 5, 19, 21, tables 2, 4; Lourenço, 2014: 37; Beron, 2018: 834; Francke, 2019: 14, 32, 38.

Preudochactas: Gromov, 1998: 1003.

DIAGNOSIS: As for subfamily.

INCLUDED TAXA: Two species: *Pseudochactas mischi* Soleglad et al., 2012; *Pseudochactas ovchinnikovi* Gromov, 1998.

DISTRIBUTION: As for subfamily.

ECOLOGY: As for subfamily.

Pseudochactas mischi Soleglad et al., 2012

Figures 6, 8B, 9, tables 2–5

Pseudochactas mischi Soleglad et al., 2012: 89–97, tables I, II, figs. 1–13, 14–18 (part), 19a, 19b, 20, 21 (part); Howard et al., 2019: 74, fig. 3G.

TYPE MATERIAL: Holotype: 1 subad. ♀ (FKPC), **AFGHANISTAN: Uruzgan [Orozgan] Prov.:** *Tarin Kowt Distr.*: Bolakh [Balagh] village, 1380 m (4300 ft), 32°32′N 65°40′E, xi.2011, M. Misch.

DIAGNOSIS: *Pseudochactas mischi* may be separated from the morphologically similar *P. ovchinnikovi*, by means of differences in coloration and carination. The coloration is paler and yellowish, the carapace, tergites, and legs immaculate, in *P. mischi* but darker and brownish, the carapace, tergites and legs infuscate, in *P. ovchinnikovi*. The lyriform anterosubmedial carinae of the carapace are absent in *P. mischi* but obsolete, granular in *P. ovchinnikovi* (fig. 10). The retrodorsal carina of the pedipalp patella is costate in *P. mischi* but costate granular in *P. ovchinnikovi* (fig. 23E, F). The pedipalp chela, metasoma, and telson vesicle are more robust (proportionally shorter and broader) in *P. mischi* than *P. ovchinnikovi* (tables 3, 6). The pectines possess 8 or 9 median lamellae and 9 or 10 teeth in *P. mischi* (tables 3, 5) but 9–12 median lamellae and 10–13 teeth in *P. ovchinnikovi* (tables 3, 5, 6). The median lateral carinae are complete on metasomal segment II, and partial on V in *P. mischi* but partial, becoming obsolete anteriorly, on II, and absent or obsolete on V in *P. ovchinnikovi* (fig. 18A, B). The telson vesicle lateral and ventral surfaces are more coarsely and densely granular in *P. mischi* than *P. ovchinnikovi* (figs. 18A, B, 20A, B).

DESCRIPTION: The following description supplements the original description of the holotype. As Soleglad et al. (2012) suggested, the holotype and only known specimen is indeed a subadult female. The adults of both sexes are unknown.

Total length: Small, 18 mm (table 3).

Color: Tegument base coloration pale yellowish orange, immaculate. Chelicerae, pedipalps (except chela fingers), legs, posterior third of tergites and sternites, metasoma, and telson slightly paler than carapace, pedipalp chela fingers, and anterior two-thirds of tergites and sternites. Pedipalp chela fingers light reddish. Sternum, genital operculum, pectines, and sternites pale yellow. Aculeus black.

Chelicerae: Fixed finger, dorsal margin with four teeth (basal, median, subdistal, distal); basal and median teeth fused into bicuspid ("conjoined on trunk"); space between median and subdistal teeth U-shaped; ventral margin with four small denticles (ventral accessory denticles). Movable finger, dorsal margin with three teeth (median, subdistal, retrolateral distal), without basal teeth; ventral margin with four small denticles (ventral accessory denticles) and serrula in distal third; retrolateral (dorsal) distal and prolateral (ventral) distal teeth subequal, retrolateral (dorsal) distal tooth smaller than prolateral (ventral) distal tooth and opposable. Ventral surface of fingers and manus with numerous long, dense macrosetae.

Carapace: Carapace slightly wider than long. Anterior margin sublinear, shallowly recessed medially; anterolateral margins entire; posteromedian margin shallowly concave (recurved); posterolateral margins angular, slanting. One pair of very small anterolateral major (ALMa) ocelli situated close to anterolateral margins of carapace, other lateral ocelli absent. Anterosubmedial depressions, medial to lateral ocelli, well developed. Median ocular tubercle situated anteromedially on carapace, distance from anterior margin 33% of carapace length (table 3); pair of median ocelli considerably larger than lateral ocelli; superciliary carinae obsolete, not protruding above ocelli; interocular sulcus shallow, obsolete. Circumocular sutures complete, connected posteriorly (postocular); circumocular triangle subtriangular (broad V-shape); median ocular curvatures present. Anteromedian depression narrow, shallow; posteromedian sulcus very shallow anteriorly,

becoming slightly deeper posteriorly; posterolateral sulci very shallow, wide, weakly curved; posteromarginal sulcus narrow, shallow. Carapacial surfaces smooth, except for sparse granulation anteromedially, and acarinate.

Pedipalps: Pedipalps relatively robust; segments almost apilose, sparsely covered in short microsetae and few macrosetae. Pedipalp femur length 67% greater than width (table 3). Femur with seven carinae evident; promedian carina obsolete, reduced to few spiniform granules in proximal two-thirds of segment; prodorsal, proventral and retrodorsal carinae well developed, granular to costate granular (serrate to crenulate); dorsomedian and retromedian carinae weak, granular rows; retroventral carina vestigial, comprising short granular row; dorsal intercarinal surface sparsely granular proximally; other intercarinal surfaces smooth. Pedipalp patella length 57% greater than width (table 3). Patella with six carinae evident; prodorsal carina well developed, granular; retrodorsal carina well developed, costate; proventral and retroventral carinae well developed, costate granular (crenulate); prolateral surface, dorsoventral "vaulted" projection ("anterior process") well developed, with prominent pair of dorsal and ventral spiniform granules ("patellar spurs") proximally, demarcating pair of vestigial, prolateral carinae ("dorsal and ventral patellar spur carinae"), reduced to two granules; dorsomedian, retromedian, and ventromedian carinae absent; intercarinal surfaces smooth. Pedipalp chela relatively short and broad; manus globose, height 4% greater than width and length 33% greater than width (table 3); length of movable finger 4% greater than length of manus. Chela with six carinae evident; dorsomedian carina reduced to few granules at base of fixed finger, becoming obsolete proximally on manus; digital carina well developed, granular in proximal sixth, remainder costate; secondary accessory and retroventral carinae entirely fused; retroventral carina well developed, granular proximally, becoming costate distally, aligned parallel to longitudinal axis of chela, with distal margin connected to retrolateral movable finger condyle; prodorsal, promedian, and proventral carinae

TABLE 9

Measurements (mm) and Counts of Male and Female Specimens of *Aemngvantom lao* (Lourenço, 2012), comb. nov. (Pseudochactidae Gromov, 1998), deposited in the American Museum of Natural History, New York

Species		*Aemngvantom lao*								
Sex		♂			subad. ♂		♀				
Total	length	24.5	28.5	29.5	21.7	26.1	37.4	23.9	26.5	36.5	34.9
Carapace	length	2.9	3.5	3.5	2.8	3.4	4.7	3.2	3.4	4.6	4.2
	ant. marg. to oc. tuber.	0.9	1.2	1.2	0.9	1.1	1.6	1.0	1.1	1.6	1.3
	ant. marg. to circumoc.	1.2	1.4	1.5	1.1	1.5	1.9	1.2	1.3	1.9	1.7
	anterior width	1.3	1.6	1.5	1.2	1.5	2.3	1.6	1.6	2.3	1.9
	posterior width	2.7	3.2	3.0	2.4	3.2	4.0	2.8	3.1	4.0	3.7
Pedipalp	total length	15.0	17.8	18.1	14.0	17.4	23.9	16.9	17.6	23.8	22.2
Trochanter	length	1.3	1.4	1.6	1.2	1.4	2.2	1.3	1.6	2.2	1.9
Femur	length	3.7	4.4	4.3	3.3	4.2	5.7	4.0	4.2	5.7	5.3
	width	0.8	1.0	1.0	0.7	0.9	1.3	0.8	0.8	1.3	1.1
	height	0.5	0.6	0.6	0.5	0.9	0.9	0.4	0.5	0.9	0.6
Patella	length	3.8	4.4	4.5	3.7	4.2	5.7	4.2	4.4	5.8	5.4
	width	0.9	1.1	1.1	0.9	1.0	1.4	0.9	0.9	1.4	1.3
	height	0.8	0.9	0.9	0.8	0.9	1.3	0.8	0.8	1.4	1.0
Chela	length	6.1	7.7	7.8	5.8	7.6	10.3	7.5	7.5	10.1	9.6
Manus	length	2.4	2.9	2.9	2.0	2.5	3.6	2.5	2.7	3.5	3.3
	width	1.2	1.5	1.5	1.0	1.1	1.7	1.1	1.1	1.7	1.5
	height	1.0	1.4	1.4	0.9	1.1	1.5	1.1	1.0	1.6	1.4
Fixed finger	length	3.7	4.7	4.8	3.8	5.1	6.7	4.9	4.8	6.6	6.3
	denticle rows (l/r)	10/10	10/10	10/10	10/10	10/10	10/10	10/10	10/10	10/10	10/10
Movable finger	length	4.0	4.8	5.0	3.8	4.9	6.8	5.0	4.9	6.6	6.3
	denticle rows (l/r)	10/10	10/10	10/10	10/10	10/10	10/10	10/10	10/10	10/10	10/10
Sternum	length	1.2	1.5	1.4	1.1	1.6	2.0	1.4	1.5	2.0	1.7
	anterior length	0.2	0.4	0.5	0.2	0.4	0.3	0.4	0.3	0.5	0.4
	anterior width	0.8	1.1	1.0	0.7	1.0	1.2	1.1	1.0	1.4	1.3
	posterior width	1.1	1.2	1.1	1.0	1.4	1.4	1.3	1.1	1.5	1.6
Leg coxa II	length	1.4	1.6	1.7	1.0	1.4	1.8	1.5	1.6	1.9	1.7
Leg coxa III	length	1.5	1.8	2.0	1.1	1.5	2.1	1.7	1.8	2.2	2.0
Leg coxa IV	length	2.3	3.0	3.1	2.0	2.7	4.0	2.9	2.9	3.7	3.4
Pectines	total length	2.6	3.4	3.2	1.8	3.0	3.1	2.2	2.0	3.3	2.9
	length dent. marg.	2.5	3.1	3.1	1.7	3.0	2.6	1.8	1.9	2.7	2.3
	marginal lamellae (l/r)	3/3	3/3	3/3	3/3	3/3	3/3	3/3	3/3	3/3	3/3
	median lamellae (l/r)	14/14	13/13	13/14	14/13	13/13	13/13	12/12	12/11	12/12	12/12
	tooth count (l/r)	15/15	14/14	14/15	15/14	14/14	14/14	13/13	13/12	13/13	13/13

TABLE 9 *continued*

Species		Aemngvantom lao								
Sex		♂			subad. ♂		♀				
Mesosoma	total length	7.3	8.1	9.0	6.5	7.8	12.5	6.7	8.5	11.1	10.6
Sternite VII	length	1.5	1.6	1.7	1.3	1.6	2.0	1.4	1.7	2.0	1.8
	width	2.2	2.5	2.6	1.9	2.4	3.1	2.4	2.7	3.3	3.2
Metasoma	total length	14.3	17.0	17.0	12.4	14.9	20.3	14.0	14.6	20.7	20.2
Metasoma I	length	1.5	1.8	1.9	1.2	1.4	1.9	1.2	1.3	1.9	2.0
	width	1.4	1.6	1.8	1.2	1.6	2.1	1.4	1.4	2.0	2.2
	height	1.2	1.5	1.6	1.0	1.4	1.8	1.2	1.3	1.7	1.6
Metasoma II	length	1.6	2.0	2.1	1.4	1.7	2.4	1.6	1.6	2.4	2.3
	width	1.4	1.6	1.6	1.1	1.4	1.7	1.2	1.2	1.8	1.7
	height	1.2	1.4	1.5	1.0	1.3	1.8	1.0	1.1	1.6	1.6
Metasoma III	length	1.7	2.2	2.3	1.5	1.8	2.7	1.8	1.7	2.7	2.4
	width	1.4	1.6	1.6	1.0	1.4	1.7	1.1	1.2	1.8	1.6
	height	1.1	1.3	1.4	1.0	1.2	1.7	1.0	1.1	1.6	1.5
Metasoma IV	length	2.4	2.8	2.9	1.9	2.4	3.4	2.3	2.3	3.4	3.3
	width	1.3	1.5	1.6	1.0	1.3	1.7	1.0	1.2	1.7	1.6
	height	1.1	1.3	1.4	0.9	1.1	1.5	1.0	1.1	1.5	1.4
Metasoma V	length	4.7	5.2	5.1	4.1	4.6	6.2	4.3	4.6	6.3	6.2
	width	1.3	1.4	1.4	1.0	1.3	1.7	1.0	1.2	1.7	1.5
	height	1.0	1.3	1.2	0.9	1.1	1.4	0.9	1.1	1.5	1.3
Telson	total length	4.1	5.2	5.0	3.9	4.8	6.3	4.6	4.7	6.8	6.4
Vesicle	length	2.8	3.8	3.7	3.3	3.7	4.5	3.4	3.4	4.7	4.6
	width	1.4	1.6	1.6	1.0	1.4	1.9	1.2	1.4	2.0	1.9
	height	1.1	1.3	1.4	0.9	1.2	1.7	1.1	1.3	1.8	1.8
Aculeus	length	1.4	1.4	1.4	0.7	1.1	1.9	1.2	1.3	2.1	1.8

weakly developed, each comprising few isolated granules; dorsal secondary, subdigital, retromedian (retrolateral secondary) and ventromedian carinae absent or obsolete; intercarinal surfaces smooth. Fixed and movable fingers, dentate margins sublinear (♀), no proximal "gap" evident when closed; median denticle rows comprising seven ($n = 2$) oblique and slightly imbricated subrows (tables 3, 4), decreasing in length distally; each subrow comprising large retrolateral denticle proximally (absent from proximal subrow, for total of six retrolateral denticles on fixed and movable fingers), several small median denticles, and large prolateral denticle distally, slightly offset (total of six and seven prolateral denticles on fixed and movable fingers, respectively); terminal (prolateral) denticle of first subrow enlarged; accessory denticles absent.

Trichobothria: Orthobothriotaxic, Type D, β configuration, trichobothrium d_2 situated on femur dorsal surface, d_3 and d_4 in same axis, parallel and closer to retrodorsal carina than d_1, angle formed by d_1, d_3 and d_4 opening toward prolateral surface, with the following segment totals: femur, 12 (6 dorsal, 3 prolateral, 3 retrolateral); patella, 10 (3 dorsal, 1 prolateral, 6 retrolateral); chela, 13 (5 manus, 8 fixed finger). Total number of trichobothria per pedipalp, 35. Five trichobothria on femur, i_4, d_1, d_2, d_4, and d_6, one on patella, est_1, and one on

TABLE 10

Measurements (mm) and Counts of the Holotype Female of *Aemngvantom thamnongpaseuam*, gen. et sp. nov., and Male and Female Specimens of *Vietbocap canhi* Lourenço, 2010 (Pseudochactidae Gromov, 1998), deposited in the American Museum of Natural History, New York

Species		A. tham.	Vietbocap canhi								subad. ♂	
Sex		Holotype ♀	♀									
Total	length	30.0	32.8	31.3	32.2	32.1	29.3	29.8	28.1	27.2	24.2	24.0
Carapace	length	4.0	4.0	3.9	3.8	3.9	3.5	3.7	3.4	3.4	3.2	3.0
	ant. marg. to oc. tuber.	1.2	1.8	1.8	1.8	1.8	1.6	1.6	1.6	1.5	1.4	1.4
	ant. marg. to circumoc.	1.7	2.3	2.3	2.2	2.3	2.0	2.1	2.0	2.0	1.9	1.8
	anterior width	2.1	2.2	2.1	2.2	2.0	1.7	1.8	1.6	1.7	1.9	1.6
	posterior width	3.9	4.1	4.0	4.0	4.0	3.4	3.5	3.1	3.5	3.4	3.0
Pedipalp	total length	19.2	21.0	21.1	21.1	21.3	19.3	20.3	19.2	19.9	17.0	16.6
Trochanter	length	1.8	2.2	2.1	1.9	2.0	1.7	2.0	2.0	1.7	1.6	1.7
Femur	length	4.6	4.8	4.9	5.1	5.1	4.7	4.8	4.6	4.9	4.1	4.1
	width	1.1	1.1	1.0	1.0	1.0	0.8	0.9	0.8	1.0	1.0	0.9
	height	0.8	1.0	0.8	0.7	0.7	0.7	0.6	0.7	0.7	0.8	0.8
Patella	length	4.6	4.8	4.7	4.6	4.7	4.3	4.6	4.3	4.4	3.9	3.7
	width	1.3	1.3	1.4	1.4	1.3	1.2	1.3	1.2	1.2	1.1	1.1
	height	1.1	1.3	1.2	1.2	1.3	1.1	1.1	1.1	1.1	1.0	1.0
Chela	length	8.3	9.3	9.4	9.4	9.5	8.5	9.0	8.3	9.0	7.4	7.2
Manus	length	3.3	4.3	4.1	4.1	4.2	3.7	3.8	3.7	3.8	3.2	3.0
	width	1.7	1.4	1.5	1.4	1.4	1.3	1.3	1.2	1.2	1.1	0.9
	height	1.5	1.6	1.5	1.5	1.4	1.4	1.4	1.2	1.3	1.2	1.0
Fixed finger	length	5.0	5.1	5.4	5.3	5.4	4.9	5.2	4.5	5.2	4.2	4.2
	denticle rows (l/r)	10/10	8/8	8/8	8/8	8/8	8/8	8/8	8/8	7/7	8/8	8/8
Movable finger	length	5.1	5.7	5.6	5.6	5.5	5.4	5.5	4.7	5.3	4.4	4.5
	denticle rows (l/r)	10/10	8/8	8/8	8/8	8/8	8/8	8/8	8/8	7/7	8/8	8/8
Sternum	length	1.6	1.6	1.7	1.7	1.6	1.6	1.5	1.5	1.5	1.4	1.4
	anterior length	0.3	0.4	0.4	0.4	0.4	0.5	0.4	0.4	0.3	0.3	0.4
	anterior width	1.2	1.1	1.1	1.2	1.2	1.1	1.2	1.1	1.1	0.9	0.9
	posterior width	1.3	1.3	1.4	1.6	1.4	1.3	1.4	1.3	1.2	1.1	1.1
Leg coxa II	length	1.7	1.8	1.6	1.5	1.6	1.4	1.5	1.4	1.4	1.3	1.3
Leg coxa III	length	1.9	1.9	2.0	1.7	1.8	1.7	1.7	1.8	1.8	1.7	1.5
Leg coxa IV	length	3.2	3.3	3.0	2.8	2.8	2.5	2.7	2.4	2.4	2.3	2.4
Pectines	total length	2.6	1.8	1.7	1.7	1.9	1.8	1.8	1.7	1.7	1.9	1.9
	length dent. marg.	2.2	1.6	1.4	1.4	1.5	1.4	1.4	1.4	1.2	1.7	1.8
	marginal lamellae (l/r)	3/3	3/3	3/3	3/3	3/3	3/3	3/3	3/3	3/3	3/3	3/3
	median lamellae (l/r)	12/11	7/7	7/7	7/7	7/7	7/7	7/7	7/6	6/5	7/8	8/8
	tooth count (l/r)	13/13	8/8	8/8	8/8	8/8	8/9	8/8	8/8	7/6	8/9	9/9

TABLE 10 continued

Species		A. tham.	Vietbocap canhi								subad. ♂	
Sex		Holotype ♀	♀									
Mesosoma	total length	9.2	10.8	10.0	10.7	10.0	9.5	9.4	8.9	7.9	6.8	7.2
Sternite VII	length	1.8	2.3	2.1	2.0	2.0	1.7	1.5	1.7	1.4	1.5	1.4
	width	2.9	3.1	3.0	2.8	2.9	2.5	2.7	2.5	2.6	2.3	2.3
Metasoma	total length	16.8	18.0	17.5	17.7	18.2	16.3	16.7	15.8	15.9	14.2	13.8
Metasoma I	length	1.6	1.7	1.6	1.7	1.6	1.5	1.6	1.5	1.6	1.4	1.2
	width	1.8	1.7	1.7	1.7	1.6	1.6	1.5	1.5	1.5	1.4	1.3
	height	1.6	1.5	1.5	1.4	1.3	1.4	1.4	1.2	1.3	1.2	1.2
Metasoma II	length	1.8	1.9	1.9	1.9	2.0	1.8	1.8	1.8	1.8	1.7	1.6
	width	1.6	1.5	1.4	1.5	1.4	1.3	1.3	1.3	1.2	1.3	1.2
	height	1.4	1.4	1.3	1.3	1.3	1.3	1.3	1.2	1.2	1.1	1.1
Metasoma III	length	2.1	2.1	2.2	2.2	2.2	2.0	2.2	1.9	1.9	1.8	1.6
	width	1.6	1.5	1.4	1.4	1.4	1.3	1.3	1.1	1.2	1.3	1.2
	height	1.4	1.3	1.2	1.2	1.2	1.2	1.3	1.1	1.1	1.0	1.1
Metasoma IV	length	2.8	2.8	2.7	2.7	2.8	2.6	2.7	2.5	2.4	2.3	2.2
	width	1.5	1.4	1.4	1.4	1.4	1.2	1.2	1.1	1.1	1.3	1.1
	height	1.3	1.3	1.1	1.2	1.2	1.1	1.2	1.0	1.0	1.0	1.0
Metasoma V	length	5.0	5.5	5.6	5.5	5.7	5.0	5.2	4.9	5.1	4.3	4.3
	width	1.5	1.4	1.3	1.4	1.2	1.2	1.3	1.1	1.0	1.2	1.0
	height	1.2	1.2	1.1	1.1	1.1	1.1	1.1	1.0	0.9	1.0	0.9
Telson	total length	5.6	6.1	5.8	5.9	6.1	5.4	5.5	5.2	5.1	4.6	4.5
Vesicle	length	4.0	4.3	4.0	4.0	4.2	3.7	3.7	3.6	3.5	3.3	4.5
	width	1.8	1.8	1.7	1.8	1.8	1.5	1.5	1.4	1.5	1.4	1.2
	height	1.5	1.6	1.4	1.6	1.5	1.4	1.4	1.3	1.4	1.2	1.1
Aculeus	length	1.6	1.9	1.7	1.9	1.9	1.7	1.8	1.5	1.5	1.3	1.0

chela fixed finger, ib_2, noticeably smaller than others ("petite"). Trichobothrium Et_1 situated distally on manus, aligned with or proximal to movable finger condyle; eb situated on fixed finger, slightly distal to movable finger condyle; esb_2 situated in proximal third of fixed finger, approximately aligned with proximal retrolateral denticle of median denticle row.

Legs: Leg I maxillary lobes (coxapophyses), distal margins rounded, unmodified (not spatulate or dilate) anteriorly, terminating flush with lobes of leg II. Legs I and II tibiae, retrolateral margins each with scattered macrosetae, without spurs; III and IV with spurs, smooth, without spinelets. Basitarsi with few scattered macrosetae, pro- and retrolateral rows of short spinules, and pair of pro- and retrolateral pedal spurs. Telotarsi with pair of ventrosubmedian rows of short spinules; proventral and retroventral rows of macrosetae absent, only few scattered macrosetae laterally; laterodistal lobes reduced and truncated; median dorsal lobe very short; ungues short, distinctly curved, equal in length; unguicular spur (dactyl) pronounced, pointed.

Sternum: Sternum, Type 1, pentagonal, length 5% greater than posterior width (table 3), lateral margins sublinear, parallel, ventral surface flat, without concave region or median furrow, posteromedian depression wide, shallow.
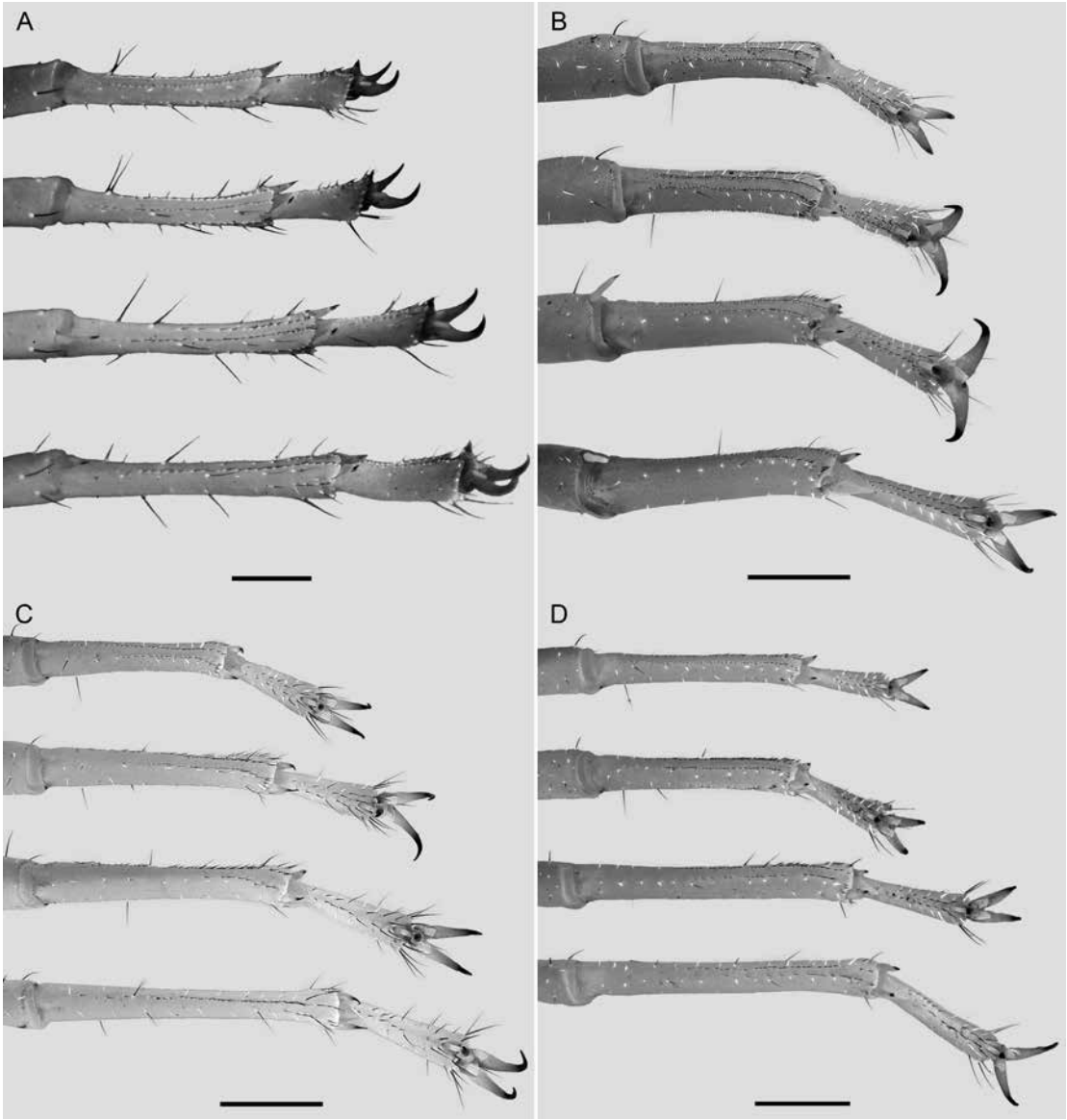
FIGURE 15. Pseudochactidae Gromov, 1998, legs I–IV, prolateral aspect. **A.** *Pseudochactas ovchinnikovi* Gromov, 1998, ♀ (AMNH), Babatag, Uzbekistan. **B.** *Troglokhammouanus steineri* Lourenço, 2007, ♀ (AMNH), Tham Xe Bang Fai, Laos. **C.** *Vietbocap canhi* Lourenço and Pham, 2010, ♀, Tiên Sơn, Vietnam (AMNH). **D.** *Aemngvantom lao* (Lourenço, 2012), comb. nov., ♀ (AMNH), Tham Nam Lot (Lod), Laos. Scale bars = 1 mm.

Pectines: Three marginal (anterior) lamellae, proximal sclerite considerably longer, distal sclerite short; eight or nine median lamellae (tables 3, 5); fulcra present, very small. Proximal median lamella and basal pectinal tooth unmodified. Pectinal teeth present along entire posterior margin of each pecten (♀); tooth count: nine or 10 (♀). Pectinal peg sensillae unknown.

Genital operculum: Opercular sclerites completely separated, genital papillae absent (♀).

Male and female reproductive organs: Unknown.

Mesosoma: Pre- and posttergites I–VI surfaces smooth, acarinate, each with pair of shallow submedian depressions; VII surface smooth, with pair of costate granular (crenulate) dorsosubmedian and dorsolateral carinae almost reaching posterior margin of segment. Sternites III–VII surfaces smooth, acarinate; III–VI, respiratory spiracles (stigmata) small, subcircular.

Metasoma: Metasoma relatively short, total length 31% greater than combined length of prosoma and mesosoma (table 3); segments I–V progressively increasing in length, I–III wider than long, width of length for segment I, 156%; II, 124%; III, 113%; IV, 89%; and V, 46%. Metasoma almost apilose, sparsely covered in short microsetae. Eight carinae on segments I, IV, and V, 10 on II and III. Dorsosubmedian carinae well developed, costate granular (crenulate) throughout length of segments I–IV, absent on V; converging posteriorly. Dorsolateral carinae well developed, costate granular (crenulate) throughout length of segments I–V; converging posteriorly on I and V, subparallel on II–IV. Dorsosubmedian and dorsolateral carinae of segments I–IV each terminating posteriorly with slightly enlarged granule. Median lateral carinae complete, costate granular (crenulate) throughout length of segments I and II, partial, reduced to posterior half on III, obsolete on IV, partial, granular, reduced to anterior half on V. Ventrolateral carinae well developed, costate granular (crenulate) on I–V; converging posteriorly on I and V, subparallel on II–IV. Ventrosubmedian carinae absent or obsolete on segment I, obsolete, granular to costate granular (crenulate) on II, well developed, costate granular (crenulate) through-

out length of III–V; subparallel on II and III, converging posteriorly on IV and V. Ventromedian carina obsolete on segment V. Intercarinal surfaces smooth.

Telson: Telson large, suboval. Vesicle globose, 4% wider than metasomal segment V (table 3), with flattened dorsal surface and rounded ventral surface, height 54% of length; dorsal surface smooth, lateral surfaces with three pairs of granular carinae, ventral surfaces with two pairs of granular carinae; anterodorsal lateral lobes ("vesicular tabs") distinct, each with two spiniform granules; subaceular tubercle very small, obsolete. Aculeus short, shallowly curved, 35% of telson length. Venom glands unknown.

Variation and sexual dimorphism: Unknown.

DISTRIBUTION: Known only from the type locality, near Bolakh [Balagh] village, in the Tarin Kowt District of the Uruzgan [Orozgan] Province of Afghanistan (fig. 6). At 1380 m, the type locality is the highest elevation recorded for the family (Soleglad et al., 2012).

ECOLOGY: The habitat and habitus of this species are consistent with the lapidicolous ecomorphotype (Prendini, 2001b). The holotype and only known specimen was collected in an arid, semidesert area, from under a stone in semiwet soil on the eastern bank of a dry riverbed (wadi) named Sarab Kariz, running from north to south (Soleglad et al., 2012). The remains of an exuvium, likely belonging to the same species, were found less than 50 m away, in the same wadi. According to Soleglad et al. (2012), the humid conditions of this microhabitat are noteworthy because *P. ovchinnikovi* also exhibits affinity to wet microhabitats (Fet et al., 2004; Prendini et al., 2006), which is unusual for Central Asian scorpions.

Soleglad et al. (2012) mention at least three species of Buthidae found in sympatry with *P. mischi* at the type locality: *Hottentotta saulcyi* (Simon, 1880), *Mesobuthus haarlovi* Vachon, 1958 and *Orthochirus afghanus* Kovařík, 2004.

CONSERVATION STATUS: *Pseudochactas mischi* is presently known from only a single locality. Although the true extent of its distribution is
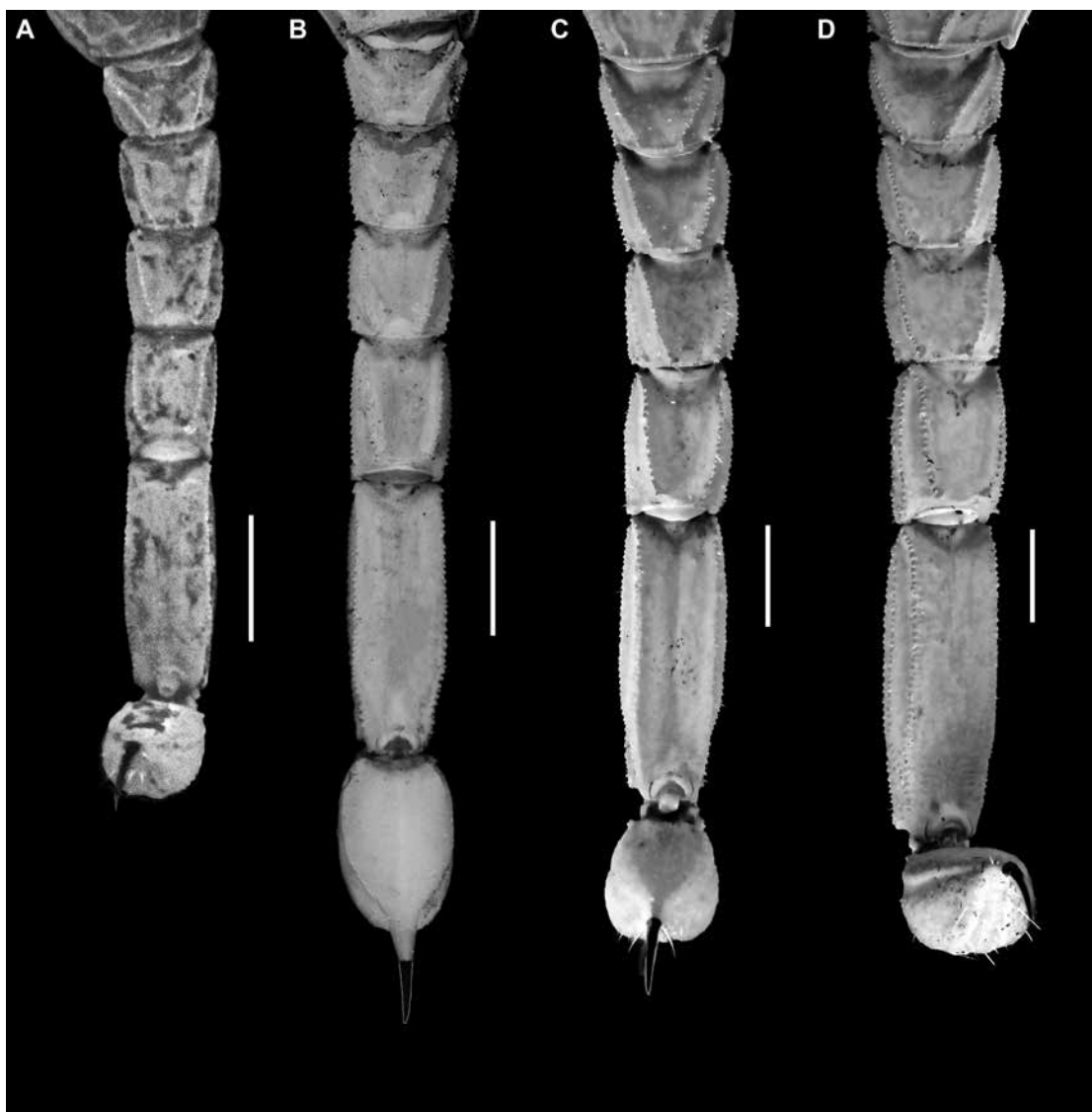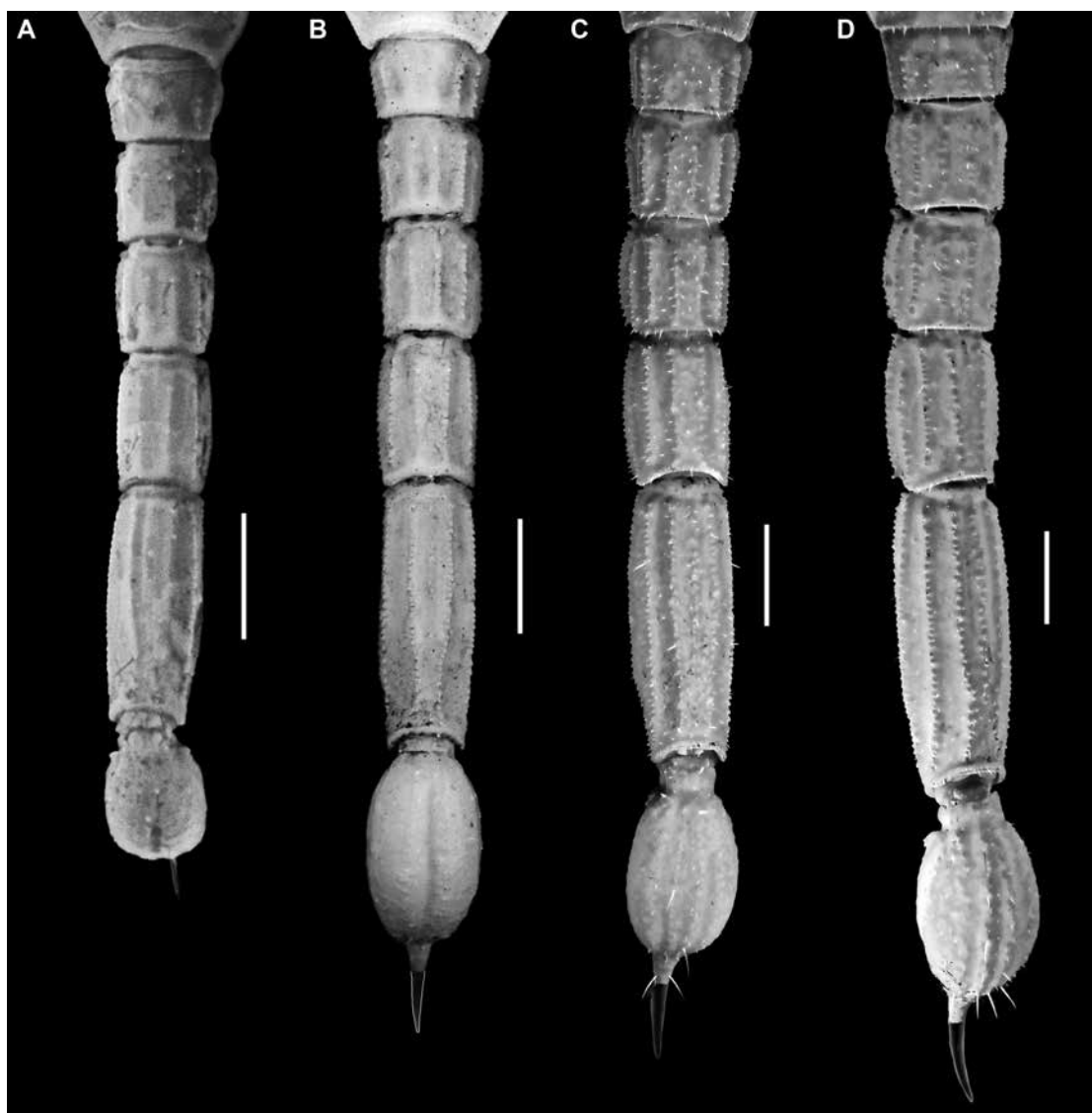
FIGURE 16. Pseudochactidae Gromov, 1998, metasoma and telson, dorsal aspect. **A, B.** *Pseudochactas ovchinnikovi* Gromov, 1998, **A.** ♂, **B.** ♀ (AMNH), Babatag, Uzbekistan. **C, D.** *Troglokhammouanus steineri* Lourenço, 2007, **C.** ♂, **D.** ♀ (AMNH), Tham Xe Bang Fai, Laos. Scale bars = 10 mm.
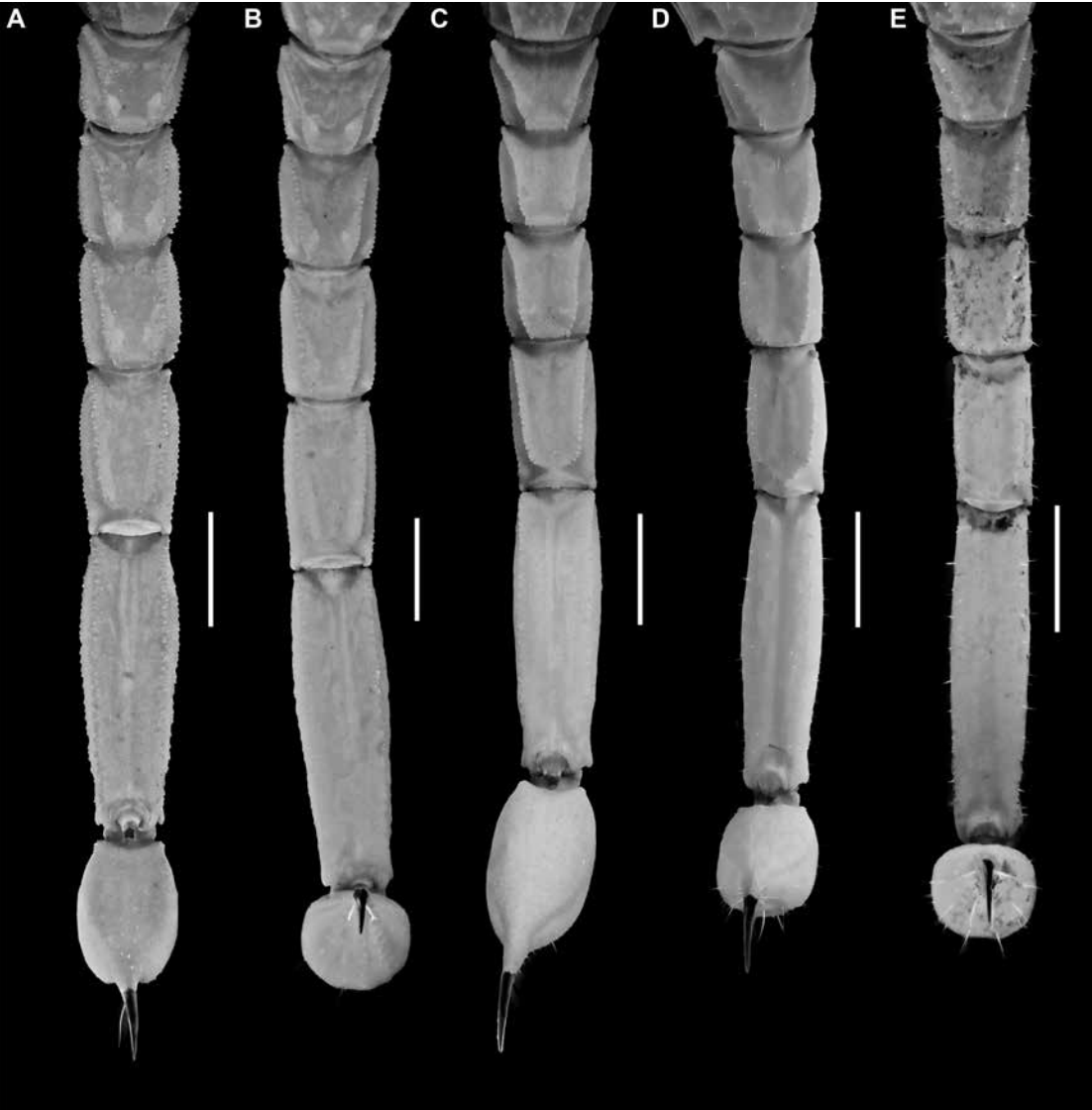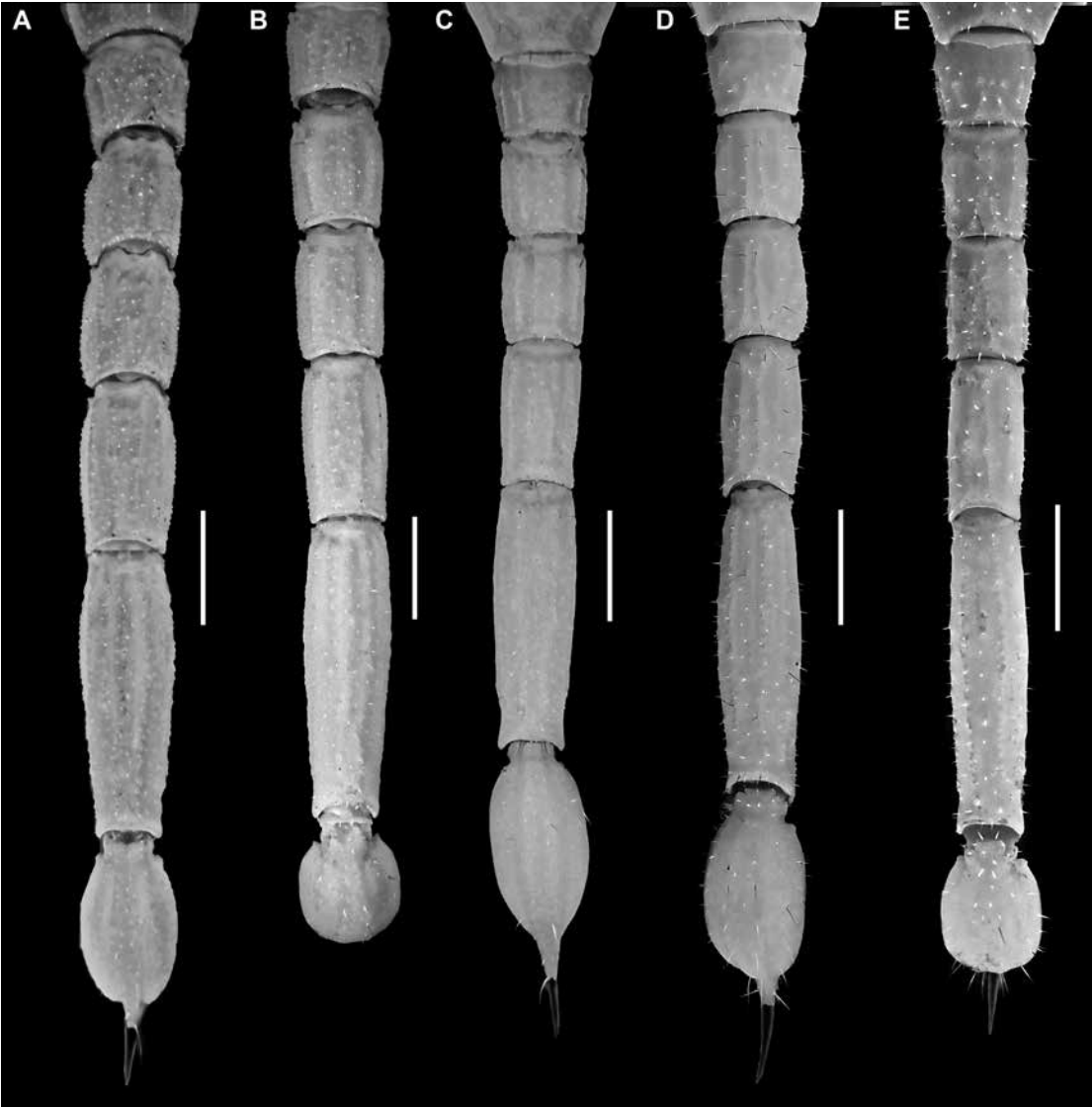
FIGURE 17. Pseudochactidae Gromov, 1998, metasoma and telson, dorsal aspect. **A, B.** *Aemngvantom lao* (Lourenço, 2012), comb. nov., **A.** ♂, **B.** ♀ (AMNH), Tham Nam Lot (Lod), Laos. **C.** *Aemngvantom tham-nongpaseuam*, gen. et sp. nov., holotype ♀ (AMNH), Tham Nong Pa Seuam, Laos. **D, E.** *Vietbocap canhi* Lourenço and Pham, 2010, **D.** ♀ (AMNH), Tiên Sơn, Vietnam, **E.** ♀ (AMNH), Thiên Đường, Vietnam. Scale bars = 10 mm.

FIGURE 18. Pseudochactidae Gromov, 1998, metasoma and telson, lateral aspect. **A, B.** *Pseudochactas ovchinnikovi* Gromov, 1998, **A.** ♂, **B.** ♀ (AMNH), Babatag, Uzbekistan. **C, D.** *Troglokhammouanus steineri* Lourenço, 2007, **C.** ♂, **D.** ♀ (AMNH), Tham Xe Bang Fai, Laos. Scale bars = 10 mm.

FIGURE 19. Pseudochactidae Gromov, 1998, metasoma and telson, lateral aspect. **A, B.** *Aemngvantom lao* (Lourenço, 2012), comb. nov., **A.** ♂, **B.** ♀ (AMNH), Tham Nam Lot (Lod), Laos. **C.** *Aemngvantom thamnongpaseuam*, gen. et sp. nov., holotype ♀ (AMNH), Tham Nong Pa Seuam, Laos. **D, E.** *Vietbocap canhi* Lourenço and Pham, 2010, **D.** ♀ (AMNH), Tiên Sơn, Vietnam, **E.** ♀ (AMNH), Thiên Đường, Vietnam. Scale bars = 10 mm.

FIGURE 20. Pseudochactidae Gromov, 1998, metasoma and telson, ventral aspect. **A, B.** *Pseudochactas ovchinnikovi* Gromov, 1998, **A.** ♂, **B.** ♀ (AMNH), Babatag, Uzbekistan. **C, D.** *Troglokhammouanus steineri* Lourenço, 2007, **C.** ♂, **D.** ♀ (AMNH), Tham Xe Bang Fai, Laos. Scale bars = 10 mm.

FIGURE 21. Pseudochactidae Gromov, 1998, ventral aspect. **A, B.** *Aemngvantom lao* (Lourenço, 2012), comb. nov., **A.** ♂, **B.** ♀ (AMNH), Tham Nam Lot (Lod), Laos. **C.** *Aemngvantom thamnongpaseuam*, gen. et sp. nov., holotype ♀ (AMNH), Tham Nong Pa Seuam, Laos. **D, E.** *Vietbocap canhi* Lourenço and Pham, 2010, **D.** ♀ (AMNH), Tiên Sơn, Vietnam, **E.** ♀ (AMNH), Thiên Đường, Vietnam. Scale bars = 10 mm.

unknown, its apparent ecological requirement for humidity suggests a restricted area of occupancy in the predominantly arid environment of south-central Afghanistan. Therefore, this species is characterized by an acute restriction in both its area of occupancy and number of known localities: it is only known to exist at a single location, the extent of occurrence is less than 5000 km², and the area of occupancy less than 500 km². Additionally, a continuing decline in the quality of its habitat is observed, inferred, and projected. According to Soleglad et al. (2012), the wadi where *P. mischi* was collected, was largely undisturbed until around the year 2000, when roads were constructed and the local population was able to collect firewood and livestock feed. The impact of this habitat degradation on *P. mischi* is unknown but presumed to be negative. The threat of habitat degradation, taken together with the restricted distributional range, which is completely unprotected, warrants its assignment to the Endangered category of the IUCN Red List. This species is expected to be prone to the effects of human activities (or stochastic events, the impact of which is increased by human activities, e.g., climate change) within a very short period of time in an unforeseeable future and is therefore considered to be facing a very high risk of extinction in the wild.

Pseudochactas ovchinnikovi Gromov, 1998

Figures 1, 2, 5, 6, 8–10, 13A, C, 15A, 16A, B, 18A, B, 20A, B, 22–25, tables 2–6

Pseudochactas ovchinnikovi Gromov, 1998: 1003–1008, figs. 1, 2 (1–12), and 3 (1–8); Fet, 2000: 426; Lourenço, 2000a: 32, fig. 6; Soleglad and Fet, 2001: 1, 22; 2003a: i, 8, 11, 12, 18, 20, 29, 30, 32, 33, 54, 60, 65, 67, 150–153, 155, figs. 1, 4, 10–12, 41, 49, 57, 92, 108, B-1, B-2, B-3, appendices B, C; 2003b: 5, 8, 18, 20, figs. 2, 3, 14; Fet et al., 2003: 2, 3, 5, fig. 1, table 1; 2004: 61, 62, 66, fig. 1; 2005: 4, 6, fig. 3; Prendini and Wheeler, 2005: 454,

table 5; Fet et al., 2006: 269, 271, table 1; Graham and Fet, 2006: 1, 4, fig. 1; Prendini et al., 2006: 211, 212, 214, 215, 217, 220–224, 228–239, tables 1, 6, 7, figs. 1–7, 11–47; Lourenço, 2007a: 771; 2007b: 5, 6; Kamenz and Prendini, 2008: 8, 21, 22, table 2, pl. 1, appendix 1; Soleglad and Fet, 2008: 29; Volschenk et al., 2008: 652, 655, 661, 663, 665, 670, 675, tables 1, 2, fig. 3C, appendix; Lourenço and Pham, 2010: 1, 2, 12; Botero-Trujillo and Noriega, 2011: 41; Lourenço, 2012a: 237, appendix A; Lourenço and Pham, 2012: 80, 84; Soleglad et al., 2012: 89, 90, 92–97, tables I, II, figs. 14–18 (part), 21 (part); Klußmann-Fricke et al., 2012: 546, table 1; Loria and Prendini, 2014: 12, fig. 3F, appendix S1: 10, appendix S2: 7; Lourenço, 2014: 36; Borges and Graham, 2016: 89; Lourenço, 2017a: 19; Lourenço et al., 2018: 265; Teruel et al., 2020: 10.

TYPE MATERIAL: **UZBEKISTAN: Surkhandarya Region:** *Uzun Distr.*: Holotype: 1 subad. ♂ (ZMMSU), Okmachit [Ak-Mechet], ca. 7 km W–4 km WSW, E slope of Babatag Mt. Range, 38°02′50″N 68°14′22″E–38°01′45″N 68°15′30″E, 760–1010 m, 29.iv–9.v.1994, A.V. Gromov. Paratypes: 2 ♀, 3 subad. ♂ (AGPC) [examined], 3 [subad.?] ♂ (VFPC), Okmachit [Ak-Mechet], ca. 7 km W–4 km WSW, E slope of Babatag Mt. Range, 38°02′50″N 68°14′22″E–38°01′45″N 68°15′30″E, 760–1010 m, 29.iv–9.v.1994, A.V. Gromov and S.V. Ovchinnikov. **TAJIKISTAN:** *Leninskii Distr.*: Paratype ♀ (AGPC), Aruktau Mt. Range, near Gandzhina village [37°58′N 68°34′E], 10.iv.1988, S.L. Zonstein and A.S. Zorkin [examined].

DIAGNOSIS: *Pseudochactas ovchinnikovi* may be separated from the morphologically similar *P. mischi*, by means of differences in coloration and carination. The coloration is darker and brownish, the carapace, tergites, and legs infuscate, in *P. ovchinnikovi* but paler and yellowish, the carapace, tergites, and legs immaculate, in *P. mischi*. The lyriform anterosubmedial carinae of the
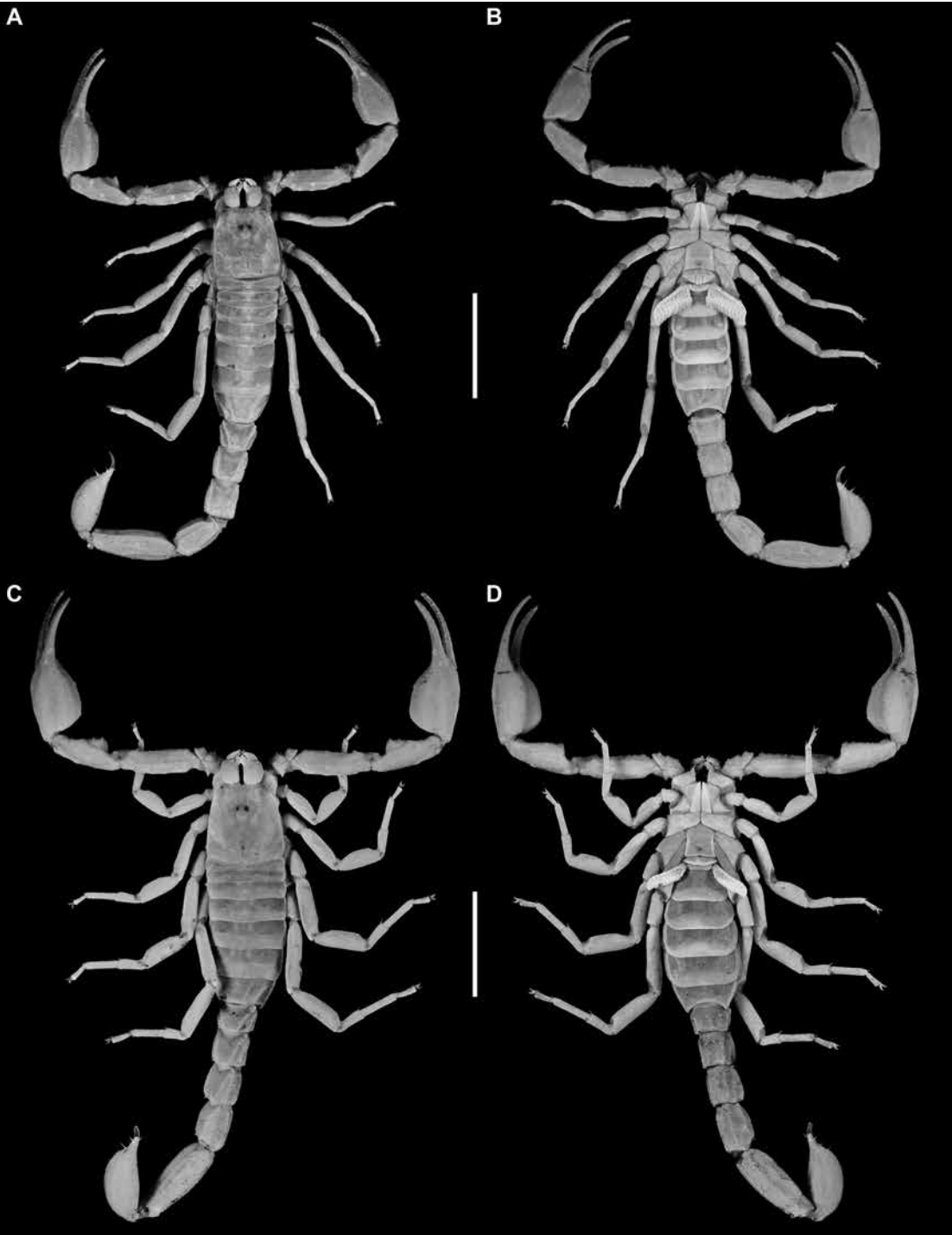
FIGURE 22. *Pseudochactas ovchinnikovi* Gromov, 1998, habitus: **A, C.** dorsal and **B, D.** ventral aspects. **A, B.** ♂, **C, D.** ♀ (AMNH), Babatag, Uzbekistan. Scale bars = 10 mm.

carapace are obsolete, granular in *P. ovchinnikovi* (fig. 10) but absent in *P. mischi*. The retrodorsal carina of the pedipalp patella is costate granular in *P. ovchinnikovi* (fig. 23E, F) but costate in *P. mischi*. The pedipalp chela, metasoma, and telson vesicle are more gracile (proportionally longer and narrower) in *P. ovchinnikovi* than *P. mischi* (tables 3, 6). The pectines possess 9–12 median lamellae and 10–13 teeth in *P. ovchinnikovi* (tables 3, 5, 6) but 8 or 9 median lamellae and 9 or 10 teeth in *P. mischi* (tables 3, 5). The median lateral carinae are partial, becoming obsolete anteriorly, on metasomal segment II, and absent or obsolete on V in *P. ovchinnikovi* (fig. 18A, B) but complete on segment II, and partial on V in *P. mischi*. The telson vesicle lateral and ventral surfaces are more finely and sparsely granular in *P. ovchinnikovi* (figs. 18A, B, 20A, B) than *P. mischi*.

DESCRIPTION: The following description, based on the material examined, including the only known adult male and 20 adult females, updates the description of Prendini et al. (2006), augmenting Gromov's (1998) original description, Soleglad and Fet's (2001) interpretation of the Type D trichobothrial pattern, Soleglad and Fet's (2003b) definition of the Type 1 sternum of *P. ovchinnikovi*, and supplemental data by Soleglad and Fet (2003a), Fet et al. (2004), and Soleglad et al. (2012).

Total length: Small, 19.4 mm (♂) or 27.6 mm (22.6–30 mm, *n* = 11) (♀) (tables 3, 6).

Color: Tegument base coloration yellow to light brown. Carapace diffusely infuscate, with brownish marbled pattern; tergites entirely infuscate or infuscate in anterior two-thirds, brownish; pedipalp chela fingers darker, lightly infuscate, reddish brown; prolateral surfaces of leg femora and patellae infuscate, brownish; other surfaces immaculate, yellowish. Chelicerae, pedipalps (except chela fingers), legs, posterior third of tergites, metasoma, and telson slightly paler than carapace (fig. 1A). Leg tibiae and tarsi, and retrolateral surfaces of femora and patellae, sternum, genital operculum, pectines and sternites pale yellow. Aculeus black.

Chelicerae: Fixed finger, dorsal margin with four teeth (basal, median, subdistal, distal); basal and median teeth fused into bicuspid ("conjoined on trunk"); space between median and subdistal teeth U-shaped; ventral margin with four or five small denticles (ventral accessory denticles). Movable finger, dorsal margin with three teeth (median, subdistal, retrolateral distal), without basal teeth; ventral margin with four or five small denticles (ventral accessory teeth) and serrula in distal third; retrolateral (dorsal) distal and prolateral (ventral) distal teeth subequal, retrolateral (dorsal) distal tooth only slightly smaller than prolateral (ventral) distal tooth, and opposable. Ventral surface of fingers and manus with numerous long, dense macrosetae.

Carapace: Carapace slightly longer than wide, anterior width 61% (♂) or 57% (55%–60%, *n* = 9) (♀) of length, posterior width 100% (♂) or 97% (92%–103%, *n* = 9) (♀) of length (table 6). Anterior margin sublinear, shallowly recessed medially; anterolateral margins entire; posteromedian margin shallowly concave (recurved); posterolateral margins angular, slanting (fig. 10). One pair of very small anterolateral major (ALMa) ocelli situated close to anterolateral margins of carapace, other lateral ocelli absent. Anterosubmedial depressions, medial to lateral ocelli, well developed. Median ocular tubercle situated anteromedially on carapace, distance from anterior margin 23% (♂) or 29% (27%–34%, *n* = 9) (♀) of carapace length (table 6); pair of median ocelli considerably larger than lateral ocelli; pair of weakly developed, smooth superciliary carinae, not protruding above ocelli; interocular sulcus shallow, obsolete. Circumocular sutures complete, connected posteriorly (postocular); circumocular triangle subtriangular (broad V-shape); median ocular curvatures present. Anteromedian depression narrow, shallow; posteromedian sulcus very shallow anteriorly, becoming slightly deeper posteriorly; posterolateral sulci very shallow, wide, weakly curved; posteromarginal sulcus narrow, shallow. Carapacial surfaces almost entirely smooth, except for scattered, fine granulation on interoc-

TABLE 11

Statistics for Two Nuclear Loci, 18S rDNA/Internal Transcribed Spacer 2 (18S/ITS2) and 28S rDNA (28S), and Three Mitochondrial Loci, 12S rDNA (12S), 16S rDNA (16S), and Cytochrome *c* Oxidase Subunit I (COI), in Phylogenetic Analysis of the Pseudochactidae Gromov, 1998

Number of Haplotypes; Length (nucleotide base-pairs) of Unaligned and Aligned Sequences; Average Percent GC Content; Number and Percent of Variable Positions (VP); Number and Percent of Parsimony-Informative Sites (PI); and Model Selected for Bayesian Inference Using the Akaike Information Criterion (AIC)

Locus	Haplotypes	Unaligned	Aligned	GC	VP	PI	AIC
18S/ITS2	12	1760–3926	4416	52	978 (22)	446 (10)	GTR + G
28S	8	1329–2193	2245	59	418 (19)	172 (8)	GTR + I + G
12S	10	337–344	371	28	217 (58)	151 (41)	GTR + G
16S	12	475–483	498	28	244 (49)	171 (34)	GTR + I + G
COI	12	1078	1078	37	388 (36)	319 (30)	GTR + I + G
COI 1st Codon	–	–	359	45	79 (7)	49 (5)	–
COI 2nd Codon	–	–	359	42	22 (2)	8 (1)	–
COI 3rd Codon	–	–	360	25	287 (27)	262 (24)	–

ular surface and along anterior margin; acarinate, except for pair of obsolete, granular anterosubmedial carinae, arranged in lyriform configuration, anterior to median ocular tubercle and prolateral to circumocular sutures.

Pedipalps: Pedipalps relatively robust; segments almost apilose, sparsely covered in short microsetae and occasional macrosetae. Pedipalp femur length 67% (♂) or 67% (64%–69%, *n* = 11) (♀) greater than width (tables 3, 6). Femur with eight carinae evident (fig. 23A–D); promedian carina obsolete, reduced to few spiniform granules in proximal two-thirds of segment; prodorsal, proventral, and retrodorsal carinae well developed, costate granular; dorsomedian carina weak, granular; retromedian carina weak, comprising short row of granules medially; retroventral and ventromedian carinae vestigial, reduced to few granules proximally; intercarinal surfaces smooth. Pedipalp patella length 56% (♂) or 54% (50%–59%, *n* = 11) (♀) greater than width (tables 3, 6). Patella with six carinae evident (fig. 23E–H); retrodorsal, retroventral, and proventral carinae well developed, costate granular to costate; prodorsal carina well developed, granular to costate granular; prolateral surface, dorsoventral "vaulted" projection ("anterior pro-

cess") well developed, with prominent pair of dorsal and ventral spiniform granules ("patellar spurs") proximally, the dorsal more strongly developed, demarcating pair of obsolete, granular prolateral carinae ("dorsal and ventral patellar spur carinae"); dorsomedian, retromedian, and ventromedian carinae absent; intercarinal surfaces smooth. Pedipalp chela relatively short and broad; manus globose, width 17% (♂) or 26% (13%–37%, *n* = 9) (♀) greater than height and length 30% (♂) or 28% (21%–38%, *n* = 11) greater than width (tables 3, 6); length of movable finger 25% (♂) or 16% (12%–21%, *n* = 11) (♀) greater than length of manus. Chela with seven carinae evident (figs. 24, 25); dorsomedian carina reduced to weak row of granules at base of fixed finger, becoming obsolete proximally on manus; digital carina well developed, granular to costate granular; dorsal secondary, subdigital and retromedian (retrolateral secondary) carinae absent; secondary accessory and retroventral carinae entirely fused; retroventral carina well developed, granular, aligned parallel to longitudinal axis of chela, with distal margin connected to retrolateral movable finger condyle; ventromedian carina vestigial, reduced to proximal granules; proventral carina obsolete, reduced to few

isolated granules near prolateral condyle of movable finger; prodorsal and promedian carinae weakly developed, each comprising series of isolated granules; intercarinal surfaces smooth except for coarse, scattered granules on prolateral surface of manus, near base of fixed and movable fingers, granulation becoming very fine and even on fingers. Fixed and movable fingers, dentate margins sublinear (♀) or slightly sinuous, movable finger with very shallow lobe, proximally and fixed finger with correspondingly shallow notch, proximally (♂), no proximal "gap" evident when closed; median denticle rows comprising seven ($n = 107$) oblique and slightly imbricated subrows (tables 4, 6), decreasing in length distally; each subrow comprising large retrolateral denticle proximally (absent from proximal subrow, for total of six retrolateral denticles on fixed and movable fingers), several small median denticles, and large prolateral denticle distally, slightly offset (total of seven prolateral denticles on fixed and movable fingers); terminal (prolateral) denticle of first subrow enlarged; accessory denticles absent.

Trichobothria: Orthobothriotaxic, Type D, β configuration, trichobothrium d_2 situated on femur dorsal surface, d_3 and d_4 in same axis, parallel and closer to retrodorsal carina than d_1, angle formed by d_1, d_3 and d_4 opening toward prolateral surface, with the following segment totals (figs. 23–25): femur, 12 (6 dorsal, 3 prolateral, 3 retrolateral); patella, 10 (3 dorsal, 1 prolateral, 6 retrolateral); chela, 13 (5 manus, 8 fixed finger). Total number of trichobothria per pedipalp, 35. Five trichobothria on femur, i_4, d_1, d_2, d_4, and d_6, one on patella, est_1, and one on chela fixed finger, ib_2, noticeably smaller than others ("petite"). Trichobothrium Et_1 situated distally on manus, aligned with or proximal to movable finger condyle; eb situated on fixed finger, slightly distal to movable finger condyle; esb_2 situated in proximal third of fixed finger, approximately aligned with proximal retrolateral denticle of median denticle row.

Legs: Leg I maxillary lobes (coxapophyses), distal margins rounded, unmodified (not spatulate or dilate) anteriorly, terminating flush with lobes of leg II (fig. 22B, D). Legs I and II tibiae, retrolateral margins each with scattered macrosetae, without spurs (fig. 15A); III and IV with spurs, smooth, without spinelets. Basitarsi with few scattered macrosetae, pro- and retrolateral rows of short spinules, and pair of pro- and retrolateral pedal spurs. Telotarsi with pair of ventrosubmedian rows of short spinules; proventral and retroventral rows of macrosetae absent, only few scattered macrosetae laterally; laterodistal lobes reduced and truncated; median dorsal lobe very short; ungues short, distinctly curved, equal in length; unguicular spur (dactyl) pronounced, pointed.

Sternum: Sternum, Type 1, pentagonal, posterior width 100% (♂) or 89% (80%–103%, $n = 11$) (♀) of length (tables 3, 6), lateral margins sublinear, parallel, ventral surface flat, without concave region or median furrow, posteromedian depression round, moderately developed, defined posteriorly by slight outer ridge (fig. 13A, C).

Pectines: Three marginal (anterior) lamellae, proximal sclerite considerably longer, distal sclerite short (fig. 13A, C); 10/11 (9–12, $n = 54$) (♂) or 10/10 (9 or 10, $n = 50$) (♀) median lamellae (tables 5, 6); fulcra present, very small. Proximal median lamella and basal pectinal tooth unmodified. Pectinal teeth present along entire posterior margin of each pecten (♂, ♀); 11/12 (10–13, $n = 54$) (♂) or 11/11 (10 or 11, $n = 53$) (♀) teeth. Pectinal peg sensillae short, stout, flattened and truncate distally, with pair of laterodistal processes; sensillar sockets smooth.

Genital operculum: Opercular sclerites completely separated, prominent genital papillae visible along entire length (♂) or absent (♀) (fig. 13A, C). Genital plugs observed in some females.

Male reproductive organs: Paraxial organ without accessory glands. Hemispermatophore lamelliform, *pars recta* absent; basal lobe present.

Female reproductive organs: Ovariuterus comprising reticulate mesh of six cells. Oocytes contained in sessile follicles directly contacting ovaruterine tubes.
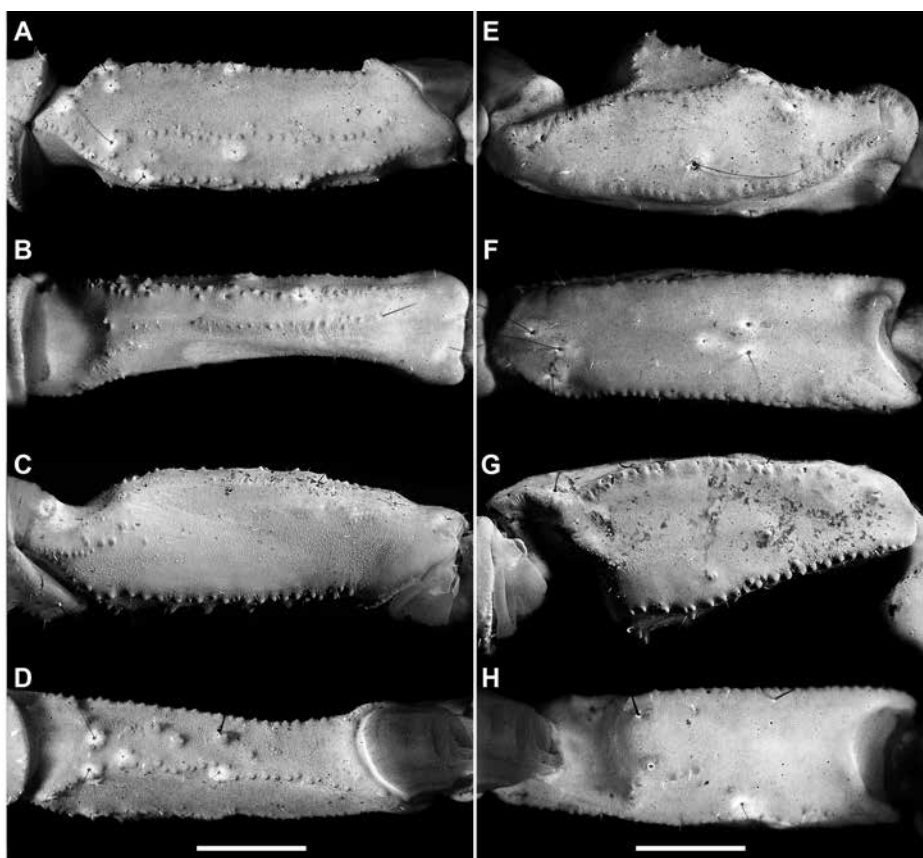
FIGURE 23. *Pseudochactas ovchinnikovi* Gromov, 1998, ♀ (AMNH), Babatag, Uzbekistan, dextral pedipalp femur (**A–D**) and patella (**E–H**): **A, E.** dorsal, **B, F.** retrolateral, **C, G.** ventral, and **D, H.** prolateral aspects. Scale bars = 1 mm.

Mesosoma: Pretergites surfaces smooth and shiny. Posttergites I–VI surfaces very finely and uniformly granular, granulation becoming slightly coarser near posterior margins, acarinate, each with pair of shallow submedian depressions (fig. 22A, C); VII surface smooth, with pair of costate granular dorsosubmedian and dorsolateral carinae almost reaching posterior margin of segment. Sternites III–VII surfaces entirely smooth, acarinate (fig. 22B, D), with scattered macrosetae, posterior margins with sparse row of macrosetae; III–VI, respiratory spiracles (stigmata) small, oval (fig. 13A, C); V posteroventral margin with pale, raised, triangular surface; VII width 38% (♂) or 41% (37%–45%, *n* = 9) (♀) greater than length (table 6).

Metasoma: Metasoma relatively short, total length 30% (♂) or 19% (12%–25%, *n* = 8) (♀) greater than combined length of prosoma and mesosoma (table 6); segments I–V progressively increasing in length, I and II wider than long, width of length for segment I, 124% (♂) or 148% (129%–169%, *n* = 11) (♀); II, 100% (♂) or 107% (97%–121%) (♀); III, 92% (♂) or 91% (86%–100%) (♀); IV, 65% (♂) or 71% (65%–76%) (♀); and V, 37% (♂) or 38% (35%–43%) (♀). Metasoma almost apilose, sparsely covered in short microsetae. Eight carinae on segments I and IV, 10 on II and III, and nine on V (figs. 16A, B, 18A, B, 20A, B). Dorsosubmedian carinae well developed, costate granular throughout length of segments I–IV, absent on V; converging posteri-

FIGURE 24. *Pseudochactas ovchinnikovi* Gromov, 1998, ♀ (AMNH), Babatag, Uzbekistan, dextral pedipalp chela: **A.** dorsal, **B.** retrolateral, **C.** ventral, and **D.** prolateral aspects. Scale bar = 1 mm.

orly. Dorsolateral carinae well developed, costate granular throughout length of segments I–V; converging posteriorly on I and V, subparallel on II–IV. Dorsosubmedian and dorsolateral carinae of segments I–III each terminating posteriorly with slightly enlarged granule. Median lateral carinae complete, costate granular throughout

length of segment I, partial, granular, becoming obsolete anteriorly on II and III, vestigial or absent on IV, reduced to few granules medially or absent on V. Ventrolateral carinae well developed, costate granular, but becoming obsolete anteriorly on segment I, continuous throughout length of II–V; converging posteriorly on I and
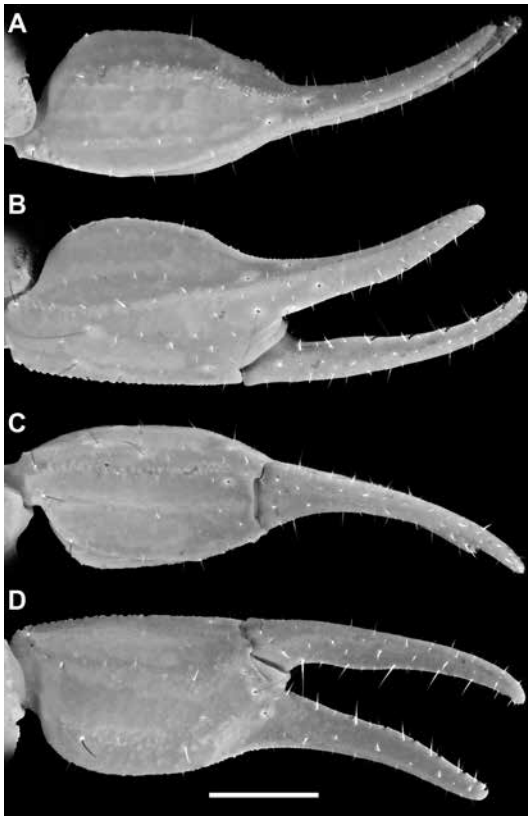
FIGURE 25. *Pseudochactas ovchinnikovi* Gromov, 1998, ♂ (AMNH), Babatag, Uzbekistan, dextral pedipalp chela: **A.** dorsal, **B.** retrodorsal, **C.** ventral, and **D.** prolateral aspects. Scale bar = 1 mm.

V, subparallel on II–IV. Ventrosubmedian carinae absent or obsolete on segment I, obsolete, costate on II, well developed, costate granular throughout length of III–V; subparallel on II and III, converging posteriorly on IV and V. Ventromedian carina absent or obsolete, comprising weak row of granules, on segment V. Intercarinal surfaces smooth.

Telson: Telson large, suboval (figs. 16A, B, 18A, B, 20A, B). Vesicle globose, 9% (♂) or 19% (11%–29%, *n* = 11) (♀) wider than metasomal segment V (tables 3, 6), with flattened dorsal surface and rounded ventral surface, height 52% (♂) or 50% (47%–54%, *n* = 11) of length; dorsal surface smooth, lateral surfaces with three pairs of obsolete, granular carinae, ventral surfaces

with two pairs of obsolete, granular carinae; anterodorsal lateral lobes ("vesicular tabs") distinct, each with two spiniform granules; subacular tubercle very small, obsolete. Aculeus short, shallowly curved, 22% (♂) or 29% (27%–30%, *n* = 10) (♀) of telson length. Venom glands thin walled, simple, and unfolded.

Intraspecific variation: No significant variation.

Ontogenetic variation: Immature stages of *P. ovchinnikovi* are paler in color and less sclerotized than adults, and the posteroventral margin of mesosomal sternite V does not exhibit a pale, raised, triangular surface as in the adults of both sexes. Males and females closely resemble one another externally until the final instar. However, immature stages are easily sexed by examination of the genital aperture. Most of the specimens identified as adult males by Gromov (1998) are subadult. These include the largest male specimens examined by Prendini et al. (2006). Upon dissection, none of these specimens possessed gonads or hemispermatophores, and are probably penultimate instars. The sole confirmed adult male specimen lacks a distended mesosoma and is slightly secondarily sexually dimorphic, but also significantly smaller (carapace length, 2.3 mm; table 6) than most of the other males examined. More adult male specimens need to be collected to determine whether penultimate instars are larger than sexually mature males or this male specimen is simply a small adult.

Sexual dimorphism: The genital papillae, visible the entire length and thus completely separating the two sclerites of the genital operculum (fig. 13A), are the characters of primary external sexual dimorphism in the male. The opercular sclerites are also separated for most of their length in the female, although genital papillae are absent (fig. 13C). Few secondary sexual characters are observed in the only confirmed adult male, compared with adult females and immature stages of both sexes. The most obvious are the slightly more developed pectines, the teeth of which are somewhat larger, although similar in number (fig. 13A, C; tables 5, 6). In addition, the adult male is proportion-

ally more slender (fig. 22), with a slightly longer metasoma and telson (table 6), slightly longer and more sinuous fingers on the pedipalp chela (figs. 24, 25), and slightly more pronounced granulation on the carapace, pedipalps, and tergites, than the adult female.

Distribution: *Pseudochactas ovchinnikovi* is known from only a few localities in the Babatag mountain range of southeastern Uzbekistan and a single locality in the Aruktau mountain range (southern foothills of Gardaniushti range) of southwestern Tajikistan (fig. 6). The localities in Uzbekistan are separated from the locality in Tajikistan by the Kofirnixon River. Most of the specimens originate from Dikhana (Dukhana or Dukhone) Canyon, on the eastern slopes of the Babatag range. All the known locality records occur at elevations ranging from 720–1010 m, in a semiarid savanna dominated by sparse grasses, xerophile perennials and Pistachio trees (Gromov, 1998; Prendini et al., 2006; Soleglad et al., 2012).

Ecology: *Pseudochactas ovchinnikovi* is a lapidicolous species (Prendini, 2001b) that inhabits the cracks and crevices of near vertical mud walls on steep, eroded riverbanks and gullies (fig. 2). Compared with the pseudochactid species inhabiting the caves of Southeast Asia, *P. ovchinnikovi* is rather compressed dorsoventrally, presumably an adaptation to its relatively arid habitat. A few specimens have been found under stones. Most of the specimens were collected during the spring months of April–May, when much of the annual rainfall is received in the region (Gromov, 1998; Soleglad and Fet, 2003a; Fet et al., 2004). Specimens collected by the first author were found to be more abundant on humid nights, especially following convectional thunderstorms that occurred during the late afternoon. Several were found very close to the edge of a small stream, sitting on moist mud banks, suggesting a requirement for high humidity. Fet et al. (2004) and Soleglad et al. (2012) likewise reported finding *P. ovchinnikovi* actively foraging at night on wet mud along the small temporary stream at the bottom of Dikhana Canyon. It is not known whether *P. ovchinnikovi*

spends most of the dry season in aestivation, as suggested by Soleglad and Fet (2003a) and Fet et al. (2004). Specimens were observed to be actively moving on the mud faces, suggesting the species is an errant forager (Bradley, 1988; Polis, 1990; Prendini, 2001b), and were very sensitive to light, retreating rapidly into cracks in the mud walls even when exposed to the UV.

At the Dikhana Canyon, *P. ovchinnikovi* was collected in sympatry with three other scorpion species, all buthids: *Mesobuthus eupeus* (C.L. Koch, 1839), *Mesobuthus kreuzbergi* Fet et al., 2018, and *Orthochirus scrobiculosus* (Grube, 1873). The much larger *M. kreuzbergi* was common in the cracks and crevices of the mud walls inhabited by *P. ovchinnikovi*, but preferred drier situations, further from the stream; *O. scrobiculosus* was also found there but was far less common. *Mesobuthus eupeus* was not syntopic with these species; it was found under stones and in burrows on flat ground between the riverbanks.

Conservation Status: Despite the low agricultural potential of the semiarid savanna in which *P. ovchinnikovi* occurs, the habitat is heavily utilized for livestock grazing by the local subsistence farming community. Much of the herbaceous layer has been heavily overgrazed, especially by goats, and widespread soil erosion is evident (fig. 2). The impact of this habitat degradation on *P. ovchinnikovi* is unknown but presumed to be negative. The threat of habitat degradation, taken together with the fairly restricted distributional range, which is completely unprotected, warrants its assignment to the Endangered category of the IUCN Red List. This species is characterized by an acute restriction in both its area of occupancy and number of known localities: it is known to exist at fewer than five fragmented locations, the extent of occurrence is estimated to be less than 5000 km^2, and the area of occupancy is estimated to be less than 500 km^2. A continuing decline in the quality of its habitat is observed, inferred, and projected. This species is expected to be prone to the effects of human activities (or stochastic events, the impact of which is increased by human activ-

TABLE 12

Mean Within-Species (boldface) and Between-Species Uncorrected Pairwise (p) Distances of Two Nuclear Loci, 18S rDNA/Internal Transcribed Spacer 2 (18S/ITS2) and 28S rDNA (28S), and Three Mitochondrial Loci, 12S rDNA (12S), 16S rDNA (16S), and Cytochrome c Oxidase Subunit I (COI), for Five Species of Pseudochactidae Gromov, 1998

Pseudochactas ovchinnikovi Gromov, 1998, *Troglokhammouanus steineri* Lourenço, 2007, *Aemngvantom lao* (Lourenço, 2012), comb. nov., *Aemngvantom thamnongpaseuam*, gen. et sp. nov., and *Vietbocap canhi* Lourenço and Pham, 2010, from Tiên Sơn (TS) and Thiên Đường (TD) caves

		P. ovchinnikovi	*T. steineri*	*A. lao*	*A. thamnong.*	*V. canhi* (TS)	*V. canhi* (TD)
18S/ITS2	*P. ovchinnikovi*	**0**					
	T. steineri	0.0128	**0**				
	A. lao	0.0155	0.0079	**0**			
	A. thamnongpaseum	0.0364	0.0264	0.0082	–		
	V. canhi (TS)	0.0182	0.0114	0.0105	0.036	**0**	
	V. canhi (TD)	0.0122	0.0060	0.0052	0.0181	**0.0002**	**0**
28S	*P. ovchinnikovi*	**0**					
	T. steineri	0.0241	**0**				
	A. lao	0.022	0.0312	**0**			
	A. thamnongpaseum	0.0197	0.0303	0.0023	–		
	V. canhi (TS)	0.0303	0.0345	0.0335	0.0322	**0**	
	V. canhi (TD)	0.0303	0.0337	0.0328	0.0314	**0.0008**	**0.0003**
12S	*P. ovchinnikovi*	**0**					
	T. steineri	0.2581	**0**				
	A. lao	0.2788	0.2273	**0.0058**			
	A. thamnongpaseum	0.2596	0.2170	0.0614	–		
	V. canhi (TS)	0.2553	0.2149	0.2216	0.2209	**0**	
	V. canhi (TD)	0.2492	0.2149	0.2119	0.2209	**0.0279**	**0.0053**
16S	*P. ovchinnikovi*	**0.0028**					
	T. steineri	0.1971	**0**				
	A. lao	0.2018	0.1863	**0.0031**			
	A. thamnongpaseum	0.2028	0.1795	0.0590	–		
	V. canhi (TS)	0.2276	0.1733	0.1665	0.1816	**0**	
	V. canhi (TD)	0.2276	0.1729	0.1703	0.1855	**0.0190**	**0.0007**
COI	*P. ovchinnikovi*	**0**					
	T. steineri	0.1879	**0.0009**				
	A. lao	0.1609	0.1632	**0.0135**			
	A. thamnongpaseum	0.1438	0.1622	0.0983	–		
	V. canhi (TS)	0.1744	0.1655	0.1517	0.1558	**0**	
	V. canhi (TD)	0.1716	0.1606	0.1524	0.1586	**0.0417**	**0.0022**
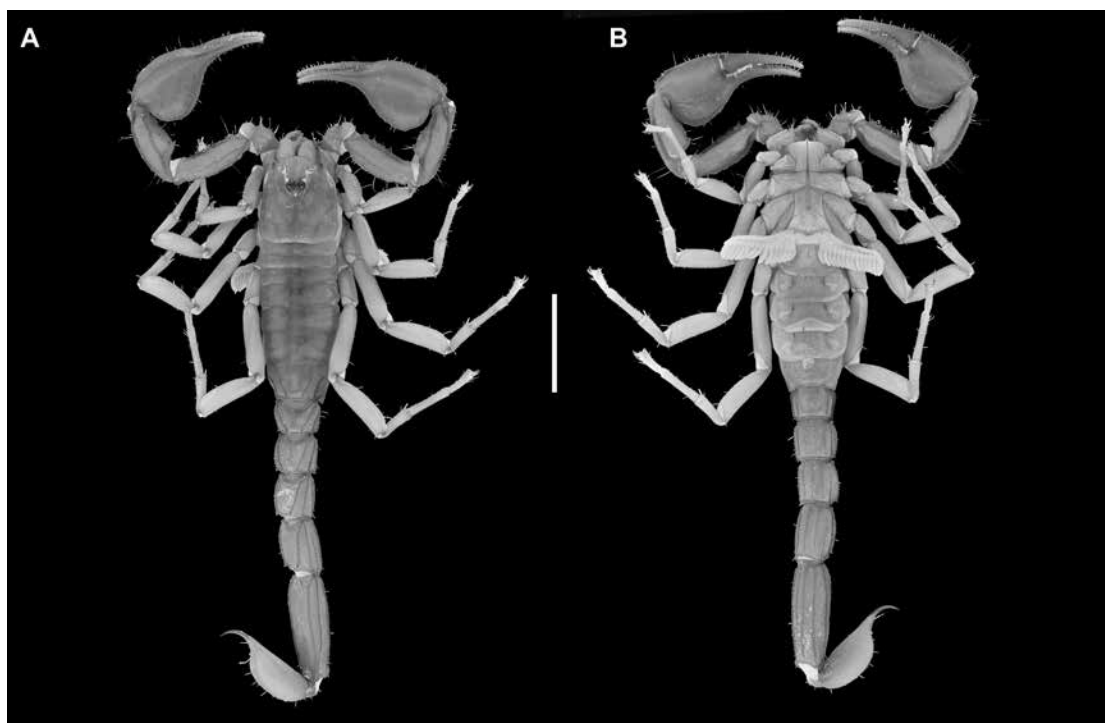
FIGURE 26. *Troglokhammouanus steineri* Lourenço, 2007, ♂ (AMNH), Tham Xe Bang Fai, Laos, habitus: **A.** dorsal and **B.** ventral aspects. Scale bar = 10 mm.

ities, e.g., climate change) within a very short period of time in an unforeseeable future, and is therefore considered to be facing a very high risk of extinction in the wild.

Material Examined: **UZBEKISTAN: Surkhandarya Region:** *Uzun Distr.*: Okmachit [Ak-Mechet], ca. 7 km W–4 km WSW, E slope of Babatag Mt. Range, 38°02′50″N 68°14′22″E–38°01′45″N 68°15′30″E, 760–1010 m, 29.iv–9.v.1994, A.V. Gromov, 1 ♀, 6 juv. (AGPC); Okmachit, ca. 7 km W, E slope of Babatag Mt. Range, 38°02′50″N 68°14′22″E, ca. 1010 m, 13.v.1995, O.V. Lyakhov, 2 juv. (AGPC); Okmachit, ca. 6.5–7 km W, E slope of Babatag Mt. Range, 38°02′50″N 68°14′22″E–38°02′04″N 68°14′51″E, 905–1010 m, 30.iv–2.v.2002, A.V. Gromov, 6 ♀, 7 subad. ♂, 1 subad. ♀, 26 juv. (AGPC); Okmachit, ca. 5 km WSW, E slope of Babatag Mt. Range, 38°02′26″N 68°14′59″E–38°02′01″N 68°15′08″E, 760–830

m, 3.v.2002, A.V. Gromov, 1 ♀, 10 juv. (AGPC); Okmachit, ca. 5–6 km WSW, E slope of Babatag Mt. Range, 38°02′01″N 68°14′03″E–38°01′36″N 68°15′00″E, 730–870 m, 4.v.2002, A.V. Gromov, 1 ♂, 1 subad. ♂ (AMNH), 3 ♀, 16 subad. ♂, 1 subad. ♀, 67 juv. (AGPC); Dikhana [Dukhana] Canyon, foothills of E slopes of Babatag Mountain Range, ca. 5 km WSW of Akmechet village, 38°01′38.3″N 68°15′11.9″E, 722 m, 20–24.v.2003, L. Prendini and A.V. Gromov, UV detection on earthen walls and rocky slopes along riverbanks and canyon walls through mountains, hard clayey soil, short grass cover with small trees and shrubs, 9 ♀, 9 subad. ♂, 3 subad. ♀, 18 juv. ♂, 10 juv. ♀ (AMNH), 3 juv. ♀ (AMCC 159928 [LP 2303A–C]); Dikhana Canyon, ca. 5.5 km WSW of Okmachit, E slope of Babatag Mt. Range, 38°01′33″N 68°14′26″E, ca. 774 m, 22.v.2003, A.V. Gromov and L. Prendini, 1 juv. (AGPC).
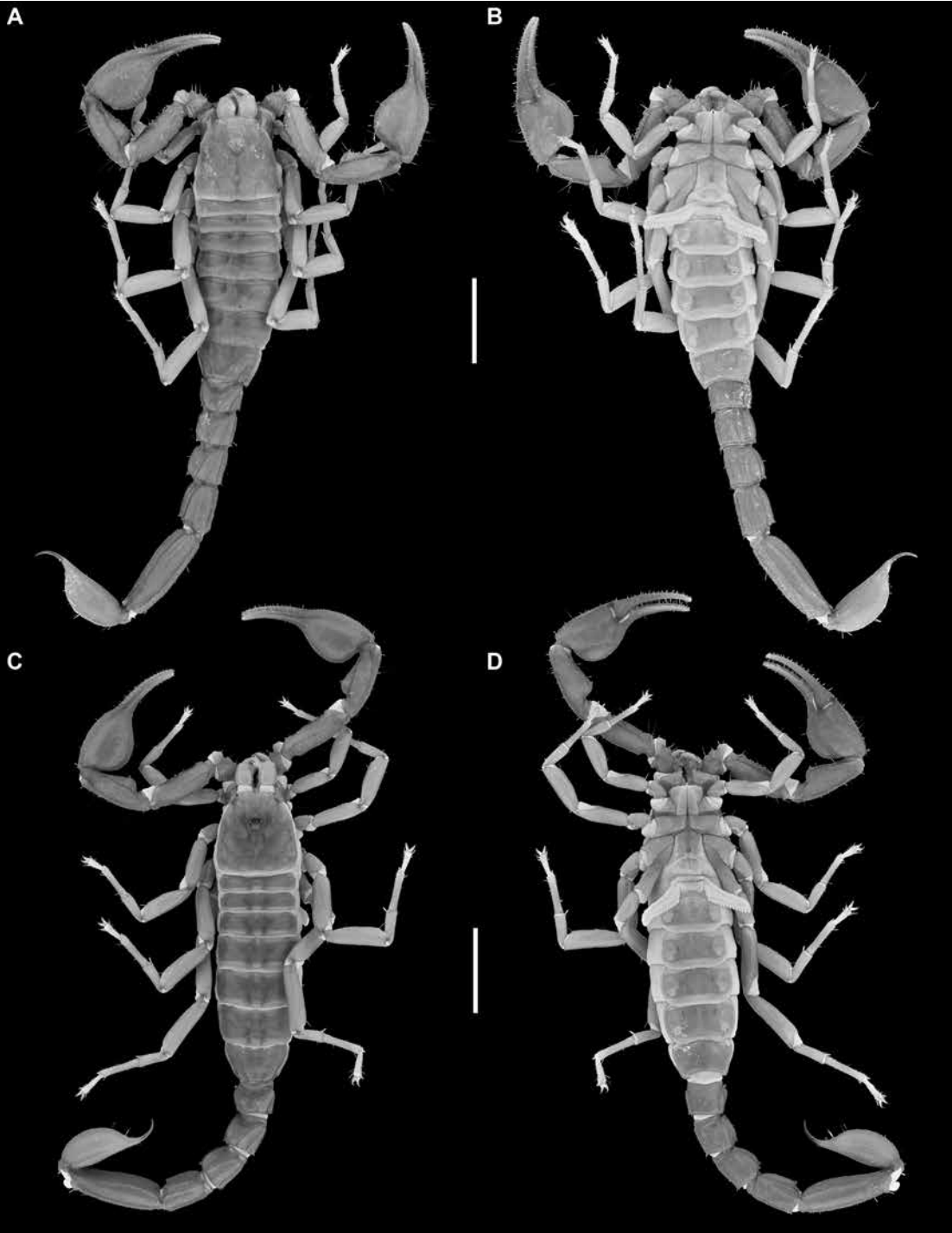
FIGURE 27. *Troglokhammouanus steineri* Lourenço, 2007, ♀♀ (AMNH), Tham Xe Bang Fai, Laos, habitus of individuals with depigmented (**A, B**) or pigmented (**C, D**) ocelli: **A, C.** dorsal and **B, D.** ventral aspects. Scale bars = 10 mm.

Subfamily Troglokhammouaninae, subfam. nov.

Figures 3, 5, 7–9, 11, 13B, D, 15B, 16C, D,
18C, D, 20C, D, 26–31, tables 1–5, 7, 8

Type genus, here designated: *Troglokhammoua-
nus* Lourenço, 2007.

DIAGNOSIS: Troglokhammouaninae may be
separated from the other two subfamilies of Pseu-
dochactidae as follows. The base coloration of the
tegument is brown in Troglokhammouaninae but
yellow in the other subfamilies. The anteromedian
margin of the carapace is convex (procurved) in
Troglokhammouaninae (fig. 11) but sublinear in
Pseudochactinae (fig. 10) and shallowly concave
(recurved) in Vietbocapinae (fig. 12). The circum-
ocular sutures of the carapace are complete but
disconnected posteriorly in Troglokhammouani-
nae (fig. 11), complete and connected posteriorly
in Pseudochactinae (fig. 10), and partial (discon-
nected) in Vietbocapinae (fig. 12). The dorsome-
dian, dorsal secondary, and subdigital carinae of
the pedipalp chela manus are vestigial, and the
retromedian and ventromedian carinae partial in
Troglokhammouaninae (figs. 29, 30), whereas the
dorsomedian, dorsal secondary, subdigital, and
retromedian carinae are absent, and the ventro-
median carina vestigial, in the other subfamilies
(figs. 24, 25, 35, 36, 39, 43). The lateral margins of
the sternum are recurved medially in Troglok-
hammouaninae (fig. 13B, D) but sublinear in the
other subfamilies (figs. 13A, C, 14). The posterior
granules of the dorsosubmedian and dorsolateral
carinae of metasomal segments I–IV are markedly
larger than the preceding granules and spiniform
in Troglokhammouaninae (fig. 16C, D) but simi-
lar in size and shape to the preceding granules, in
the other subfamilies (figs. 16A, B, 17). The
median lateral carinae of metasomal segments III
and IV are complete in Troglokhammouaninae
(fig. 18C, D) but partial, becoming obsolete ante-
riorly on III, and vestigial or absent on IV in the
other subfamilies (figs. 18A, B, 19).
Troglokhammouaninae may be further sepa-
rated from Pseudochactinae as follows. The
anteromedian margin of the carapace is protrud-

ing (anterior to the anterolateral margins) in Trog-
lokhammouaninae (fig. 11) but recessed (posterior
to the anterolateral margins) in Pseudochactinae
(fig. 10). The posterolateral margins of the cara-
pace are gently curved in Troglokhammouaninae
(fig. 11) but angular and slanting in Pseudochac-
tinae (fig. 10). The dorsoventral projection ("ante-
rior process") on the prolateral surface of the
pedipalp patella is moderately developed in Tro-
glokhammouaninae (fig. 28E, G) but pronounced
in Pseudochactinae (fig. 23E, G). The secondary
accessory and retroventral carinae of the chela
manus are incompletely fused, with a slight dis-
junction evident in the proximal third, in Troglok-
hammouaninae (figs. 29C, 30C) but entirely fused
in Pseudochactinae (figs. 24C, 25C). The ventral
surface of the sternum is shallowly concave in
Troglokhammouaninae (fig. 13B, D) but flat/pla-
nar in Pseudochactinae (fig. 13A, C). The spinules
of the basitarsi and telotarsi of legs I–IV are long
in Troglokhammouaninae (fig. 15B) but short in
Pseudochactinae (fig. 15A). The pectines possess
12–16 lamellae and 13–17 teeth in Troglokham-
mouaninae (tables 3, 5, 7, 8) but 8–12 median
lamellae and 9–13 teeth in Pseudochactinae
(tables 3, 5, 6). The peg sensillae of the pectinal
teeth are long, cylindrical, tubular or bottle
shaped, and rounded distally, without laterodistal
processes in Troglokhammouaninae but relatively
short, stout, flattened, and truncate distally, with
laterodistal processes in Pseudochactinae. The tel-
son vesicle is elongate in Troglokhammouaninae
(fig. 18C, D) but globose in Pseudochactinae (fig.
18A, B).
Troglokhammouaninae may be further sepa-
rated from Vietbocapinae as follows. The tegu-
ment is infuscate (e.g., on the carapace, tergites,
and legs) in Troglokhammouaninae but immacu-
late in Vietbocapinae. The median and lateral
ocelli are present in Troglokhammouaninae (fig.
11) but absent in Vietbocapinae (fig. 12). The
pedipalps are relatively robust, with the chela fin-
gers of the adult male sinuous and sexually dimor-
phic in Troglokhammouaninae (figs. 29, 30),
whereas the pedipalps are gracile, with the chela
fingers of the adult male sublinear and similar to

the adult female in Vietbocapinae (figs. 35, 36). The prolateral ventral carina of the pedipalp chela manus is complete in Troglokhammouaninae (figs. 29D, 30D) but absent or obsolete in Vietbocapinae (figs. 35D, 36D, 39D, 43D). Tibial spurs are present on legs III and IV in Troglokhammouaninae (fig. 15B) but absent in Vietbocapinae (fig. 15C, D). The lateral and ventral surfaces of the telson vesicle possess granular carinae in Troglokhammouaninae (figs. 18C, D, 20C, D), whereas the lateral surfaces are smooth and the ventral surfaces smooth or with sparsely granular (obsolete) carinae in Vietbocapinae (figs. 19, 21). The subaculear tubercle is obsolete (evident as a very small bump) in Troglokhammouaninae (fig. 18C, D) but absent in Vietbocapinae (fig. 19).

INCLUDED TAXA: As defined in the present contribution, Troglokhammouaninae accommodates one genus and species (table 1): *Troglokhammouanus* Lourenço, 2007.

DISTRIBUTION: Endemic to the Southeast Asian country of Laos, where it has been recorded only in Khammouane Province (fig. 7).

ECOLOGY: The sole species of Troglokhammouaninae is hypogean, having been collected below ground, in caves (fig. 3).

REMARKS: The morphological similarities between *Troglokhammouanus* and *Pseudochactas* are mostly symplesiomorphic. Phylogenetic analyses, whether based on morphology, DNA sequences or a combination thereof, place *Troglokhammouanus* as the sister group of Vietbocapinae, rendering the nominotypical subfamily, Pseudochactinae, paraphyletic. A new, monotypic subfamily, Troglokhammouaninae, is hereby created to restore the monophyly of Pseudochactinae.

Troglokhammouanus Lourenço, 2007

Figures 3, 5, 7–9, 11, 13B, D, 15B, 16C, D, 18C, D, 20C, D, 26–31, tables 1–5, 7, 8

Troglokhammouanus Lourenço, 2007a: 774, type species by monotypy: *Troglokhammouanus steineri* Lourenço, 2007a; 2007b: 1–6, figs.

1–24; Vignoli and Prendini, 2009: 3, table 1; Prendini, 2011: 117; Lourenço and Leguin, 2012: 71; Soleglad et al., 2012: 95, 96; Loria and Prendini, 2014: 5, 20, 21, tables 2, 4; Lourenço, 2014: 31, 36; Beron, 2015: 172; Sharma et al., 2015b: 4, fig. 2d; Lourenço, 2017a: 19; Loria and Prendini, 2018: 186, table 2; Lourenço et al., 2018: 265; Francke, 2019: 16, 32, 39; Sendi et al., 2020: 288.

DIAGNOSIS: As for subfamily.

INCLUDED TAXA: As redefined in the present contribution, *Troglokhammouanus* accommodates a single species: *Troglokhammouanus steineri* Lourenço, 2007.

DISTRIBUTION: As for subfamily.

ECOLOGY: The sole species of *Troglokhammouanus* is hypogean, inhabiting the dark zone of a deep cave (fig. 3).

Troglokhammouanus steineri Lourenço, 2007

Figures 3, 5, 7–9, 11, 13B, D, 15B, 16C, D, 18C, D, 20C, D, 26–31, tables 1–5, 7, 8

Troglokhammouanus steineri Lourenço, 2007a: 771, 775, 776, figs. 1, 3 (4–15), 4 (16–24); 2007b: 1–6, figs. 1–24; Lourenço and Pham, 2010: 2, 12; Botero-Trujillo and Noriega, 2011: 42; Jäger, 2012: 37; Lourenço, 2012a: 233, 236, 237, appendix A; Lourenço and Leguin, 2012: 71; Lourenço and Pham, 2012: 80, 84; Soleglad et al., 2012: 89; Steiner, 2013: 416; Loria and Prendini, 2014: appendix S1: 10, appendix S2: 7; Lourenço, 2014: 31; Beron, 2015: 184; Sharma et al., 2015a: 354; 2015b: 4, 7, figs. 1e, 2c, 3b; Lourenço, 2017a: 19–21, 23, fig. 1; Beron, 2018: 834; Lourenço et al., 2018: 265; Ballesteros et al., 2019: table S1; Francke, 2019: 32; Howard et al., 2019: 76, table 1; Santibáñez-López et al., 2019b: 26, table 3.

Troglokhammouanus louisanneorum Lourenço, 2017a: 20–23, figs. 1, 4–16; syn. nov.

TYPE MATERIAL: **LAOS: Khammouane Prov.:** *Boualapha Distr.*: Hin Namno National Biodiver-

sity Conservation Area: Holotype ♀ (MNHN RS 9098) [examined], juv. ♂ paratype (MNHN RS 9099) Boualapha, Tham Xe Bangfai (cave), Ban Nong Ping [17°22′23.6″N 105°50′11.8″E], 14.ii.2007, H. Steiner, midsection of cave [2–3 km from entrance], on sand [alluvial soil and sand bank next to river edge]. *Gnommalath Distr.*: *Troglokhammouanus louisanneorum*: Holotype ♀ (MNHN), Ban Naden, Tham Nam Lot cave (17°30′17.9″N 105°23′08.2″E), 176 m, 8.xi.2011, L. Deharveng and A. Bedos, 350–450 m from main cave entrance.

DIAGNOSIS: As for subfamily.

DESCRIPTION: The following description, based on the holotype female of *T. steineri*, and material examined, including 10 adult males and 61 adult females, supplements the original descriptions of Lourenço (2007a, 2017a) and supplemental data in Lourenço (2007b).

Total length: Small, 32.2 mm (28.4–36.4 mm, $n = 9$) (♂) or 38.5 mm (35.8–41.3 mm, $n = 13$) (♀) (tables 3, 7, 8).

Color: Tegument base coloration reddish yellow to reddish brown. Carapace diffusely infuscate, with brownish marbled pattern; tergites with paired submedial and sublateral stripes of brownish infuscation longitudinally, or immaculate; other surfaces immaculate. Carapace, pedipalps, tergites, and metasoma reddish yellow to reddish brown. Chela fingers, pedipalpal and metasomal carinae dark reddish brown. Chelicerae, legs, sternum, genital operculum, and sternites pale yellow. Pectines pale, yellowish white. Telson paler than metasomal segment V. Aculeus black.

Chelicerae: Fixed finger, dorsal margin with four teeth (basal, median, subdistal, distal); basal and median teeth fused into bicuspid ("conjoined on trunk"); space between median and subdistal teeth U-shaped; ventral margin with five or six small denticles (ventral accessory denticles). Movable finger, dorsal margin with three teeth (median, subdistal, retrolateral distal), without basal teeth; ventral margin with five or six small denticles (ventral accessory denticles) and serrula in distal third; retrolat-

eral (dorsal) distal and prolateral (ventral) distal teeth subequal, retrolateral (dorsal) distal tooth smaller than prolateral (ventral) distal tooth, and opposable. Ventral surface of fingers and manus with numerous long, dense macrosetae.

Carapace: Carapace slightly longer than wide, anterior width 51% (43%–55%, $n = 9$) (♂) or 50% (45%–57%, $n = 13$) (♀) of length, posterior width 90% (85%–94%, $n = 9$) (♂) or 95% (79%–102%, $n = 13$) (♀) of length (tables 3, 7, 8). Anterior margin convex (procurved), protruding medially; anterolateral margins entire; posteromedian margin shallowly concave (recurved); posterolateral margins gently curved (fig. 11). One pair of very small anterolateral major (ALMa) ocelli situated close to anterolateral margins of carapace, other lateral ocelli absent. Anterosubmedial depressions, medial to lateral ocelli, well developed. Median ocular tubercle situated anteromedially on carapace, distance from anterior margin 32% (26%–37%, $n = 9$) (♂) or 33% (30%–35%, $n = 11$) (♀) of carapace length (tables 7, 8); pair of median ocelli considerably larger than lateral ocelli; pair of weakly developed, smooth superciliary carinae, not protruding above ocelli; interocular sulcus shallow, obsolete. Circumocular sutures complete but disconnected posteriorly; circumocular triangle subtriangular (broad V-shape); median ocular curvatures present. Anteromedian depression narrow, shallow; posteromedian sulcus very shallow anteriorly, becoming slightly deeper posteriorly; posterolateral sulci very shallow, wide, weakly curved; posteromarginal sulcus narrow, shallow. Carapace acarinate; surfaces finely to moderately granular, except on anteromedian depression and along lateral and posterior margins.

Pedipalps: Pedipalps relatively robust; segments almost apilose, sparsely covered in short microsetae and occasional macrosetae. Pedipalp femur length 68% (65%–71%, $n = 9$) (♂) or 64% (59%–68%, $n = 13$) (♀) greater than width (tables 3, 7, 8). Femur with seven carinae evident (fig. 28A–D); promedian carina obsolete, reduced to
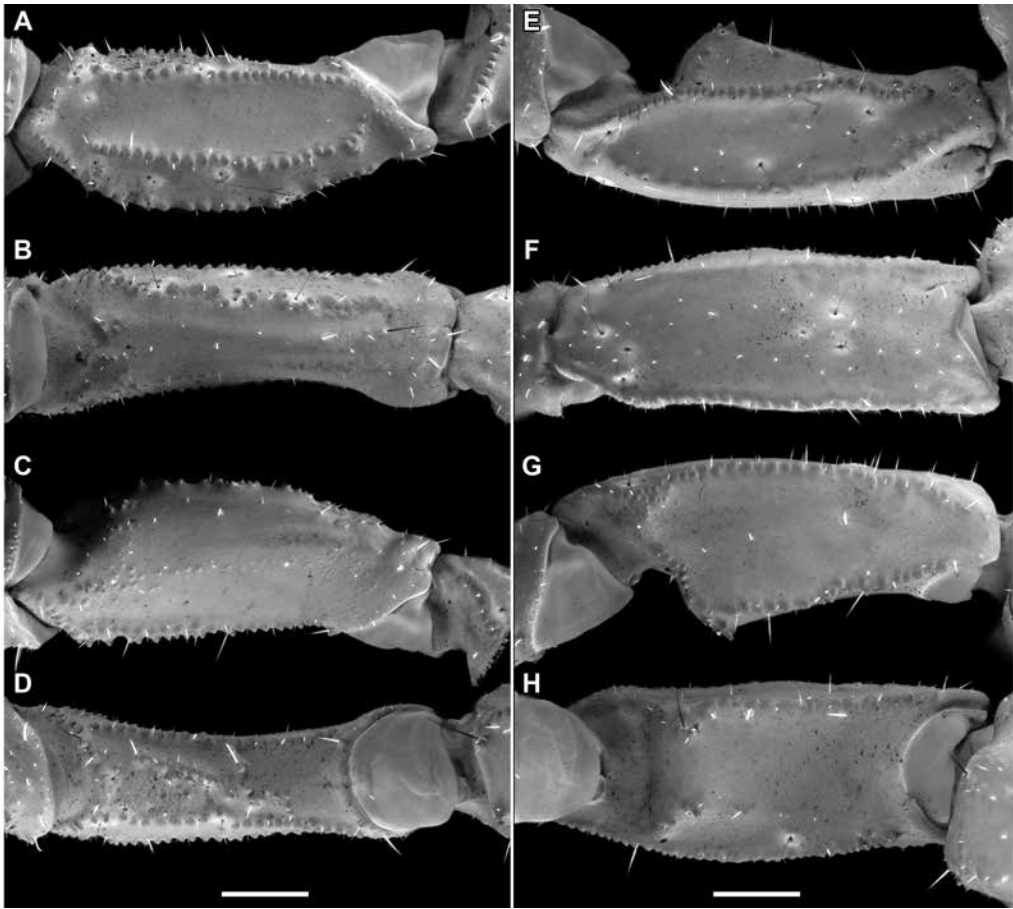
FIGURE 28. *Troglokhammouanus steineri* Lourenço, 2007, ♀ (AMNH), Tham Xe Bang Fai, Laos, dextral pedipalp femur (**A–D**) and patella (**E–H**): **A, E.** dorsal, **B, F.** retrolateral, **C, G.** ventral, and **D, H.** prolateral aspects. Scale bars = 1 mm.

few spiniform granules in proximal two-thirds of segment; prodorsal, proventral and retrodorsal carinae well developed, costate granular; dorsomedian carina moderately developed, granular; retromedian and retroventral carinae vestigial, reduced to few granules proximally; ventromedian carina absent; intercarinal surfaces smooth. Pedipalp patella length 62% (59%–70%, *n* = 9) (♂) or 61% (58%–62%, *n* = 13) (♀) greater than width (tables 3, 7, 8). Patella with six carinae evident (fig. 28E–G); retrodorsal, retroventral, and proventral carinae well developed, costate granular to costate; prodorsal carina well developed, granular to costate granular; prolateral surface,

dorsoventral "vaulted" projection ("anterior process") moderately developed, with prominent pair of dorsal and ventral spiniform granules ("patellar spurs") proximally, the dorsal more strongly developed, demarcating pair of obsolete, granular prolateral dorsal and ventral carinae ("patellar spur carinae"); ventromedian carina vestigial, reduced to proximal granules; dorsomedian and retromedian carinae absent; intercarinal surfaces smooth. Pedipalp chela relatively short and broad; manus globose, width 28% (21%–32%, *n* = 9) (♂) or 25% (18%–33%, *n* = 13) (♀) greater than height and length 14% (8%–19%, *n* = 9) (♂) or 21% (17%–26%, *n* = 11) (♀) greater
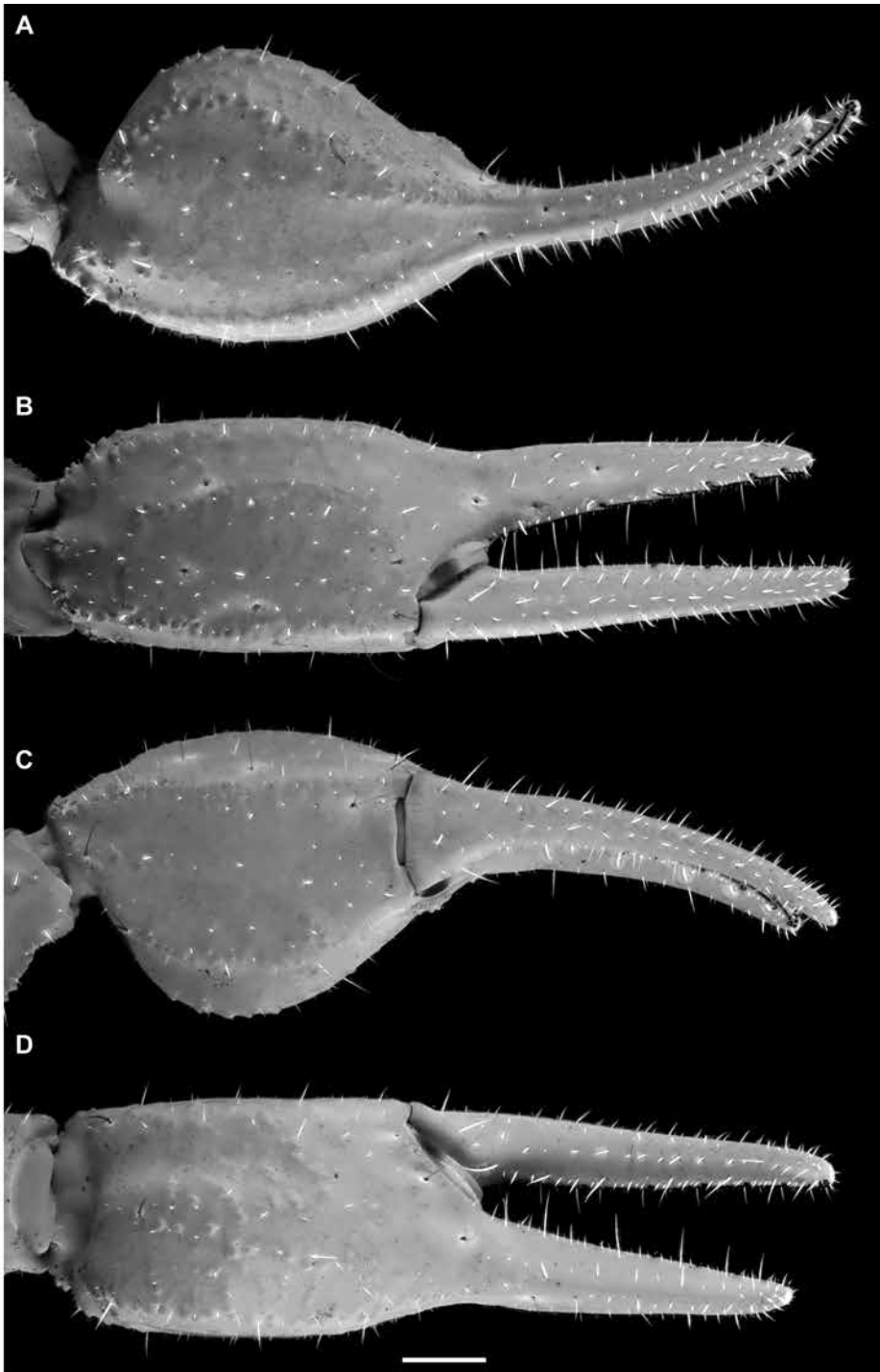
FIGURE 29. *Troglokhammouanus steineri* Lourenço, 2007, ♀ (AMNH), Tham Xe Bang Fai, Laos, dextral pedipalp chela: **A.** dorsal, **B.** retrolateral, **C.** ventral, and **D.** prolateral aspects. Scale bar = 1 mm.
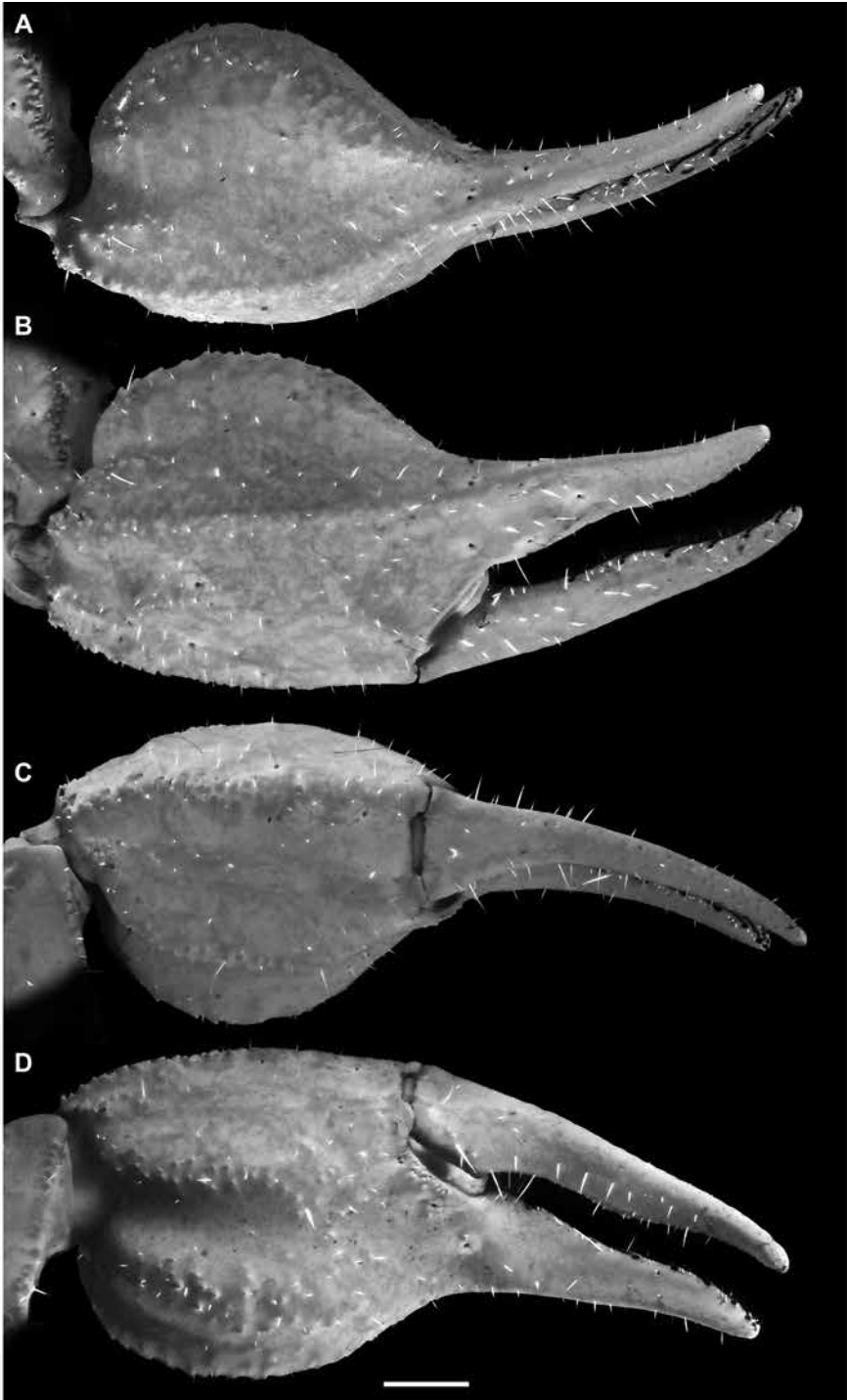
FIGURE 30. *Troglokhammouanus steineri* Lourenço, 2007, ♂ (AMNH), Tham Xe Bang Fai, Laos, dextral pedipalp chela: **A.** dorsal, **B.** retrodorsal, **C.** ventral, and **D.** proventral aspects. Scale bar = 1 mm.

than width (tables 3, 7, 8); length of movable finger 16% (8%–24%, $n = 9$) ($\male$) or 24% (16%–35%, $n = 11$) ($\female$) greater than length of manus. Chela with 10 carinae evident (figs. 29, 30); dorsomedian carina complete, granular; dorsal secondary and subdigital carinae vestigial, reduced to granules proximally on manus; digital carina well developed, costate granular; retromedian (retrolateral secondary) carina partial, comprising granular row medially; secondary accessory and retroventral carinae incompletely fused, slight disjunction evident in proximal third; retroventral carina well developed, granular, aligned parallel to longitudinal axis of chela, with distal margin connected to retrolateral movable finger condyle; ventromedian carina partial, comprising granular row in proximal quarter; prodorsal, promedian, and proventral carinae obsolete, each reduced to series of isolated granules; intercarinal surfaces smooth except for coarse, scattered granules on prolateral surface of manus, near base of fixed and movable fingers. Fixed and movable fingers, dentate margins sublinear ($\female$) or markedly sinuous, movable finger with shallow lobe, proximally and fixed finger with correspondingly shallow notch, proximally ($\male$), no proximal "gap" evident when closed; median denticle rows comprising seven (6 or 7, $n = 143$) (fixed finger) or eight (6–8, $n = 141$) (movable finger) oblique and slightly imbricated subrows (tables 3, 4, 7, 8), decreasing in length distally; each subrow comprising large retrolateral denticle proximally (absent from proximal subrow, for total of seven retrolateral denticles on fixed and movable fingers), several small median denticles, and large prolateral denticle distally, slightly offset (total of seven and eight prolateral denticles on fixed and movable fingers, respectively); terminal (prolateral) denticle of first subrow enlarged; accessory denticles absent.

Trichobothria: Orthobothriotaxic, Type D, β configuration, trichobothrium d_2 situated on femur dorsal surface, d_3 and d_4 in same axis, parallel and closer to retrodorsal carina than d_1, angle formed by d_1, d_3 and d_4 opening toward prolateral surface, with the following segment totals (figs. 28–30): femur, 12 (6 dorsal, 3 prolateral, 3 retrolateral); patella, 10 (3 dorsal, 1 prolateral, 6 retrolateral); chela, 13 (5 manus, 8 fixed finger). Total number of trichobothria per pedipalp, 35. Five trichobothria on femur, i_4, d_1, d_2, d_4, and d_6, one on patella, est_1, and one on chela fixed finger, ib_2, noticeably smaller than others ("petite"). Trichobothrium Et_1 situated distally on manus, aligned with or proximal to movable finger condyle; eb situated on fixed finger, slightly distal to movable finger condyle; esb_2 situated in proximal third of fixed finger, approximately aligned with proximal retrolateral denticle of median denticle row.

Legs: Leg I maxillary lobes (coxapophyses), distal margins rounded, unmodified (not spatulate or dilate) anteriorly, terminating flush with lobes of leg II (figs. 26B, 27B, D). Legs I and II tibiae, retrolateral margins each with scattered macrosetae, without spurs (fig. 15B); III and IV with spurs, smooth, without spinelets. Basitarsi with few scattered macrosetae, pro- and retrolateral rows of long spinules, and pair of pro- and retrolateral pedal spurs. Telotarsi with pair of ventrosubmedian rows of long spinules; proventral and retroventral rows of macrosetae absent, only few scattered macrosetae laterally; laterodistal lobes reduced and truncated; median dorsal lobe very short; ungues short, distinctly curved, equal in length; unguicular spur (dactyl) pronounced, pointed.

Sternum: Sternum, Type 1, pentagonal, posterior width 89% (80%–104%, $n = 9$) ($\male$) or 86% (79%–97%, $n = 11$) ($\female$) of length (tables 7, 8), lateral margins recurved medially, ventral surface shallowly concave, posteromedian depression round (fig. 13B, D).

Pectines: Three marginal (anterior) lamellae, proximal sclerite considerably longer, distal sclerite short (fig. 13B, D); 15/14 (13–16, $n = 92$) ($\male$) or 13/13 (12–14/12–15, $n = 190$) ($\female$) median lamellae (tables 3, 5, 7, 8); fulcra present, small. Proximal median lamella and basal pectinal tooth unmodified. Pectinal teeth present along entire posterior margin of each pecten ($\male$, $\female$); 16/15 (14–17, $n = 94$) ($\male$) or 14/14 (13–15/13–

16, n = 190) (♀) teeth. Pectinal peg sensillae long, cylindrical, tubular or bottle shaped, and rounded distally, without pair of laterodistal processes; sensillar sockets smooth.

Genital operculum: Opercular sclerites completely separated, prominent genital papillae visible along entire length (♂) or absent (♀) (fig. 13B, D). Genital plugs observed in some females.

Male reproductive organs: Paraxial organ without accessory glands. Hemispermatophore lamelliform, *pars recta* absent (fig. 31); basal lobe present.

Female reproductive organs: Ovariuterus comprising reticulate mesh of six cells. Oocytes contained in sessile follicles directly contacting ovaruterine tubes.

Mesosoma: Pretergites surfaces smooth and shiny. Posttergites I–VI surfaces moderately to coarsely granular, granulation becoming slightly coarser near posterior margins, acarinate, each with pair of shallow submedian depressions (figs. 26A, 27A, C); VII surface sparsely granular, with pair of costate granular dorsosubmedian and dorsolateral carinae reaching posterior margin of segment. Sternites III–VII surfaces entirely smooth, acarinate (figs. 26B, 27B, D), with scattered macrosetae, posterior margins with sparse row of macrosetae; III–VI, respiratory spiracles (stigmata) small, oval (fig. 13B, D); V posteroventral margin with pale, raised, triangular surface; VII width 41% (34%–47%, n = 9) (♂) or 41% (36%–46%, n = 11) (♀) greater than length (tables 7, 8).

Metasoma: Metasoma relatively short, total length 24% (16%–28%, n = 9) (♂) or 18% (13%–32%, n = 11) (♀) greater than combined length of prosoma and mesosoma (tables 7, 8); segments I–V progressively increasing in length, I and II wider than long, width of length for segment I, 126% (118%–136%, n = 9) (♂) or 138% (124%–156%, n = 13) (♀); II, 101% (92%–109%) (♂) or 107% (96%–118%) (♀); III, 88% (76%–97%) (♂) or 93% (88%–100%) (♀); IV, 65% (59%–68%) (♂) or 68% (64%–74%) (♀); and V, 35% (32%–37%) (♂) or 36% (34%–39%) (♀). Metasoma almost apilose, sparsely covered in short microsetae. Eight carinae on

segment I, 10 on II–IV, and nine on V (figs. 16C, D, 18C, D, 20C, D). Dorsosubmedian carinae well developed, costate granular throughout length of segments I–IV, absent on V; converging posteriorly. Dorsolateral carinae well developed, costate granular throughout length of segments I–V; converging posteriorly on I and V, subparallel on II–IV. Dorsosubmedian and dorsolateral carinae of segments I–IV each terminating posteriorly with enlarged, spiniform granule. Median lateral carinae complete, costate granular throughout length of segments I–V. Ventrolateral carinae well developed, costate granular, but becoming obsolete anteriorly on segments I and II, continuous throughout length of III–V; converging posteriorly on I and V, subparallel on II–IV. Ventrosubmedian carinae absent on segment I, obsolete, costate on II, well developed, costate granular throughout length of III–V; subparallel on II and III, converging posteriorly on IV and V. Ventromedian carina moderately developed, granular, on segment V. Intercarinal surfaces smooth.

Telson: Telson large, suboval (figs. 16C, D, 18C, D, 20C, D). Vesicle elongate, width 105% (101%–112%, n = 9) (♂) or 106% (97%–117%, n = 13) (♀) of metasomal segment V width (tables 3, 7, 8), with flattened dorsal surface and rounded ventral surface, height 37% (32%–44%, n = 9) (♂) or 39% (34%–47%, n = 13) (♀) of length; dorsal surface smooth, lateral surfaces with three pairs of obsolete, granular carinae, ventral surfaces with two pairs of obsolete, granular carinae; anterodorsal lateral lobes ("vesicular tabs") distinct, each with two spiniform granules; subaculear tubercle absent. Aculeus short, shallowly curved, 23% (21%–27%, n = 9) (♂) or 24% (21%–32%, n = 13) (♀) of telson length. Venom glands thin walled, simple and unfolded.

Intraspecific variation: One juvenile was completely depigmented and one adult female partially depigmented, including the ocelli (figs. 11E, 27A, B). No other significant variation was noted.

Ontogenetic variation: Immature stages of *T. steineri* are paler in color and less sclerotized than adults, and the posteroventral margin of

mesosomal sternite V does not exhibit a pale, raised, triangular surface as in the adults of both sexes. Males and females closely resemble one another externally until the final instar. However, immature stages are easily sexed by examination of the genital aperture.

Sexual dimorphism: The genital papillae, visible the entire length and thus completely separating the two sclerites of the genital operculum (fig. 13B), are the characters of primary external sexual dimorphism in the male. The opercular sclerites are also completely separated in the female, although genital papillae are absent (fig. 13D). Adult males may be further separated from adult females and immature stages based on several secondary sexual characters. The most obvious are the sexually dimorphic pedipalp chelae, the fixed and movable fingers of which are markedly sinuous in the adult male (figs. 29, 30), as well as the more developed pectines, the median lamellae of which are more numerous and the teeth somewhat larger, and more numerous (fig. 13B, D; tables 3, 5, 7, 8). In addition, the adult male is proportionally more slender (fig. 26), with a slightly longer metasoma and telson (tables 7, 8), and slightly more pronounced granulation on the carapace, pedipalps, and tergites than the adult female (fig. 27). The pale, raised, triangular surface on the posteroventral margin of sternite V is more pronounced in the adult male (fig. 26B) than the adult female.

DISTRIBUTION: Endemic to the Boualpha District of Khammouane Province, Laos, where it has been recorded from a single cave, Tham Xe Bangfai (also known as Xe Bangfai River Cave or Tham Khoun Xe), in the Hin Namno National Biodiversity Conservation Area, near Nong Ping (fig. 7). Two expeditions to the putative type locality of *T. louisanneorum*, Tham Nam Lot (Lod), near Ban Naden, in the Gnommalath District, failed to confirm the presence of this species.

ECOLOGY: Specimens collected by the first author at Tham Xe Bangfai were found with UV light detection, from the twilight zone to approximately 3 km from the downstream entrance (resurgence) (fig. 3B–D). Whereas specimens were observed in the dark zone during daytime, specimens were only observed in the twilight zone at night. It is not known how far the species extends into the river cave, which is approximately 11 km long, but the greatest abundance of individuals was observed between 300–500 m from the entrance, and their abundance appeared to decrease with increasing distance (more than 500 m upstream). Although a few specimens were collected on flowstone rock faces, the vast majority were collected close to the water, on moist muddy riverbanks at several "beaches" within the cave (fig. 3E). Most were collected in cracks between the drying mud slabs or among sticks and other vegetative debris trapped between rocks, almost always on moist soil (fig. 3F–H). None were taken on the dry sand banks or dry rock faces higher upslope. Although these moist areas presumably harbor a greater abundance of prey, the apparent preference of *T. steineri* for moist substrates, also observed in the epigean *P. mischi* and *P. ovchinnikovi* (Fet et al., 2004; Prendini et al., 2006; Soleglad et al., 2012), strongly suggests an ecological requirement for moisture.

Although no specimens of *T. steineri* have thus far been collected outside the cave, the morphology of this species suggests it is troglophilous rather than troglobitic (Prendini, 2001b; Volschenk and Prendini, 2008). The ocelli, especially the median pair, are well developed, as in some epigean scorpions from low light environments, e.g., rainforests (Loria and Prendini, 2021), the tegument of most individuals does not lack pigmentation (indeed, the base coloration is darker than in the two epigean species of *Pseudochactas*), and there is no obvious attenuation of the pedipalps or legs, as in Vietbocapinae. It is conceivable that *T. steineri* is restricted to the cave interior due to its requirement for high humidity rather than for darkness per se.

Two buthids, *Lychas aberlenci* Lourenço, 2013, and *Lychas mucronatus* (Fabricius, 1798) were collected in the deciduous forest surrounding the cave entrance. The remains of a scorpionid, *Heterometrus laoticus* Couzijn, 1981, presumably
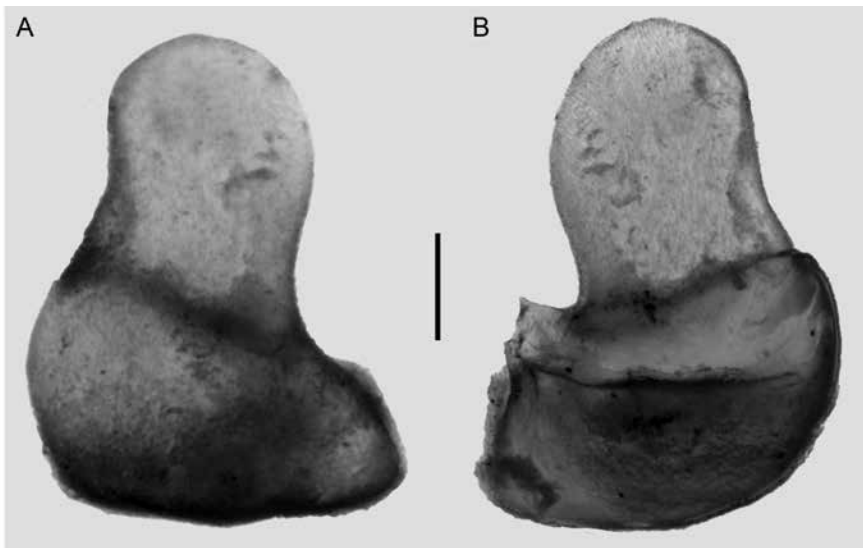
FIGURE 31. *Troglokhammouanus steineri* Lourenço, 2007, ♂ (AMNH), hemispermatophore, ectal (**A**) and ental (**B**) aspects. Scale bar = 1 mm.

washed in by the Xe Bang Fai River, were collected inside.

CONSERVATION STATUS: *Troglokhammouanus steineri* is very abundant in Tham Xe Bang Fai, which is very large (ca. 11 km long), relatively undisturbed, and situated within a protected area, the Hin Namno National Biodiversity Conservation Area. Due to difficult access, the surrounding forest is relatively intact, except for seasonal subsistence cultivation. Aside from an increase in disturbance associated with recreational ecotourism (e.g., caving and kayaking) in the cave, which could become a threat if unchecked, there appear to be few immediate threats to the survival of this species. Nevertheless, it is characterized by an acute restriction in both its area of occupancy and number of known localities: it is known to exist at one or perhaps two locations, the extent of occurrence is less than 5000 km², and the area of occupancy less than 500 km². Therefore, while presently of Least Concern, this species is prone to the effects of human activities (or stochastic events, the impact of which may be increased by human activities, e.g., climate change) within a very short period of time in an unforeseeable future, and poten-

tially faces a high risk of extinction in the wild, warranting its assignment to the Endangered category of the IUCN Red List in the future.

REMARKS: In the description of *T. louisanneorum*, Lourenço (2017a: 23) noted the following:

> The new species is very similar to the only other known species of the genus, *Troglokhammouanus steineri* … Nevertheless, a few differences can be observed: (i) a generally paler coloration in the new species, which is yellow to reddish-yellow, with pale yellow legs, (ii) the granulation on pedipalps and tergites is stronger in the new species, (iii) dorsal and ventral spinoid tubercles of pedipalp patella weaker than on *T. steineri*, (iv) some morphometric values differ between the two species, although their overall size is almost identical. Furthermore, the two species were found in separate caves that are not connected.

No other morphological differences between *T. louisanneorum* and *T. steineri* can be discerned from the diagnosis or description, in the absence of which the minor differences noted by Lourenço (2017a) cannot be considered diagnostic for the following reasons. Coloration is known to vary considerably within and between conspe-
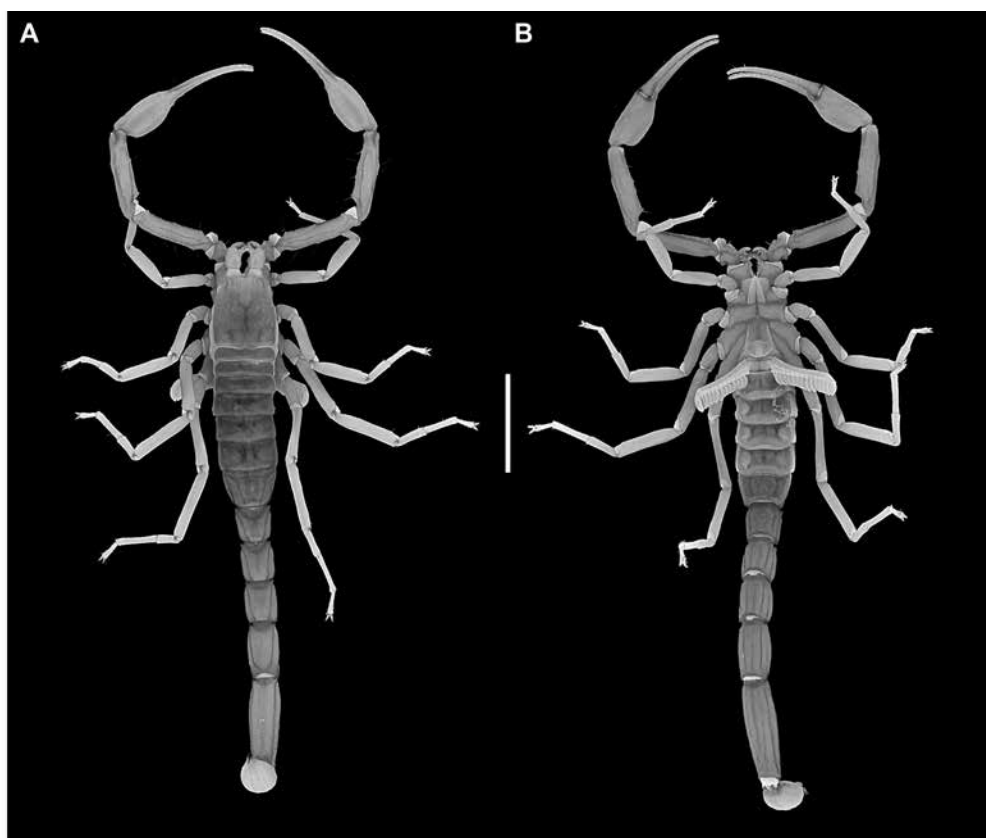
FIGURE 32. *Aemngvantom lao* (Lourenço, 2012), comb. nov., ♂ (AMNH), Tham Nam Lot (Lod), Laos, habitus: **A.** dorsal and **B.** ventral aspects. Scale bar = 10 mm.

cific populations of scorpions and the variation described falls well within the variation among the material examined from the type locality, a single cave, during the present study (e.g., although immatures of *T. steineri* are generally more infuscate than adults, a few are depigmented; figs. 11E, 27A, B). Similarly, the unspecified differences in granulation of the pedipalps and tergites between the two species, which includes the "weaker" tubercles on the pedipalp patella of *T. louisanneorum*, fall within the range of variation among the material examined from the type locality. Any possible morphometric differences offered by Lourenço (2017a) may be discounted on the grounds that two individuals (i.e., the holotypes of *T. louisanneorum* and *T. steineri*) do not comprise a statistical sample.

Moreover, multivariate statistical analysis of the morphometric data presented by Lourenço (2007a, 2017a), together with new data (tables 3–5, 7, 8; appendices 4, 5, 7), was unable to separate the holotype of *T. louisanneorum* from the holotype of *T. steineri* or other individuals from the type locality, all of which clustered together across a morphospace comparable to that of other pseudochactid species (fig. 8).

It would therefore appear that the distinction between *T. louisanneorum* and *T. steineri* rests solely on their occurrence in two caves "that are not connected," also known as the "caves as islands" paradigm (Mammola, 2019). The assumption that species occurring in different caves must be heterospecific, promulgated by others (e.g., Francke, 2009a), is problematic for three reasons.

FIGURE 33. *Aemngvantom lao* (Lourenço, 2012), comb. nov., ♀ (AMNH), Tham Nam Lot (Lod), Laos, habitus: **A.** dorsal and **B.** ventral aspects. Scale bar = 10 mm.

Firstly, geography is not heritable and cannot comprise part of a taxon diagnosis, regardless of the presence or absence of morphological (or genomic) differences. Secondly, no evidence has been presented that the caves are disconnected or, if true, that the scorpion (which appears to be troglophilous) might not occur in other caves, rock shelters or deep crevices in the 50 km between them. The type locality of *T. steineri*, Tham Xe Bang Fai, is 11 km long, but many other caves and cave networks are more than 50 km in length, e.g., the Clearwater Cave System, Malaysia (over 48 km long), Lechuguilla Cave, New Mexico (over 221 km long), the Shuanghedong Cave Network, China (over 240 km long), Optymistychna Cave, Ukraine (over 258 km long), the Sistema Ox Bel Ha (over 268 km long) and Sistema Dos Ojos (over 320 km long), both in Mexico, and the Mammoth Cave Network, Kentucky (over 652 km long). In attributing islandlike properties to caves, researchers must consider the presence of subterranean connections, as well as the vagility of the species of interest (Mammola, 2019). A network of fissures connecting two caves would make it difficult to consider the scorpion populations inhabiting them, to be isolated from one another.

Lastly, there is doubt about the accuracy of the original collection data for *T. louisanneorum*. Two expeditions to Tham Nam Lot (Lod), in different years (June 2012, May 2018), failed to confirm the presence of this species, which is extremely abundant at the type locality, Tham Xe Bang Fai, although numerous other scorpions of several taxa (including the pseudochactid, *A. lao*), were collected. Not a single specimen of this species was found during either visit to Tham Nam Lot (Lod), whereas ca. 140 specimens were collected during a single visit to Tham Xe Bang Fai, conducted during the same season.

In view of the evidence that the holotypes are conspecific, and absent any evidence to the contrary, the following new synonym is proposed: *Troglokhammouanus louisanneorum* Lourenço, 2017 = *Troglokhammouanus steineri* Lourenço, 2007, syn. nov.

MATERIAL EXAMINED: **LAOS: Khammouane Prov.:** *Boualapha Distr.*: Hin Namno National Biodiversity Conservation Area: Tham Xe Bang Fai (Xe Bang Fai River Cave), 17°22′23.6″N 105°50′11.8″E, 159 m, left bank of Xe Bang Fai River (coming from downstream entrance): 19.ii.2012, L. Prendini and P. Kanyavong, very steep muddy beach on riverbank, with few cracks and no debris, UV detection, specimen on mud bank, 1 ♂ (AMNH), muddy beach on riverbank, with moderate to steep mud bank with few rocks, UV detection, all specimens on moist mud bank, 2 ♀, 1 subad. ♂, 4 juv. ♂, 1 juv. ♀ (AMNH), rocky beach of riverbank at base of "Stairway to Heaven," with little mud except at base of rocks close to river, UV detection, 1 ♀, several imm. on moist mud, 1 imm. among vegetative debris caught between rocks, none on dry sand or rocks, 1 ♀, 1 subad. ♀, 3 juv. ♂ [1 juv. ♂ totally depigmented], 3 juv. ♀, pair of pedipalp chelae (AMNH), 1 juv. ♀ (AMCC [LP 11275]), 19–21.ii.2012, L. Prendini, P. Kanyavong, and W. Phimmathong, rocky beach on riverbank, with extensive mud and sand banks in places, UV detection, specimens mostly on mud banks, almost all on moist soil, 5 ♂, 9 ♀, 4 subad. ♂, 9 juv. ♂, 4 juv. ♀, dextral pedipalp femur and patella (AMNH),

1 juv. ♂ (AMCC [LP 11273]), 20.ii.2012, L. Prendini and P. Kanyavong, in twilight zone at cave entrance, muddy beach on riverbank, UV detection at night, specimens sitting on muddy banks (none collected at this site during daylight), 2 ♀ (AMNH), 20–21.ii.2012, L. Prendini, P. Kanyavong, and W. Phimmathong, large sandy beach of riverbank, midway through cave [type locality], with muddy bank immediately along river and muddy patches in several depressions further from river edge, UV detection, all specimens collected on moist muddy soil, some among vegetative debris (sticks, etc.) trapped between stones, others sitting in open on mud, one in mud cracks, one below stone, 7 ♀, 1 juv. ♀ (AMNH), 1 juv. ♀ (AMCC [LP 11272]); right bank of Xe Bang Fai River (coming from downstream entrance): 19–20.ii.2012, L. Prendini and P. Kanyavong, muddy beach of riverbank at bottom of "Balcony Passage," ca. 300–500 m from downstream entrance of cave, UV detection during day: specimens very common on moist mud banks, mostly in cracks between drying mud slabs or among sticks and other vegetative debris caught between rocks, all collected on moist soil, none on dry sand banks higher upslope; UV detection at night: several ♂♂ sitting on flowstone rock faces, several ♀♀ and juv. on mud banks and cracked clay, 2 ♂ (1 ♂ partly cannibalized by ♀), 22 ♀, 2 subad. ♂, 4 subad. ♀, 5 juv. ♂, 7 juv. ♀, carapace and sinistral pedipalp chela (AMNH), 1 juv. ♀ (AMCC [LP 11271]), 19–21.ii.2012, L. Prendini, P. Kanyavong, and W. Phimmathong, muddy beach of riverbank between "Balcony Passage" and "Stairway to Heaven," steep and dry with little cracked mud, relatively few rocks with trapped vegetative debris, UV detection, specimens uncommon, mostly on mud close to river edge, few higher upslope against cave walls, near moist flowstone, all specimens collected on moist mud surfaces, none on dry sand, 1 ♂, 7 ♀ (AMNH), 20.ii.2012, L. Prendini and P. Kanyavong, rocky beach of riverbank before second rapids, UV detection, several adult ♀♀ and imm. on mud bank or in rock crevices close to river, none on dry soil
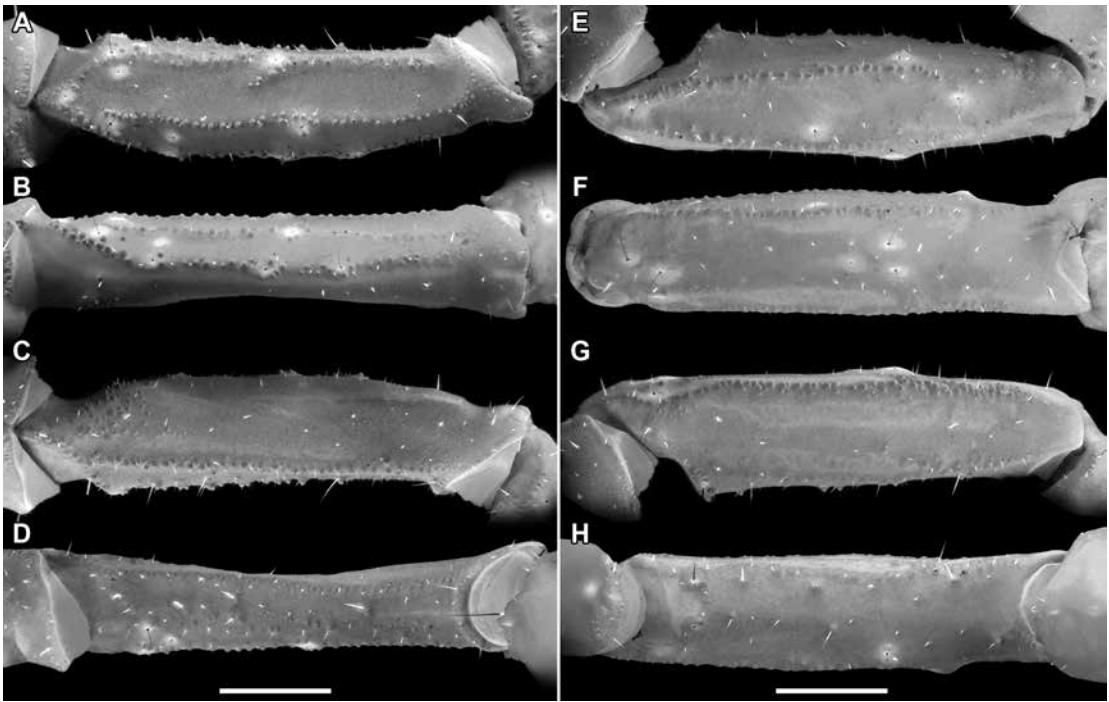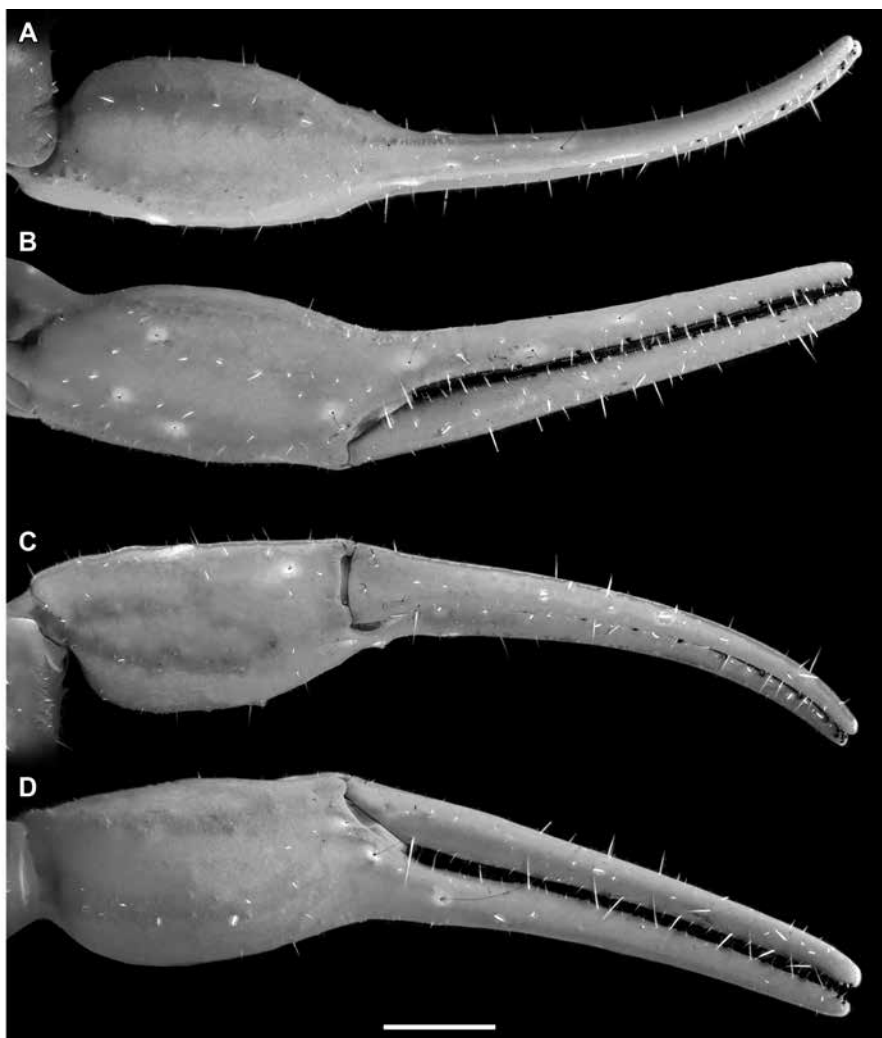
FIGURE 34. *Aemngvantom lao* (Lourenço, 2012), comb. nov., ♂ (AMNH), Tham Nam Lot (Lod), Laos, dextral pedipalp femur (**A–D**) and patella (**E–H**): **A, E.** dorsal, **B, F.** retrolateral, **C, G.** ventral, and **D, H.** prolateral aspects. Scale bars = 1 mm.

higher upslope, 5 ♀, 1 subad. ♀, 1 juv. ♂ (AMNH), 20–21.ii.2012, L. Prendini, P. Kanyavong, and W. Phimmathong, rocky/muddy beach of riverbank before "Stairway to Heaven," UV detection, several ♀♀ and imm. on muddy banks or among trapped vegetative debris between rocks, none on dry sand, 1 ♂, 4 ♀ [1 ♀ depigmented ocelli], 4 subad. ♂, 1 subad. ♀, 2 juv. ♂, 8 juv. ♀ (AMNH), 1 juv. (AMCC [LP 11274]), 21.ii.2012, L. Prendini and W. Phimmathong, Oxbow Lake, rocky beach on riverbank, UV detection, specimens on rocky shore, 2 ♀, 1 subad. ♂, dextral pedipalp chela (AMNH).

Subfamily Vietbocapinae Lourenço, 2012

Figures 4, 5, 7–9, 12, 14, 15C, D, 17, 19, 21, 32–43, tables 1–5, 9, 10

Vietbocapinae Lourenço, 2012a: 232–234, type genus, by original designation: *Vietbocap*

Lourenço and Pham, 2010; Lourenço, 2017a: 19; Pham et al., 2017: 134.

DIAGNOSIS: Vietbocapinae may be separated from the other two subfamilies of Pseudochactidae as follows. The tegument is immaculate in Vietbocapinae but usually partially infuscate (e.g., on the carapace, tergites and legs) in the other subfamilies. The anteromedian margin of the carapace is shallowly concave (recurved) in Vietbocapinae (fig. 12) but sublinear in Pseudochactinae (fig. 10) and convex (procurved) in Troglokhammouaninae (fig. 11). The median and lateral ocelli are absent in Vietbocapinae (fig. 12) but present in the other subfamilies (figs. 10, 11). The circumocular sutures of the carapace are partial (disconnected) in Vietbocapinae (fig. 12) but complete in the other subfamilies, connected posteriorly in Pseudochactinae (fig. 10) and disconnected posteriorly in Troglokhammouaninae (fig. 11). The
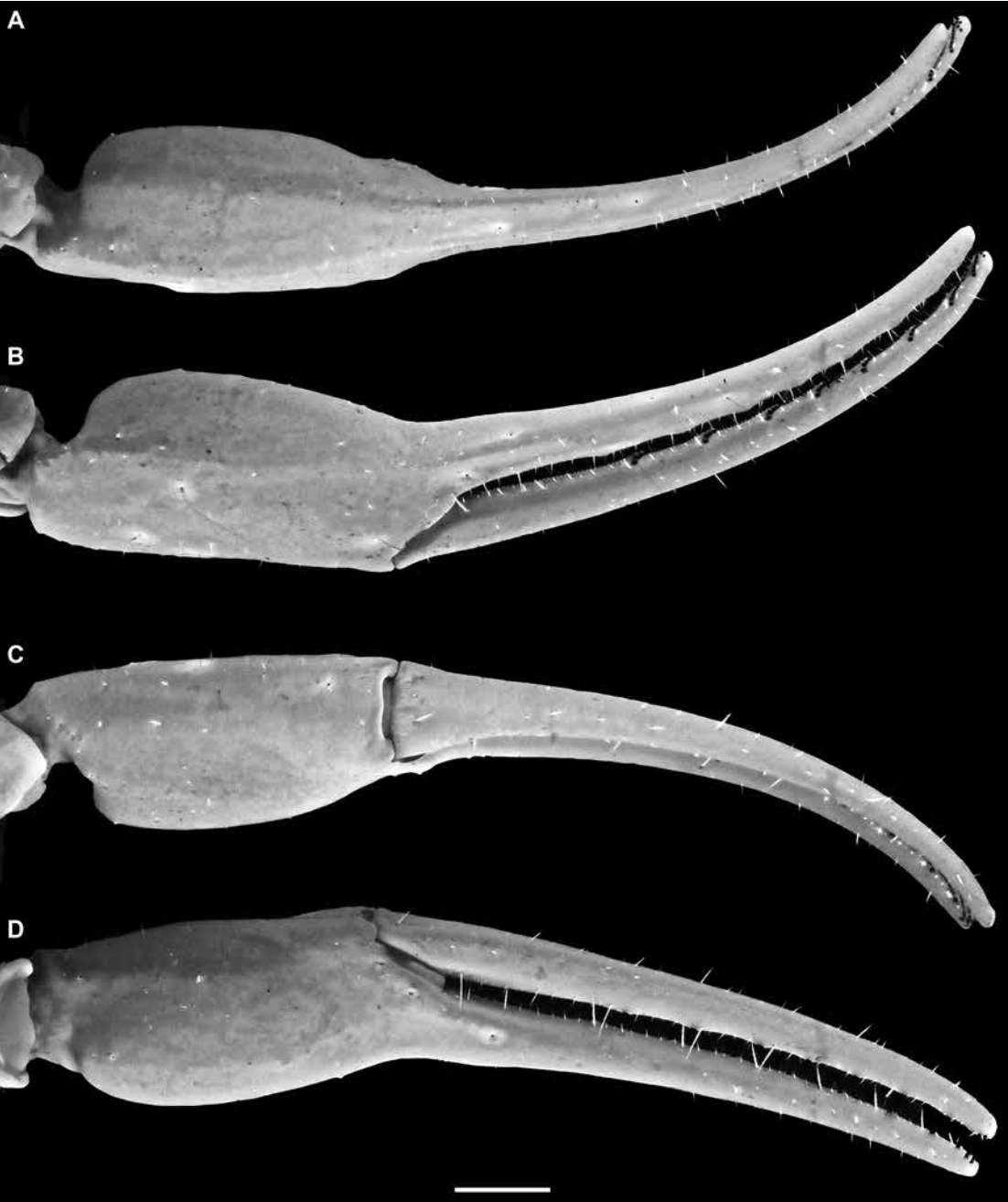
FIGURE 35. *Aemngvantom lao* (Lourenço, 2012), comb. nov., ♂ (AMNH), Tham Nam Lot (Lod), Laos, dextral pedipalp chela: **A.** dorsal, **B.** retrolateral, **C.** ventral, and **D.** prolateral aspects. Scale bar = 1 mm.

pedipalps are gracile, with the chela fingers of the adult male sublinear, and similar to the adult female in Vietbocapinae (figs. 35, 36), whereas the pedipalps are relatively robust, with the chela fingers of the adult male sinuous and sexually dimorphic in the other subfamilies (figs. 24, 25, 29, 30). The prolateral ventral carina of the pedipalp chela manus is absent or obsolete in Vietbocapinae (figs. 35D, 36D, 39D, 43D) but complete in the other subfamilies (figs. 24D, 25D, 29D, 30D). Tibial spurs are absent on legs

III and IV in Vietbocapinae (fig. 15C, D) but present in the other subfamilies (fig. 15A, B). The lateral surfaces of the telson vesicle are smooth, and the ventral surfaces smooth or with sparsely granular (obsolete) carinae in Vietbocapinae (figs. 19, 21), whereas the lateral and ventral surfaces of the vesicle possess granular carinae in the other subfamilies (figs. 18, 20). The subaculear tubercle is absent in Vietbocapinae (fig. 19) but obsolete (evident as a very small bump) in the other subfamilies (fig. 18).

FIGURE 36. *Aemngvantom lao* (Lourenço, 2012), comb. nov., ♀ (AMNH), Tham Nam Lot (Lod), Laos, dextral pedipalp chela: **A.** dorsal, **B.** retrodorsal, **C.** ventral, and **D.** prolateral aspects. Scale bar = 1 mm.

Vietbocapinae may be further separated from Pseudochactinae as follows. The anteromedian margin of the carapace is protruding (anterior to the anterolateral margins) in Vietbocapinae (fig. 12) but recessed (posterior to the anterolateral margins) in Pseudochactinae (fig. 10). The posterolateral margins of the carapace are gently curved in Vietbocapinae (fig. 12) but angular and slanting in Pseudochactinae (fig. 10). The dorsoventral projection ("anterior process") on the prolateral surface of the pedipalp patella is only moderately developed in Vietbocapinae (figs. 34E, G, 38E, G, 42E, G) but pronounced in Pseudochactinae (fig. 23E, G). The secondary accessory and retroventral carinae of the pedipalp chela manus are incompletely fused, with a slight disjunction evident in the proximal third, in Vietbocapinae (figs. 35C, 36C, 39C, 43C) but entirely fused in Pseudochactinae (figs. 24C, 25C). The ventral surface of the sternum is shallowly concave in Vietbocapinae (figs. 14) but flat/planar in Pseudochactinae (fig. 13A, C). The spinules of the basitarsi and telotarsi of legs I–IV are long in Vietbocapinae (fig. 15C, D) but short in Pseudochactinae (fig. 15A). The peg sensillae of the pectinal teeth are long, cylindrical, tubular, or bottle shaped, and rounded distally, without laterodistal processes in Vietbocapinae but relatively short, stout, flattened, and truncate distally, with laterodistal processes, in Pseudochactinae. The telson vesicle is elongate in Vietbocapinae (fig. 19) but globose in Pseudochactinae (fig. 18A, B).

Vietbocapinae may be further separated from Troglokhammouaninae as follows. The dorsomedian, dorsal secondary, subdigital, and retromedian carinae of the pedipalp chela manus are absent, and the ventromedian carina vestigial, in Vietbocapinae (figs. 35, 36, 39, 43), whereas the dorsomedian, dorsal secondary and subdigital carinae are vestigial, and the retromedian and ventromedian carinae partial in Troglokhammouaninae (figs. 29, 30). The lateral margins of the sternum are sublinear in Vietbocapinae (fig. 14) but recurved medially in Troglokhammouaninae (fig. 13B, D). The posterior granules of the dorsosubmedian and dorsolateral carinae of metasomal segments I–IV are similar in size and shape

to the preceding granules in Vietbocapinae (fig. 17) but markedly larger than the preceding granules and spiniform in Troglokhammouaninae (fig. 16C, D). The median lateral carinae are partial, becoming obsolete anteriorly on metasomal segment III, and vestigial or absent on IV in Vietbocapinae (fig. 19) but complete on III and IV in Troglokhammouaninae (fig. 18C, D).

INCLUDED TAXA: As redefined in the present contribution, Vietbocapinae accommodates three species in two genera (table 1): *Aemngvantom*, gen. nov.; *Vietbocap* Lourenço and Pham, 2010.

DISTRIBUTION: Endemic to the Southeast Asian countries of Laos and Vietnam (fig. 7).

ECOLOGY: All three species of Vietbocapinae are hypogean, having been collected in the dark zone of deep caves, 200 m to 5 km from the surface (fig. 4).

Aemngvantom, gen. nov.

Figures 4B–D, F–H, 5, 7–9, 12A, C, E, 14A, C, E, 15C, 17A–C, 19A–C, 21A–C, 32–39, tables 1–5, 9, 10

Type species: *Vietbocap lao* Lourenço, 2012 [= *Aemngvantom lao* (Lourenço, 2012), comb. nov.], here designated.

Vietbocap: Lourenço, 2012a: 232, 233 (part); Loria and Prendini, 2014: 5, 20, 21, tables 2, 4 (part); Sharma et al., 2015b: 4, fig. 2d; Pham et al., 2017: 134 (part); Lourenço et al., 2018: 264, 265, 269, 272 (part); Deharveng and Bedos 2018: 121 (part); Loria and Prendini, 2018: 186, table 2 (part); Ballesteros et al., 2019: supplementary text 2: 13; Francke, 2019: 16, 32, 39 (part); Lozano-Fernandez et al., 2019: 4, fig. 2.

Vietbokap: Beron, 2015: 172 (part).

ETYMOLOGY: The generic name is the Lao word for scorpion, "aemngvan tom."

DIAGNOSIS: In addition to the marked genetic divergence between the two genera (fig. 9; table 12), *Aemngvantom* may be separated morphologically from *Vietbocap*, as follows. The antero-
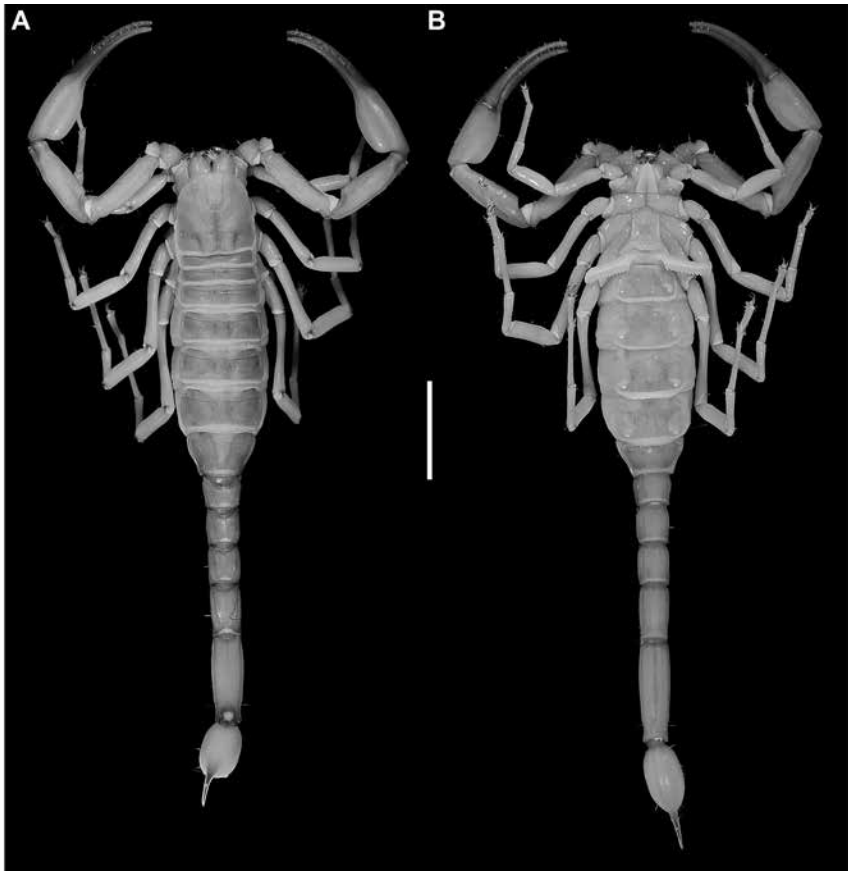
FIGURE 37. *Aemngvantom thamnongpaseuam*, gen. et sp. nov., holotype ♀ (AMNH), Tham Nong Pa Seuam, Laos, habitus: **A.** dorsal and **B.** ventral aspects. Scale bar = 10 mm.

median depression of the carapace is shallow, the circumocular triangle subtriangular (broad V-shaped), and median ocular curvatures present in *Aemngvantom* (fig. 12A, C, E), whereas the anteromedian depression of the carapace is deep, the circumocular triangle parallel sided (U-shaped) and the median ocular curvatures absent in *Vietbocap* (fig. 12B, D, F). The median ocular tubercle (demarcated by the posterior margin of the circumocular sulci) is situated anteromedially in *Aemngvantom* (fig. 12A, C, E) but medially in *Vietbocap* (fig. 12B, D, F). The anterolateral surfaces of the carapace are mostly granular in *Aemngvantom* (fig. 12A, C, E), whereas the surfaces are mostly smooth, but sparsely granular near the anterior carapace mar-

gin, in *Vietbocap* (fig. 12B, D, F). The anterolateral margins of the carapace are entire in *Aemngvantom* (fig. 12A, C, E), whereas pronounced rostrolateral incisions, lateral to the lateral ocelli, are present in *Vietbocap* (fig. 12B, D, F). The posteromedian margin of the carapace is shallowly concave (recurved) in *Aemngvantom* (fig. 12A, C, E) but sublinear to shallowly convex (procurved) in *Vietbocap* (fig. 12B, D, F). The pedipalp chela manus is globose, with the prolateral dorsal carina of the male complete in *Aemngvantom*, whereas the chela manus is elongate, with the prolateral dorsal carina of the male absent or obsolete, in *Vietbocap*. The median denticle rows of the chela fixed and movable fingers usually comprise 10 denticle subrows in *Aemngvantom*
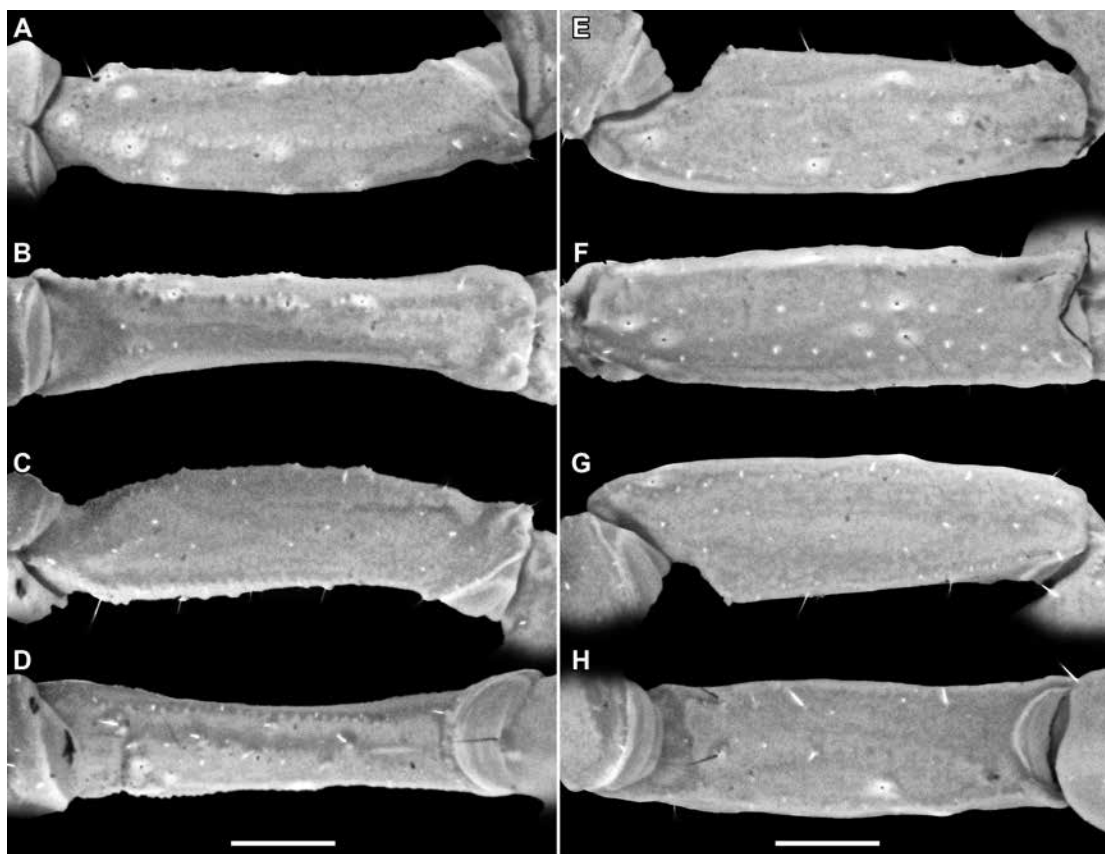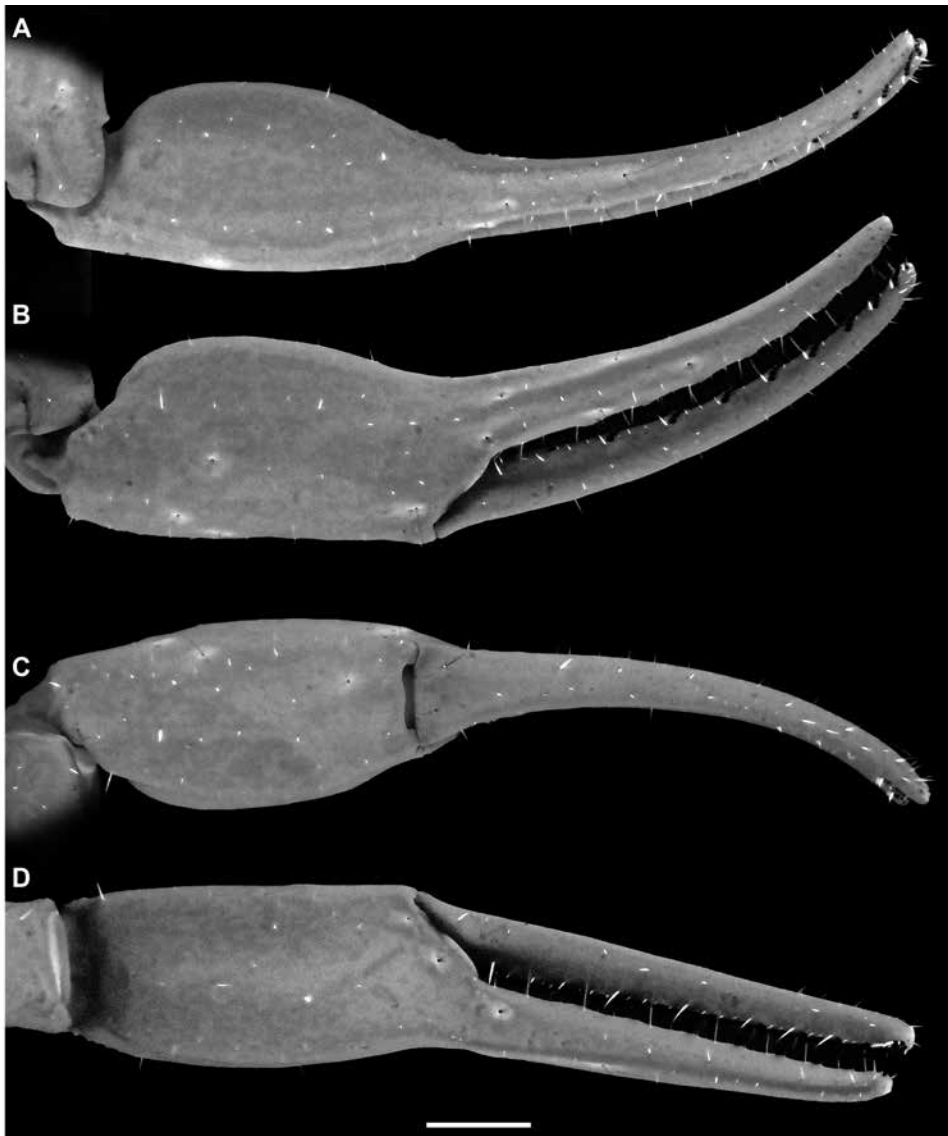
FIGURE 38. *Aemngvantom thamnongpaseuam*, gen. et sp. nov., holotype ♀ (AMNH), Tham Nong Pa Seuam, Laos, dextral pedipalp femur (**A–D**) and patella (**E–H**): **A, E.** dorsal, **B, F.** retrolateral, **C, G.** ventral, and **D, H.** prolateral aspects. Scale bars = 1 mm.

(tables 3, 4, 9, 10) but seven or eight subrows in *Vietbocap* (tables 3, 4, 10). Trichobothrium Et_1 is situated on the fixed finger, slightly distal to the movable finger condyle, and esb_2 approximately midway on the fixed finger, between the second and third most proximal retrolateral denticles of the median denticle row, in *Aemngvantom* (figs. 35B, 36B, 39B) whereas Et_1 is situated distally on the manus, aligned with or proximal to the movable finger condyle, and esb_2 in the proximal third of the fixed finger, between the first and second most proximal retrolateral denticles of the median denticle row, in *Vietbocap* (fig. 43B). The pectines possess 11–14 lamellae and 12–15 teeth in *Aemngvantom* (tables 3, 5, 9, 10) but 5–8 median lamellae and 6–10 teeth in *Vietbocap* (tables 3, 5,

10). The median lateral carinae of metasomal segment II are complete in *Aemngvantom* (fig. 19A–C) but partial, becoming obsolete anteriorly in *Vietbocap* (fig. 19D, E).

INCLUDED TAXA: Two species: *Aemngvantom lao* (Lourenço, 2012), comb. nov.; *Aemngvantom thamnongpaseuam*, gen. et sp. nov.

DISTRIBUTION: *Aemngvantom* is endemic to the Southeast Asian country of Laos, where it has been recorded from two caves in the Gnommalath and Thakhek districts of Khammouane Province (fig. 7).

ECOLOGY: The two known species of *Aemngvantom* are obligate troglobites, inhabiting the dark zone of deep caves, up to 500 m from the surface (fig. 4B–D, F–H). Both are markedly troglomorphic.

FIGURE 39. *Aemngvantom thamnongpaseuam*, gen. et sp. nov., holotype ♀ (AMNH), Tham Nong Pa Seuam, Laos, dextral pedipalp chela: **A.** dorsal, **B.** retrolateral, **C.** ventral, and **D.** prolateral aspects. Scale bar = 1 mm.

REMARKS: *Aemngvantom lao* was previously assigned to the genus *Vietbocap*. However, numerous differences are evident between this species and its sister species, *A. thamnongpaseuam*, and *V. canhi*, especially concerning the morphology of the carapace and pedipalps. The pronounced morphological differences between the taxa from Laos and Vietnam, supported by multivariate statistical analysis (fig. 8), and taken together with the high levels of genetic divergence between them (fig. 9; table 12), which are comparable to the levels of divergence among the other pseudochactid genera, justify the creation of a new genus to accommodate the two species from Laos.

Aemngvantom lao (Lourenço, 2012), comb. nov.

Figures 4D, G, H, 5, 7–9, 12A, C, 14A, C, 15C,
17A, B, 19A, B, 21A, B, 32–36, tables 1–5, 9

Vietbocap lao Lourenço, 2012a: 232, 234–237,
figs. 2, 3, appendix A; 2012b: 733, table 1;
Jäger, 2012: 37; Lourenço and Leguin, 2012:
71; Steiner, 2013: 416; Loria and Prendini,
2014: 3, table 1, appendix S1: 10, appendix
S2: 7; Lourenço, 2014: 31; Sharma et al.,
2015b: 2, 4, 7, figs. 1e, 2c, 3b; Beron, 2018:
834; Lourenço et al., 2018: 265; Howard et
al., 2019: 76, table 1; Lozano-Fernandez et
al., 2019: supplementary information: 3, 8,
13, 14, tables 1, 3, fig. 1A, B; Santibáñez-
López et al., 2019a: 5; 2019b: 26, table 3.

TYPE MATERIAL: **LAOS: Khammouane
Prov.:** *Gnommalath Distr.*: Holotype: 1 [juv.] ♀
(MNHN RS 9096), paratype: 1 [juv.] ♀ (MNHN
RS 9097), Grotte Tham Nam Lot au NO de Ban
Naden (village) [Tham Nam Lot (cave), NW of
Ban Naden village], 17°30′18″N 105°23′08″E,
176 m, 8.xi.2011, L. Deharveng and A. Bedos,
350–450 m from main cave entrance, collected
by hand, Lao11-46 [examined].

DIAGNOSIS: In addition to the marked genetic
divergence between the two species (fig. 9; table
12), *A. lao* may be separated morphologically
from *A. thamnongpaseuam* by means of the gran-
ulation and carination of the carapace, tergites
and metasoma, and the relative proportions of
the pedipalps and metasoma. The mediolateral
and posteromedian surfaces of the carapace and
the surfaces of posttergites I–VI are granular in
A. lao (fig. 12A, C) but smooth or nearly so in
A. thamnongpaseuam (fig. 12E). The ventrosub-
median carinae of metasomal segments II–IV
are distinct in *A. lao* (fig. 21A, B) but absent or
obsolete in *A. thamnongpaseuam* (fig. 21C). The
dorsolateral and ventromedian carinae are dis-
tinct, and the median lateral carinae complete on
segment V in *A. lao* (figs. 17A, B, 19A, B, 21A,
B), whereas the dorsolateral carinae are obsolete,
and the median lateral and ventromedian carina

absent or obsolete on segment V in *A. thamnong-
paseuam* (figs. 17C, 19C, 21C). Additionally, the
pedipalp segments are proportionally longer and
narrower, and the metasomal segments propor-
tionally longer and broader in *A. lao* than *A.
thamnongpaseuam* (figs. 17A–C, 19A–C, 21A–C,
34–36, 38, 39; tables 9, 10).

DESCRIPTION: The following description,
based on the type material and material exam-
ined, which includes three adult males and five
adult females, supplements the original descrip-
tion of two juvenile females, by Lourenço
(2012a). Ratios are presented for adults only
(table 9), whereas counts include immatures of
both sexes (tables 3–5, 9).

Total length: Small, 27.5 mm (24.5–29.5 mm,
n = 3) (♂) or 30.4 mm (23.4–37.4 mm, n = 6)
(♀) (tables 3, 9).

Color: Tegument base coloration pale yellow-
ish to reddish yellow (whitish in immatures),
immaculate. Chelicerae, pedipalps (except chela
fingers), legs, posterior third of tergites and
sternites, and telson slightly paler than cara-
pace, pedipalp chela fingers, anterior two-thirds
of tergites and sternites, and metasoma. Chela
fingers dark reddish; pedipalpal and metasomal
carinae reddish. Sternum, genital operculum,
pectines, and sternites pale, whitish. Aculeus
reddish black.

Chelicerae: Fixed finger, dorsal margin with
four teeth (basal, median, subdistal, distal);
basal and median teeth fused into bicuspid
("conjoined on trunk"); space between median
and subdistal teeth U-shaped; ventral margin
with four or five very small denticles (ventral
accessory denticles). Movable finger, dorsal
margin with three teeth (median, subdistal, ret-
rolateral distal), without basal teeth; ventral
margin with four or five very small denticles
(ventral accessory denticles) and serrula in dis-
tal third; retrolateral (dorsal) distal and prolat-
eral (ventral) distal teeth subequal, retrolateral
(dorsal) distal tooth slightly smaller than pro-
lateral (ventral) distal tooth, and opposable.
Ventral surface of fingers and manus with
numerous long, dense macrosetae.

Carapace: Carapace slightly longer than wide, anterior width 45% (43%–47%, $n = 3$) (♂) or 51% (44%–69%, $n = 6$) (♀) of length, posterior width 90% (85%–92%, $n = 3$) (♂) or 89% (85%–97%, $n = 6$) (♀) of length (tables 3, 9). Anterior margin protruding but shallowly concave (recurved) medially; anterolateral margins entire; posteromedian margin shallowly concave (recurved); posterolateral margins gently curved (fig. 12A, C). Median and lateral ocelli absent. Anterosubmedial depressions, medial to lateral ocelli, well developed. Median ocular tubercle represented by smooth, slightly depressed surface, situated anteromedially on carapace, distance from anterior margin 33% (32%–34%, $n = 3$) (♂) or 32% (30%–34%, $n = 5$) (♀) of carapace length (table 9); superciliary carinae absent; interocular sulcus shallow, obsolete. Circumocular sutures partial (disconnected); circumocular triangle subtriangular (broad V-shape); median ocular curvatures (regardless of absence of median ocelli) present. Anteromedian depression narrow, shallow; posteromedian sulcus shallow anteriorly, becoming deeper posteriorly; posterolateral sulci very shallow, wide, weakly curved; posteromarginal sulcus narrow, shallow. Carapace acarinate; entirely moderately and densely granular (♂) or finely and sparsely granular (♀), except on posterolateral surfaces.

Pedipalps: Pedipalps gracile; segments almost apilose, sparsely covered in short microsetae and occasional macrosetae. Pedipalp femur length 78% (77%–78%, $n = 3$) (♂) or 79% (76%–81%, $n = 6$) (♀) greater than width (tables 3, 9). Femur with five carinae evident (fig. 34A–D); promedian carina vestigial, reduced to few proximal spiniform granules; dorsomedian, prodorsal, and proventral carinae weakly developed, granular; retrodorsal carina obsolete, reduced to few granules; retromedian, retroventral, and ventromedian carinae absent; intercarinal surfaces smooth. Pedipalp patella length 76% (75%–78%, $n = 3$) (♂) or 77% (76%–79%, $n = 6$) (♀) greater than width (tables 3, 9). Patella with six carinae evident (fig. 34E–H); prodorsal, retrodorsal, proventral, and retroventral carinae weak, granular; prolateral surface, dorsoventral "vaulted" projection ("anterior process")

moderately developed, with prominent pair of dorsal and ventral spiniform granules ("patellar spurs") proximally, demarcating pair of obsolete, granular prolateral carinae ("dorsal and ventral patellar spur carinae"); dorsomedian, retromedian, and ventromedian carinae absent; intercarinal surfaces smooth. Pedipalp chela relatively short and broad; manus globose, width 10% (1%–22%, $n = 3$) (♂) or 7% (1%–12%, $n = 6$) (♀) greater than height and length 51% (50%–52%, $n = 3$) (♂) or 55% (52%–58%, $n = 5$) (♀) greater than width (tables 3, 9); length of movable finger 65% (63%–68%, $n = 3$) (♂) or 89% (82%–97%, $n = 5$) (♀) greater than length of manus. Chela with four (♀) or five (♂) carinae evident (figs. 35, 36); dorsomedian carina weakly developed, granular (♂) or absent (♀); digital carina weakly developed, granular; secondary accessory and retroventral carinae incompletely fused, slight disjunction evident in proximal third; retroventral carina weakly developed, granular (♂) or obsolete (♀), aligned parallel to longitudinal axis of chela, with distal margin connected to retrolateral movable finger condyle; ventromedian carina reduced to vestigial granules proximally; other carinae absent; intercarinal surfaces smooth. Fixed and movable fingers, dentate margins sublinear (♂, ♀), no proximal "gap" evident when closed; median denticle rows comprising 10 ($n = 65$) oblique and slightly imbricated subrows (tables 3, 4, 9), decreasing in length distally; each subrow comprising large retrolateral denticle proximally (absent from proximal subrow, for total of nine retrolateral denticles on fixed and movable fingers), several small median denticles, and large prolateral denticle distally, slightly offset (total of 10 prolateral denticles on fixed and movable fingers); terminal (prolateral) denticle of first subrow enlarged; accessory denticles absent.

Trichobothria: Orthobothriotaxic, Type D, β configuration, trichobothrium d_2 situated on femur dorsal surface, d_3 and d_4 in same axis, parallel and closer to retrodorsal carina than d_1, angle formed by d_1, d_3 and d_4 opening toward prolateral surface, with the following segment totals (figs. 34–36): femur, 12 (6 dorsal, 3 prolateral, 3 retrolateral); patella, 10 (3
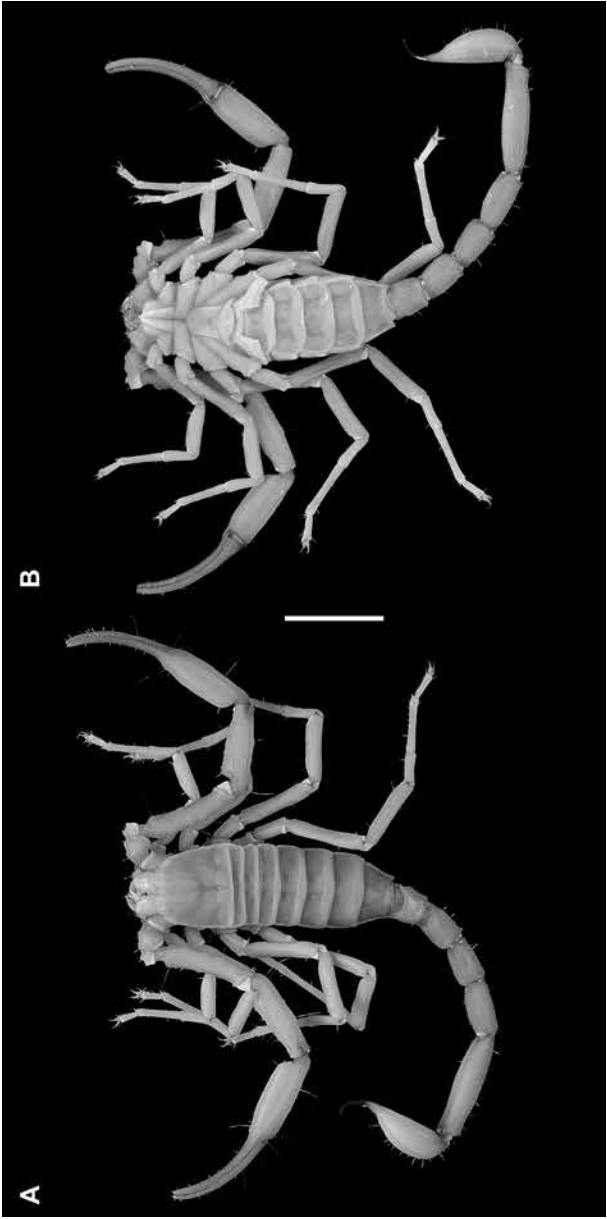
FIGURE 40. *Vietbocap canhi* Lourenço and Pham, 2010, ♀ (AMNH), Tiên Sơn, Vietnam, habitus: **A**. dorsal and **B**. ventral aspects. Scale bar = 10 mm.
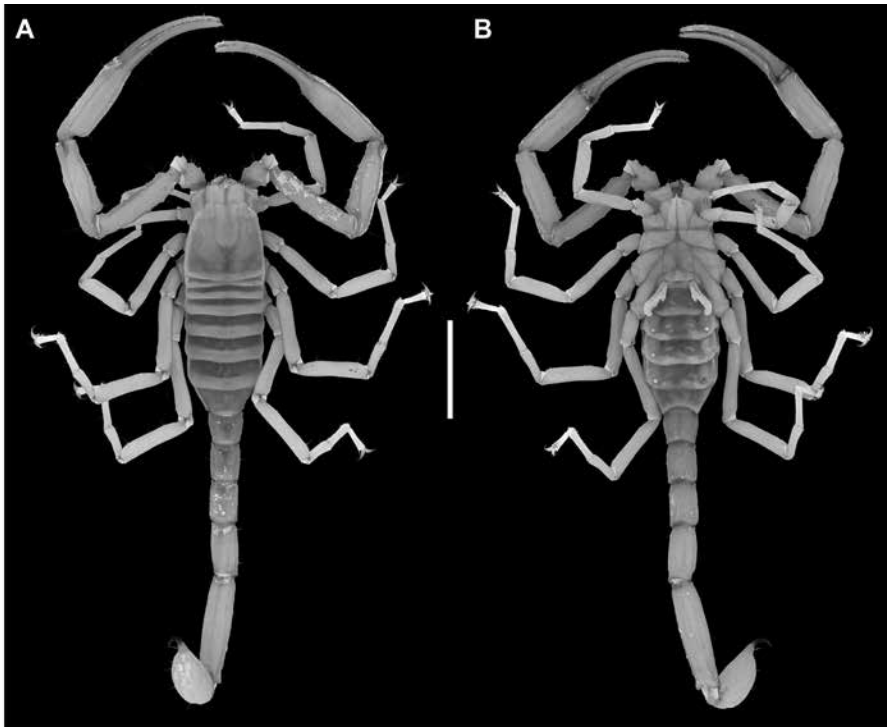
FIGURE 41. *Vietbocap canhi* Lourenço and Pham, 2010, ♀ (AMNH), Thiên Đường, Vietnam, habitus: **A.** dorsal and **B.** ventral aspects. Scale bar = 10 mm.

dorsal, 1 prolateral, 6 retrolateral); chela, 13 (5 manus, 8 fixed finger). Total number of trichobothria per pedipalp, 35. Five trichobothria on femur, i_4, d_1, d_2, d_4, and d_6, one on patella, est_1, and one on chela fixed finger, ib_2, noticeably smaller than others ("petite"). Trichobothrium Et_1 situated on fixed finger, slightly distal to movable finger condyle; *eb* situated in proximal third of fixed finger, distal to most proximal retrolateral denticle of median denticle row; esb_2 situated approximately midway on fixed finger, between second and third most proximal retrolateral denticles of median denticle row.

Legs: Leg I maxillary lobes (coxapophyses), distal margins rounded, unmodified (not spatulate or dilate) anteriorly, terminating flush with lobes of leg II (figs. 32B, 33B). Legs I and II tibiae, retrolateral margins each with scattered macrosetae, without spurs (fig. 15D); III and IV without spurs. Basitarsi with few scattered macrosetae, pro- and retrolateral rows of long spinules, and pair of pro- and retrolateral pedal spurs. Telotarsi with pair of slightly irregular ventrosubmedian rows of long spinules; proventral and retroventral rows of macrosetae absent, only few scattered macrosetae laterally; laterodistal lobes reduced and truncated; median dorsal lobe very short; ungues short, distinctly curved, equal in length; unguicular spur (dactyl) pronounced, pointed.

Sternum: Sternum, Type 1, pentagonal, length 18% (10%–23%, $n = 3$) (♂) or 19% (2%–28%, $n = 5$) (♀) greater than posterior width (table 9), lateral margins sublinear, ventral surface shallowly concave, posteromedian depression round (fig. 14A, C).

Pectines: Three marginal (anterior) lamellae, proximal sclerite considerably longer, distal sclerite short (fig. 14A, C); 13/13 (12–14/11–14,

$n = 34$) ($\male$) or 12/12 (12 or 13/11–13, $n = 29$) ($\female$) median lamellae (tables 3, 5, 9); fulcra present, very small. Proximal median lamella and basal pectinal tooth unmodified. Pectinal teeth present along entire posterior margin of each pecten ($\male$, $\female$); 14/14 (13–15/12–15, $n = 34$) ($\male$) or 13/13 (13 or 14/12–14, $n = 30$) ($\female$) teeth. Pectinal peg sensillae long, cylindrical, tubular or bottle shaped, and rounded distally, without pair of laterodistal processes; sensillar sockets smooth.

Genital operculum: Opercular sclerites completely separated, prominent genital papillae visible along entire length ($\male$) or absent ($\female$) (fig. 14A, C). Genital plugs observed in some females.

Male reproductive organs: Paraxial organ without accessory glands. Hemispermatophore lamelliform, *pars recta* absent; basal lobe present.

Female reproductive organs: Ovariuterus comprising reticulate mesh of six cells. Oocytes contained in sessile follicles directly contacting ovaruterine tubes.

Mesosoma: Pretergites surfaces smooth and shiny. Posttergites I–VI surfaces finely and sparsely granular, acarinate, each with pair of shallow submedian depressions (figs. 32A, 33A); VII surface sparsely granular, with pair of granular dorsosubmedian and dorsolateral carinae reaching posterior margin of segment. Sternites III–V surfaces entirely smooth, acarinate, and sparsely covered in microsetae (figs. 32B, 33B); VI and VII surfaces granular, VII with granular ventrosubmedian and ventrolateral carinae ($\male$) or smooth, acarinate ($\female$); III–VII surfaces with scattered macrosetae, posterior margins with sparse row of macrosetae (more densely setose in $\male$); III–VI, respiratory spiracles (stigmata) small, oval to round (fig. 14A, C); V posteroventral margin with pale, raised, triangular surface; VII width 35% (33%–36%, $n = 3$) ($\male$) or 39% (35%–44%, $n = 5$) ($\female$) greater than length (table 9).

Metasoma: Metasoma relatively short, total length 29% (27%–32%, $n = 3$) ($\male$) or 27% (15%–47%, $n = 6$) ($\female$) greater than combined length of prosoma and mesosoma (tables 3, 9); segments I–V progressively increasing in length,

I wider than long ($\female$), width of length for segment I, 92% (89%–95%, $n = 3$) ($\male$) or 106% (100%–115%, $n = 6$) ($\female$); II, 81% (78%–87%) ($\male$) or 77% (71%–87%) ($\female$); III, 75% (72%–81%) ($\male$) or 68% (58%–81%) ($\female$); IV, 55% (54%–56%) ($\male$) or 50% (44%–55%) ($\female$); and V, 27% (27%–28%) ($\male$) or 26% (23%–32%) ($\female$). Metasoma with few short macrosetae. Ten carinae on segments I–III, eight on IV, and nine on V (figs. 17A, B, 19A, B, 21A, B). Dorsosubmedian carinae moderately developed, granular throughout length of segments I–IV, absent on V; converging posteriorly. Dorsolateral carinae moderately developed, granular throughout length of segments I–V; converging posteriorly on I and V, subparallel on II–IV. Dorsosubmedian and dorsolateral carinae of segments I–IV not terminating posteriorly with enlarged, spiniform granules, granules similar to preceding granules. Median lateral carinae complete, granular throughout length of segments I, II, and V, partial, becoming obsolete anteriorly on III, vestigial or absent on IV. Ventrolateral carinae moderately developed, granular, becoming obsolete anteriorly on segments I and II, continuous throughout length of III–V; converging posteriorly on I and V, subparallel on II–IV. Ventrosubmedian carinae obsolete, granular ($\male$) or absent ($\female$) on segment I, obsolete, granular ($\male$) or costate ($\female$) on II, moderately developed, granular throughout length of III–V; subparallel on II and III, converging posteriorly on IV and V. Ventromedian carina moderately developed, granular, on segment V. Intercarinal surfaces smooth.

Telson: Telson large, suboval (figs. 17A, B, 19A, B, 21A, B). Vesicle elongate, 10% (8%–14%, $n = 3$) ($\male$) or 17% (8%–27%, $n = 6$) ($\female$) wider than metasomal segment V (tables 3, 9), with flattened dorsal surface and rounded ventral surface, height 38% (34%–41%, $n = 3$) ($\male$) or 36% (31%–39%, $n = 6$) ($\female$) of length; dorsal surface smooth, lateral surfaces with three pairs of obsolete, granular carinae, ventral surfaces with two pairs of obsolete, granular carinae ($\male$) or lateral and ventral surfaces smooth ($\female$); anterodorsal

lateral lobes ("vesicular tabs") weakly developed, granular (♂) or obsolete (♀); subaculear tubercle absent. Aculeus short, shallowly curved, 29% (27%–33%, $n = 3$) (♂) or 28% (24%–30%, $n = 6$) (♀) of telson length. Venom glands thin walled, simple and unfolded.

Intraspecific variation: No significant variation.

Ontogenetic variation: Immature stages of *A. lao* are paler in color and less sclerotized, and the posteroventral margin of mesosomal sternite V does not exhibit a pale, raised, triangular surface as in the adults of both sexes. Males and females closely resemble one another externally until the final instar. However, immature stages are easily sexed by examination of the genital aperture.

Sexual dimorphism: The genital papillae, visible the entire length and thus completely separating the two sclerites of the genital operculum (fig. 14A), are the characters of primary external sexual dimorphism in the male. The opercular sclerites are also completely separated in the female, although genital papillae are absent (fig. 14B). Several secondary sexual characters are observed in the adult male, compared with adult females and immature stages of both sexes. The most obvious are the slightly better developed pectines, the median lamellae of which are more numerous and the teeth somewhat larger, and more numerous (fig. 14A, B; tables 3, 5, 9). In addition, the adult male is smaller and proportionally more slender (fig. 32), with a slightly longer metasoma and telson (table 9), and noticeably more pronounced granulation on the carapace, pedipalps, tergites, sternites, and metasoma than the adult female (fig. 33). The pale, raised, triangular surface on the posteroventral margin of sternite V is more pronounced in the adult male (fig. 32B) than the adult female.

DISTRIBUTION: Endemic to the Gnommalath District of Khammouane Province, Laos, and presently recorded from a single cave, Tham Nam Lot (Lod), near Ban Naden (fig. 7). The cave is situated at the base of a limestone mountain, in a tropical forest at an elevation between 175–260 m (fig. 4D).

ECOLOGY: All known specimens of *A. lao* were collected from the dark zone of a moist cave with pools of water in places, ca. 300–450 m from the cave entrance. Most specimens were collected with UV light detection, under stones or in rock cracks, from crevices in mud walls below flowstone walls, or walking on the surface (fig. 4G, H).

Like other Vietbocapinae, *A. lao* is an obligate troglobite with a highly specialized morphology, characterized by the absence of ocelli and pigmentation, attenuation of the pedipalps and legs, and slight enlargement of the telson (Prendini, 2001b; Volschenk and Prendini, 2008).

Two buthids, *Lychas aberlenci* and *Lychas mucronatus*, and a scorpionid, *Heterometrus laoticus*, were collected in the forest surrounding the cave entrance.

CONSERVATION STATUS: *Aemngvantom lao* inhabits a relatively small cave, the only locality at which it has been recorded. The cave is somewhat disturbed, having been used for shelter and storage of ordnance on the Ho Chi Minh Trail during the Vietnam War. The relative proximity of the cave to a major road renders it readily accessible, access is unregulated, and it does not fall within a protected area. Limestone mining is an additional threat in the area. The threat of continued habitat degradation, taken together with the highly restricted distributional range, which is completely unprotected, warrants its assignment to the Endangered category of the IUCN Red List. This highly stenotopic species is characterized by an acute restriction in both its area of occupancy and number of known localities: it is known to exist at a single location, the extent of occurrence is less than 5000 km^2, and the area of occupancy less than 500 km^2. A continuing decline in the quality of its habitat is observed, inferred, and projected. This species is expected to be prone to the effects of human activities (or stochastic events, the impact of which may be increased by human activities, e.g., climate change) within a very short period of time in an unforeseeable future, and potentially faces a very high risk of extinction in the wild.
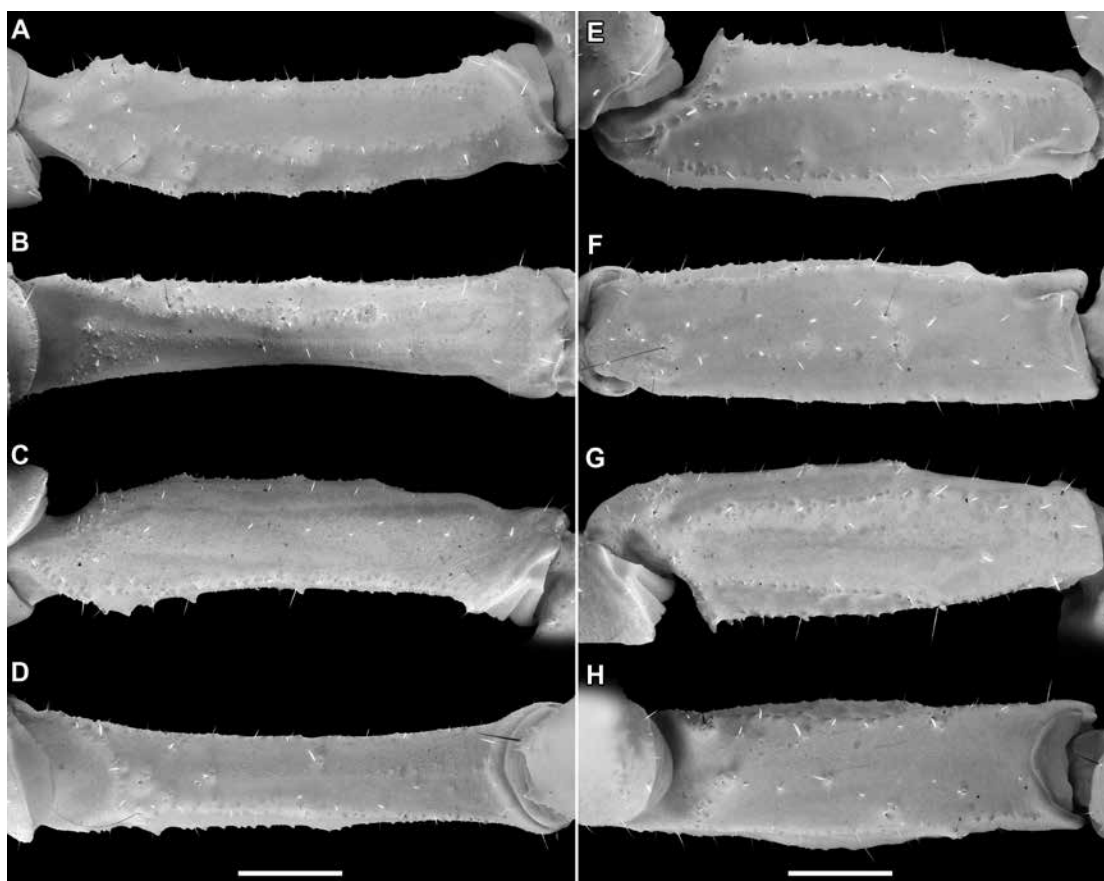
FIGURE 42. *Vietbocap canhi* Lourenço and Pham, 2010, ♀ (AMNH), Tiên Sơn, Vietnam, dextral pedipalp femur (**A–D**) and patella (**E–H**): **A, E.** dorsal, **B, F.** retrolateral, **C, G.** ventral, and **D, H.** prolateral aspects. Scale bars = 1 mm.

REMARKS: *Aemngvantom lao* was previously assigned to the genus *Vietbocap*. However, numerous differences between this species and *V. canhi*, especially concerning the morphology of the carapace and pedipalps, supported by multivariate statistical analysis (fig. 8), and taken together with the high levels of genetic divergence between them (fig. 9; table 12), which are comparable to the levels of divergence among the other pseudochactid genera, justify the creation of a new genus.

MATERIAL EXAMINED: **LAOS: Khammouane Prov.:** *Gnommalath Distr.*: Tham Nam Lot (Lod) near Ban Naden village, 17°30′13.8″N 105°23′09.2″E, 260 m, 13–14.vi.2012, L. Prendini,

S.F. Loria, and P. Kanyavong, limestone cave in primary rainforest at base of limestone mountain, fairly moist cave with pools of water in places, entrances on both sides of mountain, specimens collected with UV light detection ca. midday, uncommon, taken mostly 300–400 m (roughly halfway) from main entrance in dark zone, mostly in moist areas, sitting in crevices in mud walls below flowstone walls, 1 ♀ running on surface, several specimens (including 1 ♂) in mud walls of side room, 2 ♂, 3 ♀, 1 subad. ♂, 3 subad. ♀, 3 juv. ♂, 7 juv. ♀ (AMNH), 2 juv. ♀ (AMCC [LP 11349, 11350]); Tham Nam Lot (Lod), near Ban Naden Village, inside cave, 17°30′13.8″N 105°23′09.2″E, 260 m, 19.v.2018, S.F. Loria, L.

FIGURE 43. *Vietbocap canhi* Lourenço and Pham, 2010, ♀ (AMNH), Tiên Sơn, Vietnam, dextral pedipalp chela: **A.** dorsal, **B.** retrolateral, **C.** ventral, and **D.** prolateral aspects. Scale bar = 1 mm.

Ngo, S.T. Kangnavong, and P.T. Thon Thondet, deep in cave, walking on ground, under stones or in rock cracks, 2 ♀, 1 subad. ♀, 1 juv. ♀ (AMNH), 1 juv. ♂ (AMCC [LP 15570]), [telson] (AMCC [LP 15591]), same data except 20.v.2018, 1 ♂, 1 subad. ♂, 1 subad. ♀, 3 juv. ♀ (AMNH).

Aemngvantom thamnongpaseuam, gen. et sp. nov.

Figures 4B, C, F, 5, 7–9, 12E, 14E, 17C, 19C, 21C, 37–39, tables 1, 2, 4, 5, 10

Type Material: **LAOS: Khammouane Prov.:** *Thakhek Distr.:* Phou Hin Boun National Biodiversity Conservation Area: Holotype ♀ (AMNH/AMCC [LP 11351]), Tham Paseum [Tham Nong Paseum, Tham Nong Pa Seuam, Tham Pa Seuam, or Tham Pa Suam], 8.5 km from turnoff to Tham Phanong Pafa [Tham Nong Pa Fa or Tham Pa Fa] or Buddha Cave on main road Thakhek to Gnommalath (4 km E of Thakhek), 17°28′18″N 104°51′23.9″E, 141 m, 15.vi.2012, L. Prendini, S.F. Loria, and P. Kanyavong, limestone cave in primary rainforest, very wet cave with river running through, specimen taken from dark zone, in large terminal room [pillar room], ca. 500 m from cave entrance, with extensive rubble breakdown, stalactites, stalagmites and flowstone formations, specimen collected with UV light detection, ca. midday, sitting still on side of small stone.

Etymology: The specific epithet is a noun in apposition, taken from the name of the type locality, Tham Nong Pa Seuam.

Diagnosis: In addition to the marked genetic divergence between the two species (fig. 9; table 12), *A. thamnongpaseuam* may be separated morphologically from *A. lao* by means of the granulation and carination of the carapace, tergites, and metasoma, and the relative proportions of the pedipalps and metasoma. The mediolateral and posteromedian surfaces of the carapace and the surfaces of posttergites I–VI are smooth or nearly so in *A. thamnongpaseuam* (fig. 12E) but granular in *A. lao* (fig. 12A, C). The

ventrosubmedian carinae of metasomal segments II–IV are absent or obsolete in *A. thamnongpaseuam* (fig. 21C) but distinct in *A. lao* (fig. 21A, B). The dorsolateral carinae are obsolete, and the median lateral and ventromedian carina absent or obsolete on segment V in *A. thamnongpaseuam* (figs. 17C, 19C, 21C), whereas the dorsolateral and ventromedian carinae are distinct, and the median lateral carinae complete on segment V in *A. lao* (figs. 17A, B, 19A, B, 21A, B). Additionally, the pedipalp segments are proportionally shorter and broader, and the metasomal segments proportionally shorter and narrower in *A. thamnongpaseuam* than *A. lao* (figs. 17A–C, 19A–C, 21A–C, 34–36, 38, 39; tables 9, 10).

Description: The following description is based on the holotype female and only known specimen. The male is unknown.

Total length: Small, 30.0 mm (table 10).

Color: Tegument base coloration pale yellowish, immaculate. Chelicerae, pedipalps (except chela fingers), legs, posterior third of tergites and sternites, and telson slightly paler than carapace, pedipalp chela fingers, anterior two-thirds of tergites and sternites, and metasoma. Chela fingers dark reddish; pedipalpal and metasomal carinae reddish. Sternum, genital operculum, pectines, and sternites pale, whitish. Aculeus reddish black.

Chelicerae: Fixed finger, dorsal margin with four teeth (basal, median, subdistal, distal); basal and median teeth fused into bicuspid ("conjoined on trunk"); space between median and subdistal teeth U-shaped; ventral margin with four or five very small denticles (ventral accessory denticles). Movable finger, dorsal margin with three teeth (median, subdistal, retrolateral distal), without basal teeth; ventral margin with four or five very small denticles (ventral accessory denticles) and serrula in distal third; retrolateral (dorsal) distal and prolateral (ventral) distal teeth subequal, retrolateral (dorsal) distal tooth slightly smaller than prolateral (ventral) distal tooth, and opposable. Ventral surface of fingers and manus with numerous long, dense macrosetae.

Carapace: Carapace slightly longer than wide, anterior width 53% of length, posterior width 99% of length (table 10). Anterior margin protruding but shallowly concave (recurved) medially; anterolateral margins entire; posteromedian margin shallowly concave (recurved); posterolateral margins gently curved (fig. 12E). Median and lateral ocelli absent. Anterosubmedial depressions, medial to lateral ocelli, well developed. Median ocular tubercle represented by smooth, slightly depressed surface, situated anteromedially on carapace, distance from anterior margin 31% of carapace length (table 10); superciliary carinae absent; interocular sulcus shallow, obsolete. Circumocular sutures partial (disconnected); circumocular triangle subtriangular (broad V-shape); median ocular curvatures (regardless of absence of median ocelli) present. Anteromedian depression narrow, shallow; posteromedian sulcus shallow anteriorly, becoming deeper posteriorly; posterolateral sulci very shallow, wide, weakly curved; posteromarginal sulcus narrow, shallow. Carapace acarinate; anterolateral, interocular, circumocular, and posteromedian surfaces finely and sparsely granular, mediolateral, and posterolateral surfaces smooth.

Pedipalps: Pedipalps gracile; segments almost apilose, sparsely covered in short microsetae and occasional macrosetae. Pedipalp femur length 76% greater than width (table 10). Femur with five carinae evident (fig. 38A–D); promedian carina vestigial, reduced to few proximal spiniform granules; dorsomedian, prodorsal and proventral carinae weakly developed, granular; retrodorsal carina obsolete, reduced to few granules; retromedian, retroventral and ventromedian carinae absent; intercarinal surfaces smooth. Pedipalp patella length 71% greater than width (table 10). Patella with six carinae evident (fig. 38E–H); prodorsal, retrodorsal, proventral, and retroventral carinae weak, granular; prolateral surface, dorsoventral "vaulted" projection ("anterior process") moderately developed, with prominent pair of dorsal and ventral spiniform granules ("patellar spurs") proximally, demarcating pair of obsolete, granular prolateral carinae

("dorsal and ventral patellar spur carinae"); dorsomedian, retromedian, and ventromedian carinae absent; intercarinal surfaces smooth. Pedipalp chela relatively short and broad; manus globose, width 18% greater than height and length 47% greater than width (table 10); length of movable finger 56% greater than length of manus. Chela with three carinae evident (fig. 39); dorsomedian carina reduced to few granules at base of fixed finger, becoming obsolete on manus; digital carina weakly developed, granular; secondary accessory and retroventral carinae incompletely fused, slight disjunction evident in proximal third; retroventral carina obsolete, aligned parallel to longitudinal axis of chela, with distal margin connected to retrolateral movable finger condyle; ventromedian carina reduced to vestigial granules proximally; other carinae absent; intercarinal surfaces smooth. Fixed and movable fingers, dentate margins sublinear ($♀$), no proximal "gap" evident when closed; median denticle rows comprising 10 ($n = 2$) oblique and slightly imbricated subrows (tables 4, 10), decreasing in length distally; each subrow comprising large retrolateral denticle proximally (absent from proximal subrow, for total of nine retrolateral denticles on fixed finger and nine or 10 on movable finger), several small median denticles, and large prolateral denticle distally, slightly offset (total of 10 prolateral denticles on fixed and movable fingers); terminal (prolateral) denticle of first subrow enlarged; accessory denticles absent.

Trichobothria: Orthobothriotaxic, Type D, $β$ configuration, trichobothrium d_2 situated on femur dorsal surface, d_3 and d_4 in same axis, parallel and closer to retrodorsal carina than d_1, angle formed by d_1, d_3 and d_4 opening toward prolateral surface, with the following segment totals (figs. 38, 39): femur, 12 (6 dorsal, 3 prolateral, 3 retrolateral); patella, 10 (3 dorsal, 1 prolateral, 6 retrolateral); chela, 13 (5 manus, 8 fixed finger). Total number of trichobothria per pedipalp, 35. Five trichobothria on femur, i_4, d_1, d_2, d_4, and d_6, one on patella, est_1, and one on chela fixed finger, ib_2,

noticeably smaller than others ("petite"). Trichobothrium Et_1 situated on fixed finger, slightly distal to movable finger condyle; *eb* situated in proximal third of fixed finger, distal to most proximal retrolateral denticle of median denticle row; esb_2 situated approximately midway on fixed finger, between second and third most proximal retrolateral denticles of median denticle row.

Legs: Leg I maxillary lobes (coxapophyses), distal margins rounded, unmodified (not spatulate or dilate) anteriorly, terminating flush with lobes of leg II (fig. 37B). Legs I and II tibiae, retrolateral margins each with scattered macrosetae, without spurs; III and IV without spurs. Basitarsi with few scattered macrosetae, pro- and retrolateral rows of long spinules, and pair of pro- and retrolateral pedal spurs. Telotarsi with pair of slightly irregular ventrosubmedian rows of long spinules; proventral and retroventral rows of macrosetae absent, only few scattered macrosetae laterally; laterodistal lobes reduced and truncated; median dorsal lobe very short; ungues short, distinctly curved, equal in length; unguicular spur (dactyl) pronounced, pointed.

Sternum: Sternum, Type 1, pentagonal, length 17% greater than posterior width (table 10), lateral margins sublinear, ventral surface shallowly concave, posteromedian depression round (fig. 14E).

Pectines: Three marginal (anterior) lamellae, proximal sclerite considerably longer, distal sclerite short (fig. 14E); 12/11 ($n = 2$) ($♀$) median lamellae (tables 5, 10); fulcra present, very small. Proximal median lamella and basal pectinal tooth unmodified. Pectinal teeth present along entire posterior margin of each pecten ($♀$); 13/13 ($n = 2$) ($♀$) teeth. Pectinal peg sensillae unknown.

Genital operculum: Opercular sclerites completely separated, genital papillae absent ($♀$) (fig. 14E).

Male and female reproductive organs: Unknown.

Mesosoma: Pretergites surfaces smooth and shiny. Posttergites I–VI surfaces smooth, acarinate, each with pair of shallow submedian depressions (fig. 37A); VII surface sparsely granular, with pair of granular dorsosubmedian and dorsolateral carinae reaching posterior margin of segment. Sternites III–VII surfaces smooth, acarinate (fig. 37B), with scattered macrosetae, posterior margins with sparse row of macrosetae; III–VI, respiratory spiracles (stigmata) small, oval to round (fig. 14E); V posteroventral margin with pale, raised, triangular surface; VII width 39% greater than length (table 10).

Metasoma: Metasoma relatively short, total length 22% greater than combined length of prosoma and mesosoma (table 10); segments I–V progressively increasing in length, I wider than long, width of length for segment I, 115%; II, 89%; III, 77%; IV, 52%; and V, 29%. Metasoma with few short macrosetae. Ten carinae on segment I, eight on II and III, six on IV, and four on V (figs. 17C, 19C, 21C). Dorsosubmedian carinae moderately developed, granular throughout length of segments I–IV, absent on V; converging posteriorly. Dorsolateral carinae moderately developed, granular throughout length of segments I–IV, obsolete on V; converging posteriorly on I and V, subparallel on II–IV. Dorsosubmedian and dorsolateral carinae of segments I–IV not terminating posteriorly with enlarged, spiniform granules, granules similar to preceding granules. Median lateral carinae complete, granular throughout length of segments I and II, partial, becoming obsolete anteriorly on III, absent on IV and V. Ventrolateral carinae moderately developed, granular, becoming obsolete anteriorly on segments I and II, continuous throughout length of III–V; converging posteriorly on I and V, subparallel on II–IV. Ventrosubmedian carinae absent on segment I, obsolete on II–V; subparallel on II and III, converging posteriorly on IV and V. Ventromedian carina absent on segment V. Intercarinal surfaces smooth.

Telson: Telson large, suboval. Vesicle elongate, 21% wider than metasomal segment V (table 10), with flattened dorsal surface and rounded ventral surface (figs. 17C, 19C, 21C), height 38% of length; dorsal, lateral and ventral surfaces smooth ($♀$); anterodorsal lateral lobes ("vesicular tabs") obsolete; subaculear tubercle absent.

Aculeus short, shallowly curved, 28% of telson length. Venom glands not examined but presumed to be thin walled, simple and unfolded, as in *A. lao*.

Variation and sexual dimorphism: Unknown.

DISTRIBUTION: Endemic to the Thakhek District of Khammouane Province, Laos, and presently recorded from a single cave, Tham Nong Pa Seuam (also known as Tham Nong Paseum, Tham Paseum, Tham Pa Seuam, or Tham Pa Suam), in the Phou Hin Boun National Biodiversity Conservation Area, near Thakhek (figs. 4B, 7).

ECOLOGY: The holotype was collected from the dark zone of a very wet cave with a river running through, in a large terminal room (known as the "pillar room"), ca. 400–500 m from the cave entrance, containing extensive rubble breakdown, stalactites, stalagmites, and flowstone formations (fig. 4C, F). The specimen was collected with UV light detection, during daytime, sitting on the side of a small stone. Extensive searches, including a second expedition, failed to collect additional specimens, although numerous exuviae were observed.

Like other Vietbocapinae, *A. thamnongpaseuam* is an obligate troglobite with a highly specialized morphology, characterized by the absence of ocelli and pigmentation, attenuation of the pedipalps and legs, and slight enlargement of the telson (Prendini, 2001b; Volschenk and Prendini, 2008).

A buthid, *Lychas mucronatus*, a hormurid, *Liocheles australasiae* (Fabricius, 1775), and an unidentified euscorpiid, *Euscorpiops* sp., were collected in the forest surrounding the cave entrance.

CONSERVATION STATUS: *Aemngvantom thamnongpaseuam* inhabits a relatively small cave, the only locality at which it has been recorded. The cave is relatively undisturbed and situated within a protected area, the Phou Hin Boun National Biodiversity Conservation Area. Aside from an increase in disturbance associated with recreational ecotourism (caving), which could become a threat if unchecked, there appear to be few immediate threats to the survival of this species.

However, the relative proximity of the cave to a major road renders it readily accessible and access is unregulated, hence a continuing decline in the quality of its habitat is projected. Additionally, this highly stenotopic species is characterized by an acute restriction in both its area of occupancy and number of known localities: it is known to exist at a single location, the extent of occurrence is less than 5000 km², and the area of occupancy less than 500 km². Therefore, it is prone to the effects of human activities (or stochastic events, the impact of which may be increased by human activities, e.g., climate change) within a very short period of time in an unforeseeable future, and potentially faces a high risk of extinction in the wild, warranting its assignment to the Endangered category of the IUCN Red List.

Vietbocap Lourenço and Pham, 2010

Figures 4A, E, 5, 7–9, 12B, D, F, 14B, D, F, 15D, 17D, E, 19D, E, 21D, E, 40–43, tables 1–5, 10

Vietbocap Lourenço and Pham, 2010: 6, type species by monotypy: *Vietbocap canhi* Lourenço and Pham, 2010; Prendini, 2011: 117; Lourenço, 2012a: 232, 233, 236 (part); Lourenço and Leguin, 2012: 71 (part); Lourenço and Pham, 2012: 80, 81, 84; Soleglad et al., 2012: 89, 95, 96; Loria and Prendini, 2014: 5, 20, 21, tables 2, 4 (part); Lourenço, 2014: 31, 36; Lourenço, 2017a: 19; Pham et al., 2017: 134 (part); Deharveng and Bedos 2018: 121 (part); Loria and Prendini, 2018: 186, table 2 (part); Lourenço et al., 2018: 264, 265, 269, 272 (part); Francke, 2019: 16, 32, 39 (part); Sendi et al., 2020: 288 (part).
Vietbokap: Beron, 2015: 172 (part).

DIAGNOSIS: In addition to the marked genetic divergence between the two genera (fig. 9; table 12), *Vietbocap* may be separated morphologically from *Aemngvantom*, as follows. The anteromedian depression of the carapace is deep, the circumocular triangle parallel sided (U-shaped),

and the median ocular curvatures absent in *Vietbocap* (fig. 12B, D, F) whereas the anteromedian depression is shallow, the circumocular triangle subtriangular (broad V-shaped), and median ocular curvatures present in *Aemngvantom* (fig. 12A, C, E). The median ocular tubercle (demarcated by the posterior margin of the circumocular sulci) is situated medially in *Vietbocap* (fig. 12B, D, F) but anteromedially in *Aemngvantom* (fig. 12A, C, E). The anterolateral surfaces of the carapace are mostly smooth, but sparsely granular near the anterior carapace margin, in *Vietbocap* (fig. 12B, D, F), whereas the surfaces are mostly granular in *Aemngvantom* (fig. 12A, C, E). Pronounced rostrolateral incisions in the anterolateral margins of the carapace, lateral to the lateral ocelli, are present in *Vietbocap* (fig. 12B, D, F), whereas the anterolateral margins are entire in *Aemngvantom* (fig. 12A, C, E). The posteromedian margin of the carapace is sublinear to shallowly convex (procurved) in *Vietbocap* (fig. 12B, D, F) but shallowly concave (recurved) in *Aemngvantom* (fig. 12A, C, E). The pedipalp chela manus is elongate, with the prolateral dorsal carina of the male absent or obsolete in *Vietbocap*, whereas the chela manus is globose, with the prolateral dorsal carina of the male complete, in *Aemngvantom*. The median denticle rows of the chela fixed and movable fingers comprise seven or eight denticle subrows in *Vietbocap* (tables 3, 4, 10) but usually 10 subrows in *Aemngvantom* (tables 3, 4, 9, 10). Trichobothrium Et_1 is situated distally on the manus, aligned with or proximal to the movable finger condyle, and esb_2 in the proximal third of the fixed finger, between the first and second most proximal retrolateral denticles of the median denticle row, in *Vietbocap* (fig. 43B) whereas Et_1 is situated on the fixed finger, slightly distal to the movable finger condyle, and esb_2 approximately midway on the fixed finger, between the second and third most proximal retrolateral denticles of the median denticle row, in *Aemngvantom* (figs. 35B, 36B, 39B). The pectines possess 5–8 median lamellae and 6–10 teeth in *Vietbocap* (tables 3, 5, 10) but 11–14 lamellae and 12–15 teeth in *Aemngvantom*

(tables 3, 5, 9, 10). The median lateral carinae of metasomal segment II are partial, becoming obsolete anteriorly in *Vietbocap* (fig. 19D, E) but complete in *Aemngvantom* (fig. 19A–C).

INCLUDED TAXA: As redefined in the present contribution, *Vietbocap* accommodates a single species: *Vietbocap canhi* Lourenço and Pham, 2010.

DISTRIBUTION: *Vietbocap* is endemic to the Southeast Asian country of Vietnam, where it has been recorded from two caves, Tiên Sơn and Thiên Đường, in the Bố Trạch District of Quảng Bình Province (figs. 4A, 7).

ECOLOGY: The sole species of *Vietbocap* is an obligate troglobite, inhabiting the dark zone of deep caves, 200 m to 5 km from the surface (fig. 4E). The species is markedly troglomorphic.

Vietbocap canhi Lourenço and Pham, 2010

Figures 4A, E, 5, 7–9, 12B, D, F, 14B, D, F, 15D, 17D, E, 19D, E, 21D, E, 40–43, tables 1–5, 10

Scorpionida sp. nov.: Moulds et al., 2010: 4–6, 17, 18, 20, 34, fig. 3.3, table 1.
Vietbocap canhi Lourenço and Pham, 2010: 7–12, figs. 3–24; Fet et al., 2011a: 15; Lourenço, 2012a: 233, 235–237, fig. 3G, appendix A; 2012b: 733, table 1; Lourenço and Leguin, 2012: 71; Lourenço and Pham, 2012: 81–84, fig. 3B, E, H; Soleglad et al., 2012: 89; Moulds et al., 2013: 14; Loria and Prendini, 2014: 3, table 1; Lourenço, 2014: 31; Beron, 2015: 184; Pham et al., 2017: 134, 135, fig. 1; Beron, 2018: 834; Lourenço et al., 2018: 265; Francke, 2019: 32.
Vietbocap thienduongensis Lourenço and Pham, 2012: 82–85, fig. 3A, C, D, F, G; Lourenço, 2012a: 236, 237, appendix A; 2012b: 732, 733, table 1, fig. 2; Lourenço and Leguin, 2012: 71; Soleglad et al., 2012: 89; Moulds et al., 2013: 14; Loria and Prendini, 2014: 3, table 1; Lourenço, 2014: 31, 37, fig. 6; Pham et al., 2017: 134, 136, figs. 1, 4; Beron, 2018: 834; Lourenço, 2018: 2, fig. 2; Lourenço et al., 2018: 264–267, 269, 271; syn. nov.

Vietbocap aurantiacus Lourenço et al., 2018: 268, 269, 271, figs. 6, 7; syn. nov.

Vietbocap quinquemilia Lourenço et al., 2018: 269–271, figs. 8–11; syn. nov.

Type Material: **VIETNAM: Quảng Bình Prov.:** *Bố Trạch Distr.*: Phong Nha-Kẻ Bàng National Park: Holotype: 1 [juv.] ♂ (MNHN RS 8850), paratypes: 1 [juv.] ♀ (MNHN RS 8851), 2 [juv.] ♀ (IEBR), Tiên Sơn cave, 17°32′N 106°16′E, 16.v.2010, D.-S. Pham, mid section of the cave (200 m from cave entrance), No. VNS-01. *Vietbocap thienduongensis*: Holotype [subad.] ♂ (MNHH), paratype [juv.] ♂ (IEBR), Thiên Đường cave, mid section of cave (1800 m from cave entrance), 9.viii.2011, N.K. Dang. *Vietbocap aurantiacus*: Holotype ♀, paratype [juv.] ♀ (MNHN), paratype [juv.] ♀ (IEBR), Thiên Đường cave (17°31′10.3″N 106°13′22.9″E), midsection of cave (3000 m from cave entrance), 23.v.2013, D.-S. Pham. *Vietbocap quinquemilia*: Holotype: [juv.] ♂, paratype: [juv.] ♀ (MNHN), paratype ♀ (IEBR), Thiên Đường cave (17°31′10.3″N 106°13′22.9″E), midsection of cave (5000 m from cave entrance), 6.iv.2015, D.-S. Pham. It is apparent from the measurements and illustrations provided in the descriptions (Lourenço and Pham, 2010, 2012; Lourenço et al., 2018) that all except the holotype of *V. aurantiacus* are immature.

Diagnosis: As for genus.

Description: The following description, based on the material examined, which includes eight adult females, supplements the descriptions of Lourenço and Pham (2010, 2012) and Lourenço et al. (2018). It is unclear from the published photographs and measurements whether any of the males collected thus far are adult (no adult males were examined in the present study). Based on size and coloration, the holotypes of *V. canhi* and *V. quinquemilia* are immature, whereas the holotype of *V. thienduongensis* appears to be subadult. Ratios are presented for adult females only (tables 3, 10) whereas counts include immatures of both sexes (tables 3–5, 10).

Total length: Small, 31 mm (27.2–35.8 mm, *n* = 9) (tables 3, 10).

Color: Tegument base coloration pale yellowish to reddish yellow (whitish in immatures), immaculate. Chelicerae, pedipalps (except chela fingers), legs, posterior third of tergites and sternites, and telson slightly paler than carapace, pedipalp chela fingers, anterior two-thirds of tergites and sternites, and metasoma. Chela fingers dark reddish; pedipalpal and metasomal carinae reddish. Sternum, genital operculum, pectines, and sternites pale, whitish. Aculeus reddish black.

Chelicerae: Fixed finger, dorsal margin with four teeth (basal, median, subdistal, distal); basal and median teeth fused into bicuspid ("conjoined on trunk"); space between median and subdistal teeth U-shaped; ventral margin with three to five very small denticles (ventral accessory denticles). Movable finger, dorsal margin with three teeth (median, subdistal, retrolateral distal), without basal teeth; ventral margin with four or five very small denticles (ventral accessory denticles) and serrula in distal third; retrolateral (dorsal) distal and prolateral (ventral) distal teeth subequal, retrolateral (dorsal) distal tooth smaller than prolateral (ventral) distal tooth, and opposable. Ventral surface of fingers and manus with numerous long, dense macrosetae.

Carapace: Carapace slightly wider than long, anterior width 52% (47%–60%, *n* = 9) of length, length 101% (90%–107%, *n* = 9) of posterior width (tables 3, 10). Anterior margin protruding but shallowly concave (recurved) medially; anterolateral margins with pronounced rostrolateral incisions, lateral to lateral ocelli; posteromedian margin shallowly concave (recurved); posterolateral margins gently curved (fig. 12B, D, F). Median and lateral ocelli absent. Anterosubmedial depressions, medial to lateral ocelli, well developed. Median ocular tubercle represented by smooth, flat to slightly depressed surface, situated approximately medially on carapace, distance from anterior margin 46% (44%–47%, *n* = 8) of carapace length (table 10); superciliary carinae absent; interocular sulcus obsolete, shallow to deep. Circumocular sutures partial (discon-

nected); circumocular triangle parallel sided (U-shape), median ocular curvatures (regardless of absence of median ocelli) absent. Anteromedian depression narrow, deep; posteromedian sulcus shallow anteriorly, becoming deeper posteriorly; posterolateral sulci very shallow, wide, weakly curved; posteromarginal sulcus narrow, shallow. Carapace surfaces entirely smooth, except near anterior margin, and acarinate.

Pedipalps: Pedipalps gracile; segments apilose. Pedipalp femur width 80% (78%–82%, n = 9) greater than length (tables 3, 10). Femur with five carinae evident (fig. 42A–D); promedian carina vestigial, reduced to few proximal spiniform granules; dorsomedian, prodorsal and proventral carinae weakly developed, granular; retrodorsal carina obsolete, reduced to few granules; retromedian, retroventral, and ventromedian carinae absent; intercarinal surfaces smooth. Pedipalp patella length 71% (70%–72%, n = 9) greater than width (tables 3, 10). Patella with six carinae evident (fig. 42E–H); prodorsal, retrodorsal, proventral, and retroventral carinae weak, granular; prolateral surface, dorsoventral "vaulted" projection ("anterior process") moderately developed, with prominent pair of dorsal and ventral spiniform granules ("patellar spurs") proximally, demarcating pair of obsolete, granular prolateral carinae ("dorsal and ventral patellar spur carinae"); dorsomedian, retromedian, and ventromedian carinae absent; intercarinal surfaces smooth. Pedipalp chela relatively short and broad; manus elongate, width 97% (87%–106%, n = 9) of height and 34% (32%–37%, n = 8) of length (tables 3, 10); length of movable finger 37% (25%–45%, n = 8) greater than length of manus. Chela with three or four carinae evident (fig. 43); dorsomedian carina reduced to vestigial granules proximally or absent; digital carina weakly developed, granular; secondary accessory and retroventral carinae incompletely fused, slight disjunction evident in proximal third; retroventral carina weakly developed, granular, aligned parallel to longitudinal axis of chela, with distal margin connected to retrolateral movable finger condyle; ventromedian carina reduced to

vestigial granules proximally; other carinae absent; intercarinal surfaces smooth. Fixed and movable fingers, dentate margins sublinear, no proximal "gap" evident when closed; median denticle rows comprising eight (7 or 8, n = 68) oblique and slightly imbricated subrows (tables 3, 4, 10), decreasing in length distally; each subrow comprising large retrolateral denticle proximally (absent from proximal subrow, for total of six or seven retrolateral denticles on fixed and movable fingers), several small median denticles, and large prolateral denticle distally, slightly offset (total of seven or eight prolateral denticles on fixed and movable fingers); terminal (prolateral) denticle of first subrow enlarged; accessory denticles absent.

Trichobothria: Orthobothriotaxic, Type D, β configuration, trichobothrium d_2 situated on femur dorsal surface, d_3 and d_4 in same axis, parallel and closer to retrodorsal carina than d_1, angle formed by d_1, d_3 and d_4 opening toward prolateral surface, with the following segment totals (figs. 42, 43): femur, 12 (6 dorsal, 3 prolateral, 3 retrolateral); patella, 10 (3 dorsal, 1 prolateral, 6 retrolateral); chela, 13 (5 manus, 8 fixed finger). Total number of trichobothria per pedipalp, 35. Five trichobothria on femur, i_4, d_1, d_2, d_4, and d_6, one on patella, est_1, and one on chela fixed finger, ib_2, noticeably smaller than others ("petite"). Trichobothrium Et_1 situated distally on manus, aligned with or proximal to movable finger condyle; eb situated on fixed finger, slightly distal to movable finger condyle; esb_2 situated in proximal third of fixed finger, between first and second most proximal retrolateral denticles of median denticle row.

Legs: Leg I maxillary lobes (coxapophyses), distal margins rounded, unmodified (not spatulate or dilate) anteriorly, terminating flush with lobes of leg II (figs. 40B, 41B). Legs I and II tibiae, retrolateral margins each with scattered macrosetae, without spurs (fig. 15D); III and IV without spurs. Basitarsi with few scattered macrosetae, pro- and retrolateral rows of long spinules, and pair of pro- and retrolateral pedal spurs. Telotarsi with pair of slightly irregular ventrosubmedian rows of long

spinules; proventral and retroventral rows of macrosetae absent, only few scattered macrosetae laterally; laterodistal lobes reduced and truncated; median dorsal lobe very short; ungues short, distinctly curved, equal in length; unguicular spur (dactyl) pronounced, pointed.

Sternum: Sternum, Type 1, pentagonal, length 15% (7%–21%, $n = 9$) greater than posterior width (tables 3, 10), lateral margins sublinear, ventral surface shallowly concave, posteromedian depression round (fig. 14B, D, F).

Pectines: Three marginal (anterior) lamellae, proximal sclerite considerably longer, distal sclerite short (fig. 14B, D, F); 8/8 (7 or 8, $n = 15$) (♂) or 7/7 (5–7/5–8, $n = 34$) (♀) median lamellae (tables 3, 10); fulcra present, very small. Proximal median lamella and basal pectinal tooth unmodified. Pectinal teeth present along entire posterior margin of each pecten; 9/9 (8–10/8 or 9, $n = 18$) (♂) or 7/8 (6–8/6–9, $n = 46$) (♀) teeth. Pectinal peg sensillae long, cylindrical, tubular, or bottle shaped, and rounded distally, without pair of laterodistal processes; sensillar sockets smooth.

Genital operculum: Opercular sclerites completely separated, prominent genital papillae visible along entire length (♂) or absent (♀) (fig. 14B, D, F). Genital plugs observed in some females.

Male reproductive organs: Unknown.

Female reproductive organs: Ovariuterus comprising reticulate mesh of six cells. Oocytes contained in sessile follicles directly contacting ovaruterine tubes.

Mesosoma: Pretergites surfaces smooth and shiny. Posttergites I–VI surfaces smooth or nearly so, acarinate, each with pair of shallow submedian depressions (figs. 40A, 41A); VII surface sparsely granular, with pair of granular dorsosubmedian and dorsolateral carinae reaching posterior margin of segment. Sternites III–VII surfaces entirely smooth, acarinate (figs. 40B, 41B), with scattered macrosetae, posterior margins with sparse row of macrosetae; III–VI, respiratory spiracles (stigmata) small, oval (fig. 14B, D, F); V posteroventral margin with pale,

raised, triangular surface; VII width 34% (25%–45%, $n = 8$) greater than length (table 10).

Metasoma: Metasoma relatively short, total length 24% (18%–44%, $n = 9$) greater than combined length of prosoma and mesosoma (tables 3, 10); segments I–V progressively increasing in length, I wider than long, width of length for segment I, 101% (95%–116%, $n = 9$); II, 76% (68%–86%); III, 65% (59%–72%); IV, 48% (44%–53%); and V, 23% (20%–25%). Metasoma with few short macrosetae. Ten carinae on segments I–III, eight on IV, and four on V (figs. 17D, E, 19D, E, 21D, E). Dorsosubmedian carinae moderately developed, granular throughout length of segments I–IV, absent on V; converging posteriorly. Dorsolateral carinae moderately developed, granular throughout length of segments I–IV, obsolete on V; converging posteriorly on I and V, subparallel on II–IV. Dorsosubmedian and dorsolateral carinae of segments I–IV not terminating posteriorly with enlarged, spiniform granules, granules similar to preceding granules. Median lateral carinae complete, granular throughout length of segment I, partial, becoming obsolete anteriorly on II and III, absent on IV and V. Ventrolateral carinae moderately developed, granular, becoming obsolete anteriorly on segments I and II, continuous throughout length of III–V; converging posteriorly on I and V, subparallel on II–IV. Ventrosubmedian carinae absent on segment I, obsolete, costate on II, moderately developed, granular throughout length of III–V; subparallel on II and III, converging posteriorly on IV and V. Ventromedian carina absent on segment V. Intercarinal surfaces smooth.

Telson: Telson large, suboval (figs. 17D, E, 19D, E, 21D, E). Vesicle elongate, 32% (20%–45%, $n = 9$) wider than metasomal segment V (tables 3, 10), with flattened dorsal surface and rounded ventral surface, height 37% (35%–39%, $n = 8$) of length; dorsal, lateral, and ventral surfaces smooth or nearly so (♀); anterodorsal lateral lobes ("vesicular tabs") obsolete; subaculear tubercle absent. Aculeus short, shallowly curved, 31% (29%–33%, $n = 8$) of telson length. Venom glands thin walled, simple, and unfolded.

Intraspecific variation: The only morphological difference between the material from the two caves, which does not constitute ontogenetic variation or sexual dimorphism, concerns the median denticle rows on the fixed and movable fingers of the pedipalp chela, which comprise eight subrows in material from Tiên Sơn, the type locality of *V. canhi*, and seven subrows in material from Động Thiên Đường (Paradise Cave), the type locality of *V. aurantiacus*, *V. quinquemilia*, and *V. thienduongensis* (tables 3, 4, 10). This single difference is not considered sufficient to merit recognition at the species level, in the face of morphological similarity (fig. 8) and low genetic divergence (fig. 9; table 12).

Ontogenetic variation: Immature stages, including the types of *V. canhi*, *V. quinquemilia*, and *V. thienduongensis*, are paler in color and less sclerotized, and the posteroventral margin of mesosomal sternite V does not exhibit a pale, raised, triangular surface as in the adult stage. However, immature stages are easily sexed by examination of the genital aperture.

Sexual dimorphism: The genital papillae, visible the entire length and thus completely separating the two sclerites of the genital operculum (fig. 14B), are the characters of primary external sexual dimorphism in the male. The opercular sclerites are also completely separated in the female, although genital papillae are absent (fig. 14D, F). The only apparent secondary sexual characters observed in the male are the slightly better developed pectines, the median lamellae of which are more usually numerous and the teeth somewhat larger, and usually more numerous (fig. 14B, D, F; tables 3, 5, 10).

DISTRIBUTION: Endemic to the Bố Trạch District of Quảng Bình Province, Vietnam, where it has been recorded from two caves, Tiên Sơn and Động Thiên Đường (Paradise Cave), near Sơn Trạch, in the Phong Nha-Kẻ Bàng National Park (fig. 7). The caves are situated in a karstic landscape, in tropical forest at an elevation of 200–250 m (fig. 4A).

ECOLOGY: Specimens from Tiên Sơn were collected with UV detection in the dark zone of the cave, ca. 200–500 m from the entrance, sitting in rock crevices or under small stones, in a moist area with abundant speleothems, including dripstone and flowstone formations, stalactites, and stalagmites (fig. 4E). None were found in dry areas of cave. Specimens from Động Thiên Đường were also collected with UV detection in the dark zone, but much deeper, at sites between 1–5 km from the cave entrance, under rocks, in limestone cracks, or walking on the surface. Động Thiên Đường is approximately 31 km in length.

Vietbocap canhi is an obligate troglobite, characterized by the absence of ocelli and pigmentation, attenuation of the pedipalps and legs, and slight enlargement of the telson (Prendini, 2001b; Volschenk and Prendini, 2008). It appears to be the most cave-adapted member of the family, displaying the most elongated pedipalp chela and distinct dorsoventral compression of the carapace.

CONSERVATION STATUS: *Vietbocap canhi* is presently known from two caves, ca. 2.5 km apart, in the Phong Nha-Kẻ Bàng National Park. Whereas Tiên Sơn is a relatively small cave, Động Thiên Đường is very deep (ca. 31 km long), and *V. canhi* has been collected up to 5 km from the entrance of the latter. The anterior section of both caves is heavily disturbed: a concrete walkway and metal railings have been installed, and the cave brightly illuminated to display the speleothems. Few scorpions were observed in the illuminated parts of either cave. Access is restricted beyond the illuminated sections of both caves, however, where the habitat remains largely undisturbed. Despite the high level of protection afforded to its habitat, this highly stenotopic species is characterized by an acute restriction in both its area of occupancy and number of known localities: it is known to exist at only two locations, the extent of occurrence is less than 5000 km^2, and the area of occupancy less than 500 km^2. Therefore, it remains prone to the effects of human activities (or stochastic events, the impact of which may be increased by human activities, e.g., climate change) within a

very short period of time in an unforeseeable future, and potentially faces a high risk of extinction in the wild, warranting its assignment to the Endangered category of the IUCN Red List.

REMARKS: Lourenço and Pham (2012) described *V. thienduongensis* from Động Thiên Đường, a cave ca. 2.5 km from Tiên Sơn, the type locality of *V. canhi*. Lourenço and Pham (2012: 84) separated *V. thienduongensis* from *V. canhi* as follows:

> (i) bigger size and distinct morphometric values; (ii) complete and more strongly marked circumocular sutures; (iii) chela fingers proportionally shorter (ratios of chela length/movable finger length 7.1/4.2 = 1.69 for *V. canhi* and 8.3/4.6 = 1.80 for *V. thienduongensis* sp. n. and with 8 subrows of granules vs. 7 sub-rows); (iv) sternum only slightly longer than wide (ratio 1.15 for *V. canhi* and 1.30 for *V. thienduongensis* sp. n.); (v) metasomal segments less carinated and granulated and with a weaker chaetotaxy; (vi) pedipalp carinae better marked; (vii) pectines shorter and more bulkier with 8 teeth. Moreover, the caves where the species have been found are totally isolated from one other and belong to distinct cave systems. Given that the two caves are only a few kilometres apart, it can be suggested that both *Vietbocap* species may have a common epigean ancestor that colonized the caves independently.

Lourenço et al. (2018) subsequently described the female of *V. thienduongensis*, and two new species from deeper in the same cave. Whereas the specimens of *V. thienduongensis* were collected 750–1800 m from the cave entrance, the holotype of *V. aurantiacus* was collected 3000 m from the entrance, and the types of *V. quinquemilia*, 5000 m from the entrance. According to Lourenço et al. (2018: 269, 271, 272):

> *Vietbocap thienduongensis* and *Vietbocap aurantiacus* sp. n. are the two most geographically close species found in the cave, distant of 1.0 to 1.5 km. *V. aurantiacus* sp. n. can, however, be distinguished by a number of features: bigger size (35.8 vs 23.9 mm) and distinct morphometric values …; darker coloration, more to orange-yellow; anterior mar-

gin of carapace not depressed; sternum longer than wide …; metasomal segments and pedipalps better carinated and granulated; sternite V with a conspicuous white posterior inflated triangular zone; moderate serrula on chelicera movable finger.…

> *Vietbocap quinquemilia* sp. n. is geographically separated of *Vietbocap aurantiacus* sp. n. by 2 km. Their general morphology although similar presents a number of differences and in fact *V. quinquemilia* seems more closely related to *V. thienduongensis*. This new species can however be characterized by a number of particular features: small size (only 20.2 mm for female) and distinct morphometric values (see measurements and ratios following the description); a very pale coloration almost whitish; this is the paler species known for the genus; median ocular tubercle on carapace only slightly depressed; cheliceral serrula moderately marked; tergites globally smooth; pedipalp carinae very weakly marked.…

> It is difficult to estimate from the sole morphological study of these "populations" of *Vietbocap* living in the Thien Duong cave what is their precise degree of differentiation … Consequently, the question to be addressed is: are we faced with species, subspecies or only morphs of a large polymorphic species? For three of these populations, a specific status is here suggested in association with their possible allopatric distribution, though the number of available specimens is small to evaluate the robustness of the observed differences.… The presence of syntopic and closely related troglobitic species of a same genus in a same cave [sic] is quite exceptional. Molecular approaches will be necessary to evaluate the robustness of the observed differences between the species which have been recognized.

The hypothesis that three allopatric populations or species of *Vietbocap* inhabit Động Thiên Đường was tested and falsified in the present study by comparing DNA sequences of two nuclear (18S-ITS and 28S) and three mitochondrial (12S, 16S, and COI) gene loci from five samples collected at several sites along a transect 1–5 km from the entrance. The extremely low

genetic divergence among the samples along this transect (fig. 9; table 12) are consistent with panmixis. In addition, the same loci were sequenced from three samples collected in Tiên Sơn, the type locality of *V. canhi*, only 2.5 km away. Similar levels of divergence among the samples from Tiên Sơn, and between those samples and the samples from Động Thiên Đường, falsified the hypothesis that the two caves harbor different species, refuting the unsubstantiated statement that the caves "are totally isolated from one other and belong to distinct cave systems." The assumption that species occurring in different caves must be heterospecific, also known as the "caves as islands" paradigm (Mammola, 2019) suggested earlier by others (e.g., Francke, 2009a), is problematic for two reasons, noted earlier. Firstly, geography is not heritable and cannot comprise part of a taxon diagnosis, regardless of the presence or absence of morphological (or genomic) differences. Secondly, no conclusive evidence has been presented that the caves are disconnected or that these scorpions might not occur in other caves or passages in the 2.5 km between them. Several caves and cave networks in Southeast Asia are far longer than the distance between Tiên Sơn and Động Thiên Đường, e.g., Hang Sơn Đoòng (over 9 km long), Tham Xe Bang Fai (11 km long), and Phong Nha Cave (over 44 km long). Even Thiên Đường is more than 20 km long. As noted earlier, in attributing islandlike properties to caves, researchers should consider the presence of subterranean connections, as well as the vagility of the species of interest (Mammola, 2019). A network of fissures connecting two caves would make it difficult to consider the scorpion populations inhabiting them, to be isolated from one another.

Multivariate statistical analysis of the morphometric data presented by Lourenço and Pham (2010, 2012) and Lourenço et al. (2018), together with new data (tables 3–5, 10; appendices 4, 6, 7), was similarly unable to discriminate among the individuals from the two caves, which clustered together across a morphospace comparable to that of other pseudochactid species (fig. 8). It is apparent that ontogenetic differences were mistaken as diagnostic by Lourenço and Pham (2010, 2012) and Lourenço et al. (2018). Putatively diagnostic differences concerning size and morphometrics (table 3), coloration, granulation and/or carination, and the relative development of the circumocular sutures (affected by the sclerotization of the carapace tegument) reflect different stages of sexual maturity. Smaller size (and associated morphometric differences; tables 3, 10; appendices 4, 6, 7), paler coloration, weaker granulation and/or carination, and weakly developed circumocular sutures, as exemplified by the types of *V. canhi* and *V. quinquemilia*, are consistent with the immature stages, whereas larger size (and associated morphometric differences; tables 3, 10; appendices 4, 6, 7), darker coloration, stronger granulation and/or carination, and well developed sutures, as well as the presence of a pale, raised, triangular surface on the posteroventral margin of sternite V, exemplified by the holotype of *V. aurantiacus*, are consistent with the adult stage. The only characters that are ontogenetically invariant and offer any potential for species diagnosis are the counts of median denticle subrows on the fixed and movable fingers of the pedipalp chela, and the counts of pectinal teeth and lamellae. However, setting aside the absence of a statistical sample, the variation in these counts (e.g., a difference of one denticle subrow between individuals from the two caves, or of one pectinal lamella or tooth between individuals of the same sex in the same or different caves; tables 3–5) spans the normal levels of variation observed in other scorpion taxa, including pseudochactids.

In view of the overwhelming molecular and morphological evidence that the scorpions inhabiting both caves are conspecific, the following new synonyms are proposed: *Vietbocap thienduongensis* Lourenço and Pham, 2012 = *Vietbocap canhi* Lourenço and Pham, 2010, syn. nov.; *Vietbocap aurantiacus* Lourenço et al., 2018 = *V. canhi*, syn. nov.; *Vietbocap quinquemilia* Lourenço et al., 2018 = *V. canhi*, syn. nov.

Material Examined: **VIETNAM: Quảng Bình Prov.:** *Bố Trạch Distr.*: Phong Nha-Kẻ Bàng National Park: Tiên Sơn (Cave), 17°31′58.8″N 106°16′01.2″E, 200 m, 23.ii.2012, L. Prendini and V.A. Dang, dark zone of cave, ca. 200–500 m from entrance, UV detection in moist cave environment with abundant dripstone and flowstone formations, stalactites and stalagmites, specimens usually sitting in rock crevices or under small stones, mostly in moist situations (near areas where water collects from dripstone formations), none found in dry areas of cave, 7 ♀, 2 subad. ♂, 1 subad. ♀, 4 juv. ♂, 4 juv. ♀, pedipalp fragments (AMNH), 3 juv. ♀ (AMCC [LP 11270, 16750, 16751]); Thiên Đường (Cave), 200 m, 12.xi.2011, ex D.-S. Pham, cave, No. 1279, 1 juv. ♀ (AMCC [LP 11348]), Động Thiên Đường (Paradise Cave), 17°31′11.1″N 106°13′23″E, 248 m, 12–13.xi.2018, S.F. Loria, V.L. Ehrenthal, B.Đ. Trần, and H.V. Dương, blacklight in cave, specimens collected between 1 km and 5 km deep in cave, walking on ground, under rocks or in limestone cracks, ca. 1 km from cave entrance, 1 ♀ (AMNH), 1 subad. ♀ (IEBR), [leg] (AMCC [LP 16533]), between 1 km and 5 km from cave entrance, 1 subad. ♂ (IEBR), [leg] (AMCC [LP 16535]), 1 subad. ♀ (AMCC [LP 16536]), ca. 5 km from cave entrance, 1 juv. ♂ (PNKB), [leg] (AMCC [LP 16534]), 1 juv. ♀ (PNKB), [leg] (AMCC [LP 16537]).

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APPENDIX 1

FAMILIES, GENERA, AND SPECIES OF
CAVERNICOLOUS, TROGLOBITIC, AND
TROGLOMORPHIC SCORPIONS, WITH HABITAT,
TROGLOMORPHIES, AND PAST AND PRESENT
ASSESSMENTS OF ECOLOGICAL CLASSIFICATION

Family Akravidae Levy, 2007.

Akrav israchanani Levy, 2007: ISRAEL. Habitat: inside cave. Troglomorphies: median and lateral ocelli absent; pigmentation and sclerotization absent; pedipalps and legs attenuate. Previous assessments: troglobite (Levy, 2007; Volschenk and Prendini, 2008; Fet et al., 2011b; Deharveng and Bedos, 2018). Current assessment: **hypogean: troglobite**. Citations: Levy (2007); Volschenk and Prendini (2008); Fet et al. (2011b, 2017); Deharveng and Bedos (2018).

Family Belisariidae Lourenço, 1998.

Belisarius ibericus Lourenço, 2015: SPAIN. Habitat: under rocks near to cave entrance. Troglomorphies: median ocelli absent; lateral ocelli reduced; pigmentation and sclerotization reduced; telson vesicle enlarged. Previous assessments: endogean hygrophile lapidicolous (Karaman, 2020); endogean (Tropea and Onnis, 2020). Current assessment: **endogean**. Citations: Lourenço (2015); Karaman (2020); Tropea and Onnis (2020). Remarks: The type locality is dubious and this species is probably a junior synonym of *B. xambeui.*

Belisarius xambeui Simon, 1879: FRANCE, SPAIN. Habitat: leaf litter; inside caves. Troglomorphies: median and lateral ocelli absent; pigmentation and sclerotization reduced; telson vesicle enlarged. Previous assessments: troglophile (Jeannel, 1926; Jaulin et al., 2010; Deharveng and Bedos, 2018; Karaman, 2020); hypogée (Vachon, 1945); endogean (Gertsch and Soleglad, 1972; Francke, 1982; Lourenço, 2009; Tropea and Onnis, 2020); hipogea, que tant es pot trobar sota les pedres enfonsades … com dins de les coves (Vives, 1981); found in caves but also inhabits deep soil and litter (Reddell, 1981); vivant préférentiellement dans les grottes, mais également dans la litière forestière et sous les pierres (Emerit et al., 1996); troglophylus (Vignoli et al., 2008); humicolous, not a troglobite (Volschenk and Prendini, 2008); endogean hygrophile lapidicolous (Fet, 2010; Karaman, 2020); hypogé, litiéricole (Jaulin et al., 2010); troglomorphic endogean (Prendini et al., 2010; Botero-Trujillo et al., 2017); troglobite (Reddell, 2019; Santibáñez-López et al., 2019a). Current assessment: **endogean, hypogean: troglobite**. Citations: Simon (1879); Jeannel (1926); Wolf (1937); Kästner (1941); Vachon (1945); Auber (1959); Gertsch and Soleglad (1972); Reddell (1981, 2019); Vives (1981); Francke (1982); Emerit et al. (1996); Kovařík (2000a); Volschenk and Prendini (2008); Vignoli et al. (2008); Botero-Trujillo and Francke (2009); Lourenço (2009); Jaulin et al. (2010); Prendini et al. (2010); Botero-Trujillo et al. (2017); Deharveng and Bedos (2018); Santibáñez-López et al. (2019a); Karaman (2020); Tropea and Onnis (2020).

Sardoscorpius troglophilus Tropea and Onnis, 2020: ITALY (Sardinia). Habitat: under stones inside cave. Troglomorphies: median and lateral ocelli reduced; pigmentation and sclerotization absent; pedipalps and legs attenuate. Previous assessments: eutroglophile (Tropea and Onnis, 2020). Current assessment: **hypogean: troglophile (eutroglophile)**. Citations: Tropea and Onnis (2020).

Family Buthidae C.L. Koch, 1837.

Alayotityus delacruzi Armas, 1973: CUBA. Habitat: inside cave. Troglomorphies: median and lateral ocelli reduced; pigmentation and sclerotization slightly reduced. Previous assessments: une espèce néotroglobionte en train d'inféodation dans le milieu cavernicole (Vachon, 1977); mais dans tous les cas, elles ont été considérées uniquement comme des trogloxènes réguliers ou, à la rigueur, comme des troglophiles (Lourenço and Francke, 1985); troglobite

(Armas, 2000; Gallão and Bichuette, 2016); non-troglomorph troglobite (Teruel and Kovařík, 2012); guanobitic-troglobitic (Deharveng and Bedos, 2018). Current assessment: **hypogean: troglophile (eutroglophile)**. Citations: Armas (1973); Vachon (1977); Lourenço and Francke (1985); Armas (2000); Teruel and Kovařík (2012); Gallão and Bichuette (2016); Deharveng and Bedos (2018).

Alayotityus juraguaensis Armas, 1973: CUBA. Habitat: under stones near seashore, arid area. Previous assessments: neotroglobiont (Vachon, 1977); troglobio-guanobio (Decou, 1981); troglófila del primer orden (Armas and Alayón Garcia, 1984); trogloxene/troglophile (Lourenço and Duhem, 2010a). Current assessment: **epigean, hypogean: accidental**. Citations: Armas (1973); Armas and Alayón Garcia (1984); Lourenço and Duhem (2010a); Teruel and Kovařík (2012).

Babycurus johnstonii Pocock, 1896: CAMEROON. Habitat: surface, forest. Previous assessments: trogloxene/troglophile (Lourenço and Duhem, 2010a). Current assessment: **epigean: accidental**. Citations: Lourenço and Duhem (2010a).

Centruroides gracilis (Latreille, 1804): CUBA. Habitat: inside cave; surface. Previous assessments: troglófila del primer orden (Armas and Alayón Garcia, 1984); accidental (Sissom and Reddell, 2009). Current assessment: **epigean: accidental**. Citations: Armas and Alayón Garcia (1984); Sissom and Reddell (2009).

Heteroctenus junceus (Herbst, 1800): CUBA. Habitat: inside cave; surface. Previous assessments: troglófila del primer orden (Armas and Alayón Garcia, 1984). Current assessment: **epigean: accidental**. Citations: Armas and Alayón Garcia (1984); Armas (2000).

Lychas hosei Pocock, 1891: MALAYSIA. Habitat: inside cave; surface (forest). Previous assessments: probablement troglophile mais, il se pourrait qu'elle soit uniquement trogloxène (Vachon and Lourenço, 1985); trogloxene/troglophile (Lourenço and Duhem, 2010a); troglophile (Beron, 2015). Current assessment: **epigean, hypogean: trogloxene (subtroglophile)**. Citations: Vachon and Lourenço (1985); Lourenço (2007c); Lourenço and Duhem (2010a); Beron (2015); Kovařík (2019). A monotypic genus of dubious validity, *Spelaeolychas* Kovařík, 2019, was erected to accommodate this species; it is retained in the genus *Lychas* C.L. Koch, 1845, in the present contribution. The subspecies, *Lychas hosei cavernicola* Lourenço, 2007 appears to be a junior synonym of the nominotypical form.

Reddyanus deharvengi (Lourenço and Duhem, 2010): VIETNAM. Habitat: inside cave; in litter. Previous assessments: troglophile (Lourenço and Duhem, 2010a; Beron, 2015). Current assessment: **epigean, hypogean: accidental**. Citations: Lourenço and Duhem (2010a); Beron (2015). Remarks: The holotype male closely resembles the males of other epigean *Reddyanus* Vachon, 1972, including *Reddyanus petrzelkai* Kovařík, 2003, with which it may be conspecific. *Reddyanus* are typically attenuate, consistent with the lithophilous ecomorphotype (Prendini, 2001b).

Tityopsis inexpectata (Moreno, 1940): CUBA. Habitat: inside cave; surface. Previous assessments: troglófila del primer orden (Armas and Alayón Garcia, 1984). Current assessment: **epigean: accidental**. Citations: Armas and Alayón Garcia (1984); Armas (2000); Teruel and Rodríguez-Cabrera (2020).

Tityopsis sheylae Teruel and Rodríguez-Cabrera, 2020: CUBA. Habitat: inside cave. Troglomorphies: pigmentation and sclerotization slightly reduced; pedipalps, legs, and metasoma attenuate. Previous assessments: troglobite (Teruel and Rodríguez-Cabrera, 2020). Current assessment: **hypogean: troglophile (eutroglophile)**. Citations: Teruel and Rodríguez-Cabrera (2020).

Tityus demangei Lourenço, 1981: ECUADOR. Habitat: inside cave; surface, forest. Previous assessments: trogloxene (Lourenço, 1981); not a troglobite (Volschenk and Prendini, 2008); trogloxene/troglophile (Lourenço and Duhem, 2010a). Current assessment: **epigean, hypogean: accidental**. Citations: Lourenço (1981); Lourenço and Francke (1985); Volschenk and Pren-

dini (2008); Lourenço and Duhem (2010a); Botero-Trujillo and Flórez (2014). Remarks: According to Lourenço (1981) and Lourenço and Duhem (2010a), this species is a trogloxene, but only the holotype was recorded in a cave, with other specimens collected far from caves (Botero-Trujillo and Flórez, 2014). The yellowish coloration of this species resembles that of many epigean species of the genus and meets the criterion of an accidental.

Tityus jussarae Lourenço, 1988: ECUADOR. Habitat: inside cave. Current assessment: **hypogean: trogloxene (subtroglophile)**. Citations: Lourenço (1988).

Tityus grottoedensis Botero-Trujillo and Flórez, 2014: COLOMBIA. Habitat: inside cave, under stone; outside cave. Previous assessments: eutroglophile/subtroglophile (Botero-Trujillo and Flórez, 2014). Current assessment: **epigean, hypogean: trogloxene (subtroglophile)**. Citations: Botero-Trujillo and Flórez (2014).

Tityus magnimanus Pocock, 1897: BRAZIL, COLOMBIA, VENEZUELA. Habitat: surface, forest; inside cave and surrounding areas. Previous assessments: mais dans tous les cas, elles ont été considérées uniquement comme des trogloxènes réguliers ou, à la rigueur, comme des troglophiles (Lourenço and Francke, 1985); troglophile (Galan and Herrera, 2006); trogloxene/troglophile (Lourenço and Duhem, 2010a). Current assessment: **epigean, hypogean: accidental**. Citations: González-Sponga (1974, 1996); Lourenço and Francke (1985); Linares and Bordon (1987); Rojas-Runjaic (2004); Galan and Herrera (2006); Lourenço and Duhem (2010a). Remarks: *Tityus falconensis* González-Sponga, 1974 is a junior synonym of *T. magnimanus*, which is why the species was listed as hypogean by Lourenço and Duhem (2010a). Cave records and citations from Lourenço and Francke (1985), Linares and Bordon (1987), Rojas-Runjaic (2004), and Galan and Herrera (2006) refer to *T. falconensis*.

Tityus monaguensis González-Sponga, 1974: VENEZUELA. Habitat: forested areas and caves. Previous assessments: mais dans tous les cas, elles ont été considérées uniquement comme des trogloxènes réguliers ou, à la rigueur, comme des troglophiles (Lourenço and Francke, 1985); troglophile (Galan and Herrera, 2006); trogloxene/troglophile (Lourenço and Duhem, 2010a). Current assessment: **epigean, hypogean: accidental**. Citations: González-Sponga (1974, 1996); Lourenço and Francke (1985); Linares and Bordon (1987); Rojas-Runjaic (2004); Galan and Herrera (2006); Lourenço and Duhem (2010a).

Troglorhopalurus lacrau (Lourenço and Pinto-da-Rocha, 1997): BRAZIL. Habitat: inside caves. Troglomorphies: pigmentation and sclerotization slightly reduced. Previous assessments: trogloxene; non-cavernicolous (Lourenço and Pinto-da-Rocha, 1997); obligatory cave-dwelling life habitat, troglobite (Gallão and Bichuette, 2016); troglophile (Esposito et al., 2017). Current assessment: **hypogean: troglophile (eutroglophile)**. Citations: Lourenço and Pinto-da-Rocha (1997); Gallão and Bichuette (2016); Esposito et al. (2017).

Troglorhopalurus translucidus Lourenço et al., 2004: BRAZIL. Habitat: inside cave. Troglomorphies: median and lateral ocelli reduced; pigmentation and sclerotization reduced; pedipalps, legs and metasoma attenuate; prolateral and retrolateral pedal spurs reduced. Previous assessments: troglobite (Lourenço et al., 2004; Volschenk and Prendini, 2008; Trajano and Bichuette, 2010; Botero-Trujillo and Flórez, 2014; Gallão and Bichuette, 2016; Esposito et al., 2017); unequivocal troglobitic characteristics (Lourenço and Duhem, 2010a; Lourenço and Pham, 2013). Current assessment: **hypogean: troglobite**. Citations: Lourenço et al. (2004); Volschenk and Prendini (2008); Lourenço and Duhem (2010a); Ochoa et al. (2010); Trajano and Bichuette (2010); Lourenço and Pham (2013); Botero-Trujillo and Flórez (2014); Gallão and Bichuette (2016); Esposito et al. (2017).

Troglotityobuthus gracilis (Fage, 1946): MADAGASCAR. Habitat: inside cave. Troglomorphies: pigmentation and sclerotization unknown (old, faded specimen; pale coloration likely due to preservation); pedipalps, legs, and metasoma attenuate; telson vesicle slightly

enlarged. Previous assessments: troglobie (Fage, 1946); troglobite (Lourenço, 2000b; Lourenço and Goodman, 2008; Lourenço and Duhem, 2010a; Gallão and Bichuette, 2016); perhaps a troglobite (Volschenk and Prendini, 2008); unequivocal troglobitic characteristics (Lourenço and Pham, 2013). Current assessment: **hypogean: troglophile (eutroglophile)**. Citations: Fage (1946); Lourenço (2000b); Lourenço and Goodman (2008); Volschenk and Prendini (2008); Lourenço and Duhem (2010a); Lourenço and Pham (2013); Gallão and Bichuette (2016). Remarks: Although this species may be troglomorphic, it seems likely the pale coloration is an artefact of age and preservation. If so, only the attenuation and presence in a cave would be consistent with its classification in the Schiner-Racovitza system. However, many lithophilous epigean buthids are highly attenuated (Volschenk and Prendini, 2008).

Family Chactidae Pocock, 1893

Broteochactas trezzii (Vignoli and Kovařík, 2003): VENEZUELA. Habitat: under a stone inside Sima Aonda, a long narrow gorge, ca. 50 m deep, the remains of a cave, the ceiling of which collapsed; the biotope was characterized as dark and extremely humid. Troglomorphies: median ocelli reduced; pigmentation and sclerotization reduced; pedipalps, legs, and metasoma attenuate; prolateral and retrolateral pedal spurs absent; telson vesicle enlarged. Previous assessments: troglobite (Vignoli and Kovařík, 2003; Rojas-Runjaic, 2004; Galan and Herrera, 2006; Vignoli and Prendini, 2009); perhaps a troglobite (Volschenk and Prendini, 2008). Current assessment: **endogean**. Citations: Vignoli and Kovařík (2003); Rojas-Runjaic (2004); Galan and Herrera (2006); Volschenk and Prendini (2008); Ochoa et al. (2010); Rossi (2018a); Ochoa and Rojas-Runjaic (2019). Remarks: A monotypic genus of dubious validity, *Antridiscalceatus* Rossi, 2018, was erected to accommodate this species; it is retained in the genus *Broteochactas* Pocock, 1893, in the present contribution.

Chactas vilorai Rojas-Runjaic, 2004: VENEZUELA. Habitat: under stones, hypogean, twilight zone. Previous assessments: trogloxene (Rojas-Runjaic, 2004); troglóxenas y troglófilas (Galan and Herrera, 2006). Current assessment: **hypogean: troglophile (eutroglophile)**. Citations: Rojas-Runjaic (2004); Galan and Herrera (2006).

Chactas vanbenedenii (Gervais, 1843): COLOMBIA, VENEZUELA. Habitat: inside cave; surface. Previous assessments: troglófila (Galan and Herrera, 2006). Current assessment: **epigean, hypogean: accidental**. Citations: Galan and Herrera (2006).

Chactas yupai González-Sponga, 1994: VENEZUELA. Habitat: high altitude tropical forest and savanna. Previous assessments: troglóxenas y troglófilas? (Galan and Herrera, 2006). Current assessment: **epigean: accidental**. Citations: González-Sponga (1994); Galan and Herrera (2006).

Family Chaerilidae Pocock, 1893

Chaerilus agilis Pocock, 1899: MALAYSIA. Habitat: inside cave. Troglomorphies: median and lateral ocelli reduced; pigmentation and sclerotization reduced; pedipalps, legs, and metasoma attenuate. Previous assessments: troglobite (McClure et al., 1967); probably troglophile (Lourenço and Francke, 1985); cavernicoles (Deharveng and Leclerc, 1989); troglophile/trogloxene (Dittmar et al., 2005); suspected of having a subterranean way of life, mainly because found inside caves, but more formal evidence may be necessary (Lourenço and Rossi, 2019). Current assessment: **hypogean: troglobite**. Citations: Pocock (1899); Bristowe (1952); McClure et al. (1967); Lourenço and Francke (1985); Deharveng and Leclerc (1989); Kovařík (2000b); Dittmar et al. (2005); Lourenço (2008); Beron (2015); Lourenço and Rossi (2019). Remarks: McClure et al. (1967) listed this species as *Chaerilus* prob. *celebensis*.

Chaerilus agnellivanniorum Lourenço and Rossi, 2019: PHILIPPINES. Habitat: inside cave. Troglomorphies: pigmentation and sclerotization

reduced; pedipalps, legs, and metasoma attenuate. Previous assessments: may also be a true troglobitic element, but with a less marked degree of regression for several characters (Lourenço and Rossi, 2019). Current assessment: **hypogean: troglobite**. Citations: Lourenço and Rossi (2019).

Chaerilus cavernicola Pocock, 1894: INDONESIA. Habitat: inside cave. Troglomorphies: pedipalps, legs, and metasoma attenuate. Previous assessments: probably troglophile (Lourenço and Francke, 1985); probably not a troglobite (Volschenk and Prendini, 2008); suspected of having a subterranean way of life, mainly because found inside caves, but more formal evidence may be necessary (Lourenço and Rossi, 2019). Current assessment: **hypogean: troglophile (eutroglophile)**. Citations: Pocock (1894); Wolf (1937); Lourenço and Francke (1985); Kovařík (2000b); Volschenk and Prendini (2008); Lourenço and Rossi (2019).

Chaerilus chapmani Vachon and Lourenço, 1981: MALAYSIA. Habitat: inside cave. Troglomorphies: median and lateral ocelli reduced; pigmentation and sclerotization absent; pedipalps, legs and metasoma attenuate. Previous assessments: troglobie (Lourenço and Francke, 1985; Lourenço, 1995); cavernicoles (Deharveng and Leclerc, 1989); apparently to some extent troglobitic, a facultative troglobite (Kovařík, 2000a); troglobite (Lourenço, 2008, 2009; Lourenço and Goodman, 2008; Volschenk and Prendini, 2008; Moulds et al., 2013; Lourenço and Rossi, 2019). Current assessment: **hypogean: troglobite**. Citations: Lourenço and Francke (1985); Deharveng and Leclerc (1989); Lourenço (1995, 2009); Kovařík (2000a, 2000b); Lourenço and Goodman (2008); Volschenk and Prendini (2008); Moulds et al. (2013); Beron (2015); Lourenço and Rossi (2019).

Chaerilus pathom Lourenço and Pham, 2014: VIETNAM. Habitat: inside cave. Current assessment: **hypogean: troglophile (eutroglophile)**. Citations: Lourenço and Pham (2014b).

Chaerilus sabinae Lourenço, 1995: INDONESIA. Habitat: inside cave. Troglomorphies: median and lateral ocelli absent; pigmentation and sclerotization absent; pedipalps and legs attenuate; telson vesicle enlarged. Previous assessments: cavernicoles, anophtalme (Deharveng and Leclerc, 1989); troglobie (Lourenço, 1995); troglobite (Volschenk and Prendini, 2008; Lourenço, 2009; Lourenço and Rossi, 2019). Current assessment: **hypogean: troglobite**. Citations: Deharveng and Leclerc (1989); Lourenço (1995, 2009); Kovařík (2000a, 2000b); Volschenk and Prendini (2008); Deharveng and Bedos (2018); Rossi (2018b); Lourenço and Rossi (2019). Remarks: A monotypic genus of dubious validity, *Chaerilourencous* Rossi, 2018, was erected to accommodate this species; it is retained in the genus *Chaerilus* Simon, 1877 in the present contribution.

Chaerilus spinatus Lourenço and Duhem, 2010: INDONESIA. Habitat: inside cave. Previous assessments: no characteristics of a troglobitic species (Lourenço and Duhem, 2010b); definitely epigean (Lourenço, 2012b). Current assessment: **hypogean: troglophile (eutroglophile)**. Citations: Lourenço and Duhem (2010b); Lourenço (2012b).

Chaerilus telnovi Lourenço, 2009: INDONESIA. Habitat: leaf litter. Troglomorphies: median ocelli absent; lateral ocelli reduced; pigmentation and sclerotization absent; pedipalps, legs, and metasoma attenuate. Previous assessments: litter dwelling (Lourenço, 2009); eyeless forest litter scorpion (Lourenço and Duhem, 2010b); not an epigean species, but a soil dweller (Lourenço, 2012b). Current assessment: **endogean**. Citations: Lourenço (2009, 2012b); Lourenço and Duhem (2010b); Loria and Prendini (2014); Deharveng and Bedos (2018).

Family Diplocentridae Karsch, 1880

Cryptoiclus rodriguezi Teruel and Kovařík, 2012: CUBA. Habitat: exclusively in interstitial spaces of soil, deep inside rocky taluses in cave entrances at the base of coastal cliffs. Troglomorphies: median and lateral ocelli reduced; pigmentation and sclerotization reduced. Previous assessments: lives exclusively in interstitial spaces

of soil, deep inside rocky taluses in cave entrances at the base of coastal limestone cliffs 10–52 m (Teruel and Kovařík, 2012). Current assessment: **endogean**. Citations: Teruel and Kovařík (2012).

Diplocentrus actun Armas and Palacios-Vargas, 2002: MEXICO. Habitat: inside cave. Troglomorphies: median ocelli absent; lateral ocelli reduced; pigmentation and sclerotization absent; pedipalps and legs attenuate. Previous assessments: troglobite (Armas and Palacios-Vargas, 2002; Volschenk and Prendini, 2008; Sissom and Reddell, 2009); troglobio (Palacios-Vargas and Reddell, 2013). Current assessment: **hypogean: troglobite**. Citations: Armas and Palacios-Vargas (2002); Volschenk and Prendini (2008); Sissom and Reddell (2009); Palacios-Vargas and Reddell (2013). Remarks: This species is probably a junior synonym of *D. anophthalmus.*

Diplocentrus anophthalmus Francke, 1977: MEXICO. Habitat: inside cave. Troglomorphies: median ocelli absent; lateral ocelli reduced; pigmentation and sclerotization absent; pedipalps and legs attenuate; telson vesicle enlarged. Previous assessments: troglobite (Francke, 1977, 1978; Reddell, 1977, 1981; Armas, 1994; Armas and Palacios-Vargas, 2002; Volschenk and Prendini, 2008; Sissom and Reddell, 2009); troglobie (Lourenço and Francke, 1985); troglobio (Palacios-Vargas and Reddell, 2013); troglobiont (Santibáñez-López et al., 2014a). Current assessment: **hypogean: troglobite**. Citations: Francke (1977, 1978); Reddell (1977, 1981); Lourenço (1981); Muchmore (1982); Lourenço and Francke (1985); Beutelspacher and López-Forment (1991); Armas (1994); Palacios-Vargas (1994); Armas and Palacios-Vargas (2002); Volschenk and Prendini (2008); Sissom and Reddell (2009); Palacios-Vargas and Reddell (2013); Santibáñez-López et al. (2014b); Rossi (2018a). Remarks: A monotypic genus of dubious validity, *Troglopolyphemos* Rossi, 2018, was erected to accommodate this species; it is retained in the genus *Diplocentrus* Peters, 1861, in the present contribution.

Diplocentrus cueva Francke, 1978: MEXICO. Habitat: inside cave. Troglomorphies: median

ocelli reduced; pigmentation and sclerotization reduced; pedipalps and legs attenuate. Previous assessments: troglobite (Francke, 1978; Reddell, 1981; Armas, 1994; Volshenk and Prendini, 2008); troglobie (Lourenço and Francke, 1985); in initial stages of regressive evolution (Sissom, 1986); troglobio (Palacios-Vargas and Reddell, 2013). Current assessment: **hypogean: troglobite**. Citations: Francke (1978); Lourenço (1981); Reddell (1981); Lourenço and Francke (1985); Sissom (1986); Beutelspacher and López-Forment (1991); Armas (1994); Palacios-Vargas (1994); Volschenk and Prendini (2008); Sissom and Reddell (2009); Palacios-Vargas and Reddell (2013).

Diplocentrus mitchelli Francke, 1977: MEXICO. Habitat: inside cave. Previous assessments: troglobite (Francke, 1977, 1978; Reddell, 1977, 1981; Armas, 1994; Armas and Palacios-Vargas, 2002); troglobie (Lourenço and Francke, 1985); probably not a troglobite (Volschenk and Prendini, 2008); possibly troglobitic (Sissom and Reddell, 2009); troglobio (Palacios-Vargas and Reddell, 2013). Current assessment: **epigean: accidental**. Citations: Francke (1977, 1978); Reddell (1977, 1981); Lourenço (1981); Lourenço and Francke (1985); Beutelspacher and López-Forment (1991); Armas (1994); Palacios-Vargas (1994); Armas and Palacios-Vargas (2002); Volschenk and Prendini (2008); Sissom and Reddell (2009); Palacios-Vargas and Reddell (2013). Remarks: The holotype is an early instar juvenile suggesting the absence of pigmentation is the juvenile condition as observed in most other diplocentrids (Volschenk and Prendini, 2008). This species is probably a junior synonym of *D. reddelli.*

Diplocentrus reddelli Francke, 1977: MEXICO. Habitat: inside sinkhole; outside cave. Previous assessments: smallest epigean species (Francke, 1977); troglophile (Reddell, 1977); probably an accidental (Sissom and Reddell, 2009); especies conocidas solo de cuevas, pero probablemente no restringidas a los hábitats subterráneos (Palacios-Vargas and Reddell, 2013). Current assessment: **epigean: accidental**. Citations: Francke

(1977); Reddell (1977, 1981); Sissom and Reddell (2009); Palacios-Vargas and Reddell (2013); Santibáñez-López et al. (2014a).

Kolotl magnus (Beutelspacher and López-Forment, 1991): MEXICO. Habitat: inside cave but also inhabits cracks and crevices in rocks. Previous assessments: troglobite (Beutelspacher and López-Forment, 1991); not a troglobite (Volschenk and Prendini, 2008); probably an accidental (Sissom and Reddell, 2009); semilithophilous (Santibáñez-López et al., 2014a). Current assessment: **epigean: accidental**. Citations: Beutelspacher and López-Forment (1991); Volschenk and Prendini (2008); Sissom and Reddell (2009); Santibáñez-López et al. (2014a, 2014b).

Heteronebo clareae Armas, 2001: UNITED STATES OF AMERICA. (Navassa Island). Habitat: inside "dark zone" of vertical "cave" ca. 1.2 m in diameter and only 5 m deep. Troglomorphies: median and lateral ocelli reduced; pigmentation and sclerotization absent; pedipalps and legs attenuate. Previous assessments: troglobite (Armas, 2001); probably not a troglobite (Volschenk and Prendini, 2008). Current assessment: **endogean or hypogean: trogloxene (subtroglophile)**. Citations: Armas (2001); Volschenk and Prenndini (2008). Remarks: The shallowness of the cave suggests this is a trogloxene, if not an accidental.

Family Euscorpiidae Laurie, 1896

Euscorpius aquilejensis (C.L. Koch, 1837): CROATIA, ITALY, SLOVENIA. Habitat: inside cave; surface. Previous assessments: it is quite possible that some *Euscorpius* Thorell, 1876, species are more or less troglophilic, opportunistic taxa, and, where an opportunity presents itself, spend part or all of their lives inside a cave or similar habitat (Tropea and Fet, 2015; Tropea and Ozimec, 2019, 2020); troglophile (Karaman, 2020). Current assessment: **epigean, hypogean: accidental**. Citations: Boldori (1977); Tropea and Fet (2015); Tropea and Ozimec (2019, 2020); Karaman (2020).

Euscorpius biokovensis Tropea and Ozimec, 2020: BOSNIA-HERZEGOVINA, CROATIA. Habitat: primarily inside cave but also mines and underground tunnels. Troglomorphies: pigmentation and sclerotization reduced; pedipalps, legs, and metasoma attenuate; telson vesicle enlarged. Previous assessments: troglophile (Karaman, 2020); subtroglophile (Tropea and Ozimec, 2020). Current assessment: **hypogean: trogloxene (subtroglophile)**. Citations: Karaman (2020); Tropea and Ozimec (2020).

Euscorpius birulai Fet et al., 2014: GREECE. Habitat: inside cave. Troglomorphies: median ocelli reduced; pigmentation and sclerotization reduced; pedipalps, legs, and metasoma attenuate; telson vesicle enlarged. Previous assessments: clearly exhibits general attenuation of appendages (pedipalps) although it does not have other typical cave adaptations (depigmentation, eye reduction) (Fet et al., 2014a); it is quite possible that some *Euscorpius* species are more or less troglophilic, opportunistic taxa, and, where an opportunity presents itself, spend part or all of their lives inside a cave or similar habitat (Tropea and Ozimec, 2019, 2020); troglophile (Karaman, 2020). Current assessment: **hypogean: troglophile (eutroglophile) or trogloxene (subtroglophile)**. Citations: Fet et al. (2014a, 2018); Tropea and Ozimec (2019, 2020); Karaman (2020).

Euscorpius concinnus (C.L. Koch, 1837): FRANCE, ITALY. Habitat: inside cave; surface. Previous assessments: non cavernicola (Di Caporriaco, 1950); troglossena (Bologna and Taglianti, 1985). Current assessment: **epigean, hypogean: accidental**. Citations: Wolf (1937); Caporiacco (1950); Boldori (1977); Bologna and Taglianti (1985). Remarks: Records from Wolf (1937), Bologna and Taglianti (1985) and Boldori (1977) were originally identified as *Euscorpius carpathicus* L., 1767. However, this species is no longer recognized in Italy and the records are probably referable to *E. concinnus*.

Euscorpius croaticus Caporiacco, 1950: CROATIA. Habitat: inside cave. Previous assessments: troglophile (Karaman, 2020); our investigation did not uncover any morphological features indi-

cating that the specimens may be troglomorphic (Graham et al., 2012). Current assessment: **epigean, hypogean: accidental**. Citations: Graham et al. (2012); Fet et al. (2016); Karaman (2020).

Euscorpius deltshevi Fet et al., 2014: BULGARIA, SERBIA. Habitat: inside cave; surface habitats. Previous assessments: trogloxène (Guéorguiev and Beron, 1962). Current assessment: **epigean, hypogean: accidental.** Citations: Guéorguiev and Beron (1962); Fet et al. (2014b). Remarks: Guéorguiev and Beron (1962) identified scorpions from two caves in northwestern Bulgaria as *E. carpathicus* and labelled this species as a trogloxene. A phylogenetic analysis of the *E. carpathicus* species complex using mitochondrial COI data (Fet et al., 2014b) identified *E. carpathicus* records from northwestern Bulgaria as a distinct species and described it as *E. deltshevi*.

Euscorpius feti Tropea, 2013: BOSNIA-HERZEGOVINA, CROATIA, ?MONTENEGRO. Habitat: inside cave; outside cave. Troglomorphies: pigmentation and sclerotization reduced; pedipalps, legs, and metasoma attenuate; telson vesicle enlarged. Previous assessments: it is quite possible that some *Euscorpius* species are more or less troglophilic, and, where an opportunity presents itself, spend part or all of their lives inside a cave or similar habitat (Tropea and Fet, 2015; Tropea and Ozimec, 2019); opportunistic eutroglophile/subtroglophile (Tropea and Ozimec, 2019); troglophile (Karaman, 2020). Current assessment: **epigean, hypogean: trogloxene (subtroglophile)**. Citations: Tropea and Fet (2015); Tropea and Ozimec (2019, 2020); Karaman (2020).

Euscorpius giachinoi Tropea and Fet, 2015: GREECE. Habitat: both inside caves and outside (typical *Euscorpius* habitats). Troglomorphies: median ocelli reduced; pigmentation and sclerotization reduced; pedipalps, legs, and metasoma attenuate; telson vesicle enlarged. Previous assessments: elongated features and smaller median eyes suggest beginning or partial adaptation to cave life; it is quite possible that some *Euscorpius* species are more or less troglophilic,

and, where an opportunity presents itself, spend part or all of their lives inside a cave or similar habitat (Tropea and Fet, 2015; Tropea and Ozimec, 2019, 2020); troglophile (Karaman, 2020). Current assessment: **epigean, hypogean: trogloxene (subtroglophile)**. Citations: Tropea and Fet (2015); Fet et al. (2018); Tropea and Ozimec (2019, 2020); Karaman (2020).

Euscorpius studentium Karaman, 2020: ?BOSNIA-HERZEGOVINA, MONTENEGRO. Habitat: inside cave. Troglomorphies: median ocelli absent; lateral ocelli reduced; pigmentation and sclerotization absent; pedipalps, legs and metasoma attenuate; telson vesicle slightly enlarged. Previous assessments: troglobite (Karaman, 2020). Current assessment: **hypogean: troglobite**. Citations: Apfelbeck (1895); Karaman (2020). Remarks: Apfelbeck (1895) noted a blind cave scorpion from caves in Bosnia that may be conspecific, given the geographical proximity.

Megacormus gertschi Díaz Najera, 1966: MEXICO. Habitat: inside cave; surface habitats. Previous assessments: possible troglophile (Sissom and Reddell, 2009). Current assessment: **epigean: accidental**. Citations: Sissom and Reddell (2009).

Family Hormuridae Laurie, 1896

Hormurus polisorum (Volschenk et. al., 2001): AUSTRALIA (Christmas Island). Habitat: inside cave. Troglomorphies: median ocelli reduced or absent; lateral ocelli reduced; pigmentation and sclerotization reduced; pedipalps, legs, and metasoma attenuate; telson vesicle enlarged. Previous assessments: troglobitic (Humphreys, 2001); troglobite (Volschenk et al., 2001; Volschenk and Prendini, 2008; Moulds and Bannik, 2012). Current assessment: **hypogean: troglobite**. Citations: Humphreys (2001); Volschenk et al. (2001); Volschenk and Prendini (2008); Moulds and Bannik (2012).

Opisthacanthus pauliani Lourenço and Goodman, 2008: MADAGASCAR. Habitat: inside cave, 30 m from entry. Previous assessments: obligate cave-dwelling animal, may represent second tro-

globitic scorpion species in Madagascar (Lourenço and Goodman, 2008). Current assessment: **epigean, hypogean: accidental**. Citations: Lourenço and Goodman (2008). Remarks: The faded coloration of this old specimen is likely due to age and preservation although several epigean Malagasy hormurids are relatively pale in color, e.g., *Palaeocheloctonus pauliani* Lourenço, 1996. This species is likely to be conspecific with one of several common epigean Malagasy hormurids.

Family Iuridae Thorell, 1876

Protoiurus kadleci (Kovařík et al., 2010): TURKEY. Habitat: inside and at cave entrance. Troglomorphies: pigmentation and sclerotization slightly reduced; pedipalps and legs slightly attenuate. Previous assessments: presence deep in cave, where it has been found hiding in a rock crevice might indicate its lithophilic and/or troglophilic nature; somewhat slender habitus, especially metasoma, suggests some degree of cave adaptation, however, holotype and paratypes were not found in caves (Kovařík et al., 2010); found in cave as well as outside, and exhibits no troglomorphic features (Yağmur et al., 2015a). Current assessment: **epigean, hypogean: trogloxene (subtroglophile)**. Citations: Kovařík et al. (2010); Yağmur et al. (2015a, 2015b).

Protoiurus kumlutasi Yağmur et al., 2015: TURKEY. Habitat: inside and at entrances of cave. Previous assessments: collected deep inside cave and also at cave entrance; shows no troglomorphic characteristics and resembles other epigean species of the genus (Yağmur et al., 2015a, 2015b). Current assessment: **epigean, hypogean: trogloxene (subtroglophile)**. Citations: Yağmur et al. (2015a, 2015b).

Family Pseudochactidae Gromov, 1998

Aemngvantom lao (Lourenço, 2012): LAOS. Habitat: inside cave. Troglomorphies: median and lateral ocelli absent; pigmentation and sclerotization absent; pedipalps, legs, and metasoma attenuate; tibial spurs absent; telson vesicle enlarged. Previous assessments: troglobiont (Lourenço, 2012a); troglobite (Lourenço, 2012b; Beron, 2015; Lourenço et al., 2018); troglobitic element (Pham et al., 2017); strong troglomorphic features (Steiner, 2013). Current assessment: **hypogean: troglobite**. Citations: Lourenço (2012a, 2012b); Steiner (2013); Beron (2015); Pham et al. (2017); Lourenço et al. (2018); present contribution.

Aemngvantom thamnongpaseuam, sp. nov.: LAOS. Habitat: inside cave. Troglomorphies: median and lateral ocelli absent; pigmentation and sclerotization absent; pedipalps, legs, and metasoma attenuate; tibial spurs absent; telson vesicle enlarged. Current assessment: **hypogean: troglobite**. Citations: present contribution.

Troglokhammouanus steineri Lourenço, 2007: LAOS. Habitat: inside cave. Troglomorphies: pigmentation and sclerotization present (two individuals partially or entirely depigmented). Previous assessments: troglobite (Lourenço, 2012b; Beron, 2015); found 2000–3000 m from main cave entrance, but its morphological characteristics are not those of a troglobitic element (Lourenço, 2012a); morphological characteristics do not correspond to a troglobitic element (Lourenço and Pham, 2012); found in caves and considered troglomorphic or troglobitic (Soleglad et al., 2012); troglobitic element (Pham et al., 2017); although this species was found inside a cave, its morphological characteristics do not correspond to a totally troglobitic element (Lourenço et al., 2018). Current assessment: **hypogean: troglophile (eutroglophile)**. Citations: Lourenço (2007a, 2007b, 2012a, 2012b, 2017a); Lourenço and Pham (2010, 2012); Soleglad et al. (2012); Steiner (2013); Beron (2015); Pham et al. (2017); Lourenço et al. (2018); present contribution.

Vietbocap canhi Lourenço and Pham, 2010: VIETNAM. Habitat: inside cave. Troglomorphies: median and lateral ocelli absent; pigmentation and sclerotization absent; pedipalps, legs, and metasoma attenuate; tibial spurs absent; telson vesicle enlarged. Previous assessments: troglobite (Lourenço and Pham, 2010; Lourenço, 2012a, 2012b; Lourenço and Pham, 2012; Soleglad et al., 2012; Beron, 2015; Lourenço et

al., 2018); strong troglomorphic features (Steiner, 2013); troglobitic element (Pham et al., 2017). Current assessment: **hypogean: troglobite**. Citations: Lourenço and Pham (2010, 2012); Lourenço (2012a, 2012b); Soleglad et al. (2012); Steiner (2013); Beron (2015); Pham et al. (2017); Lourenço et al. (2018); present contribution.

Family Scorpiopidae Latreille, 1802

Alloscorpiops troglodytes Lourenço and Pham, 2015: VIETNAM. Habitat: inside cave, approximately 60 m from entry. Current assessment: **hypogean: trogloxene (subtroglophile)**. Citations: Lourenço and Pham (2015). Remarks: Although Kovařík et al. (2020) transferred this species to *Scorpiops* Peters, 1861, it is retained in *Alloscorpiops* Vachon, 1980, in the present contribution.

Euscorpiops cavernicola Lourenço and Pham, 2013: VIETNAM. Habitat: inside cave, 120 m from main entrance, on walls of cave. Previous assessments: presents most features of genus *Euscorpiops* Vachon, 1980, but may represent first Scorpiopinae Latreille, 1802, species exhibiting certain adaptations to cave life (Lourenço and Pham, 2013). Current assessment: **hypogean: trogloxene (subtroglophile)**. Citations: Lourenço and Pham (2013); Pham (2016). Remarks: Although Kovařík et al. (2020) transferred this species to *Scorpiops* Peters, 1861, it is retained in *Euscorpiops* in the present contribution.

Euscorpiops dakrong Lourenço and Pham, 2014: VIETNAM. Habitat: inside cave, 60–70 m from entrance. Previous assessments: some morphological features indicate certain degree of adaptation to cave life (Lourenço and Pham, 2014b). Current assessment: **hypogean: trogloxene (subtroglophile)**. Citations: Lourenço and Pham (2014a). Remarks: Although Kovařík et al. (2020) transferred this species to *Scorpiops* Peters, 1861, it is retained in *Euscorpiops* in the present contribution.

Plethoscorpiops profusus Lourenço, 2017: MYANMAR. Habitat: inside cave, about 90 m from entry, hidden in wall crevices. Current assessment: **hypogean: trogloxene (subtroglophile)**. Citations: Lourenço (2017b). Remarks: Although Kovařík et al. (2020) transferred this species to *Scorpiops* Peters, 1861, it is retained in *Plethoscorpiops* Lourenço, 2017 in the present contribution.

Troglocormus ciego Francke, 1981: MEXICO. Habitat: inside cave. Troglomorphies: median ocelli absent; lateral ocelli reduced; pigmentation and sclerotization reduced; pedipalps and legs attenuate; telson vesicle enlarged. Previous assessments: troglobite (Francke, 1981; Armas, 1994; Volschenk and Prendini, 2008; Sissom and Reddell, 2009); troglobie (Lourenço and Francke, 1985); troglobio (Palacios-Vargas and Reddell, 2013). Current assessment: **hypogean: troglobite**. Citations: Francke (1981); Lourenço and Francke (1985); Armas (1994); Soleglad and Sissom (2001); Volschenk and Prendini (2008); Sissom and Reddell (2009); Palacios-Vargas and Reddell (2013).

Troglocormus willis Francke, 1981: MEXICO. Habitat: inside cave. Troglomorphies: median ocelli absent; lateral ocelli reduced; pigmentation and sclerotization reduced; pedipalps and legs attenuate; telson vesicle enlarged. Previous assessments: troglobite (Francke, 1981; Armas, 1994; Volschenk and Prendini, 2008; Sissom and Reddell, 2009); troglobie (Lourenço and Francke, 1985); troglobio (Palacios-Vargas and Reddell, 2013). Current assessment: **hypogean: troglobite**. Citations: Francke (1981); Lourenço and Francke (1985); Armas (1994); Soleglad and Sissom (2001); Volschenk and Prendini (2008); Sissom and Reddell (2009); Palacios-Vargas and Reddell (2013).

Family Troglotayosicidae Lourenço, 1998

Troglotayosicus hirsutus Botero-Trujillo et al., 2012: COLOMBIA. Habitat: leaf litter. Troglomorphies: median ocelli absent; second pair of lateral ocelli reduced; pigmentation and sclerotization reduced; retrolateral pedal spurs vestigial. Previous assessments: humicolous (Botero-Trujillo et al., 2012); endogean (humicolous) (Botero-Trujillo et al., 2017; Sánchez-Vialas et

al., 2020). Current assessment: **endogean**. Citations: Botero-Trujillo et al. (2012, 2017); Sánchez-Vialas et al. (2020).

Troglotayosicus humiculum Botero-Trujillo and Francke, 2009: COLOMBIA. Habitat: leaf litter. Troglomorphies: median ocelli absent; second pair of lateral ocelli reduced; pigmentation and sclerotization reduced; retrolateral pedal spurs vestigial. Previous assessments: leaf litter dweller (Botero-Trujillo and Francke, 2009); endogean (humicolous) (Ochoa et al., 2010; Botero-Trujillo et al., 2017); humicolous (Botero-Trujillo et al., 2012). Current assessment: **endogean**. Citations: Botero-Trujillo and Francke (2009); Lourenço (2009); Ochoa et al. (2010); Fet et al. (2011b); Botero-Trujillo et al. (2012, 2017); Sánchez-Vialas et al. (2020).

Troglotayosicus meijdeni Botero-Trujillo et al., 2017: COLOMBIA. Habitat: leaf litter. Troglomorphies: median ocelli absent; second pair of lateral ocelli reduced; pigmentation and sclerotization reduced; retrolateral pedal spurs vestigial. Previous assessments: endogean (Botero-Trujillo et al., 2017; Sánchez-Vialas et al., 2020). Current assessment: **endogean**. Citations: Botero-Trujillo et al. (2017); Sánchez-Vialas et al. (2020).

Troglotayosicus muranunkae Lourenço et al., 2020: ECUADOR. Habitat: on ground. Troglomorphies: median ocelli absent; second pair of lateral ocelli reduced; pigmentation and sclerotization reduced; retrolateral pedal spurs vestigial. Previous assessments: endogean (Sánchez-Vialas et al., 2020). Current assessment: **endogean**. Citations: Sánchez-Vialas et al. (2020).

Troglotayosicus vachoni Lourenço, 1981: ECUADOR. Habitat: inside cave. Troglomorphies: median ocelli absent; second pair of lateral ocelli reduced; pigmentation and sclerotization reduced; retrolateral pedal spurs vestigial; telson vesicle enlarged. Previous assessments: troglobitic (Lourenço, 1981, 2006; Graham and Fet, 2006; Lourenço and Goodman, 2008; Volschenk and Prendini, 2008; Ochoa et al., 2010; Botero-Trujillo et al., 2012); troglobie (Lourenço and Francke, 1985); hypogean (Ochoa et al., 2010; Sánchez-Vialas et al., 2020); hypogean (troglo-

bitic) (Prendini et al., 2010; Botero-Trujillo et al., 2017; Sánchez-Vialas et al., 2020). Current assessment: **hypogean: troglobite**. Citations: Lourenço (1981, 2006); Lourenço and Francke (1985); Armas (1994); Graham and Fet (2006); Lourenço and Goodman (2008); Volschenk and Prendini (2008); Jaulin et al. (2010); Ochoa et al. (2010); Prendini et al. (2010); Fet et al. (2011b); Botero-Trujillo et al. (2012, 2017); Brito and Borges (2015); Sánchez-Vialas et al. (2020).

Family Typhlochactidae Mitchell, 1971

Alacran chamuco Francke, 2009: MEXICO. Habitat: inside cave. Troglomorphies: median and lateral ocelli absent; pigmentation and sclerotization absent; pedipalps, legs, and metasoma attenuate; retrolateral pedal spurs absent; telson vesicle greatly enlarged. Previous assessments: troglobite (Francke, 2009a; Santibáñez-López et al., 2014c; Deharveng and Bedos, 2018); troglobio (Palacios-Vargas and Reddell, 2013). Current assessment: **hypogean: troglobite**. Citations: Francke (2009a); Vignoli and Prendini (2009); Fet et al. (2011b); Palacios-Vargas and Reddell (2013); Santibáñez-López et al. (2014c); Deharveng and Bedos (2018). Remarks: This species, which is probably a junior synonym of *A. tartarus*, was listed as *Alacran* sp. by Vignoli and Prendini (2009).

Alacran tartarus Francke, 1982: MEXICO. Habitat: inside cave. Troglomorphies: median and lateral ocelli absent; pigmentation and sclerotization absent; pedipalps, legs and metasoma attenuate; retrolateral pedal spurs absent; telson vesicle greatly enlarged. Previous assessments: troglobite (Francke, 1982, 2009a; Armas, 1994; Graham and Fet, 2006; Volschenk and Prendini, 2008; Vignoli and Prendini, 2009; Prendini et al., 2010; Santibáñez-López et al., 2014c; Deharveng and Bedos, 2018); troglobitic (Francke, 1986); troglobie (Lourenço and Francke, 1985); most highly cave-adapted scorpion in the world (Sissom and Reddell, 2009); troglobio (Palacios-Vargas and Reddell, 2013). Current assessment: **hypogean: troglobite**. Citations: Francke (1982,

1986, 2009a); Lourenço and Francke (1985); Armas (1994); Palacios-Vargas (1994); Sissom and Cokendolpher (1998); Graham and Fet (2006); Volschenk and Prendini (2008); Sissom and Reddell (2009); Vignoli and Prendini (2009); Prendini et al. (2010); Fet et al. (2011b); Palacios-Vargas and Reddell (2013); Santibáñez-López et al. (2014c); Deharveng and Bedos (2018).

Alacran triquimera Santibáñez-López et al., 2014: MEXICO. Habitat: inside cave. Troglomorphies: median and lateral ocelli absent; pigmentation and sclerotization absent; pedipalps, legs and metasoma attenuate; retrolateral pedal spurs absent; telson vesicle greatly enlarged. Previous assessments: troglobite (Santibáñez-López et al., 2014c; Deharveng and Bedos, 2018). Current assessment: **hypogean: troglobite**. Citations: Santibáñez-López et al. (2014c); Deharveng and Bedos (2018).

Sotanochactas elliotti (Mitchell, 1971): MEXICO. Habitat: inside cave. Troglomorphies: median and lateral ocelli absent; pigmentation and sclerotization absent; pedipalps, legs, and metasoma attenuate; prolateral and retrolateral pedal spurs absent; telson vesicle slightly enlarged. Previous assessments: troglobite (Mitchell, 1971; Reddell and Mitchell, 1971a; Reddell and Elliott, 1973a; Reddell, 1981; Francke, 1982, 1986; Armas, 1994; Graham and Fet, 2006; Volschenk and Prendini, 2008; Vignoli and Prendini, 2009; Prendini et al., 2010); probably troglobite (Reddell, 1973); troglobie (Lourenço and Francke, 1985); highly troglomorphic eyeless species (Sissom and Reddell, 2009); troglobio (Palacios-Vargas and Reddell, 2013). Current assessment: **hypogean: troglobite**. Citations: Mitchell (1971); Reddell and Mitchell (1971a); Reddell (1973, 1981); Reddell and Elliott (1973a); González-Sponga (1974); Soleglad (1976); Mitchell and Peck (1977); Lourenço (1981); Francke (1982, 1986); Lourenço and Francke (1985); Sissom (1988); Armas (1994); Palacios-Vargas (1994); Graham and Fet (2006); Volschenk and Prendini (2008); Sissom and Reddell (2009); Vignoli and Prendini (2009); Jaulin et al. (2010); Prendini et al. (2010); Fet et al. (2011b); Palacios-Vargas and Reddell (2013).

Stygochactas granulosus (Sissom and Cokendolpher, 1998): MEXICO. Habitat: inside cave. Troglomorphies: median and lateral ocelli absent; pigmentation and sclerotization absent; pedipalps, legs and metasoma attenuate; prolateral and retrolateral pedal spurs absent; telson vesicle enlarged. Previous assessments: troglobite (Sissom and Cokendolpher, 1998; Volschenk and Prendini, 2008; Francke et al., 2009; Vignoli and Prendini, 2009; Prendini et al., 2010); eyeless species (Sissom and Reddell, 2009); troglobio (Palacios-Vargas and Reddell, 2013). Current assessment: **hypogean: troglobite**. Citations: Sissom and Cokendolpher (1998); Volschenk and Prendini (2008); Francke et al. (2009); Sissom and Reddell (2009); Vignoli and Prendini (2009); Prendini et al. (2010); Fet et al. (2011b); Palacios-Vargas and Reddell (2013); Santibáñez-López et al. (2014c).

Typhlochactas cavicola Francke, 1986: MEXICO. Habitat: inside cave. Troglomorphies: median and lateral ocelli absent; pigmentation and sclerotization absent; pedipalps and legs attenuate; prolateral and retrolateral pedal spurs absent; telson vesicle enlarged. Previous assessments: troglobie (Lourenço and Francke, 1985); troglobite (Francke, 1986; Armas, 1994; Sissom and Cokendolpher, 1998; Volschenk and Prendini, 2008; Vignoli and Prendini, 2009; Prendini et al., 2010); eyeless species (Sissom and Reddell, 2009); troglobio (Palacios-Vargas and Reddell, 2013). Current assessment: **hypogean: troglobite**. Citations: Lourenço and Francke (1985); Francke (1986); Sissom (1988); Armas (1994); Palacios-Vargas (1994); Sissom and Cokendolpher (1998); Kovařík (2000a); Volschenk and Prendini (2008); Francke et al. (2009); Sissom and Reddell (2009); Vignoli and Prendini (2009); Prendini et al. (2010); Fet et al. (2011b); Palacios-Vargas and Reddell (2013).

Typhlochactas mitchelli Sissom, 1988: MEXICO. Habitat: montane forest litter. Troglomorphies: median and lateral ocelli absent; pigmentation and sclerotization absent; retrolateral pedal spurs absent; telson vesicle enlarged. Previous assessments: montane forest litter (Sis-

som, 1988); forest litter in mountains (Sissom and Cokendolpher, 1998); endogean, not a troglobite (Volschenk and Prendini, 2008); humicolous (Francke et al., 2009); leaf litter (Lourenço, 2009); endogean (humicolous) (Vignoli and Prendini, 2009); endogean (Prendini et al., 2010). Current assessment: **endogean**. Citations: Sissom (1988); Sissom and Cokendolpher (1998); Volschenk and Prendini (2008); Botero-Trujillo and Francke (2009); Francke et al. (2009); Lourenço (2009); Vignoli and Prendini (2009); Prendini et al. (2010); Fet et al. (2011b).

Typhlochactas reddelli Mitchell, 1968: MEXICO. Habitat: inside cave. Troglomorphies: median and lateral ocelli absent; pigmentation and sclerotization absent; pedipalps and legs attenuate; retrolateral pedal spurs absent; telson vesicle enlarged. Previous assessments: troglobite (Mitchell, 1968, 1971; Reddell, 1971a, 1971b, 1981; Francke, 1982, 1986; Muchmore, 1972; Armas, 1994; Sissom and Cokendolpher, 1998; Lourenço and Goodman, 2008; Volschenk and Prendini, 2008; Francke et al., 2009; Vignoli and Prendini, 2009; Prendini et al., 2010; Lourenço and Pham, 2013, 2014a; Deharveng and Bedos, 2018); probable troglobite (Reddell, 1973); troglobias (González-Sponga, 1974); troglòbies (Vives, 1981); troglobie (Lourenço and Francke, 1985); eyeless species (Sissom and Reddell, 2009); troglobio (Palacios-Vargas and Reddell, 2013). Current assessment: **hypogean: troglobite**. Citations: Mitchell (1968, 1971); Reddell (1971a, 1971b, 1973, 1981); Muchmore (1972); González-Sponga (1974); Vachon (1974); Soleglad (1976); Mitchell and Peck (1977); Lourenço (1981); Vives (1981); Francke (1982, 1986); Lourenço and Francke (1985); Sissom (1988); Armas (1994); Palacios-Vargas (1994); Sissom and Cokendolpher (1998); Kovařík (2000a); Graham and Fet (2006); Lourenço and Goodman (2008); Volschenk and Prendini (2008); Francke et al. (2009); Sissom and Reddell (2009); Vignoli and Prendini (2009); Prendini et al. (2010); Fet et al. (2011b); Lourenço and Pham (2013, 2014a); Palacios-Vargas and Reddell (2013); Deharveng and Bedos (2018).

Typhlochactas rhodesi Mitchell, 1968: MEXICO. Habitat: inside cave. Troglomorphies: median and lateral ocelli absent; pigmentation and sclerotization absent; pedipalps and legs attenuate; prolateral and retrolateral pedal spurs absent; telson vesicle enlarged. Previous assessments: troglobite (Mitchell, 1968, 1971; Reddell, 1971a, 1971b, 1981; Reddell and Mitchell, 1971b; Mitchell and Kawakatsu, 1973; Reddell and Elliott, 1973b; Francke, 1982, 1986; Armas, 1994; Sissom and Cokendolpher, 1998; Lourenço and Goodman, 2008; Volschenk and Prendini, 2008; Francke et al., 2009; Vignoli and Prendini, 2009; Prendini et al., 2010; Lourenço and Pham, 2013, 2014a); probable troglobite (Reddell, 1973); troglobias (González-Sponga, 1974); troglòbies (Vives, 1981); troglobie (Lourenço and Francke, 1985); eyeless species (Sissom and Reddell, 2009); troglobio (Palacios-Vargas and Reddell, 2013). Current assessment: **hypogean: troglobite**. Citations: Mitchell (1968, 1971); Reddell (1971a, 1971b, 1973, 1981); Reddell and Mitchell (1971b); Mitchell and Kawakatsu (1973); Reddell and Elliott (1973b); González-Sponga (1974); Soleglad (1976); Mitchell and Peck (1977); Lourenço (1981); Vives (1981); Francke (1982, 1986); Lourenço and Francke (1985); Sissom (1988); Armas (1994); Palacios-Vargas (1994); Sissom and Cokendolpher (1998); Graham and Fet (2006); Lourenço and Goodman (2008); Volschenk and Prendini (2008); Francke et al. (2009); Sissom and Reddell (2009); Vignoli and Prendini (2009); Prendini et al. (2010); Fet et al. (2011b); Lourenço and Pham (2013, 2014a); Palacios-Vargas and Reddell (2013); Santibáñez-López et al. (2014c).

Typhlochactas sissomi Francke et al., 2009: MEXICO. Habitat: mesophilous forest, under stone. Troglomorphies: median and lateral ocelli absent; pigmentation and sclerotization absent; retrolateral pedal spurs absent; telson vesicle enlarged. Previous assessments: probably humicolous (Francke et al., 2009); endogean (Vignoli and Prendini, 2009; Prendini et al., 2010). Current assessment: **endogean**. Citations: Botero-Trujillo and Francke (2009); Francke et al. (2009); Vignoli and Prendini (2009); Prendini et al. (2010); Fet et al. (2011b); Santibáñez-López et al. (2014c).

Typhlochactas sylvestris Mitchell and Peck, 1977: MEXICO. Habitat: montane forest litter. Troglomorphies: median and lateral ocelli absent; pigmentation and sclerotization absent; retrolateral pedal spurs absent; telson vesicle enlarged. Previous assessments: known eyeless epigean/montane forest litter habitat (Mitchell and Peck, 1977; Francke, 1986; Sissom, 1988); litéricole (Emerit et al., 1996); forest litter in mountains (Sissom and Cokendolpher, 1998); leaf litter in cloud forest (Kovařík, 2000a); endogean, not a troglobite (Volschenk and Prendini, 2008); humicolous (Francke et al., 2009); litter (Lourenço, 2009); humicolous (endogean) (Vignoli and Prendini, 2009); endogean (Prendini et al., 2010). Current assessment: **endogean**. Citations: Mitchell and Peck (1977); Francke (1982, 1986); Sissom (1988); Emerit et al. (1996); Sissom and Cokendolpher (1998); Kovařík (2000a); Volschenk and Prendini (2008); Botero-Trujillo and Francke (2009); Francke et al. (2009); Lourenço (2009); Vignoli and Prendini (2009); Prendini et al. (2010); Fet et al. (2011b).

Family Urodacidae Pocock, 1893

Aops oncodactylus Volschenk and Prendini, 2008: AUSTRALIA (Barrow Island). Habitat: inside cave. Troglomorphies: median and lateral ocelli absent; pigmentation and sclerotization absent; pedipalps, legs, and metasoma attenuate; retrolateral pedal spurs absent. Previous assessments: troglobite (Volschenk and Prendini, 2008; Moulds and Bannik, 2012; Deharveng and Bedos, 2018). Current assessment: **hypogean: troglobite**. Citations: Volschenk and Prendini (2008); Moulds and Bannik (2012); Deharveng and Bedos (2018).

Family Vaejovidae Thorell, 1876

Franckeus minckleyi (Williams, 1968): MEXICO. Habitat: inside cave, 20 m from entrance on exposed wall; known from surface. Previous assessments: possibly a troglophile (Sissom and Reddell, 2009). Current assessment: **epigean: accidental**. Citations: Sissom and Reddell (2009).

Graemeloweus iviei (Gertsch and Soleglad, 1972): UNITED STATES OF AMERICA. Habitat: in cave entrances and under rocks and ground detritus outside caves. Previous assessments: troglophile (Gertsch and Soleglad, 1972; Reddell, 1981); probably a troglophile (Sissom and Reddell, 2009). Current assessment: **epigean, hypogean: trogloxene (subtroglophile) or accidental**. Citations: Gertsch and Soleglad (1972); Reddell (1981); Sissom and Reddell (2009).

Pseudouroctonus apacheanus (Gertsch and Soleglad, 1972): MEXICO, UNITED STATES OF AMERICA. Habitat: surface and cave habitats. Previous assessments: common on surface near entrance to caves, but none were detected with UV light or by any other means in the caves (Cokedolpher and Polyak, 2004); might be considered troglophilic, probably a troglophile (Sissom and Reddell, 2009). Current assessment: **epigean, hypogean: trogloxene (subtroglophile) or accidental**. Citations: Gertsch and Soleglad (1972); Cokendolpher and Polyak (2004); Sissom and Reddell (2009); Rossi (2018a). Remarks: A genus of dubious validity, *Ruberhieronymus* Rossi, 2018, was erected to accommodate this species, which is retained in *Pseudouroctonus* Stahnke, 1974, in the present contribution.

Pseudouroctonus reddelli Gertsch and Soleglad, 1972: MEXICO, UNITED STATES OF AMERICA. Habitat: inside and outside cave habitats. Previous assessments: troglophile (Reddell, 1965a, 1965b, 1981, 1988a; Barr and Reddell, 1967; Veni, 1988; Francke and Savary, 2006; Cokendolpher and Reddell, 2009; Bryson et al., 2014); common troglophile (Mitchell and Reddell, 1971; Reddell and Cokendolpher, 2001); common troglophile, holotype found in first room of cave in darkness about 50 feet from entrance outside cave (Gertsch and Soleglad, 1972); troglophilic (Reddell, 1994; Brown, 1997); troglophile, seasonally abundant in some caves and reproduces in caves (Sissom and Reddell,

2009); exploits both epigean (surface) and hypogean (subterranean) habitats (Bryson et al., 2014); troglomorphic (Ayrey and Soleglad, 2015). Current assessment: **epigean, hypogean: trogloxene (subtroglophile)**. Citations: Reddell (1965a, 1965b, 1981, 1988a, 1988b 1994); Barr and Reddell (1967); Mitchell and Reddell (1971); Gertsch and Soleglad (1972); Stahnke (1974); Veni (1988); Brown (1997); Reddell and Cokendolpher (2001); Francke and Savary (2006); Soleglad and Fet (2006); Cokendolpher and Reddell (2009); Sissom and Reddell (2009); Bryson et al. (2014); Ayrey and Soleglad (2015).

Pseudouroctonus savvasi Francke, 2009: MEXICO. Habitat: inside cave. Troglomorphies: median ocelli slightly reduced; pigmentation and sclerotization reduced; pedipalps, legs and metasoma attenuate. Previous assessments: troglophile (Francke, 2009b); troglophile, no troglomorphic adaptations (Sissom and Reddell, 2009); especies conocidas solo de cuevas, pero probablemente no restringidas a los hábitats subterráneos (Palacios-Vargas and Reddell, 2013). Current assessment: **hypogean: troglophile (eutroglophile)**. Citations: Francke (2009b); Sissom and Reddell (2009); Palacios-Vargas and Reddell (2013).

Pseudouroctonus sprousei Francke and Savary, 2006: MEXICO. Habitat: inside cave. Troglomorphies: median and lateral ocelli reduced; pedipalps, legs and metasoma attenuate; telson vesicle enlarged. Previous assessments: troglobite (Francke and Savary, 2006; Volschenk and Prendini, 2008; Bryson et al., 2014); has slightly reduced eyes and pigmentation and is more attenuated than closest relative, *P. reddelli* (Sissom and Reddell, 2009); troglobio (Palacios-Vargas and Reddell, 2013); troglobitic/troglomorphic (Ayrey and Soleglad, 2015). Current assessment: **hypogean: troglophile (eutroglophile)**. Citations: Francke and Savary (2006); Volschenk and Prendini (2008); Francke (2009b); Sissom and Reddell (2009); Palacios-Vargas and Reddell (2013); Bryson et al. (2014); Ayrey and Soleglad (2015).

Uroctonites sequoia (Gertsch and Soleglad, 1972): UNITED STATES OF AMERICA. Habitat: inside cave, under rocks. Troglomorphies: median ocelli reduced; lateral ocelli reduced (two pairs; third pair obsolete). Previous assessments: troglophile (Gertsch and Soleglad, 1972; Reddell, 1981; Francke and Savary, 2006; Elliott et al., 2017); no adaptations for cave existence and is at best a troglophile (Sissom and Reddell, 2009). Current assessment: **hypogean: troglophile (eutroglophile)**. Citations: Gertsch and Soleglad (1972); Reddell (1981); Francke and Savary (2006); Sissom and Reddell (2009); Elliott et al. (2017).

Uroctonus grahami Gertsch and Soleglad, 1972: UNITED STATES OF AMERICA. Habitat: inside cave, 8 foot depth in back end of main entrance; deep soil recesses. Troglomorphies: median ocelli reduced; pigmentation and sclerotization reduced; pedipalps and legs attenuate. Previous assessments: cave adapted/endogean? (Gertsch and Soleglad, 1972); probably a troglobite (Reddell, 1981); endogean (Sissom, 1986); true troglobite (Francke and Savary, 2006); troglobite (Volschenk and Prendini, 2008; Elliott et al., 2017); probable troglobite (Sissom and Reddell, 2009). Current assessment: **endogean, hypogean: troglobite**. Citations: Gertsch and Soleglad (1972); Reddell (1981); Sissom (1986); Francke and Savary (2006); Volschenk and Prendini (2008); Sissom and Reddell (2009); Elliott et al. (2017).

Vaejovis davidi Soleglad and Fet, 2005: MEXICO. Habitat: inside cave. Troglomorphies: pedipalps, legs, and metasoma attenuate. Previous assessments: troglophile (Reddell, 1981; Francke and Savary, 2006); not exhibiting noticeable cave adaptedness (Soleglad and Fet, 2005); probably not a troglobite (Volschenk and Prendini, 2008); possibly a troglobite (Sissom and Reddell, 2009); troglobio (Palacios-Vargas and Reddell, 2013). Current assessment: **hypogean: troglophile (eutroglophile)**. Citations: Soleglad (1975); Reddell (1981); Soleglad and Fet (2005); Francke and Savary (2006); Volschenk and Prendini (2008);

Sissom and Reddell (2009); Palacios-Vargas and Reddell (2013).

Vaejovis gracilis Gertsch and Soleglad, 1972: MEXICO. Habitat: inside cave. Troglomorphies: median and lateral ocelli reduced; pigmentation and sclerotization reduced; pedipalps, legs, and metasoma attenuate. Previous assessments: cave adaptations but exact status uncertain (Gertsch and Soleglad, 1972); [holotype] is cave adapted due in part to its pale coloration, weak sclerotization, and slender appendages … additional specimens were also collected in caves but do not exhibit cave adaptation (Soleglad, 1975); troglobite (Reddell, 1981; Armas, 1994; Volschenk and Prendini, 2008); troglobie (Lourenço and Francke, 1985); troglophile; in initial stages of regressive evolution (Sissom, 1986); true troglobite (Francke and Savary, 2006); troglobio (Palacios-Vargas and Reddell, 2013). Current assessment: **hypogean: troglophile (eutroglophile)**. Citations: Gertsch and Soleglad (1972); Reddell (1973, 1981); Soleglad (1975); Lourenço and Francke (1985); Sissom (1986); Armas (1994); Palacios-Vargas (1994); Sissom and González-Santillán (2004); Soleglad and Fet (2005); Francke and Savary (2006); Volschenk and Prendini (2008); Sissom and Reddell (2009); Palacios-Vargas and Reddell (2013).

Vaejovis mitchelli Sissom, 1991: MEXICO. Habitat: inside cave; surface. Previous assessments: possible troglophile (Sissom and Reddell, 2009). Current assessment: **epigean: accidental**. Citations: Sissom (1991); Sissom and Reddell (2009).

Vaejovis norteno Sissom and González-Santillán, 2004: MEXICO. Habitat: inside cave. Troglomorphies: telson vesicle slightly enlarged. Previous assessments: does not exhibit any significant troglobitic adaptations, and should be regarded as troglophilic (Sissom and González-Santillán, 2004); troglophile (Francke and Savary, 2006; Sissom and Reddell, 2009). Current assessment: **hypogean: troglophile (eutroglophile)**. Citations: Sissom and González-Santillán (2004); Soleglad and Fet (2005); Francke and Savary (2006); Sissom and Reddell (2009).

Vaejovis rossmani Sissom, 1989: MEXICO. Habitat: inside cave; surface. Previous assessments: troglophile (Sissom and Reddell, 2009). Current assessment: **epigean, hypogean: trogloxene (subtroglophile) or accidental**. Citations: Sissom and Reddell (2009).

Vaejovis sprousei Sissom, 1990: MEXICO. Habitat: inside cave; surface. Previous assessments: probable troglophile (Sissom and Reddell, 2009). Current assessment: **epigean, hypogean: trogloxene (subtroglophile) or accidental**. Citations: González Santillán et al. (2004); Sissom and Reddell (2009).

APPENDIX 2

DISTRIBUTION OF MORPHOLOGICAL CHARACTERS USED FOR PHYLOGENETIC ANALYSIS OF THE RELICTUAL ASIAN SCORPION FAMILY PSEUDOCHACTIDAE GROMOV, 1998

Numbers following terminal taxon names correspond to samples from which DNA was extracted and sequenced (appendix 8). Character states scored 0–4, inapplicable (-) or unknown (?). Character descriptions in appendix 3.

Outgroup
Buthus atlantis **3489**
```
0010002000  0000020000  ---0000000  0002111010  1001100000  1000111011
0000000010  0000010010  1010110000  00001-200-  -001011000  0011000000
0000000000  0101000100
```
Chaerilus sejnai **3685**
```
1130111101  0001101010  ---1001110  0100000111  0110120111  0110000011
0111100102  2120101000  0020101323  3221001110  -01010011-  00--441200
0211000111  02-1000001
```

Ingroup
Pseudochactas mischi
```
0001100111  0001201011  ?011101101  1101101001  1121011100  2001100100
10?1111000  0100010201  010101?334  3330010011  01????001  ?2?1?2???1
??100101?1  00100?0?11
```
Pseudochactas ovchinnikovi **2303A–2303C**
```
0130100111  0001211011  0001101101  1101101001  1121011100  2001100100
1011111000  0100010201  0101011333  3330010011  0110000001  0211221111
0210000011  0010000011
```
Troglokhammouanus steineri **11271–11275**
```
1121100111  1101201011  1011101100  0001101001  1121011100  1001100100
1011111001  1111010201  0102011323  2220001021  0110000001  0122111200
0211011211  0011100011
```
Aemngvantom lao **11349 11350 15570 15591**
```
0001100111  1201201111  2001111100  0002101001  1121011100  1001100100
1010111000  0101010102  0301010111  1110011121  1110000001  1222111200
1110010201  0011101001
```
Aemngvantom thamnongpaseuam **11351**
```
0001100111  1201201111  2001111100  1002101001  1121011100  1001100100
10?0111000  0101010102  030101?111  1110011121  11????001  ?2?2?1???1
??10110 0?1  10101?1?01
```
Vietbocap canhi **11270 16750 16751**
```
0001100110  1212200101  2121111101  1013101001  1121011100  1001100100
1000111000  0101010201  0201010222  2220011121  1110000001  0200331201
0?10100011  0010111001
```
Vietbocap canhi **11348 16533–16537**
```
0001100110  1212200111  2121111101  1013101001  1121011100  1001100100
1000111000  0101010201  0201010333  3330011121  1110000001  0200331201
0?10100011  0010111001
```

APPENDIX 3

MORPHOLOGICAL CHARACTERS AND CHARACTER STATES USED FOR PHYLOGENETIC ANALYSIS OF THE RELICTUAL ASIAN SCORPION FAMILY PSEUDOCHACTIDAE GROMOV, 1998

Terminology, including trichobothrial homology, follows Prendini et al. (2006). Characters corresponding to lists of Lamoral (1980), Stockwell (1989), Prendini (2000), Soleglad and Sissom (2001), Soleglad and Fet (2001), Soleglad and Fet (2003b, table 4), Soleglad and Fet (2003b, table 5) and Prendini (2004) denoted, respectively, by abbreviations L80, S89, P00, S&S01, S&F01, S&F03.4, S&F03.5, and P04, followed by the corresponding number. Character matrix in appendix 2. Fifty-eight uninformative characters are indicated by †.

Coloration and infuscation

1. Tegument base coloration: **0,** yellowish; **1,** brown.

2. Carapace infuscation: **0,** absent (immaculate); **1,** present.

3. Mesosomal tergites infuscation: **0,** absent (immaculate); **1,** median stripe and pair of lateral bands; **2,** paired submedian and sublateral stripes; **3,** entirely or mostly (anterior two-thirds) infuscate.

4. Legs, femoral and patellar prolateral surfaces infuscation: **0,** present; **1,** absent (immaculate).

Chelicerae

†5. Cheliceral fixed finger, ventral surface, teeth or denticles: **0,** two major teeth; **1,** four or five small denticles (ventral accessory denticles). [S&S01/8, S&F03.5/45, P04/1]

†6. Cheliceral fixed finger, median and basal teeth, fusion: **0,** fused into bicuspid ("conjoined on trunk"); **1,** separate. [S&S01⁄9, S&F03.5⁄44]

†7. Cheliceral movable finger, dorsal margin, basal teeth: **0,** absent; **1,** one; **2,** two. [S89/33, S&S01/2, S&F03.5/40]

†8. Cheliceral movable finger, ventral margin, teeth or denticles: **0,** two large, subequal median teeth; **1,** four or five ventral accessory denticles (crenulate margin). [S89/34–36, S&S01/4, S&F03.5/42, 43]

9. Cheliceral movable finger, ventral margin, serrula: **0,** absent; **1,** present. [S89/34–36, S&S01/4, S&F03.5/42, 43]

Carapace

10. Carapace posterior width, relative to length: **0,** posterior width greater than length; **1,** posterior width similar to or less than length.

11. Carapace anteromedian margin, alignment relative to anterolateral margins: **0,** anteromedian margin recessed, posterior to anterolateral margins; **1,** anteromedian margin protruding, anterior to anterolateral margins.

12. Carapace anteromedian margin, curvature: **0,** sublinear; **1,** convex (procurved); **2,** shallowly concave (recurved).

13. Carapace anterolateral margins: **0,** entire; **1,** with pronounced incision lateral to lateral ocelli (rostrolateral incision).

14. Carapace anteromedian depression, dimensions: **0,** broad, deep; **1,** narrow, shallow; **2,** narrow, deep.

†15. Carapace anterosubmedial depressions, medial to lateral ocelli: **0,** absent; **1,** vestigial; **2,** well developed.

16. Carapace anterosubmedial lyriform carinae, vertical development and macrosculpture: **0,** absent; **1,** obsolete, granular; **2,** pronounced, costate-granular.

17. Carapace median ocular tubercle (or eyeless surface representing ocular tubercle), distance from anterior margin relative to carapace length: **0,** medial; **1,** anteromedial.

18. Carapace median ocelli: **0,** present; **1,** absent.

19. Carapace interocular sulcus (regardless of presence or absence of median ocelli), depth: **0,** deep; **1,** shallow.

20. Carapace circumocular sutures: **0,** absent; **1,** present.

21. Carapace circumocular sutures, development: **0,** complete, connected posteriorly (postocular); **1,** complete, disconnected posteriorly; **2,** partial (disconnected); **?,** unknown; **-,** inapplicable.

22. Carapace circumocular triangle (regardless of presence or absence of median ocelli), shape: **0,** subtriangular (broad V-shape), median ocular curvatures present; **1,** parallel sided (U-shape), median ocular curvatures absent; **-,** inapplicable.

23. Carapace circumocular sulci, posterior margin, distance from anterior margin relative to carapace length: **0,** anteromedial; **1,** medial; **2,** posteromedial; **-,** inapplicable.

†24. Carapace lateral ocelli, anterolateral major (ALMa) ocelli: **0,** present; **1,** absent.

25. Carapace lateral ocelli, mediolateral major (MLMa) ocelli: **0,** present; **1,** absent.

26. Carapace lateral ocelli, posterolateral major (PLMa) ocelli: **0,** present; **1,** absent.

†27. Carapace lateral ocelli, anterodorsal minor (ADMi) ocelli: **0,** present; **1,** absent.

†28. Carapace lateral ocelli, posterodorsal minor (PDMi) ocelli: **0,** present; **1,** absent.

†29. Carapace lateral eyespot: **0,** absent; **1,** present.

30. Carapace anterolateral, circumocular, and posteromedian surfaces, macrosculpture: **0,** anterolateral, circumocular, and posteromedian surfaces mostly granular; **1,** anterolateral and posteromedian surfaces smooth, circumocular surfaces mostly smooth except for sparse granulation near anterior carapace margin.

31. Carapace mediolateral surfaces, macrosculpture: **0,** granular; **1,** smooth.

32. Carapace posterolateral margins, curvature: **0,** gently curved; **1,** angular, slanting.

33. Carapace posteromedian margin, curvature: **0,** shallowly concave (recurved); **1,** sublinear to shallowly convex (procurved).

Pedipalps

34. Pedipalps shape: **0,** segments very robust, chela manus incrassate; **1,** segments moderately robust, chela manus globose; **2,** segments gracile, chela manus globose; **3,** segments gracile, chela manus elongate.

†35. Pedipalp femur trichobothrium i_2: **0,** absent; **1,** present. [Prendini et al. (2006) preferred hypothesis]

†36. Pedipalp femur petite trichobothrium i_3: **0,** absent; **1,** present. [Prendini et al. (2006) preferred hypothesis]

†37. Pedipalp femur petite trichobothrium i_4: **0,** absent; **1,** present. [Prendini et al. (2006) preferred hypothesis]

†38. Pedipalp femur prodorsal carina, longitudinal development: **0,** complete; **1,** partial.

39. Pedipalp femur trichobothrium d_1, size: **0,** petite; **1,** full size. [Prendini et al. (2006) preferred hypothesis]

†40. Pedipalp femur trichobothria d_1 and i_{1-4}, relative alignment: **0,** d_1 aligned with or distal to i_{1-4}; **1,** d_1 proximal to i_{1-4}. [S&S01/38, S&F03.5/5]

†41. Pedipalp femur petite trichobothrium d_2: **0,** absent; **1,** present. [Prendini et al. (2006) preferred hypothesis]

†42. Pedipalp femur trichobothrium d_3, size: **0,** petite; **1,** full size. [Prendini et al. (2006) preferred hypothesis]

†43. Pedipalp femur trichobothrium d_4, size: **0,** absent; **1,** petite; **2,** full size. [Prendini et al. (2006) preferred hypothesis]

†44. Pedipalp femur trichobothrium d_5: **0,** absent; **1,** present. [Prendini et al. (2006) preferred hypothesis]

45. Pedipalp femur trichobothrium d_6, size: **0,** petite; **1,** full size. [Prendini et al. (2006) preferred hypothesis]

†46. Pedipalp femur trichobothria d_3 and d_4 alignment relative to retrodorsal carina: **0,** d_4 prolateral to d_3 such that d_3–d_4 directed away from retrodorsal carina (β configuration); **1,** d_3 and d_4 in same axis, such that d_3–d_4 parallel to retrodorsal carina; **2,** d_4 retrolateral to d_3 such that d_3–d_4 directed toward retrodorsal carina (α configuration). [S&F03.5/3, P04/11]

47. Pedipalp femur retrodorsal carina, vertical development: **0,** absent or obsolete; **1,** present, distinct.

†48. Pedipalp femur trichobothrium e_3: **0,** absent; **1,** present. [Prendini et al. (2006) preferred hypothesis]

†49. Pedipalp femur trichobothrium e_4: **0,** absent; **1,** present. [S&F01/62, S&F03.4/62]

†50. Pedipalp patella promedian carina ("dorsal patellar spur carina"): **0,** present; **1,** absent. [S&F03.5/94 (part)]

51. Pedipalp patella prolateral surface, dorsoventral "vaulted" projection ("anterior process"): **0,** absent; **1,** moderate; **2,** pronounced. [P00/18, S&S01/16,17, S&F03.5/97, 98]

†52. Pedipalp patella prolateral surface, dorsoventral "vaulted" projection, pair of spiniform granules proximally (dorsal and ventral "patellar spurs" situated proximally on dorsal and ventral prolateral carinae, respectively): **0,** present; **1,** absent. [P00/18, S&S01/16,17, S&F03.5/97, 98]

†53. Pedipalp patella trichobothrium i_2: **0,** absent; **1,** present. [S&F01/28, S&F03.4/28]

54. Pedipalp patella dorsomedian carina: **0,** present; **1,** absent. [S&F03.5/95]

†55. Pedipalp patella trichobothium d_3: **0,** absent; **1,** present. [S&F01/31, S&F03.4/31]

†56. Pedipalp patella trichobothium d_4: **0,** absent; **1,** present. [S&F01/32, S&F03.4/32]

†57. Pedipalp patella petite trichobothium d_5: **0,** absent; **1,** present. [S&F01/33, S&F03.4/33]

58. Pedipalp patella retromedian carina: **0,** present; **1,** absent.

59. Pedipalp patella trichobothium em_1: **0,** absent; **1,** present. [S&F01/41, S&F03.4/41]

60. Pedipalp patella trichobothium est, size: **0,** petite; **1,** full size. [S&F01/43, S&F03.4/43]

61. Pedipalp patella ventromedian carina: **0,** present; **1,** absent.

†62. Pedipalp patella trichobothria v_1, v_2 and v_3: **0,** absent; **1,** present. [S&F01/47–49, S&F03.4/47–49]

63. Pedipalp chela manus prolateral dorsal carina (♂), longitudinal development: **0,** absent or obsolete; **1,** complete; **?,** unknown.

64. Pedipalp chela manus prolateral ventral carina (♂, ♀), longitudinal development: **0,** absent or obsolete; **1,** complete.

†65. Pedipalp chela manus trichobothrium ib_1: **0,** absent; **1,** present. [S&F01/1, S&F03.4/1]

66. Pedipalp chela manus petite trichobothrium ib_2: **0,** absent; **1,** present. [Prendini et al. (2006) preferred hypothesis]

67. Pedipalp chela fixed finger trichobothrium it_1 (it situated at base of fixed finger): **0,** absent; **1,** present. [S89/70–72, P00/47, S&S01/40, S&F03.5/11, 14]

†68. Pedipalp chela fixed finger trichobothrium it_2 (it situated in proximal third of fixed finger): **0,** absent; **1,** present. [S89/70–72, P00/47, S&S01/40, S&F03.5/11, 14]

†69. Pedipalp chela fixed finger trichobothrium it_3 (it situated distally on finger): **0,** absent; **1,** present. [S89/70–72, P00/47, S&S01/40, S&F03.5/11, 14]

70. Pedipalp chela manus dorsomedian carina, longitudinal development: **0,** absent or obsolete; **1,** vestigial; **2,** complete.

71. Pedipalp chela manus dorsal secondary and subdigital carinae, longitudinal development: **0,** absent or obsolete; **1,** vestigial; **2,** complete.

†72. Pedipalp chela manus digital carina, longitudinal development: **0,** absent or obsolete; **1,** complete.

73. Pedipalp chela manus retromedian carina, longitudinal development: **0,** absent or obsolete; **1,** partial; **2,** complete.

74. Pedipalp chela manus secondary accessory and retroventral carinae, fusion: **0,** entire; **1,** incomplete, slight disjunction evident in proximal third.

†75. Pedipalp chela manus trichobothrium Eb_3, size: **0,** petite; **1,** full size. [Prendini et al. (2006) preferred hypothesis]

†76. Pedipalp chela manus trichobothrium Est_1 (*Est* situated distal on chela manus): **0,** absent; **1,** present. [S89/86]

†77. Pedipalp chela manus trichobothrium Est_2 (*Est* situated proximal to movable finger condyle): **0,** absent; **1,** present. [S89/86]

78. Pedipalp chela manus/fixed finger trichobothrium Et_1 (in Pseudochactidae, and positionally homologous trichobothrium *eb* in Buthidae and Chaerilidae), position: **0,** situated proximally on fixed finger; **1,** situated on fixed finger, slightly distal to movable finger condyle; **2,** situated distally on manus, aligned with or proximal to movable finger condyle.

†79. Pedipalp chela manus petite trichobothrium Et_4: **0,** absent; **1,** present. [S&F01/21, S&F03.4/21]

80. Pedipalp chela trichobothrium *eb* (not positionally homologous with *eb* in Buthidae and Chaerilidae), position: **0,** absent; **1,** present, situated on fixed finger, slightly distal to movable finger condyle; **2,** present, situated in proximal third of fixed finger, distal to most proximal retrolateral denticle of median denticle row.

†81. Pedipalp chela fixed finger petite trichobothrium esb_1 (*esb* situated in proximal quarter of fixed finger, between second and third most proximal retrolateral denticles of median denticle row): **0,** absent; **1,** present. [Prendini et al. (2006) preferred hypothesis]

82. Pedipalp chela fixed finger trichobothrium esb_2 (in Pseudochactidae, not positionally homologous with *esb* in Buthidae and Chaerilidae), position: **0,** absent; **1,** situated in proximal third of fixed finger, approximately aligned with proximal retrolateral denticle of median denticle row; **2,** situated in proximal third of fixed finger, between first and second most proximal retrolateral denticles of median denticle row; **3,** situated approximately midway on fixed finger, between second and third most proximal retrolateral denticles of median denticle row.

†83. Pedipalp chela fixed finger trichobothria *est* and *et*, position: **0,** absent; **1,** situated medially on finger; **2,** situated distally on finger. [Prendini et al. (2006) preferred hypothesis]

84. Pedipalp chela manus ventromedian carina, longitudinal development: **0,** absent or obsolete; **1,** vestigial; **2,** partial.

85. Pedipalp chela manus V_1: **0,** absent; **1,** present. [Prendini et al. (2006) preferred hypothesis]

†86. Pedipalp chela manus V_2: **0,** absent; **1,** present. [Prendini et al. (2006) preferred hypothesis]

87. Pedipalp chela fixed and movable fingers, shape lateral aspect (adult ♂): **0,** sublinear, similar to adult ♀; **1,** sinuous, sexually dimorphic; **?,** unknown.

88. Pedipalp chela fixed finger, median denticle rows, number of subrows: **0,** 11; **1,** 10; **2,** 8; **3,** 7.

89. Pedipalp chela movable finger, median denticle rows, number of subrows: **0,** 11 or 12; **1,** 10; **2,** 8; **3,** 7.

90. Pedipalp chela fixed finger, median denticle rows, number of prolateral denticles: **0,** 11; **1,** 10; **2,** 8; **3,** 7; **4,** 6.

91. Pedipalp chela movable finger, median denticle rows, number of prolateral denticles: **0,** 11 or 12; **1,** 10; **2,** 8; **3,** 7.

92. Pedipalp chela fixed finger, median denticle rows, number of retrolateral denticles: **0,** 11 or 12; **1,** 9; **2,** 7; **3,** 6.

93. Pedipalp chela movable finger, median denticle rows, number of retrolateral denticles: **0,** 12; **1,** 9; **2,** 7; **3,** 6.

Coxosternum

†94. Leg I, maxillary lobes (coxapophyses): **0,** distal margins unexpanded (nonspatulate); **1,** distal margins distinctly expanded (spatulate). [L80/5, S&S01/68, S&F03.5/70]

†95. Sternum shape: **0,** pentagonal; **1,** subtriangular. [L80/3, 18, S89/28, P00/9, S&S01/69, S&F03.5/64]

96. Sternum lateral margins, curvature: **0,** curved medially; **1,** sublinear.

97. Sternum ventral surface: **0,** flat/planar ("no concave region, minimal outer ridge"); **1,** shallowly concave ("marginal concave region, minimal outer ridge"); **2,** markedly concave ("well-developed concave region and outer ridge"). [L80/3, 18, S89/28, P00/9, S&S01/69, S&F03.5/64]

Legs

98. Legs III and IV, tibial spurs: **0,** present; **1,** absent. [S89/89, S&F03.5/59, P04/15]

99. Legs I–IV basitarsi and telotarsi, spinules: **0,** absent; **1,** short; **2,** long.

†100. Legs I–IV telotarsi, spinule rows: **0,** single ventromedian row; **1,** paired ventrosubmedian rows; **-,** inapplicable. [L80/9, S89/93, 94, 97, P00/68, 70, S&S01/83, 84, 88, 89, S&F03.5/57, 58]

101. Legs I–IV telotarsi, paired ventrosubmedian rows of spinules: **0,** regular; **1,** slightly irregular; **-,** inapplicable.

102. Legs I–IV telotarsi, proventral and retroventral rows of (socketed) macrosetae: **0,** present; **1,** absent. [L80/9, S89/93, 94, 97, P00/68, 70, S&S01/83, 84, 88, 89, S&F03.5/57, 58]

Genital operculum

†103. Genital papillae (♂), length relative to genital opercula: **0,** inconspicuous; **1,** conspicuously visible along entire length of opercula; **?,** unknown. [S&S01/72, S&F03.5/81]

Reproductive anatomy

†104. Paraxial organ, accessory glands: **0,** absent; **1,** present; **?,** unknown. [S89/113]

†105. Hemispermatophore, basal lobe: **0,** present; **1,** absent; **?,** unknown. [S89/112]

†106. Hemispermatophore, *pars recta*: **0,** absent; **1,** present; **?,** unknown. [L80/2 (part), S89/110, 111, P00/82, S&S01/74, S&F03.5/73]

†107. Ovariuterus, number of "cells" in ovariuterine net (reticulate mesh): **0,** six; **1,** eight; **?,** unknown. [S89/102, S&F03.5/100]

Pectines

†108. Pectines, marginal lamellae, fusion: **0,** three; **1,** two (fusion of proximal and medial marginal lamellae).

†109. Pectines, marginal and median lamellae, fusion: **0,** separate, longitudinal suture between marginal and median lamellae present; **1,** fused, longitudinal suture between marginal and median lamellae absent.

†110. Pectines, median lamellae, fusion and number: **0,** variously fused, many fewer than pectinal teeth; **1,** separate, similar number to pectinal teeth; **-,** inapplicable.

111. Pectines, proximal median lamella (scape), angle (♂): **0,** acute; **1,** obtuse; **?,** unknown.

112. Pectines, fulcra: **0,** moderate to large; **1,** small; **2,** very small (vestigial).

113. Pectines, median lamellae, count (♂): **0,** 7 or 8; **1,** 9 or 10; **2,** 14 or 15; **?,** unknown; **-,** inapplicable.

114. Pectines, median lamellae, count (♀): **0,** 5–7; **1,** 8–10; **2,** 11–13; **-,** inapplicable.

115. Pectines, tooth count (♂): **0,** 30 or 31; **1,** 15 or 16; **2,** 10–13; **3,** 8 or 9; **4,** 4; **?,** unknown.

116. Pectines, tooth count (♀): **0,** 25; **1,** 13 or 14; **2,** 9–11; **3,** 6–8; **4,** 3.

†117. Pectinal teeth, peg sensillae, sockets: **0,** papillate; **1,** smooth; **?,** unknown.

118. Pectinal teeth, peg sensillae, length and shape: **0,** short, barely protruding from sensilla socket, stout, subcylindrical basally, flattened and truncate distally; **1,** intermediate, protruding from sensillla socket stout, flattened and truncate distally; **2,** long, protruding from sensilla socket, cylindrical, tubular or bottle shaped, and rounded distally; **?,** unknown.

119. Pectinal teeth, peg sensilla, laterodistal processes: **0,** absent; **1,** present; **?,** unknown.

Tergites

120. Posttergites I–VI surfaces, macrosculpture: **0,** granular; **1,** smooth or nearly so.

Sternites

121. Sternites VI and VII, ventral surface, macrosculpture (♂): **0,** smooth; **1,** granular; **?,** unknown.

122. Sternite VII, ventral surface, ventrosubmedian and ventrolateral carinae (adult ♂): **0,** well developed, costate; **1,** obsolete, granular; **2,** absent; **?,** unknown.

†123. Sternites III–VI, respiratory spiracles (stigmata), shape: **0,** long, slitlike; **1,** small, circular or oval. [L80/20 (part), S&F03.5/101]

Metasoma

124. Metasomal segments I–IV, dorsosubmedian and dorsolateral carinae, posterior granules size relative to preceding granules: **0,** similar; **1,** markedly larger and spiniform.

125. Metasomal segment V, dorsolateral carinae, vertical development: **0,** distinct; **1,** obsolete.

126. Metasomal segments I and II, median lateral carinae, longitudinal development: **0,** complete (segment I), partial, becoming obsolete anteriorly (segment II); **1,** complete (segments I and II).

127. Metasomal segments III and IV, median lateral carinae, longitudinal development: **0,** partial, becoming obsolete anteriorly (segment III), vestigial or absent (segment IV); **1,** complete (segments III and IV).

128. Metasomal segment V, median lateral carinae, longitudinal development: **0,** absent or obsolete; **1,** partial; **2,** complete. [S&F03.5/86]

129. Metasomal segment I, ventrosubmedian carinae (♂): **0,** distinct; **1,** absent or obsolete; **?,** unknown.

†130. Metasomal segment I, ventrosubmedian carinae, vertical development: **0,** distinct; **1,** absent or obsolete.

†131. Metasomal segments II–IV, ventrosubmedian carinae, vertical development: **0,** distinct; **1,** absent or obsolete.

†132. Metasomal segment V, ventrosubmedian carinae, longitudinal development: **0,** complete; **1,** partial; **2,** absent. [S&F03.5/84]

†133. Metasomal segment V, ventrosubmedian carinae, posterior orientation: **0,** diverging; **1,** converging; **-,** inapplicable. [S&F03.5/84]

134. Metasomal segment V, ventromedian carina, vertical development: **0,** absent or obsolete; **1,** distinct.

Telson

135. Telson vesicle, shape: **0,** globose; **1,** elongate.

136. Telson vesicle surfaces, macrosculpture (♂): **0,** lateral and ventral surfaces with granular carinae; **1,** lateral and ventral surfaces smooth or nearly so; **?,** unknown.

137. Telson vesicle surfaces, macrosculpture (♀): **0,** lateral and ventral surfaces with granular carinae; **1,** lateral and ventral surfaces smooth or nearly so.

†138. Telson vesicle, venom gland epithelium walls, folding: **0,** simple, unfolded; **1,** complex, folded; **?,** unknown. [S89/137, P00/113, S&S01/14, S&F03.5/99]

139. Telson subaculear tubercle: **0,** absent; **1,** obsolete, very small bump.

†140. Telson aculeus, length and shape: **0,** long, deeply curved; **1,** short, shallowly curved.

APPENDIX 4

Ratios and Counts for Males Used in Nonmetric Multidimensional Scaling Analysis of the Relictual Asian Scorpion Family Pseudochactidae Gromov, 1998

Abbreviations: Char., Character; Holo, Holotype; *P. ovc.*, *P. ovchinnikovi*; *V. qui.*, *V. quinquemilia*; *V. thi.*, *V. thienduongensis*. Ratios for holotypes calculated from data in table 3, rest from data in tables 6, 7, 9, and 10.

Char.	P. ovc.	T. steineri									A. lao					V. canhi		V. thi.	V. thi.	V. qui.
	♂	♂	♂	♂	♂	♂	♂	♂	♂	♂	♂	♂	♂	subad. ♂	subad. ♂	subad. ♂	subad. ♂	Holo. subad. ♂	Holo. juv. ♂	Holo. juv. ♂
1	0.12	0.14	0.14	0.14	0.13	0.14	0.14	0.13	0.13	0.14	0.12	0.12	0.12	0.13	0.13	0.13	0.13	0.13	0.13	0.13
2	0.61	0.54	0.43	0.53	0.51	0.51	0.54	0.51	0.55	0.49	0.45	0.47	0.43	0.43	0.46	0.60	0.54	0.61	0.69	0.63
3	1.00	0.94	0.90	0.87	0.90	0.90	0.93	0.91	0.85	0.94	0.92	0.92	0.85	0.85	0.95	1.09	1.00	0.97	1.10	1.03
4	0.33	0.35	0.30	0.32	0.32	0.32	0.33	0.29	0.34	0.32	0.22	0.23	0.22	0.22	0.21	0.24	0.21	0.20	0.24	0.24
5	0.44	0.37	0.30	0.39	0.39	0.41	0.38	0.39	0.39	0.40	0.22	0.25	0.24	0.23	0.23	0.28	0.30	0.28	0.31	0.28
6	0.31	0.42	0.40	0.40	0.41	0.42	0.43	0.41	0.44	0.43	0.19	0.19	0.19	0.16	0.15	0.15	0.13	0.16	0.17	0.16
7	0.86	0.76	0.78	0.78	0.76	0.80	0.76	0.80	0.78	0.83	0.82	0.99	0.93	0.97	0.94	1.04	1.13	0.92	0.83	0.92
8	0.56	0.57	0.55	0.59	0.53	0.59	0.58	0.54	0.58	0.54	0.65	0.62	0.64	0.65	0.64	0.60	0.62	0.55	0.59	0.59
9	7	7	7	7	7	7	7	7	7	7	10	10	10	10	10	8	8	7	8	7
10	7	7	7	7	7	7	7	7	7	7	10	10	10	10	10	8	8	7	8	7
11	7	8	8	8	8	8	8	8	8	8	10	10	10	10	10	8	8	7	8	7
12	7	8	8	8	8	8	8	8	8	7	10	10	10	10	10	8	8	7	8	7
13	10	15	15	14	14	15	13	14	13	14	14	13	13	14	13	7	8	7	8	7
14	9	15	15	15	14	14	14	14	14	14	14	13	14	13	13	8	8	8	9	8
15	11	16	16	15	15	16	14	15	14	15	15	14	14	15	14	8	9	8	9	8
16	10	15	16	16	15	15	15	15	15	15	15	14	15	14	14	9	9	8	9	8
17	0.59	0.58	0.57	0.56	0.57	0.54	0.58	0.55	0.58	0.57	0.58	0.60	0.58	0.57	0.57	0.59	0.57	0.62	0.63	0.58
18	1.24	1.26	1.18	1.31	1.24	1.25	1.27	1.29	1.21	1.36	0.93	0.89	0.95	1.04	1.13	0.98	1.06	1.14	1.17	1.33
19	1.00	0.92	0.96	1.02	0.99	1.09	1.07	1.02	1.01	1.05	0.87	0.78	0.78	0.80	0.86	0.80	0.75	0.82	0.93	1.00
20	0.92	0.84	0.84	0.86	0.76	0.97	0.97	0.91	0.86	0.90	0.81	0.72	0.73	0.66	0.75	0.69	0.71	0.70	0.80	0.81
21	0.65	0.65	0.62	0.63	0.59	0.67	0.68	0.66	0.65	0.66	0.56	0.54	0.54	0.52	0.55	0.56	0.51	0.57	0.52	0.57
22	0.37	0.35	0.32	0.35	0.33	0.37	0.35	0.35	0.34	0.35	0.28	0.27	0.27	0.24	0.27	0.28	0.24	0.27	0.28	0.29
23	0.88	0.75	0.83	0.81	0.92	0.88	0.85	0.82	0.84	0.83	0.97	0.88	0.89	0.84	0.85	0.84	0.79	0.82	0.86	0.86
24	0.92	0.92	0.92	0.89	0.80	0.89	0.93	0.94	0.87	0.92	0.94	0.94	0.93	0.91	0.93	0.91	0.96	0.85	0.93	0.88
25	0.76	0.79	0.75	0.75	0.79	0.72	0.71	0.74	0.82	0.75	0.71	0.76	0.77	0.79	0.74	0.82	0.73	0.87	0.71	0.76
26	0.57	0.54	0.52	0.57	0.55	0.61	0.55	0.55	0.53	0.55	0.51	0.55	0.57	0.47	0.52	0.52	0.52	0.48	0.54	0.50
27	0.95	0.93	0.92	0.92	0.95	0.79	0.85	0.89	0.86	0.87	1.13	1.00	1.02	1.04	0.97	0.94	0.95	1.00	1.00	0.98
28	0.92	0.95	0.96	0.99	0.95	0.97	0.95	0.89	0.93	0.99	0.93	0.91	0.88	0.93	0.89	0.88	0.83	0.81	0.85	0.86
29	0.38	0.34	0.31	0.33	0.33	0.31	0.31	0.35	0.32	0.31	0.34	0.30	0.31	0.27	0.30	0.30	0.27	0.33	0.33	0.33
30	0.35	0.32	0.26	0.29	0.27	0.29	0.28	0.29	0.25	0.28	0.27	0.25	0.28	0.24	0.25	0.25	0.25	0.29	0.31	0.28

APPENDIX 5

RATIOS AND COUNTS FOR FEMALES USED IN NONMETRIC MULTIDIMENSIONAL SCALING ANALYSIS OF THE RELICTUAL ASIAN SCORPION FAMILY PSEUDOCHACTIDAE GROMOV, 1998

Abbreviations: Char., Character; Holo., Holotype; *T. lou.*, *T. louisanneorum*. Ratios for holotypes calculated from data in table 3, rest from data in tables 6 and 8.

Char.	*P. mischi* Holo. subad. ♀	*P. ovchinnikovi* ♀	♀	♀	♀	♀	♀	♀	Holo. ♀	*T. lou.* Holo. ♀	*T. steineri* ♀	♀	♀	♀	♀	♀	♀	♀	♀	♀	♀	♀	♀	♀
1	0.15	0.12	0.13	0.13	0.12	0.13	0.13	0.13	0.14	0.17	0.14	0.14	0.14	0.14	0.14	0.14	0.14	0.14	0.14	0.14	0.14	0.14	0.14	0.14
2	0.33	0.57	0.56	0.56	0.58	0.58	0.56	0.60	0.57	0.47	0.55	0.45	0.51	0.48	0.45	0.54	0.50	0.53	0.54	0.53	0.51	0.54	0.53	0.51
3	0.54	1.00	0.96	0.92	0.96	0.94	0.95	1.03	1.02	0.79	1.01	0.97	0.93	0.96	0.92	0.96	0.96	1.02	0.98	0.96	1.01	0.98	0.94	0.92
4	0.33	0.33	0.35	0.32	0.33	0.33	0.33	0.33	0.39	0.41	0.36	0.36	0.33	0.32	0.35	0.35	0.36	0.33	0.37	0.36	0.38	0.37	0.39	0.36
5	0.43	0.47	0.50	0.48	0.46	0.47	0.45	0.45	0.38	0.41	0.40	0.38	0.42	0.38	0.39	0.39	0.39	0.42	0.38	0.39	0.38	0.40	0.39	0.40
6	0.35	0.34	0.37	0.36	0.34	0.32	0.33	0.34	0.37	0.38	0.37	0.36	0.36	0.35	0.37	0.39	0.37	0.36	0.37	0.37	0.35	0.38	0.38	0.37
7	1.04	0.80	0.78	0.73	0.83	0.80	0.79	0.79	0.79	0.80	0.75	0.82	0.84	0.84	0.79	0.79	0.79	0.84	0.79	0.78	0.79	0.82	0.79	0.82
8	0.54	0.51	0.55	0.53	0.53	0.53	0.54	0.52	0.57	0.55	0.56	0.58	0.62	0.57	0.57	0.59	0.58	0.58	0.59	0.58	0.57	0.58	0.59	0.57
9	7	7	7	7	7	7	7	7	7	7	7	6	7	7	7	7	7	7	7	7	7	7	7	7
10	7	7	7	7	7	7	7	7	7	7	6	7	7	7	7	7	7	7	8	7	7	7	8	7
11	7	7	7	7	7	7	7	7	8	7	8	8	8	8	8	8	8	8	8	8	8	8	7	7
12	7	7	7	7	7	7	7	7	8	7	7	8	8	8	8	8	8	8	7	8	8	7	7	7
13	9	10	10	10	10	9	10	10	13	13	13	13	12	14	13	13	12	13	13	14	13	12	12	13
14	8	9	10	10	10	9	9	9	14	14	12	13	13	13	13	13	13	13	14	13	13	12	12	13
15	10	11	11	11	10	10	11	11	14	14	14	15	14	15	15	14	13	14	15	14	14	13	13	14
16	9	10	11	11	10	11	10	10	14	14	13	14	14	15	14	14	14	15	14	14	13	13	13	14
17	0.59	0.57	0.56	0.54	0.57	0.55	0.56	0.53	0.58	0.61	0.55	0.54	0.53	0.54	0.55	0.55	0.54	0.55	0.54	0.53	0.54	0.54	0.55	0.55
18	1.56	1.29	1.57	1.67	1.69	1.35	1.42	1.65	1.45	1.53	1.56	1.30	1.24	1.30	1.30	1.32	1.50	1.30	1.40	1.30	1.31	1.50	1.36	1.31
19	1.24	1.00	1.06	1.09	1.12	1.14	1.07	1.21	1.18	1.09	1.06	0.96	0.96	1.02	1.05	1.06	1.09	1.02	1.08	1.02	1.04	1.09	1.17	1.04
20	1.13	0.86	0.95	0.89	0.95	1.00	0.91	0.93	1.00	0.96	0.98	0.96	0.89	0.89	0.91	0.93	0.96	0.89	0.89	0.91	0.88	0.96	0.98	0.88
21	0.89	0.65	0.76	0.71	0.68	0.73	0.70	0.75	0.74	0.68	0.64	0.71	0.71	0.65	0.69	0.70	0.71	0.68	0.69	0.65	0.67	0.71	0.64	0.67
22	0.46	0.38	0.43	0.38	0.37	0.39	0.38	0.38	0.39	0.38	0.35	0.34	0.35	0.36	0.35	0.38	0.39	0.35	0.35	0.36	0.37	0.39	0.35	0.37
23	0.86	0.89	0.78	0.75	0.76	0.93	0.86	0.83	0.91	0.83	0.75	0.80	0.85	0.84	0.83	0.85	0.79	0.83	0.82	0.84	0.80	0.79	0.89	0.80
24	0.95	0.86	0.90	0.84	0.85	0.93	0.88	0.80	0.88	0.88	0.95	0.80	0.84	1.00	0.92	0.92	0.92	0.90	0.87	0.92	0.89	0.92	0.86	0.89
25	0.82	0.81	0.80	0.79	0.80	0.75	0.80	0.83	0.81	0.76	0.70	0.81	0.79	0.74	0.78	0.78	0.76	0.71	0.79	0.74	0.77	0.76	0.71	0.77
26	0.52	0.59	0.58	0.57	0.58	0.57	0.56	0.53	0.53	0.54	0.58	0.53	0.49	0.56	0.56	0.51	0.56	0.58	0.53	0.56	0.56	0.56	0.56	0.56
27	0.90	0.89	0.86	0.85	0.84	0.83	0.88	0.87	0.86	0.93	0.91	0.92	0.93	0.89	0.93	0.87	0.93	0.88	0.96	0.91	0.89	0.89	0.91	0.89
28	0.96	0.88	0.88	0.84	0.80	0.90	0.84	0.87	0.88	0.96	1.02	0.85	0.93	0.93	0.93	0.91	0.97	0.86	0.98	0.98	1.03	0.97	0.98	1.03
29	0.43	0.39	0.42	0.38	0.39	0.36	0.39	0.38	0.38	0.37	0.32	0.35	0.36	0.34	0.34	0.34	0.34	0.35	0.33	0.34	0.32	0.34	0.33	0.32
30	0.35	0.35	0.37	0.32	0.36	0.33	0.37	0.33	0.33	0.31	0.31	0.28	0.30	0.28	0.29	0.28	0.30	0.28	0.30	0.28	0.27	0.27	0.28	0.27

APPENDIX 6

RATIOS AND COUNTS FOR FEMALES USED IN NONMETRIC MULTIDIMENSIONAL SCALING ANALYSIS OF THE RELICTUAL ASIAN SCORPION FAMILY PSEUDOCHACTIDAE GROMOV, 1998

Abbreviations: Char., Character; Holo., Holotype; Para., Paratype; V. aur., V. aurantiacus; V. qui., V. quinquemilia. Ratios for holotypes (except A. thamnongpaseuam) and paratypes calculated from data in table 3, rest from data in tables 9 and 10.

Char.	A. lao Holo. ♀	A. lao ♀	A. lao ♀	A. lao ♀	A. lao ♀	A. lao ♀	A. thamnongpaseuam Holo. ♀	V. canhi ♀	V. canhi ♀	V. canhi ♀	V. canhi ♀	V. canhi ♀	V. canhi ♀	V. canhi ♀	V. canhi ♀	V. aur. Holo. ♀	V. aur. subad. ♀	Para. juv. ♀	V. qui. Para. juv. ♀
1	0.14	0.13	0.13	0.13	0.13	0.12	0.13	0.12	0.12	0.12	0.12	0.12	0.12	0.12	0.13	0.13	0.13	0.13	0.12
2	0.69	0.48	0.48	0.48	0.49	0.44	0.53	0.54	0.54	0.56	0.52	0.47	0.48	0.47	0.49	0.60	0.67	0.64	0.72
3	0.97	0.86	0.87	0.92	0.85	0.89	0.99	1.02	1.04	1.05	1.04	0.98	0.96	0.90	1.01	1.07	1.07	1.04	1.08
4	0.24	0.22	0.20	0.19	0.22	0.22	0.24	0.22	0.21	0.20	0.20	0.18	0.19	0.18	0.20	0.22	0.25	0.23	0.28
5	0.22	0.24	0.21	0.21	0.24	0.23	0.29	0.28	0.29	0.30	0.29	0.28	0.28	0.29	0.28	0.29	0.32	0.28	0.29
6	0.18	0.16	0.14	0.15	0.17	0.16	0.21	0.14	0.16	0.14	0.14	0.15	0.15	0.15	0.13	0.16	0.16	0.17	0.18
7	0.92	0.89	0.99	0.90	0.95	0.96	0.84	1.16	1.01	1.07	1.04	1.04	1.04	0.97	1.07	0.94	1.00	0.90	0.90
8	0.66	0.66	0.67	0.65	0.66	0.66	0.62	0.61	0.59	0.60	0.58	0.63	0.61	0.57	0.59	0.59	0.59	0.67	0.60
9	10	10	10	10	10	10	10	8	8	8	8	8	8	8	7	7	7	8	7
10	10	10	10	10	10	10	10	8	8	8	8	8	8	8	7	7	7	8	7
11	10	10	10	10	10	10	10	8	8	8	8	8	8	8	7	7	7	8	7
12	10	10	10	10	10	10	10	8	8	8	8	8	8	8	7	7	7	8	7
13	12	13	12	12	12	12	12	7	7	7	7	7	7	7	6	7	6	7	7
14	12	13	12	11	12	12	11	7	7	7	7	7	6	6	5	8	7	7	8
15	13	13	13	13	13	13	13	8	8	8	8	8	8	8	7	7	7	7	7
16	13	14	13	13	13	13	13	8	8	8	8	9	8	8	6	7	7	7	7
17	0.65	0.54	0.59	0.55	0.57	0.58	0.56	0.55	0.56	0.55	0.57	0.56	0.56	0.56	0.59	0.64	0.64	0.57	0.57
18	1.00	1.08	1.15	1.03	1.02	1.06	1.15	1.02	1.04	0.98	1.01	1.01	0.97	0.95	0.98	1.16	1.25	1.20	1.20
19	0.87	0.71	0.77	0.78	0.76	0.75	0.89	0.83	0.77	0.81	0.70	0.75	0.73	0.74	0.68	0.86	0.86	0.83	0.83
20	0.81	0.63	0.58	0.72	0.67	0.67	0.77	0.72	0.64	0.65	0.63	0.63	0.59	0.61	0.63	0.72	0.65	0.64	0.69
21	0.55	0.50	0.44	0.52	0.50	0.47	0.52	0.51	0.51	0.51	0.48	0.47	0.46	0.45	0.44	0.53	0.50	0.47	0.50
22	0.32	0.26	0.23	0.26	0.27	0.25	0.29	0.25	0.23	0.25	0.21	0.24	0.24	0.23	0.20	0.25	0.23	0.25	0.25
23	0.93	0.79	0.78	0.84	0.81	0.89	0.87	0.91	0.85	0.93	0.80	0.87	0.88	0.87	0.87	0.86	0.86	0.83	0.83
24	0.94	0.91	0.87	0.93	0.89	0.94	0.89	0.89	0.87	0.85	0.92	0.87	0.82	0.94	0.95	0.88	0.82	0.86	0.92
25	0.73	0.79	0.79	0.73	0.78	0.74	0.73	0.74	0.81	0.79	0.76	0.79	0.80	0.75	0.78	0.78	0.77	0.82	0.81
26	0.54	0.54	0.53	0.50	0.54	0.53	0.57	0.51	0.50	0.50	0.50	0.52	0.53	0.52	0.47	0.51	0.51	0.53	0.50
27	0.91	0.98	0.94	0.98	0.93	0.97	0.88	0.90	0.92	0.92	0.94	0.94	0.94	0.94	1.00	0.93	0.93	0.89	0.97
28	0.93	0.86	0.79	0.88	0.85	0.82	0.83	0.76	0.77	0.69	0.81	0.83	0.81	0.81	0.69	0.73	0.71	0.80	0.73
29	0.31	0.30	0.27	0.29	0.29	0.29	0.31	0.29	0.30	0.30	0.29	0.28	0.27	0.27	0.30	0.32	0.30	0.28	0.33
30	0.27	0.26	0.23	0.27	0.27	0.28	0.27	0.27	0.24	0.26	0.24	0.25	0.26	0.25	0.27	0.28	0.26	0.25	0.27

APPENDIX 7

List of Ratios and Counts for Males and Females used in Nonmetric Multidimensional Scaling Analysis of the Relictual Asian Scorpion Family Pseudochactidae Gromov, 1998

1. Carapace length : total length
2. Carapace anterior width : length
3. Carapace posterior width : length
4. Pedipalp femur width : length
5. Pedipalp patella width : length
6. Pedipalp chela manus width : chela length
7. Pedipalp chela manus height : width
8. Pedipalp chela movable finger length : chela length
9. Pedipalp chela fixed finger median denticle subrows (left)
10. Pedipalp chela fixed finger median denticle subrows (right)
11. Pedipalp chela movable finger median denticle subrows (left)
12. Pedipalp chela movable finger median denticle subrows (right)
13. Pectinal median lamellae (left)
14. Pectinal median lamellae (right)
15. Pectinal teeth (left)
16. Pectinal teeth (right)
17. Metasoma–telson length : total length
18. Metasomal segment I width : length
19. Metasomal segment II width : length
20. Metasomal segment III width : length
21. Metasomal segment IV width : length
22. Metasomal segment V width : length
23. Metasomal segment I length : segment II length
24. Metasomal segment II length : segment III length
25. Metasomal segment III length : segment IV length
26. Metasomal segment IV length : segment V length
27. Metasomal segment V length: telson length
28. Metasomal segment V width : telson vesicle width
29. Telson vesicle width : telson length
30. Telson vesicle height : telson length

APPENDIX 8

Tissue Samples and GenBank Accession Codes of DNA Sequences Used for Phylogenetic Analysis of the Relictual Asian Scorpion Family Pseudochactidae Gromov, 1998

Sequences of the 18S rDNA (18S), internal transcribed spacer 2 (ITS2), 28S rDNA (28S), 12S rDNA (12S), 16S rDNA (16S), and cytochrome *c* oxidase subunit I (COI) loci. Tissue samples deposited in the Ambrose Monell Collection for Molecular and Microbial Research (AMCC) at the American Museum of Natural History, New York. Asterisks denote partial sequences.

Species	AMCC	Country	18S/18S-ITS2	28S	12S	16S	COI
Buthidae C.L. Koch, 1837							
Buthus atlantis Pocock, 1889	LP 3489	Morocco	MZ041717	MZ041765	MZ041686	MZ041735	MZ032877
Chaerilidae Pocock, 1893							
Chaerilus sejnai Kovařík, 2005	LP 3685	Malaysia	MZ041718	MZ041766	MZ041687	MZ041736	MZ032878
Pseudochactidae Gromov, 1998							
Pseudochactas ovchinnikovi Gromov, 1998	LP 2303A	Uzbekistan	MZ041759*	MZ041767*	MZ041688	MZ041737	MZ032879
	LP 2303B		MZ041719	MZ041768*	MZ041689	MZ041738	MZ032880
	LP 2303C		MZ041720	MZ041769*	MZ041690	MZ041739	MZ032881
Troglokhammouanus steineri Lourenço, 2007	LP 11271	Laos	MZ041760	MZ041770	MZ041691	MZ041740	MZ032882
	LP 11272		MZ041721	MZ041771	MZ041692	MZ041741	MZ032883
	LP 11273		MZ041722	MZ041772	MZ041693	MZ041742	MZ032884
	LP 11274		MZ041723	MZ041773	MZ041694	MZ041743	MZ032885
	LP 11275		MZ041724	MZ041774	MZ041695	MZ041744	MZ032886
Aemngvantom lao (Lourenço, 2012), comb. nov.	LP 11349		MZ041761	MZ041775	MZ041696	MZ041745	MZ032887
	LP 11350		MZ041725	MZ041776	MZ041697	MZ041746	MZ032888
	LP 15570		MZ041726	MZ041777	MZ041698	MZ041747	MZ032889
	LP 15591		MZ041727	MZ041778	MZ041699	MZ041748	MZ032890
Aemngvantom thamnongpaseuam, sp. nov.	LP 11351		MZ041762	MZ041779	MZ041700	MZ041749	MZ032891
Vietbocap canhi Lourenço and Pham, 2010	LP 11270	Vietnam	MZ041763	MZ041780	MZ041701	MZ041750	MZ032892
	LP 16750		MZ041733	MZ041787	MZ041708	MZ041757	MZ032899
	LP 16751		MZ041734	MZ041788	MZ041709	MZ041758	MZ032900
	LP 11348		MZ041728	MZ041781	MZ041702	MZ041751	MZ032893
	LP 16533		MZ041764	MZ041782	MZ041703	MZ041752	MZ032894
	LP 16534		MZ041729	MZ041783	MZ041704	MZ041753	MZ032895
	LP 16535		MZ041730	MZ041784	MZ041705	MZ041754	MZ032896
	LP 16536		MZ041731	MZ041785	MZ041706	MZ041755	MZ032897
	LP 16537		MZ041732	MZ041786	MZ041707	MZ041756	MZ032898

APPENDIX 9

Nucleotide Base-Pair Lengths of DNA Sequences used for Phylogenetic Analysis of the Relictual Asian Scorpion Family Pseudochactidae Gromov, 1998

Sequences of the 18S rDNA (18S), internal transcribed spacer 2 (ITS2), 28S rDNA (28S), 12S rDNA (12S), 16S rDNA (16S), and cytochrome *c* oxidase subunit I (COI) loci. Tissue samples deposited in the Ambrose Monell Collection for Molecular and Microbial Research (AMCC) at the American Museum of Natural History, New York. Asterisks denote partial sequences.

Species	AMCC	Country	18S/18S-ITS2	28S	12S	16S	COI
Buthidae C.L. Koch, 1837							
Buthus atlantis Pocock, 1889	LP 3489	Morocco	1762	2088	338	475	1078
Chaerilidae Pocock, 1893							
Chaerilus sejnai Kovařík, 2005	LP 3685	Malaysia	1761	2173	337	482	1078
Pseudochactidae Gromov, 1998							
Pseudochactas ovchinnikovi Gromov, 1998	LP 2303A	Uzbekistan	1760/2981*	1329*	344	480	1078
	LP 2303B		1760	1329*	344	480	1078
	LP 2303C		1760	1329*	344	480	1078
Troglokhammouanus steineri Lourenço, 2007	LP 11271	Laos	1760/3624	2193	344	481	1078
	LP 11272		1760	2193	344	481	1078
	LP 11273		1760	2193	344	481	1078
	LP 11274		1760	2193	344	481	1078
	LP 11275		1760	2193	344	481	1078
Aemngvantom lao (Lourenço, 2012), comb. nov.	LP 11349		1760/3926	2182	342	479	1078
	LP 11350		1760	2182	342	479	1078
	LP 15570		1760	2182	342	479	1078
	LP 15591		1760	2182	342	479	1078
Aemngvantom thamnongpaseuam, sp. nov.	LP 11351		1760/3384	2179	342	479	1078
Vietbocap canhi Lourenço and Pham, 2010	LP 11270	Vietnam	1760/3682	2188	341	483	1078
	LP 16750		1760	2188	341	483	1078
	LP 16751		1760	2188	341	483	1078
	LP 11348		1760	2188	341	483	1078
	LP 16533		1760/3682	2188	341	483	1078
	LP 16534		1760	2188	341	483	1078
	LP 16535		1760	2188	341	483	1078
	LP 16536		1760	2188	341	483	1078
	LP 16537		1760	2188	341	483	1078

On the cover: Pseudochactas ovchinnikovi Gromov, 1998, adult ♀ (AMNH), Babatag, habitus in life. Photograph by L. Prendini.