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A 'living fossil' from Central Asia: The morphology of *Pseudochactas ovchinnikovi* Gromov, 1998 (Scorpiones: Pseudochactidae), with comments on its phylogenetic position

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Abstract

Pseudochactas ovchinnikovi Gromov, 1998, arguably the most remarkable scorpion discovered during the last century, inhabits an isolated, mountainous region of southeastern Uzbekistan and southwestern Tajikistan, Central Asia. This scorpion displays several morphological characters unique among Recent (extant) scorpions, including a unique trichobothrial pattern and a mixture of other characters, some potentially synapomorphic with Buthidae C.L. Koch, 1837, others with the nonbuthid scorpion families, particularly Chaerilidae Pocock, 1893. Consequently, a monotypic family, Pseudochactidae Gromov, 1998 was created to accommodate it. Although there is widespread agreement that *Pseudochactas* Gromov, 1998 is basal within Recent scorpions, its precise phylogenetic position remains a matter of debate. Three competing hypotheses have been proposed to account for its position: (1) sister group of all Recent scorpions; (2) sister group of Buthidae; (3) sister group of Chaerilidae. Despite the importance of *Pseudochactas* in determining the basal relationships among Recent scorpions, several important character systems, including the hemispermatophore and the ovariuterus, have not yet been studied in the genus. There are also several misconceptions regarding some of the character systems (e.g., trichobothria and carinae) that have been studied. In this contribution, we provide a detailed, fully illustrated reexamination of the morphology of *Pseudochactas*, including the first descriptions of its hemispermatophore, ovariuterus, and pectinal peg sensillae. We discuss the implications of these and other characters for the phylogenetic position of this 'living fossil' and conclude that Hypothesis 2, sister group of Buthidae, is the most plausible of the alternatives, all of which await further testing in a rigorous phylogenetic analysis.
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1. Introduction

Pseudochactas ovchinnikovi Gromov, 1998 (Figs. 1 and 2), arguably the most remarkable scorpion discovered during the last century, inhabits an isolated, mountainous region of southeastern Uzbekistan and

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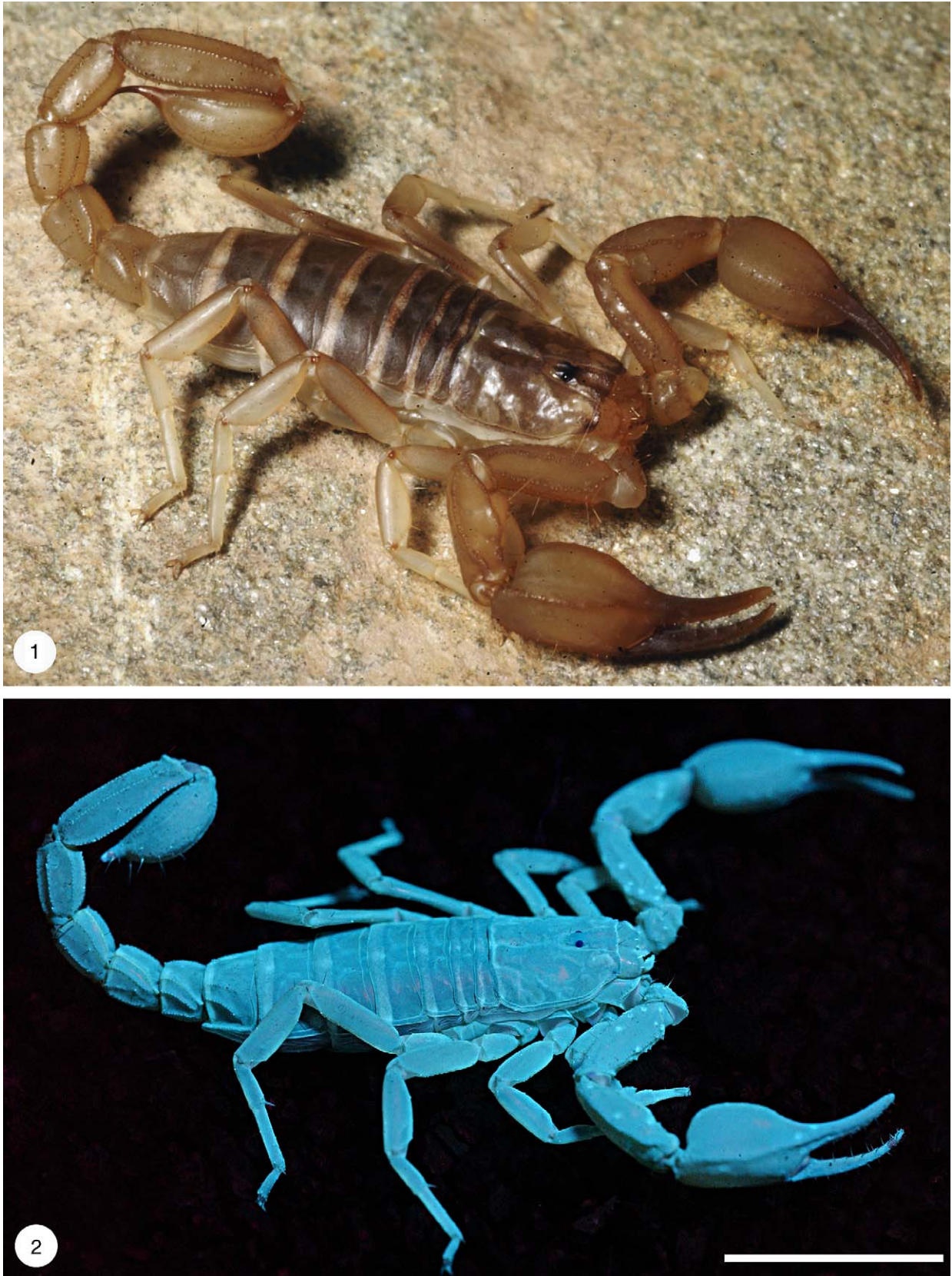
Figs. 1–2. *Pseudochactas ovchinnikovi* Gromov, 1998, adult ♀, in life: (**1**) natural light and (**2**) ultraviolet light. Scale bar = 10 mm.

southwestern Tajikistan, Central Asia (Figs. 3–7). As observed in the original description by Gromov (1998), several characters of this species suggest a close phylogenetic relationship to the largest and most widely distributed scorpion family, Buthidae C.L. Koch, 1837 (*sensu lato*, i.e., including Microcharmidae Lourenço, 1996). Other characters suggest a closer relationship to the so-called 'nonbuthid' scorpion families—widely thought to constitute a single monophyletic lineage, sister to the Buthidae *s. l.* (Lamoral 1980; Sissom 1990; Prendini 2000a; Soleglad and Fet 2001, 2003b; Coddington et al. 2004)—especially Chaerilidae Pocock, 1893. The phylogenetic position of Chaerilidae, comprising a single genus, *Chaerilus* Simon, 1877, with ca. 22 species endemic to tropical South and Southeast Asia (Khatoon 1999; Fet 2000a; Kovařík 2000, 2005; Qui et al. 2005), is also contentious (Lamoral 1980; Stockwell 1989; Sissom 1990; Prendini 2000a; Soleglad and Fet 2001, 2003b; Coddington et al. 2004). Some authors place it as the sister group of Buthidae *s. l.*, whereas others place it as the sister group of the nonbuthid families.

Besides the mixture of characters shared with buthid and nonbuthid scorpions, Gromov (1998) noted several characters of *Pseudochactas* that are unique among Recent (extant) scorpions. Among the most important is the trichobothrial pattern of its pedipalps, which cannot be accommodated in any of the three 'fundamental' (orthobothriotaxic) patterns first defined by Vachon (1974; Table 1) and so influential in scorpion systematics since.

The unique combination of characters that *Pseudochactas* shares with Buthidae, on one hand, and the nonbuthid families, on the other, lead 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 (Fig. 8), and create a monotypic family, Pseudochactidae Gromov, 1998, to accommodate it.

Subsequent authors have not reached a consensus regarding the phylogenetic position of this enigmatic scorpion. In Fet's (2000b) opinion, the peculiar trichobothrial pattern of *Pseudochactas* suggested a relationship to the most plesiomorphic Buthidae (Fig. 9) or to Chaerilidae (Fig. 10). Lourenço (2000) placed *Pseudochactas* in a new superfamily, Chaeriloidea Pocock, 1893, implying that he considered it to be the sister group of *Chaerilus* (Fig. 10).

In the first issue of their online journal, *Euscorpius*, Soleglad and Fet (2001) set out to quantitatively determine the phylogenetic position of *Pseudochactas* by studying its trichobothia in more detail. Soleglad and Fet (2001) amended Gromov's (1998) designations of the individual trichobothria of *Pseudochactas* (Table 1), formalised the definition of its trichobothrial pattern, which they named 'Type D', and presented a cladistic analysis of the four orthobothriotaxic patterns of scorpions (Table 2), on the basis of which *Pseudochactas* was placed as the sister group of Buthidae (Fig. 9). 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 1982a, b; Sissom 1990; Prendini 2000a; Prendini and Wheeler 2005), while other sources of evidence were ignored (Coddington et al. 2004), and was rooted on a hypothetical outroup, with consequent problems for determining character polarity (Prendini 2001a; Prendini and Wheeler 2005). The phylogenetic placement of *Pseudochactas* was therefore not rigorously tested in the analysis by Soleglad and Fet (2001). Fet et al. (2003) nevertheless cited the finding as justification for using *Pseudochactas* as the sole outgroup in their 'first molecular phylogeny' of Buthidae, casting doubt on the results of that analysis as well.

Next, Soleglad and Fet (2003a) presented a quantitative assessment of the sternum of *Pseudochactas*, as part of a survey of sternum morphology across all scorpions, in which they demonstrated similarities among the sterna of *Pseudochactas*, Buthidae *s. l.*, and Chaerilidae, which they formally designated as 'Type 1' sterna. Soleglad and Fet (2003a) concluded that the sternum of *Pseudochactas* is the most plesiomorphic of any Recent scorpion, showing a close affinity with that of the Carboniferous fossil, *Palaeopisthacanthus* Petrunkevitch, 1913.

Soleglad and Fet (2003b) subsequently suggested further affinities between *Pseudochactas* and *Palaeopisthacanthus*, and presented a new cladistic analysis of the higher phylogeny of Recent scorpions, based on trichobothria and other morphological characters, according to which *Pseudochactas* was placed basal to all Recent scorpions, echoing the earlier view of Gromov (1998). Besides the incorporation of problematic data from their earlier analysis (Soleglad and Fet 2001), there are many other fundamental problems with Soleglad and Fet's (2003b) analysis (Prendini and Wheeler 2004, 2005).

More recently, Fet et al. (2004) republished Soleglad and Fet's (2003b) diagnosis of *Pseudochactas*, elaborated their biogeographical discussion and published a few additional illustrations. Fet et al. (2004, p. 63) maintained Soleglad and Fet's (2003b) placement of *Pseudochactas* as the basal sister group of all Recent scorpions.

In all, three competing hypotheses have been proposed to account for the phylogenetic position of *Pseudochactas*: (1) sister group of all Recent (extant) scorpions (Fig. 8); (2) sister group of Buthidae (Fig. 9); (3) sister group of Chaerilidae (Fig. 10). As noted by Coddington et al. (2004), neither of the hypotheses based on evidence (Soleglad and Fet 2001, 2003b) supports Lourenço's (2000) placement of *Pseudochactas* as the sister group of *Chaerilus*, in a unique superfamily Chaeriloidea (Hypothesis 3) and there are fundamental problems with the phylogenetic analyses presented by
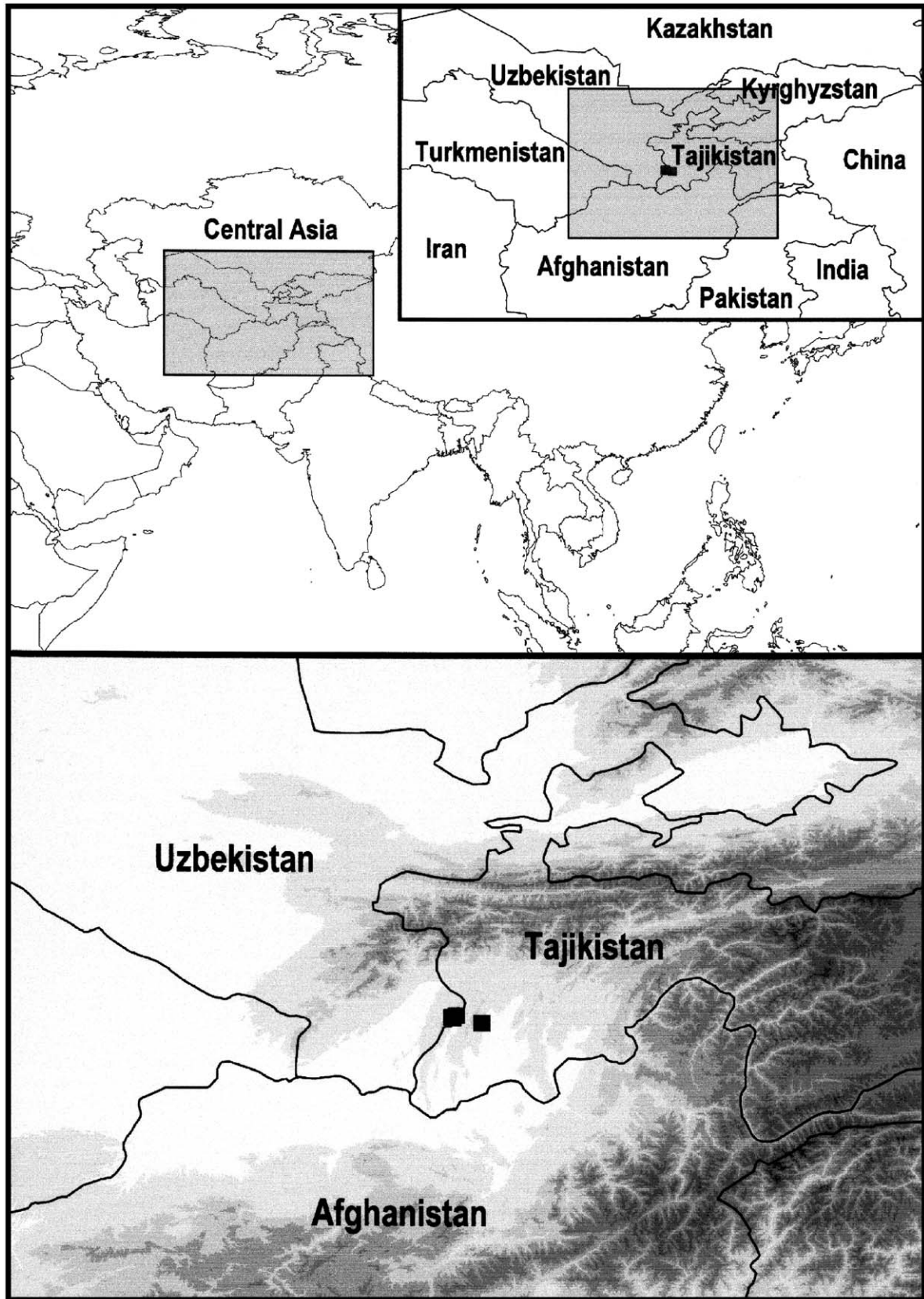
Fig. 3. Map showing the known distribution of *Pseudochactas ovchinnikovi* Gromov, 1998 in Central Asia (■). Contour interval 500 m.

Figs. 4–7. Dikhana Canyon, Babatag Mountains, SE Uzbekistan, collection locality for *Pseudochactas ovchinnikovi* Gromov, 1998. (**4**) Aerial view of canyon. (**5**) Canyon, facing upstream. (**6**) Side gully in canyon, where several specimens were collected. (**7**) Microhabitat of *P. ovchinnikovi*. Specimens were observed sitting and walking on mud walls, often close to the stream at night.

Table 1. Alternative interpretations for the trichobothrial pattern on the pedipalps (femur, patella, chela manus and fixed finger) of *Pseudochactas* Gromov 1998 proposed by Gromov (1998), Soleglad and Fet (2001) and here (1–4)

			Gromov (1998)	Soleglad and Fet (2001)	New interpretations				
					1	2	3	4	Preferred
Chela	Finger	Internal surface	it	it	it	it	it	it	it
			ib	ib	**ib_1**	ib_1	ib_1	ib_1	ib_1
					$[ib_2]^a$	$[ib_2]$	$[ib_2]$	$[ib_2]$	$[ib_2]$
		Dorsal surface	dt	dt	dt	dt	dt	dt	dt
			db	db	db	db	db	db	db
		External surface	et	et	et	et	et	**esb**	esb
			est	est	est	est	est	**eb**	Eb
	Manus	External surface	eb	eb	eb	eb	**Et_1**	Et_1	Et_1
			Est	Et_1	Et_1	**Est**	Est	Est	Est
			Em	Est	**Eb_1**	Eb_1	Eb_1	Eb_1	Eb_1
			Eb_2	Eb_2	**$[Eb_3]$**	$[Eb_3]$	$[Eb_3]$	$[Eb_3]$	$[Eb_3]$
			Eb_1	Eb_1	**Eb_2**	Eb_2	Eb_2	Eb_2	Eb_2
		Ventral surface	V	**V_1**	**V_2**	V_2	V_2	V_2	V_2
Patella		Internal surface	i	**i_1**	i_1	i_1	i_1	i_1	i_1
		Dorsal surface	d_3	d_3	d_3	d_3	d_3	d_3	d_3
			d_2	d_2	d_2	d_2	d_2	d_2	d_2
			d_1	d_1	d_1	d_1	d_1	d_1	d_1
		External surface	est_1	**et_1**	et_1	et_1	et_1	et_1	et_1
			est_2	**et_2**	et_2	et_2	et_2	et_2	et_2
			em	**est_1**	$[est_1]$	$[est_1]$	$[est_1]$	$[est_1]$	$[est_1]$
			eb_2	**esb_1**	esb_1	esb_1	esb_1	esb_1	esb_1
			eb_3	**eb_2**	eb_2	eb_2	eb_2	eb_2	eb_2
			eb_1	eb_1	eb_1	eb_1	eb_1	eb_1	eb_1
Femur		Internal surface	i_3	i_3	**$[i_4]$**	$[i_4]$	$[i_4]$	$[i_4]$	$[i_4]$
			i_2	i_2	**i_3**	**i_2**	i_2	i_2	i_2
			i_1	i_1	**i_2**	**i_1**	i_1	i_1	i_1
		Dorsal surface	d_5	d_5	**$[d_6]$**	$[d_6]$	$[d_6]$	$[d_6]$	$[d_6]$
			i_4	i_4	**d_5**	d_5	d_5	d_5	d_5
			d_4	d_4	**$[d_4]$**	$[d_4]$	$[d_4]$	$[d_4]$	$[d_4]$
			d_3	d_3	d_3	d_3	d_3	d_3	d_3
			d_2	d_2	**$[i_1]$**	**$[d_2]$**	$[d_2]$	$[d_2]$	$[d_2]$
			d_1	d_1	**$[d_1]$**	$[d_1]$	$[d_1]$	$[d_1]$	$[d_1]$
		External surface	e_3	e_3	e_3	e_3	e_3	e_3	e_3
			e_2	e_2	e_2	e_2	e_2	e_2	e_2
			e_1	e_1	e_1	e_1	e_1	e_1	e_1

'Petite' trichobothria (*sensu* Vachon 1974) are denoted by square brackets. Trichobothria in boldface differ from previous column.

[a]Additional 'petite' trichobothrium, ib_2, not observed by Gromov (1998) or Soleglad and Fet (2001, 2003b); ib renamed ib_1. Preferred interpretation illustrated in Figs. 22–31.

Soleglad and Fet (2001, 2003b), which produced alternative positions for *Pseudochactas* (Hypotheses 1 and 2). Furthermore, several important character systems, e.g., the hemispermatophore and ovariuterus, have not been studied at all in *Pseudochactas*. Concerning the hemispermatophore, Soleglad and Fet (2003b, p. 76) stated:

> We also do not yet know the structure of the hemispermatophore for [*Pseudochactas*], presumably the most primitive of all Recent scorpions. Repeated attempts by us and others (personal communications of David Sissom and Graeme Lowe) to find and remove such a structure have failed. The reason for this

failure may have several possible reasons: since all male specimens examined were collected at the same time of the year (early May), possibly the structure is not developed in adult males at this season; or the structure as we know it in other scorpions may be so different in *Pseudochactas*, it was unrecognizable as a hemispermatophore; or *Pseudochactas* employs altogether a totally different mechanism for mating.

There are also several misconceptions regarding some of the character systems (e.g., trichobothria, pedipalpal and metasomal carinae) that have been studied by previous authors, as we will demonstrate. We agree with
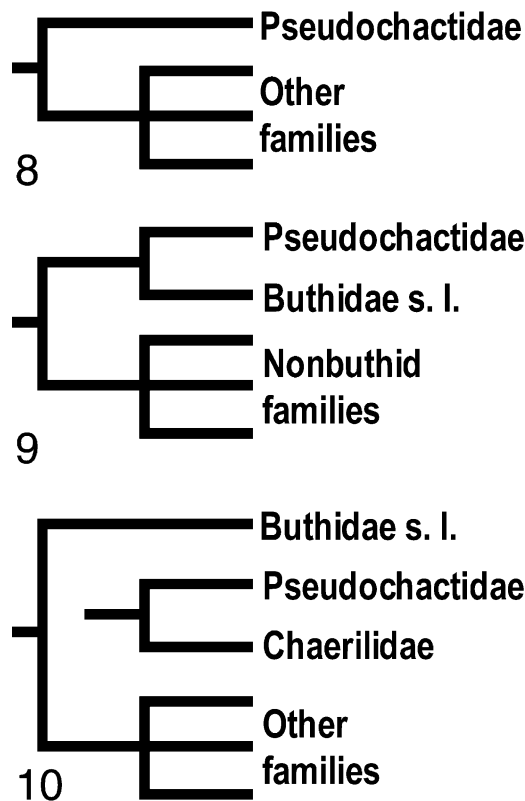
Figs. 8–10. Three competing hypotheses proposed to account for the phylogenetic position of *Pseudochactas* Gromov, 1998. (**8**) Sister group of all Recent (extant) scorpions (Gromov 1998; Soleglad and Fet 2003b). (**9**) Sister group of Buthidae C.L. Koch, 1837 (Fet 2000b; Soleglad and Fet 2001; Fet et al. 2003). (**10**) Sister group of Chaerilidae Pocock, 1893 (Fet 2000b; Lourenço 2000).

Soleglad and Fet (2003b) and Fet et al. (2004) that this remarkable scorpion requires further study in all aspects. Indeed, we believe it is premature to consider its phylogenetic position resolved before its morphology has been more intensively studied and putative homology statements with other scorpions have been more rigorously evaluated. In this contribution, we provide a detailed, fully illustrated reexamination of the morphology of *Pseudochactas*, based on most of the previously collected specimens and a new series obtained in 2003. We present the first descriptions of the hemispermatophore, ovariuterus, and pectinal peg sensillae of *Pseudochactas*, and discuss the implications of these and other characters for the phylogenetic position of this 'living fossil'.

2. Material and methods

2.1. Fieldwork

New specimens and natural history observations reported in this study were obtained by L. Prendini

and A.V. Gromov during an expedition through the Central Asian countries of Kazakhstan and Uzbekistan in May and June, 2003. All specimens were located at night with the aid of ultraviolet (UV) light detection (Honetschlager 1965; Stahnke 1972; Sissom et al. 1990; Fig. 2) and captured with forceps. Portable UV lamps, each comprising two mercury-vapor tubes attached to a chromium parabolic reflector and powered by a rechargeable 7 A/h, 12 V battery, were used for fieldwork. A portable Garmin[TM] GPS II Plus device was used for recording the geographical coordinates of collection localities in the field.

2.2. Material

Material examined is deposited in the following collections: American Museum of Natural History, New York, USA (AMNH); Zoological Museum, Moscow State University, Moscow, Russia (ZMMSU); Zoological Museum, Institute for Animal Systematics and Ecology, Novosibirsk, Russia (IASE); Alexander V. Gromov Personal Collection, Almaty, Kazakhstan (AVG); Antonio Melic Personal Collection, Zaragoza, Spain (AM); František Kovařík Personal Collection, Prague, Czech Republic (FK); Sergei V. Ovchinnikov Personal Collection, Bishkek, Kyrghyzstan (SVO); Valerio Vignoli Personal Collection, Siena, Italy (VV); Victor Fet Personal Collection, Huntington, West Virginia, USA (VF). Tissue samples of *P. ovchinnikovi* are stored (in the vapour phase of liquid nitrogen at $-150\,°C$) in the Ambrose Monell Collection for Molecular and Microbial Research (AMCC) at the AMNH.

2.3. Morphology and anatomy

Measurements and other meristic data were recorded using a Nikon SMZ-1500 stereomicroscope. Color designation follows Smithe (1974, 1975, 1981) and mensuration follows Stahnke (1970). Unless noted otherwise, morphological terminology follows papers by Prendini (2000a, b).

Trichobothrial notation follows Vachon (1974). Given the well-known problems with assigning trichobothrial homology across the major patterns in scorpions (Lamoral 1979; Francke and Soleglad 1981; Francke 1982a, b; Sissom 1990; Prendini 2000a; Prendini and Wheeler 2005), we did not assume that the trichobothria identified in *Pseudochactas* by Gromov (1998) or Soleglad and Fet (2001), who reassigned many of Gromov's (1998) original designations (Table 1), were homologous with those assigned the same designations in other scorpions (Table 2). Instead, we reassessed the trichobothrial pattern of *Pseudochactas* by direct comparison with those of other scorpions, without

Table 2. The four fundamental (orthobothriotaxic) trichobothrial patterns on the pedipalps (femur, patella, chela manus and fixed finger) of extant scorpions, proposed to date for the Buthidae C.L. Koch 1837 (*sensu lato*, i.e., including Microcharmidae Lourenço 1996), Chaerilidae Pocock 1893, Pseudochactidae Gromov 1998, and the remaining extant families (Vachon 1974; Sissom 1990; Gromov 1998; Soleglad and Fet 2001)

Type (Family)	Segment	Internal surface	Dorsal surface	External surface	Ventral surface	No
A (Buthidae *s.l.*)	Finger	1 (it)	2 (db, dt)	4 (eb, [esb], est, et)		7
	Manus			6 (Eb_1, Eb_2, [Eb_3], Est, Et_1, [Et_4])	2 (V_1, V_2)	8
	Patella	1 (i_1)	5 (d_1–d_4, [d_5])	7 (eb_1, eb_2, esb_1, em_1, est, et_1, et_2)		13
	Femur	4 (i_1, i_2, [i_3], [i_4])	5 (d_1, [d_2], d_3–d_5)	2 (e_1, e_2)		11
	Total					39
B (Chaerilidae)	Finger	2 (ib_1, it)	2 (db, dt)	4 (eb, esb, est, et)		8
	Manus			5 (Eb_1–Eb_3, Est, Et_1)	1 (V_1)	6
	Patella	2 (i_1, i_2)	2 (d_1, d_2)	7 (eb_1, eb_2, esb_1, em_1, est, et_1, et_2)	3 (v_1–v_3)	14
	Femur	1 (i_1)	4 (d_1, d_3–d_5)	4 (e_1–e_4)		9
	Total					37
C (other families)	Finger	2 (ib_1, it)	4 (db, dsb, dst, dt)	4 (eb, esb, est, et)		10
	Manus		2 (Db, Dt)	10 (Eb_1–Eb_3, [Esb], Est, Et_1–Et_3, [Et_4], Et_5)	4 (V_1–V_4)	16
	Patella	1 (i_1)	2 (d_1, d_2)	13 (eb_1–eb_5, esb_1, [esb_2], em_1, em_2, est, et_1–et_3)	3 (v_1–v_3)	19
	Femur	1 (i_1)	1 (d_1)	1 (e_1)		3
	Total					48
D (Pseudochactidae)	Finger	3 ([ib_2][a], ib_1, it)	2 (db, dt)	3 (eb, est, et)		8
	Manus			4 (Eb_1, Eb_2, Est, Et_1)	1 (V_1)	5
	Patella	1 (i_1)	3 (d_1–d_3)	6 (eb_1, eb_2, esb_1, [esf], et_1, et_2)		10
	Femur	4 (i_1, i_2, [i_3], i_4)	5 ([d_1], [d_2], d_3, [d_4], d_5)	3 (e_1–e_3)		12
	Total					35

Trichobothrial designations and putative homologies follow Soleglad and Fet (2001, 2003b). 'Petite' trichobothria (*sensu* Vachon 1974) are denoted by square brackets.
[a] Additional 'petite' trichobothrium, ib_2, not observed by Gromov (1998) or Soleglad and Fet (2001, 2003b); ib renamed ib_1.

recourse to the designations of Vachon (1974) and subsequent workers, paying particular attention to the trichobothrial patterns of buthid scorpions that deviate from Type A orthobothriotaxy.

Photographs of the external morphology and internal anatomy of *Pseudochactas* were taken in visible light as well as under long wave UV light using a Nikon D1X camera and a Microptics™ ML-1000 digital imaging system. Scanning electron micrographs of the pectines were prepared using a Hitachi scanning electron microscope at the AMNH Microscopy and Imaging Facility.

Sexual maturity of males and females was confirmed by the observation of testicular tubules or hemispermatophores in males, and ovariuterine tubules in females. Dissections, undertaken to expose the mesosomal organs, involved the removal of at least the anterior tergites in males, or the carapace and tergites in females. Using dissection needles constructed from minuten entomology pins, the hepatopancreas was teased away to reveal the gonads. Dissections were hindered by the hardened hepatopancreas, an apparent preservation artefact, of many specimens examined. Attempts to soften the hepatopancreas of these specimens, by soaking them in 30% ethanol for 2 days, were largely unsuccessful.

During the course of this study, we examined 28 male specimens, identified externally by the presence of their distinctive genital papillae. We selected 18, suspected to be adult based on size or external morphological characteristics, for dissection. Only one of these specimens was obviously secondarily sexually dimorphic, and only slightly so. Upon dissection, this was the only specimen that could be confirmed as an adult male due to the possession of hemispermatophores and testes. Among the specimens examined are most of those listed as adult males in Gromov's (1998) description, including the holotype. None of these specimens are adult, in our opinion. Most possess a distinctly distended mesosoma, those dissected containing a large mass of hepatopancreas, as is typical of juvenile and female scorpions. Three specimens of similar overall size and proportions to the sole confirmed adult male, also lacked hemispermatophores and gonads.

Several techniques were used to study and render illustrations of the single pair of male hemispermatophores that were obtained. The right hemispermatophore was broken into three parts during its preparation for examination under light microscopy. The parts were subsequently mounted on a permanent slide in Euparal, examined and reconstructed in 3D using a Zeiss ConFocal Laser Scanning Microscope and Imaris Version 4.1 (BitPlane AG™), in the AMNH Microscopy and Imaging Facility, according to protocols outlined in Klaus et al. (2003). As this hemispermatophore was mounted in a slide, only its ventral surface could be photographed. Additional data about the hemispermatophore were gathered by clearing the intact left paraxial organ in clove oil, mounting it on a wet slide, and examining it under a compound microscope (Olympus BH2) fitted with a drawing attachment.

The anatomy of the female reproductive system was determined and illustrated by dissecting three specimens, as follows. The genital opercula were first dissected, by cutting through the surrounding membrane, then cleared and mounted in 85% lactic acid, on temporary slides, and examined with compound and stereo microscopes. After examination, the genital opercula were transferred to glass genitalia vials stored with the specimens from which they originated. In order to examine the ovariuterus, the carapace and tergites were dissected from the specimens by cutting through the pleural membrane of the mesosoma, around the lateral and anterior margins of the carapace, and the posterior margin of tergite VII, and then carefully lifting the tergites and carapace from the specimen to reveal the internal anatomy. The outline of the ovariuterine tubules was exposed and traced by gradually and carefully dissecting away the hepatopancreas.

2.4. Distribution

A distribution map was produced using ArcView GIS Version 3.2 (Environmental Systems Research Institute, Redlands, CA, USA), by superimposing point locality records on coverages depicting the topography (500 m contour interval) and political boundaries of Central Asia. A topographic contour coverage was created from the GTOPO30 raster grid coverage, obtained from the website of the US Government Public Information Exchange Resource: ⟨http://edcdaac.usgs.gov/gtopo30/gtopo30.html⟩.

2.5. Conservation status

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

3. Systematics

3.1. Family Pseudochactidae Gromov, 1998

Pseudochactidae Gromov, 1998: 1003. Type genus: *Pseudochactas* Gromov, 1998.

Pseudochactidae: Fet 2000b, p. 426; Lourenço 2000, p. 24, 32; Soleglad and Fet 2001, p. 1, 7, 9, 10–16, 18, 20–22, 24–26, 35, 38, Figs. 2–9, 12, 13, and B-1, Table 6, Appendices B and C; Soleglad and Fet 2003a, p. 1, 5, 9, 10, 12, 25, 28–30, Figs. 3 and 44, Table 1; Soleglad and Fet 2003b, p. 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, and E-1, Tables 9 and 11, Appendices A, B, and E; Fet et al. 2003, p. 2, 3, Table 1; Coddington et al. 2004, p. 309, 310, Fig. 18.5; Prendini and Wheeler 2005, p. 448, 460, 463–465, 473, 482, 491–494, Tables 2, 8, and 10.

3.1.1. Diagnosis

Pseudochactas is unique among extant scorpions in possessing the following morphological character states: cheliceral movable finger, dorsal edge with three teeth (medial, subdistal, external distal; Fig. 15); only one pair of lateral ocelli, i.e., a single ocellus on each side of the carapace (Fig. 16); a pair of circumocular sutures with a U-shaped configuration, originating at the anterior margin of the carapace, between the lateral ocelli, and converging in the anteromedian region of the carapace, immediately posterior to the median ocular tubercle; the Type D trichobothrial pattern (Soleglad and Fet 2001, 2003b), with 35 trichobothria per pedipalp (Table 2): 12 on the femur (five dorsal, three internal, four external), 10 on the patella (three dorsal, one internal, six external, trichobothria absent on the ventral surface), and 13 on the chela (five manus, eight fixed finger); pectinal peg sensillae stout, square distally, with pair of processes at laterodistal margins (Fig. 21); paraxial organ and hemispermatophore unlike any other scorpion, extremely small (1.45 mm long and 0.45 mm wide) and associated with a single glandular structure (Figs. 41–44); telotarsi each with a pair of ventrosubmedian rows of spinules; metasomal segment V with a well developed pair of ventrosubmedian carinae, continuous throughout length of segment (Fig. 36).

Pseudochactas is further distinguished from other scorpions by the following combination of morphological character states: cheliceral fixed finger, ventral edge with four or five denticles; cheliceral movable finger, dorsal edge with a single subdistal tooth, without basal teeth, ventral edge crenulated, with numerous denticles (ventral accessory teeth *sensu* Stockwell 1989), external distal and internal distal teeth subequal, external distal tooth only slightly smaller than internal distal tooth, and opposable; carapace with a pair of anterosubmedial carinae, arranged in a lyriform configuration, anterior to the median ocular tubercle and internal to the circumocular sutures; pedipalp femur dorsal trichobothria with β configuration, d_2 situated on dorsal surface, d_3 and d_4 in same axis, parallel and closer to dorsoexternal carina than d_1, angle formed by d_1, d_3 and d_4 opening toward

internal surface (Fig. 23); pedipalp patella with seven discernable carinae; pedipalp chela with eight discernable carinae; pedipalp chela fixed and movable fingers, dentate margins with median denticle row comprising oblique granular subrows; maxillary lobes (coxapophyses) I, distal edges rounded, unexpanded (not spatulate or dilate) anteriorly, terminating flush with lobes II (Figs. 12 and 14); sternum pentagonal, Type 1 (Soleglad and Fet 2003a), not horizontally compressed; genital operculum completely divided longitudinally, with prominent genital papillae visible entire length in male; respiratory spiracles small, oval in shape; ovariuterus comprising reticulate mesh of six cells; tibial spurs present on legs III and IV only; pro- and retrolateral pedal spurs present on legs I–IV; telson vesicle with venom glands thin-walled, simple and unfolded.

3.1.2. Included taxa

A single monotypic genus, *Pseudochactas* Gromov, 1998.

3.1.3. Distribution

Endemic to the Central Asian countries of Uzbekistan and Tajikistan. Not recorded from Afghanistan, but may also occur there.

3.2. *Pseudochactas* Gromov, 1998

Pseudochactas Gromov, 1998, p. 1003. Type species by monotypy: *Pseudochactas ovchinnikovi* Gromov, 1998.

Preudochactas (lapsus): Gromov, 1998, p. 1003.

Pseudochactas: Fet 2000b, p. 426; Lourenço 2000, p. 24, 32, Fig. 6; Soleglad and Fet 2001, pp. 1–4, 8, 12, 13, 19, 21, 22, 24, 28, 34, Appendix B; Soleglad and Fet 2003a, p. 5, 8, 9, 12, 18, 19, 20, 22, 24, 26, Figs. 2, 3, 14; Soleglad and Fet 2003b, p. 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, and B-3, Tables 3, 4, and 9, Appendices A–C; Fet et al. 2003, p. 2, 3, 5, 10, Fig. 1, Table 1, Appendix; Prendini and Wheeler 2005, p. 451, 454, 459–462, 470, 474, 482, Tables 3, 5, and 10.

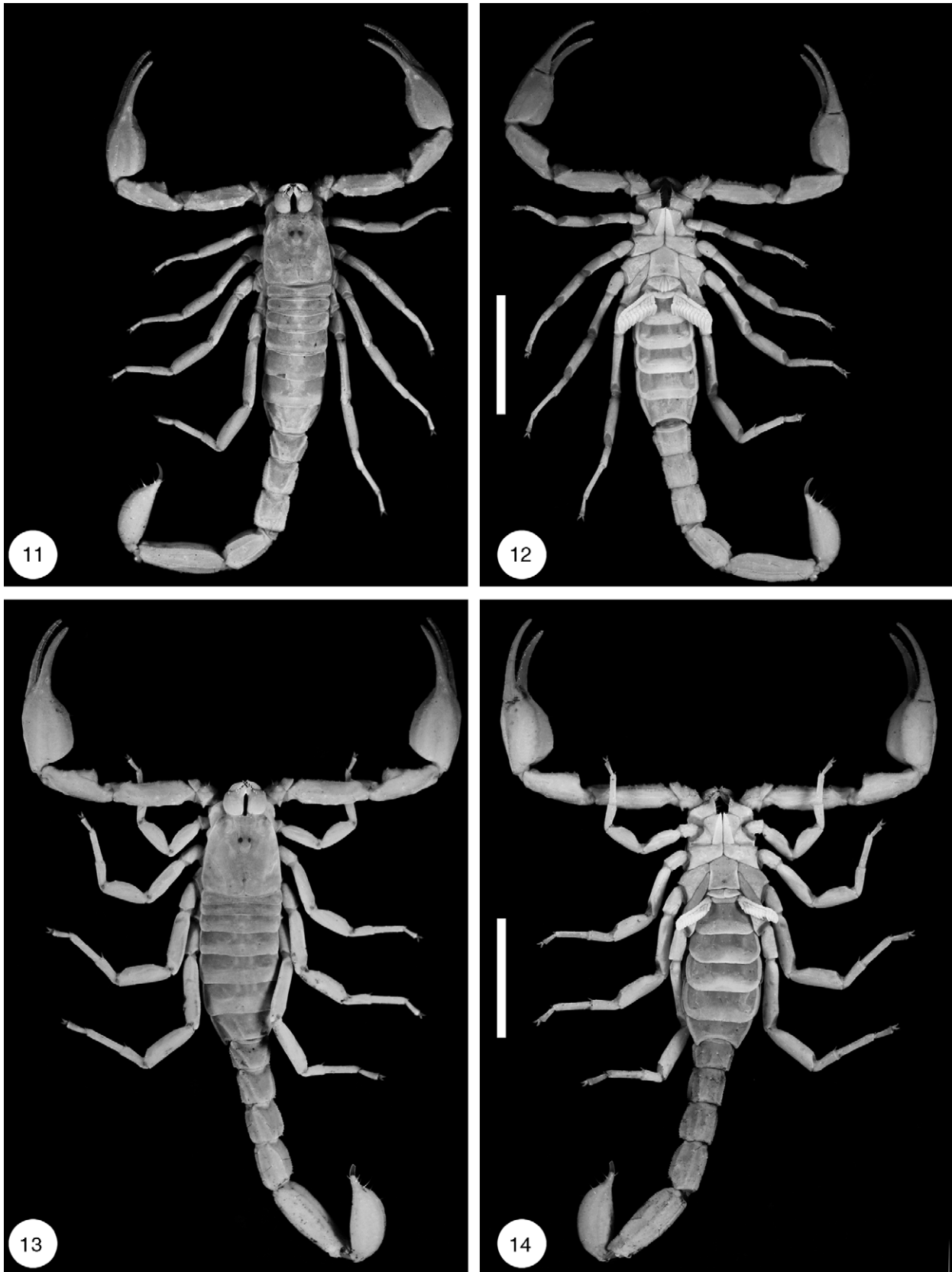### 3.2.1. Diagnosis
As for Pseudochactidae.

3.2.2. Included taxa
A single species, *Pseudochactas ovchinnikovi* Gromov, 1998.

3.2.3. Distribution
As for Pseudochactidae.

Figs. 11–14. *Pseudochactas ovchinnikovi* Gromov, 1998, habitus of ♂ and ♀ (AMNH). (**11**) Dorsal aspect, ♂. (**12**) Ventral aspect, ♂. (**13**) Dorsal aspect, ♀. (**14**) Ventral aspect, ♀. Scale bars = 10 mm.

3.3. Pseudochactas ovchinnikovi Gromov, 1998

Pseudochactas ovchinnikovi Gromov, 1998, pp. 1003–1008, Figs. 1, 2 (1–12), and 3 (1–8).

Pseudochactas ovchinnikovi: Fet 2000b, p. 426; Lourenço 2000, p. 32, Fig. 6; Soleglad and Fet 2001, p. 1, 22; Soleglad and Fet 2003a, p. 5, 8, 18, 20, Figs. 2, 3, and 14; Soleglad and Fet 2003b, p. i, 8, 11, 12, 18, 20, 29, 30, 32, 33, 54, 60, 65, 67, 150, 151–153, 155, Figs. 1, 4, 10–12, 41, 49, 57, 92, 108, B-1, B-2, and B-3, Appendices B and C; Fet et al. 2003, p. 2, 3, 5, Fig. 1, Table 1; Prendini and Wheeler 2005, p. 454, Table 5.

3.3.1. Type material

UZBEKISTAN: Surkhandarya Region: *Uzun District*: Holotype, subad. ♂ (ZMMSU), Okmachit [Akmechet], ca. 7 km W–4 km WSW, 38°02′50″N 68°14′22″E–38°01′45″N 68°15′30″E, E slope of Babatag Mt. Range, 760–1010 m, 29.iv–9.v.1994, A.V. Gromov. Paratypes: same data as holotype, except 'A.V. Gromov & S.V. Ovchinnikov', 2 ♀ 3 subad. ♂ (AVG), 3 [subadult?] ♂ (VF). TAJIKISTAN: *Leninskii District*: Aruktau Mt. Range, near Gandzhina village [37°58′N 68°34′E], 10.iv.1988, S.L. Zonstein & A.S. Zorkin, 1 ♀ (AVG).

3.3.2. Additional material

UZBEKISTAN: Surkhandarya Region: *Uzun District*: same data as holotype, 1 ♀ 6 juv. (AVG); Okmachit, ca. 7 km W, 38°02′50″N 68°14′22″E, E slope of Babatag Mt. Range, ca. 1010 m, 28.iv.1995, S.V. Ovchinnikov, 6 juv. (SVO); same data, except '13.v.1995, O.V. Lyakhov', 1 juv. (IASE), 2 juv. (AVG); Okmachit, ca. 6.5–7 km W, 38°02′50″N 68°14′22″E–38°02′4″N 68°14′51″E, E slope of Babatag Mt. Range, 905–1010 m, 30.iv–2.v.2002, A.V. Gromov, 6 ♀ 7 subad. ♂ 1 subad. ♀ 26 juv. (AVG), 1 subad. ♂ 1 juv. (VV); 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. (AVG), 1 ♀ 1 [subad.] ♂ (FK); Okmachit, ca. 5–6 km WSW, 38°02′01″N 68°14′03″E–38°01′36″N 68°15′00″E, E slope of Babatag Mt. Range, 730–870 m, 4.v.2002, A.V. Gromov, 1 ♂ [dissected] 1 subad. ♂ [dissected] (AMNH), 3 ♀ 16 subad. ♂ [all dissected] 1 subad. ♀ 67 juv. (AVG), 1 ♀ 1 [subad.?] ♂ (FK), 1 juv. (AM); Dikhana Canyon, foothills of E slopes of Babatag Mountain Range, ca. 5 km WSW of Akmechet village, 38°01.638′N 68°15.198′E, 722 m, 20–24.v.2003, L. Prendini & A.V. Gromov, 9 ♀ [3 dissected] 8 subad. ♂ 4 subad. ♀ 17 juv. ♂ 9 juv. ♀ (AMNH), 1 juv. ♀ (AMCC 159928); Dikhana Canyon, ca. 5.5 km WSW of Okmachit, 38°01′33″N, 68°14′26″E, E slope of Babatag Mt. Range, ca. 774 m, 22.v.2003, A.V. Gromov & L. Prendini, 1 juv. (AVG).

3.3.3. Diagnosis

As for Pseudochactidae.

3.3.4. Description

The following description and Figs. 11–47 supplement Gromov's (1998) original description, Soleglad and Fet's (2001) definition of the Type D trichobothrial pattern, Soleglad and Fet's (2001) definition of the Type 1 sternum of *Pseudochactas*, and supplemental data on its morphology by Soleglad and Fet (2003b) and Fet et al. (2004). Table 5 records meristic data for 10 adult specimens (1 ♂ and 9 ♀) in the AMNH collection.

Color: Chelicerae, pedipalps (except chela fingers), legs, posterior third of tergites, metasoma, and telson slightly paler than carapace, pedipalp chela fingers, and anterior two-thirds of tergites (Fig. 1). Prolateral surfaces of leg femora and patellae darker than rest of legs. Carapace and anterior two-thirds of tergites: Natal Brown No. 219A. Pedipalp chela fingers: Burnt Umber No. 22. Chelicerae, pedipalps (except chela fingers), prolateral surfaces of leg femora and patellae, posterior third of tergites, metasoma and telson: Cinnamon Brown No. 33. Legs (except prolateral surfaces of leg femora and patellae), genital operculum, pectines and sternites: Pale Horn Color No. 92. Aculeus: Jet Black No. 89.

Chelicerae: Fixed finger, dorsal edge with four teeth (basal, medial, subdistal, distal); space between medial and subdistal teeth U-shaped; ventral edge with four or five denticles (Fig. 15). Cheliceral movable finger, dorsal edge with three teeth (medial, subdistal, external distal), without basal teeth; ventral edge crenulated, with numerous small denticles (ventral accessory teeth *sensu* Stockwell 1989); external distal and internal distal teeth subequal, external distal tooth only slightly smaller than internal distal tooth, and opposable. Ventral aspect of fingers and manus with numerous long, dense macrosetae.

Carapace: Anterior margin almost straight, posterior margin shallowly recurved (Fig. 16). One pair of very small lateral ocelli, i.e., a single ocellus situated close to anterolateral margin of each side of carapace. Median ocular tubercle situated anteromedially, comprising pair of median ocelli, considerably larger than lateral ocelli, with pair of weak, smooth superciliary carinae, not protruding above ocelli; interocular sulcus obsolete. Pair of circumocular sutures with a broad U-shaped configuration, originating at carapace anterior margin, between lateral ocelli, and converging in anteromedian region of carapace, immediately posterior to median ocular tubercle. Anteromedian sulcus shallow; posteromedian sulcus very shallow anteriorly, becoming slightly deeper posteriorly; posterolateral sulci very shallow, wide, weakly curved; posteromarginal sulcus narrow, shallow. Carapacial surface almost entirely smooth, except for scattered, fine granulation on
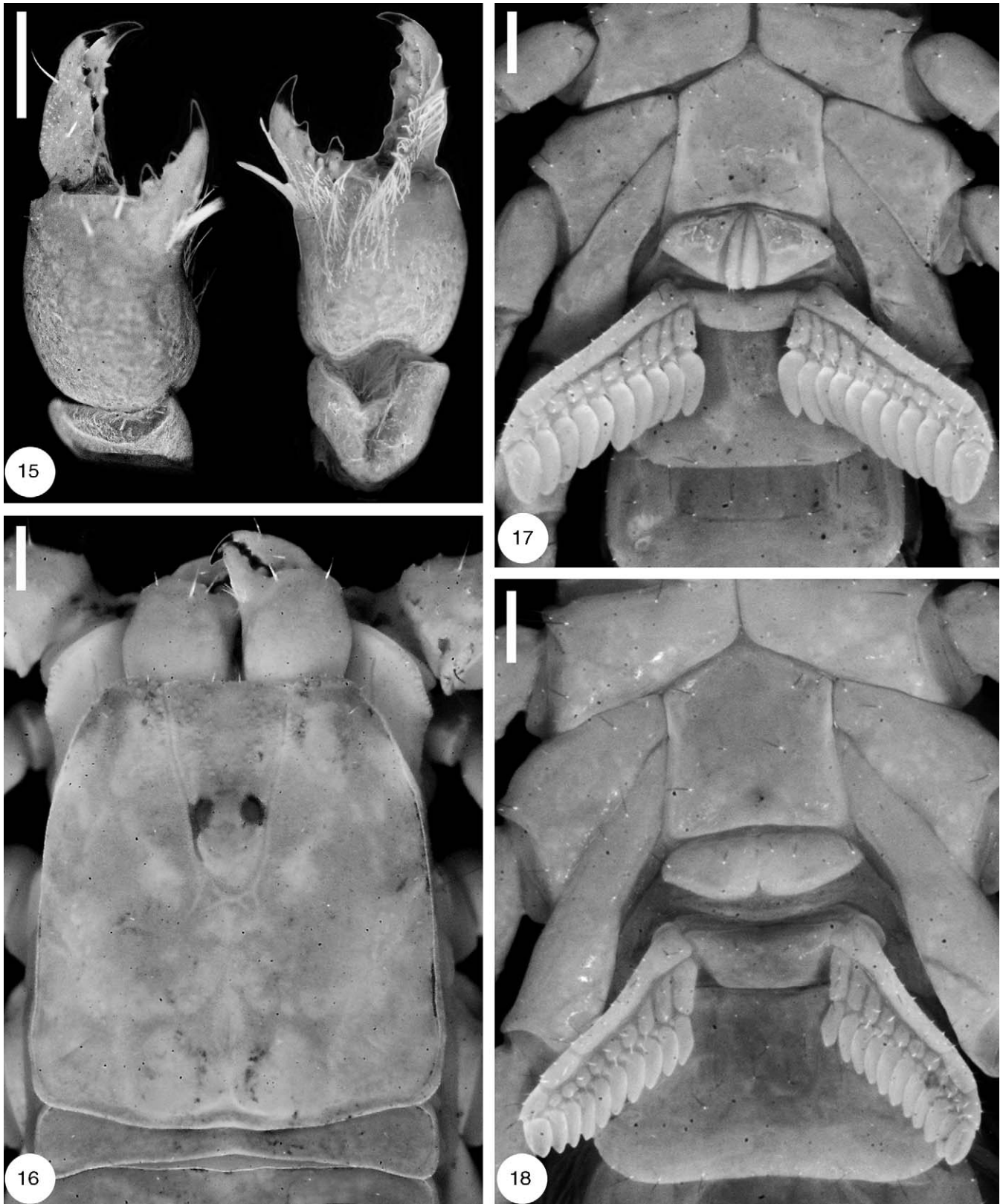
Figs. 15–18. *Pseudochactas ovchinnikovi* Gromov, 1998, diagnostic characters in ♂ and ♀ (AMNH). (**15**) Chelicerae, ♀, dorsal and ventral aspects. (**16**) Carapace, ♀. (**17**) Sternum, genital operculum and pectines, ♂. (**18**) Sternum, genital operculum and pectines, ♀. Scale bars = 1 mm.

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

Pedipalps: Segments almost apilose, sparsely covered in short microsetae and occasional macrosetae. Pedipalp femur length 66% (64–68%) greater than width (Table 5). Femur with seven discernable carinae; internomedian carina obsolete, reduced to a few spiniform granules in proximal two-thirds of segment (Fig. 22); dorsoexternal, dorsointernal, and ventrointernal carinae well developed, costate granular (Figs. 22–24); dorsomedian carina weak, granular (Figs. 23 and 24); externomedian carina weak, comprising short row of granules medially; ventromedian carina vestigial, reduced to a few granules proximally (Fig. 24); intercarinal surfaces smooth.

Pedipalp patella length 53% (50–56%) greater than width (Table 5). Patella with seven discernable carinae; dorsoexternal, ventroexternal and ventrointernal carinae well developed, costate granular to costate (Figs. 25–27); dorsointernal carina well developed, granular to costate granular (Fig. 26); anterior process ('vaulted projection' *sensu* Soleglad and Fet 2003b) well developed, comprising a pair of dorsal and ventral 'spurs' (*sensu* Soleglad and Sissom 2001), the dorsal more strongly developed (Figs. 25 and 26), demarcated by a pair of obsolete, granular internal carinae (dorsal and ventral 'patellar spur carinae' *sensu* Soleglad and Fet 2003b); externomedian carina absent (Fig. 27); intercarinal surfaces smooth.

Pedipalp chela short, broad, width 19.5% (12–27%) greater than height (Table 5); length (along ventroexternal carina) 23.5% (21–30%) greater than width; length of movable finger 25% less than chela length (along ventroexternal carina) in ♂, 16.5% (12–21%) less in ♀. Chela with eight discernable carinae; dorsomedian carina reduced to a weak row of granules at base of fixed finger, becoming obsolete proximally on manus (Fig. 28); digital carina well developed, granular to costate granular (Figs. 28 and 29); external secondary carina absent (Fig. 29); ventroexternal carina well developed, granular, aligned parallel to longitudinal axis of chela, with distal edge connected to external movable finger condyle (Figs. 29 and 30); ventromedian carina obsolete, reduced to a vestigial granule(s) proximally (Fig. 30); ventrointernal carina also obsolete, reduced to a few isolated granules near internal condyle of movable finger (Figs. 30 and 31); internomedian and dorsointernal carinae weakly developed, each comprising a series of isolated granules (Fig. 31); intercarinal surfaces smooth except for coarse, scattered granules on internal surface of manus, near base of fixed and movable fingers, granulation becoming very fine and even on fingers. Movable finger, dentate margin with very weak lobe proximally; fixed finger, dentate margin

with corresponding notch, proximally linear when fingers closed (no proximal 'gap' evident). Fixed and movable fingers, dentate margins each with median denticle row comprising seven oblique granular subrows (Figs. 32 and 33); each subrow comprising several small granules and a large proximal granule (absent from the basal row); all except basal subrow flanked proximally by one internal granule but no external accessory granules; first subrow of each finger with an enlarged terminal denticle; supernumerary granules absent.

Trichobothria: Orthobothriotaxic, Type D (Soleglad and Fet 2001, 2003b), β configuration, d_2 situated on dorsal surface, d_3 and d_4 in same axis, parallel and closer to dorsoexternal carina than d_1, angle formed by d_1, d_3 and d_4 opening toward internal surface (Fig. 23), with the following segment totals (Tables 1 and 2): femur, 12 (five dorsal, three internal, four external); patella, 10 (three dorsal, one internal, six external); chela, 13 (five manus, eight fixed finger). Total number of trichobothria per pedipalp, 35. This is the second lowest number of trichobothria recorded in scorpions, the lowest being 34 in buthids with minor neobothriotaxy, e.g., *Lissothus* Vachon, 1948 (Vachon 1974).

Previous authors (Gromov 1998; Soleglad and Fet 2001, 2003b) did not report that one patellar trichobothrium, est_1 (Fig. 27) and five femoral trichobothria, here designated i_4, d_1, d_2, d_4, and d_6 (Figs. 22 and 23), are noticeably smaller than the others ('petite' *sensu* Vachon 1974; also see Soleglad and Fet 2001), and missed a third, petite internal trichobothrium on the fixed finger of the pedipalp chela, basal to the trichobothrium previously designated ib (Fig. 31). We designate this trichobothrium ib_2 and reassign the designation of the middle trichobothrium ib_1 (= ib of previous authors) (Tables 1, 2 and 4).

Based on our comparisons with the trichobothrial patterns of buthid scorpions, particularly those that deviate from Type A orthobothriotaxy, we conclude that the trichobothrial pattern of *Pseudochactas* is homologous, fundamentally, with that of Buthidae, which is to say that we identify more similarities (potentially synapomorphic trichobothria) than differences between the two patterns, even if Soleglad and Fet's (2001) interpretation is adopted (Table 3). We propose a reinterpretation of the trichobothrial pattern of *Pseudochactas* (Figs. 22–31), however, that is more similar to the buthid pattern (Table 4) than either the interpretations of Gromov (1998) or Soleglad and Fet (2001), with which it is compared directly in Table 1. This reinterpretation is only one of various possible reinterpretations for particular trichobothria. Others imply even more potential synapomorphies with Buthidae. The Type D pattern of *Pseudochactas* shares few similarities with the Type B pattern of *Chaerilus* (Tables 3 and 4).

Legs: Legs I–IV, femora and patellae each with weak granular ventromedian carina, II–IV, femora each with

Table 3. Pedipalp trichobothria of extant scorpion families supporting alternative hypotheses for the phylogenetic position of *Pseudochactas* Gromov 1998, according to the trichobothrial interpretations for Buthidae C.L. Koch 1837 (Type A), Chaerilidae Pocock 1893 (Type B) and Pseudochactidae Gromov 1998 (Type D) proposed by Soleglad and Fet (2001)

			Buthidae	Pseudochactidae *Pseudochactas*	Chaerilidae *Chaerilus*	H1	H2	H2b	H3	H4
Chela	Finger	Internal surface	it	it	it					
				ib	ib			X		X
		Dorsal surface	dt	dt	dt					
			db	db	db					
		External surface	et	et	et					
			est	est	est					
			$[esb]$		esb	X				
	Manus	External surface	Eb	eb	eb					
			$[Et_4]$							
			Et_1	et_1	Et_1					
			Est	Est	Est					
			$[Eb_3]$		Eb_3	X				
			Eb_2	Eb_2	Eb_2					
			Eb_1	Eb_1	Eb_1					
		Ventral surface	V_1	V_1	V_1					
			V_2					X	X	
Patella		Internal surface	i_1	i_1	i_1					
					i_2					
		Dorsal surface	$[d_5]$					X		
			d_4					X		
			d_3	d_3			X			
			d_2	d_2	d_2					
			d_1	d_1	d_1					
		External surface	et_1	et_1	et_1					
			et_2	et_2	et_2					
			est_1	Est_1	est_1					
			em_1		em_1	X		X		
			esb_1	esb_1	esb_1					
			eb_2	eb_2	eb_2					
			eb_1	eb_1	eb_1					
		Ventral surface			v_3					
					v_2					
					v_1					
Femur		Internal surface	$[i_4]$	i_4			X			
			$[i_3]$	i_3			X			
			i_2	i_2			X			
			i_1	i_1	i_1					
		Dorsal surface	d_5	d_5	d_5					
			d_4	d_4	d_4					
			$[d_3]$	d_3	d_3					
			$[d_2]$	d_2			X			
			d_1	d_1	d_1					
		External surface			e_4					
				e_3	e_3				X	
			e_2	e_2	e_2					
			e_1	e_1	e_1					
Total						3	5	5	2	1

Trichobothrial patterns of the extinct Palaeopisthacanthidae Kjellesvig-Waering 1986 and Archaeobuthidae Lourenço, 2001 are too incomplete for meaningful comparison, in our opinion. 'Petite' trichobothria (*sensu* Vachon 1974) are denoted by square brackets. Hypothesis 1 (H1) is supported by the absence of chelal manus Eb_3, finger esb, and patellar em_1 in *Pseudochactas*, potential (unambiguous) synapomorphies for all Recent scorpions excluding *Pseudochactas*. Hypothesis 2 (H2) is supported by the presence of patellar d_3 and femoral d_2, i_2, i_3 and i_4 in *Pseudochactas*, potential (unambiguous) synapomorphies for *Pseudochactas* and the Buthidae *s. l.* The absence of chelal ib and V_2, patellar em_1, and femoral d_4 and d_5 unambiguously exclude *Pseudochactas* from Buthidae (H2b). Hypothesis 3 (H3) is supported by the presence of femoral e_3 in *Pseudochactas*, a potential (ambiguous) synapomorphy with Chaerilidae (e_3 also occurs in some Buthidae), and the absence of chelal manus V_2. The presence of chelal manus ib provides a potential (unambiguous) synapomorphy with Chaerilidae and other nonbuthids (Hypothesis 4).

Table 4. Pedipalp trichobothria of extant scorpion families supporting alternative hypotheses for the phylogenetic position of *Pseudochactas* Gromov 1998, according to the trichobothrial interpretations for Buthidae C.L. Koch 1837 (Type A), Chaerilidae Pocock 1893 (Type B) and Pseudochactidae Gromov 1998 (Type D) proposed here

		Buthidae						Pseudochactidae					Chaerilidae	Hypothesis				
		Androctonus	*Buthiscus*	*Centruroides*	*Liobuthus*	*Microbuthus*[a]	*Vachoniolus*	*Pseudochactas* 1	2	3	4	Preferred	*Chaerilus*	H1	H2	H2b	H3	H4
Chela — Finger — Internal surface	it	it	it	it	it	it	it	it	it	it	it	it	it					X
								ib₁	ib₁	ib₁	ib₁	ib₁	ib₁		X			
								[ib₂]	[ib₂]	[ib₂]	[ib₂]	[ib₂]						
Dorsal surface		dt	dt	dt	dt	dt	dt	dt	dt	dt	dt	dt	dt					
		db	db	db	db	db	db	db	db	db	db	db	db					
External surface		et	et	et	et	et	et	et	et	et	et	et	**et**	X				
		est	est	est	est	est	est	est	est	est	est	est	**est**	X				
Manus — External surface		[esb]	[esb]	[esb]	[esb]	[esb]	[esb]				**esb**	esb	esb	X				
		eb	eb	eb	eb	eb	eb	eb	eb	eb	**eb**	eb	eb	X				
		[et₄]	[et₄]	[et₄]	[et₄]		[et₄]											
		et₁	et₁	et₁	et₁	et₁	et₁	et₁	**Est**	**et₁**	et₁	et₁	et₁	X				
		Est	Est	Est	Est	Est	Est	**Est**	Est	Est	Est	Est	Est	X				
		[Eb₃]	[Eb₃]	[Eb₃]		[Eb₃]	[Eb₃]	[Eb₃]	[Eb₃]	[Eb₃]	[Eb₃]	[Eb₃]	Eb₃				X	
		Eb₂	Eb₂	Eb₂	Eb₂	Eb₂	Eb₂	Eb₂	Eb₂	Eb₂	Eb₂	Eb₂	Eb₂					
		Eb₁	Eb₁	Eb₁	Eb₁	Eb₁	Eb₁	Eb₁	Eb₁	Eb₁	Eb₁	Eb₁	Eb₁					
Ventral surface		V₁	V₁	V₁	V₁	V₁	V₁						**V₁**		X			
		V₂	V₂	V₂	V₂	V₂	V₂	V₂	V₂	V₂	V₂	V₂						
Patella — Internal surface		i₁	i₁	i₁	i₁	i₁	i₁	i₁	i₁	i₁	i₁	i₁	i₁					
													i₂			X		
Dorsal surface		[d₅]	[d₅]	[d₅]	[d₅]	[d₅]	[d₅]											
		d₄	d₄	d₄	d₄	d₄	d₄											
		d₃	d₃	d₃	d₃	d₃	d₃	d₃	d₃	d₃	d₃	d₃						
		d₂	d₂	d₂	d₂	d₂	d₂	d₂	d₂	d₂	d₂	d₂	d₂					
		d₁	d₁	d₁	d₁	d₁	d₁	d₁	d₁	d₁	d₁	d₁	d₁					
External surface		et₁	et₁	et₁	et₁	et₁	et₁	et₁	et₁	et₁	et₁	et₁	et₁					
		et₂	et₂	et₂	et₂	et₂	et₂	et₂	et₂	et₂	et₂	et₂	et₂					
		est₁	est₁	est₁	est₁	est₁	est₁	**[est₁]**	[est₁]	[est₁]	[est₁]	[est₁]	est₁					
		em₁	em₁	em₁	em₁	em₁	em₁	em₁	em₁	em₁	em₁	em₁	**em₁**		X			
					em₂		**em₂**											

Femur														3	6	5	2	1
Ventral surface																		
	esb_2 eb_1	esb_2 eb_1	esb_2 eb_1	esb_2 eb_1	esb_2 eb_1	esb_2 eb_1	esb_2 eb_1	esb_2 eb_1	esb_2 eb_1	esb_2 eb_1	esb_2 eb_1	esb_2 eb_1	esb_2 eb_1 $\boldsymbol{v_3}$ $\boldsymbol{v_2}$ $\boldsymbol{v_1}$				X	
Internal surface																X		
	$[i_4]$	$[i_4]$	i_4	$\boldsymbol{i_4}$	$[i_4]$	$[i_4]$	$[i_4]$	$[i_4]$	$[i_4]$	$[i_4]$	$[i_4]$					X		
	$[i_3]$	$[i_3]$	i_3	$[i_3]$	$[i_3]$	i_3										X		
	i_2	i_2	i_2	i_2	i_2	i_2	i_2	i_2	i_2	i_2	i_2							
	i_1	i_1	i_1	i_1	i_1	$\boldsymbol{i_1}$	i_1	i_1	i_1	i_1	i_1		i_1					
Dorsal surface																X		X
	$\boldsymbol{d_6}$	d_6	d_6	$\boldsymbol{d_6}$	d_6	$[d_6]$	$[d_6]$	$[d_6]$	$[d_6]$	$[d_6]$	$[d_6]$		d_6					
	d_5	d_5	d_5	d_5	d_5	d_5	d_5	d_5	d_5	d_5	d_5							
	$\boldsymbol{d_4}$					$[d_4]$	$[d_4]$	$[d_4]$	$[d_4]$	$[d_4]$	$[d_4]$		d_4					X
	d_3	$[d_3]$	d_3	$\boldsymbol{d_3}$	$[d_3]$	d_3	d_3	d_3	d_3	d_3	d_3		d_3					
	$[d_2]$	$[d_2]$	$\boldsymbol{[d_2]}$	$[d_2]$	$[d_2]$	$\boldsymbol{d_2}$	$[d_2]$	$[d_2]$	$[d_2]$	$[d_2]$	$[d_2]$							X
	d_1	$\boldsymbol{[d_2]}$	d_1	d_1	d_1	$[d_1]$	$[d_1]$	$[d_1]$	$[d_1]$	$[d_1]$	$[d_1]$		$\boldsymbol{d_1}$					
External surface													$\boldsymbol{e_4}$					
		$\boldsymbol{e_3}$	e_3	$\boldsymbol{e_3}$	e_3	$\boldsymbol{e_3}$	e_3	e_3	e_3	e_3	e_3		e_3				X	
	e_2	e_2	e_2	e_2	e_2	e_2	e_2	e_2	e_2	e_2	e_2		e_2					
	e_1	e_1	e_1	e_1	e_1	e_1	e_1	e_1	e_1	e_1	e_1		e_1					
Total														3	6	5	2	1

Trichobothrial patterns of the extinct Palaeopisthacanthidae Kjellesvig-Waering 1986 and Archaeobuthidae Lourenço 2001 are too incomplete for meaningful comparison, in our opinion. 'Petite' trichobothria (*sensu* Vachon 1974) are denoted by square brackets. Trichobothria in boldface differ from previous column. Preferred interpretation illustrated in Figs. 22–31. Hypothesis 1 (H1) is supported by the absence of three trichobothria on the chela of *Pseudochactas*, potential (unambiguous) synapomorphies for all other Recent scorpions: chelal manus *Est* and finger *esb* (interpretation 1), chelal manus Et_1 and finger *esb* (interpretation 2), chelal finger *eb* and *esb* (interpretation 3), or chelal finger *est* and *et* (interpretation 4, preferred); patellar em_1. Hypothesis 2 (H2) is supported by the presence of patellar d_3, femoral d_5, i_2, i_4 and i_3 (interpretation 1) or petite d_2 (interpretation 2, preferred), and the petite condition of chelal manus chela Eb_3, six potential (unambiguous) synapomorphies for *Pseudochactas* and the Buthidae. The absence of chelal manus *ib* and V_1, patellar em_1, presence of femoral d_4 and d_5 unambiguously exclude *Pseudochactas* from Buthidae (H2b). Hypothesis 3 (H3) is supported by the presence of femoral d_4 and e_3 in *Pseudochactas*, two potential (ambiguous) synapomorphies for *Pseudochactas* and Chaerilidae (d_4 and e_3 also occur in some Buthidae). The presence of ib_1 provides a potential (unambiguous) synapomorphy with Chaerilidae and other nonbuthids (Hypothesis 4).

a Other buthids in which trichobothria absent (Vachon 1974; Lamoral 1979; Sissom 1990; Lourenço and Vachon 1996; Soleglad and Fet 2001; Kovařík 2004; Prendini 2005): chelal manus Eb_3; *Karasbergia* Hewitt, 1913 (variable); *Microbuthus* Kraepelin, 1898; chelal manus Et_4: *Microbuthus*; patellar d_5: *Apistobuthus* Finnegan, 1932; *Karasbergia*; *Parabuthus* Pocock, 1890; *Razianus* Farzanpay, 1987; femoral d_2: *Alayotityus* Armas, 1973; *Apistobuthus* (variable); *Baloorthochirus* Kovařík, 1996; *Karasbergia*; *Lissothus* Vachon, 1948; *Microbuthus*; *Microtityus* Kjellesvig-Waering, 1966 (variable); *Orthochiroides* Kovařík, 1998; *Orthochirus* Karsch, 1891 (variable); *Pakistanorthochirus* Lourenço, 1997; *Zabius* Thorell, 1893.

weak granular dorsomedian carina; other surfaces of leg segments smooth. Legs I and II, tibiae, retrolateral margins each with scattered macrosetae, without spurs (Figs. 37 and 38); III and IV with spurs (Figs. 39 and 40). Basitarsi each with a few scattered macrosetae, a pro- and a retrolateral row of spinules, and a pair of pro- and retrolateral pedal spurs. Telotarsi each with a pair of ventrosubmedian rows of spinules, each spinule exhibiting subtle striations basally, extending to the midpoint or further (Soleglad and Fet 2003b, p. 18, 20, figs. 10–12); ventrosubmedian rows of macrosetae absent, only a few scattered macrosetae laterally; laterodistal lobes reduced and truncated; median dorsal lobe very short (ca. 10% of telotarsus length); ungues short (ca. 50% of telotarsus length), distinctly curved, equal in length; dactyl pronounced.

Coxosternum: Maxillary lobes (coxapophyses) I, distal edges rounded, unexpanded (not spatulate or dilate) anteriorly, terminating flush with lobes II (Figs. 12 and 14).

Sternum, Type 1 (Soleglad and Fet 2003a), pentagonal, not horizontally compressed, lateral sides parallel, slightly longer than wide (Figs. 17 and 18), external aspect flat, without a concave region or median furrow, posteromedian depression round, moderately developed, defined posteriorly by slight outer ridge; internal aspect flat, lacking significant three-dimensional (3D) form, single internal process subtle, mirroring external form. Mean coxosternal morphometric ratios, with mean values from Soleglad and Fet's (2003a, p. 25) table 1 provided (parentheses) for comparison: coxa II length/sternum anterior length: 1.19 (2.11); sternum posterior width/anterior width: 1.11 (1.19); coxa III length/II length: 1.01 (1.05); coxa IV length/II length: 1.67 (1.08); sternum length/posterior width: 1.11 (1.58).

Pectines: Each pecten with two distinct marginal lamellae present in ♂ (Fig. 17), three in ♀ (Fig. 18), 9–10 well delineated median lamellae present in ♂ and ♀. Fulcra present and distinct. Pectinal teeth present along entire posterior margin of each pecten (♂, ♀). First
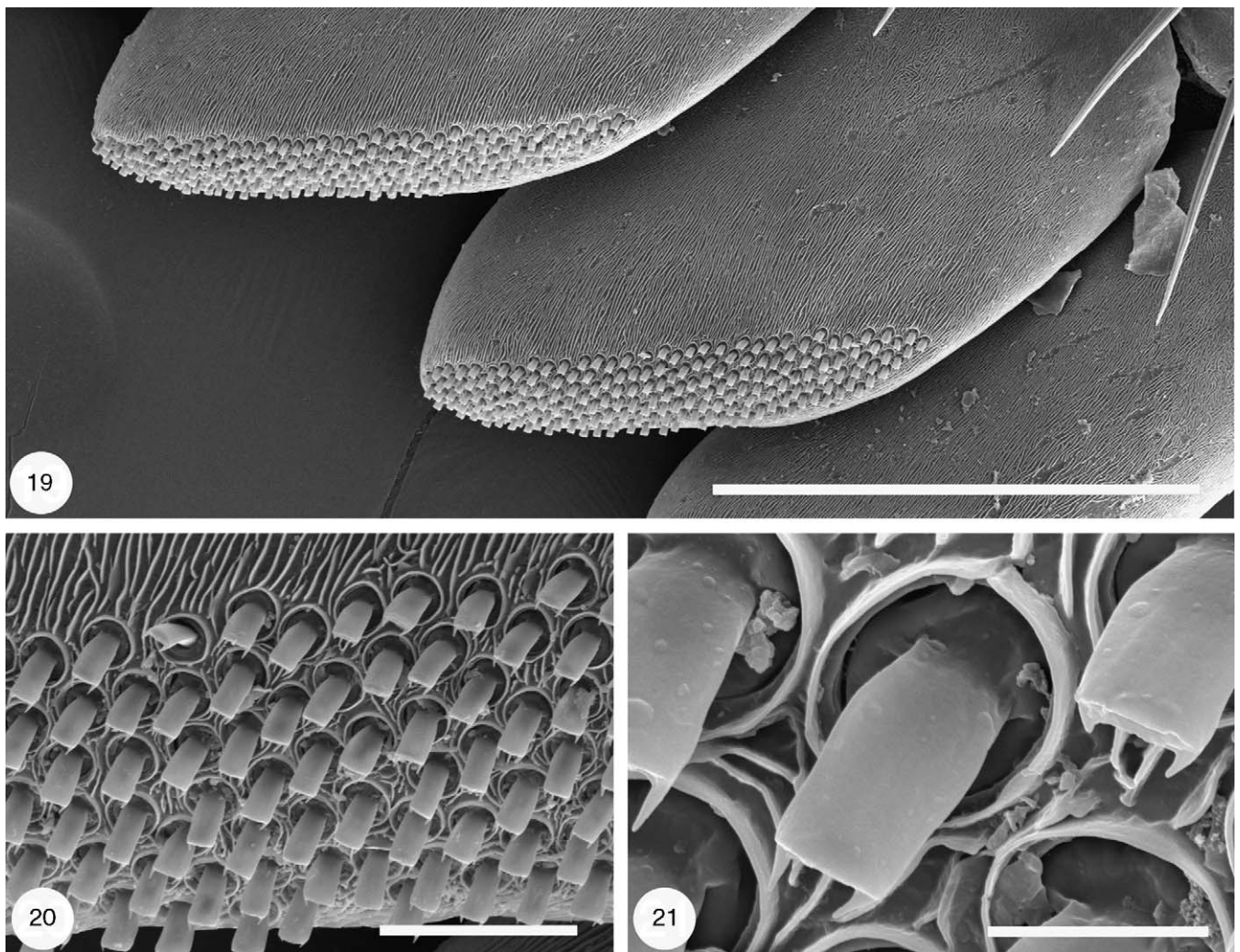
Figs. 19–21. *Pseudochactas ovchinnikovi* Gromov, 1998, SEM micrographs of dextral pecten of ♀ (AMNH). (19) Whole pecten. Scale bar = 200 µm. (20) Sensilla field. Scale bar = 20 µm. (21) Sensillae. Scale bar = 5 µm.

proximal median lamella and basal pectinal tooth unmodified. Pectinal tooth count: 10–11/10–11 ($\male$, $\female$).

Pectinal peg sensillae stout, square distally, with pair of processes at laterodistal margins (Figs. 19–21). Although the fine structure of the pectines has been studied sporadically for at least 20 years (e.g., Ivanov 1981), the potential significance of the sensillar field at the distal margin of each pectinal tooth was only appreciated more recently. For example, in several recent taxonomic papers, Lourenço (2002a, b, 2003a, b) incorporated scanning electron micrographs of the peg sensillae into descriptions of scorpion species and higher taxa. The variation in sensillar morphology documented thus far confirms their potential value as systematic characters for scorpions at multiple levels in the taxonomic hierarchy. Based on published data, we observe several simple characters pertaining to the shape of the individual sensillae: overall length; relative width of the distal end; shape of the distal end. The first of these is a continuous variable, difficult to define unambiguously. The length of the sensillae also varies spatially, i.e., sensillae become shorter at the anterior and basal margins and longer at the posterior margin.

Table 6 summarises some of these characters from published descriptions and our observations on *Pseudochactas*. The peg sensillae of *P. ovchinnikovi* are stout and square distally, as seen in buthid and liochelid scorpions, but differ from those of all other scorpions thus far studied in possessing a pair of processes at the laterodistal margins (Fig. 17), potentially adding another character, 'ornamentation', for the peg sensillae. The significance of these processes will only become apparent when the morphology of the peg sensillae has been studied in a wider taxon sample of scorpions (e.g., the peg sensillar morphology is currently undocumented in *Chaerilus*) than is possible at this time. It is also not yet understood how variation in sensillar morphology relates to environmental variables such as humidity or aridity.

Genital operculum: Operculum completely divided longitudinally. Prominent genital papillae visible entire length of operculum ($\male$), absent ($\female$). Genital plugs observed in some females (Fig. 45).

Mesosoma: Pre-tergites smooth and shiny. Post-tergites I–VI very finely and uniformly granular, granulation becoming slightly coarser near posterior
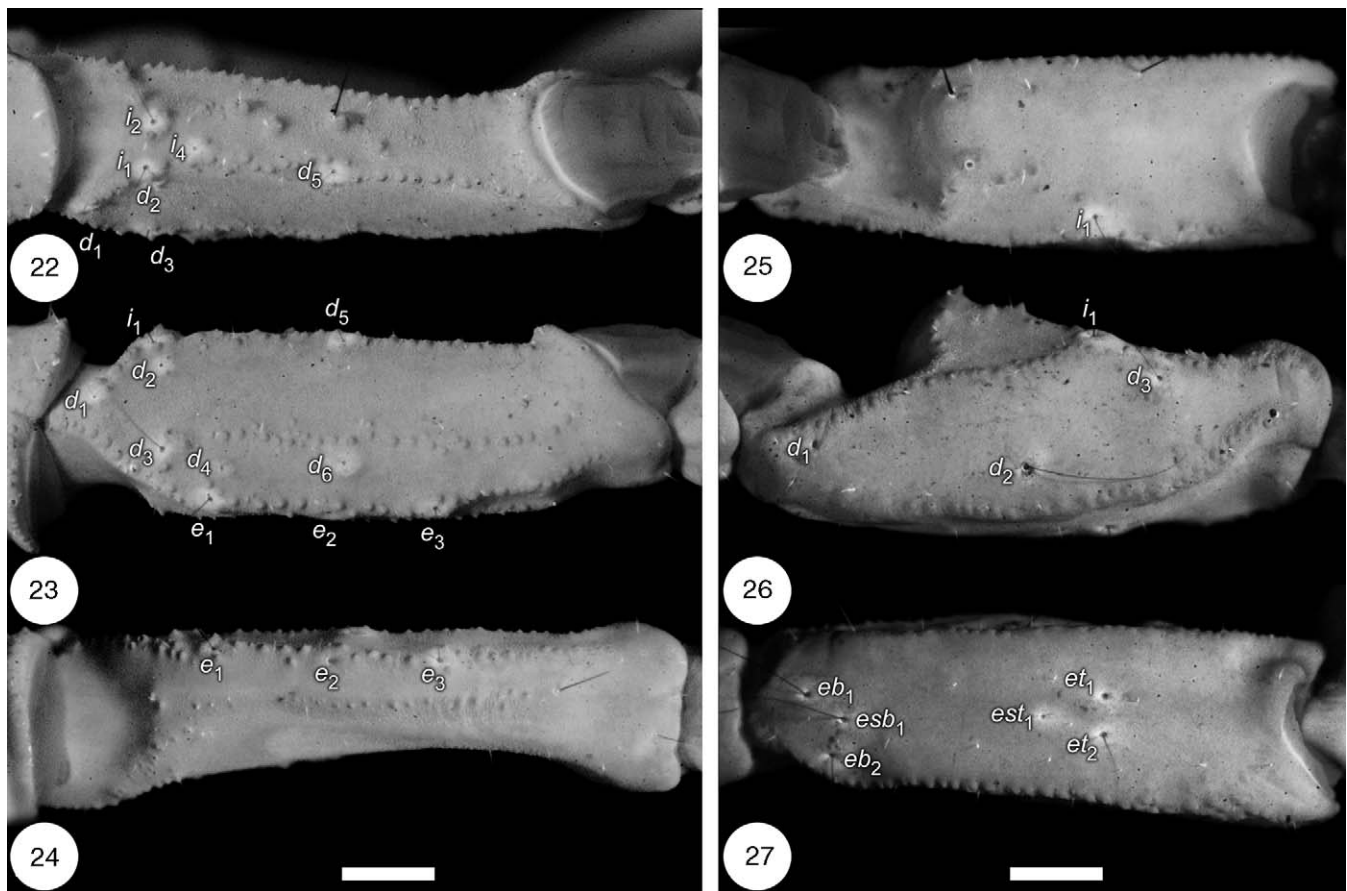
Figs. 22–27. *Pseudochactas ovchinnikovi* Gromov, 1998, carinae, trichobothria and macrosetae on dextral pedipalp segments of $\female$ (AMNH). (**22**) Femur, internal aspect. (**23**) Femur, dorsal aspect. (**24**) Femur, external aspect. (**25**) Patella, internal aspect. (**26**) Patella, dorsal aspect. (**27**) Patella, external aspect. Scale bars = 1 mm.
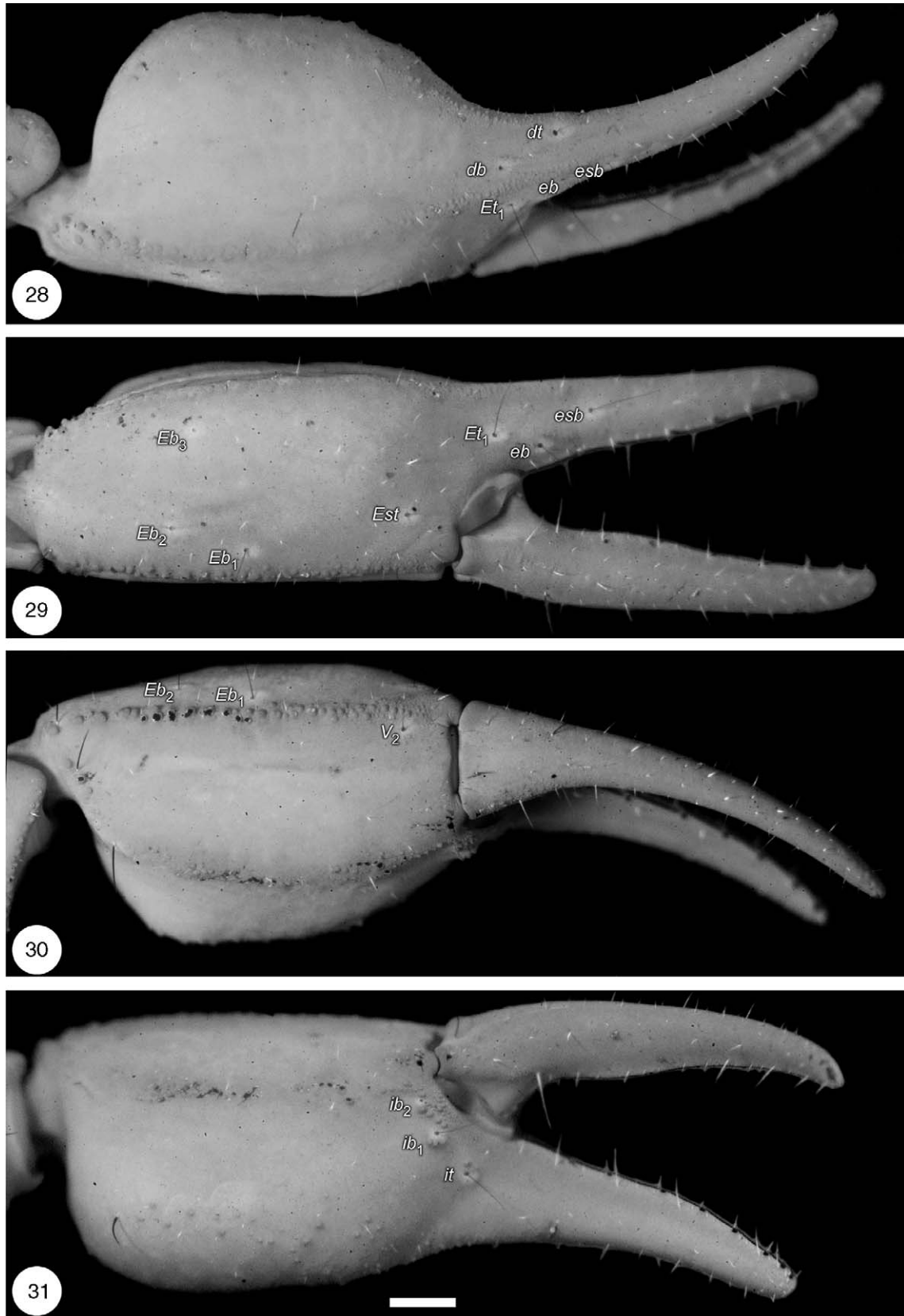
Figs. 28–31. *Pseudochactas ovchinnikovi* Gromov, 1998, carinae, trichobothria and macrosetae on dextral pedipalp chela of ♀ (AMNH). (**28**) Dorsal aspect. (**29**) External aspect. (**30**) Ventral aspect. (**31**) Internal aspect. Scale bar = 1 mm.
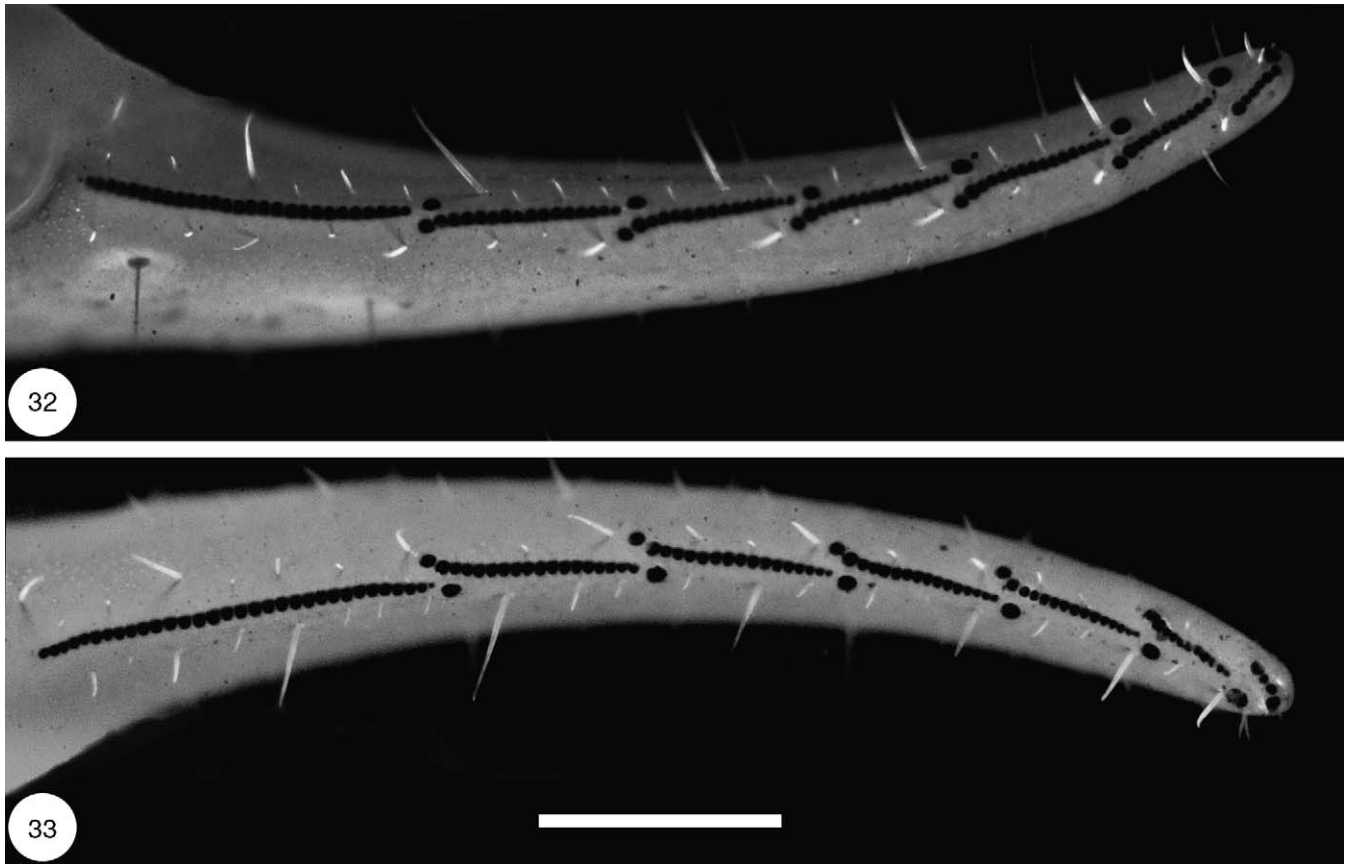
Figs. 32–33. *Pseudochactas ovchinnikovi* Gromov, 1998, oblique granular subrows of median denticle rows on sinstral pedipalp chela fingers of ♀ (AMNH). (**32**) Fixed finger. (**33**) Movable finger. Scale bar = 1 mm.

edges, acarinate, each with a pair of shallow submedian depressions (Figs. 11 and 13); VII smooth, with pair of costate granular dorsosubmedian and dorsolateral carinae almost reaching posterior edge of segment. Sternites entirely smooth, acarinate (Figs. 12 and 14); surfaces with scattered macrosetae; distal margins each with sparse row of macrosetae; respiratory spiracles small, oval in shape (Fig. 17). Sternite VII width 41% (37–45%) greater than length (Table 5).

Metasoma and telson: Metasoma relatively short, total length 30% greater than combined length of prosoma and mesosoma in ♂, 19% (12–26%) greater in ♀ (Table 5); segments I–V progressively increasing in length, width of length for segment I, 124% in ♂, 149% (129–169%) in ♀; for II, 100% in ♂, 110% (100–121%) in ♀; for III, 92% in ♂, 93% (86–100%) in ♀; for IV, 65% in ♂, 70% (65–76%) in ♀; and for V, 37% in ♂, 40% (37–43%) in ♀. Telson large, 8% wider than metasomal segment V in ♂, 15% (10–20%) wider in ♀, suboval, with flattened dorsal surface and rounded ventral surface (Figs. 34–36), height 35% (31–39%) of length. Aculeus short, shallowly curved, 22% of vesicle length in ♂, 29% (28–30%) in ♀.

Metasoma almost apilose, very sparsely covered in short microsetae. Ten carinae on segments I–III, eight on segment IV, nine on segment V (Figs. 34–36). Dorsosubmedian carinae well developed, costate granular throughout length of segments I–IV, absent on segment V; each terminating distally with a slightly enlarged granule on segments I–III; converging distally. Dorsolateral carinae well developed, costate granular throughout length of segments I–V; converging distally on segments I and V, subparallel on segments II–IV. Median lateral carinae well developed, costate granular throughout length of segment I, weak, granular, becoming obsolete proximally on segments II and III, absent on segment IV, reduced to a few granules medially or absent on segment V. Ventrolateral carinae well developed, costate granular, but becoming obsolete distally on segment I, continuous throughout length of segments II–V, converging distally on segments I and V, subparallel on segments II–IV. Ventrosubmedian carinae absent or obsolete on segment I, obsolete, costate on segment II, well developed, costate granular throughout length of segments III–V, subparallel on segments II and III, converging distally on segments IV and V. Ventromedian carina on segment V observed in some specimens as a weak medial row of granules between ventrosubmedian carinae. Intercarinal surfaces smooth. Telson vesicle smooth dorsally, with scattered

Table 5. Meristic data for *Pseudochactas ovchinnikovi* Gromov, 1998

		♂	♀	♀	♀	♀	♀	♀	♀	♀	♀
Total length[a]		19.4	31.95	30.46	30.10	29.65	–	25.20	24.85	24.00	22.55
Carapace	Length	2.30	3.70	3.85	3.75	3.80	3.50	3.30	3.20	3.00	2.90
	Anterior width	1.40	2.10	2.15	2.10	2.20	1.95	1.90	1.80	1.80	1.60
	Posterior width	2.30	3.70	3.70	3.60	3.50	3.40	3.10	3.05	3.10	2.90
Pedipalp	Total length	10.15	16.80	16.45	15.65	16.55	15.10	14.05	13.30	12.90	12.05
Chela	Length[b]	4.50	7.40	7.30	6.85	7.20	6.80	6.20	5.70	5.60	5.20
	Width	1.40	2.50	2.70	2.30	2.60	2.30	2.00	1.90	1.90	1.70
	Height	1.20	2.00	2.10	1.90	1.90	1.80	1.60	1.50	1.50	1.50
	Length of ventroexternal carina	2.00	3.30	3.40	3.20	3.30	3.10	2.80	2.70	2.60	2.40
	Length of movable finger	2.50	3.75	4.00	3.60	3.80	3.60	3.30	3.10	2.90	2.90
	Granular rows, fixed finger (left/right)	7/7	7/7	7/7	7/7	7/7	7/7	7/7	7/7	7/7	7/7
	Granular rows, movable finger (left/right)	7/7	7/7	7/–[c]	7/7	7/7	7/7	7/7	7/7	7/7	7/7
Patella	Length	2.25	3.70	3.60	3.50	3.55	3.20	3.00	2.90	2.90	2.70
	Width	1.00	1.75	1.80	1.60	1.70	1.50	1.40	1.30	1.30	1.25
	Height	0.85	1.40	1.38	1.19	1.30	1.10	1.03	1.00	0.98	0.98
Femur	Length	2.40	3.80	3.75	3.60	3.80	3.50	3.20	3.15	3.00	2.75
	Height	0.68	1.18	1.05	1.00	1.15	0.98	0.93	0.90	0.83	0.80
	Width	0.80	1.25	1.30	1.20	1.20	1.20	1.05	1.05	1.00	1.00
Trochanter	Length	1.00	1.90	1.80	1.70	2.00	1.60	1.65	1.55	1.40	1.40
Mesosoma	Total length[d]	5.70	10.00	9.61	10.10	8.95	8.60	8.00	7.75	8.20	7.55
Sternum	Length	1.05	1.75	1.70	1.63	1.75	1.63	1.53	1.43	1.30	1.25
	Anterior length	0.56	0.85	0.85	0.86	0.85	0.78	0.78	0.73	0.68	0.68
	Anterior width	0.93	1.35	1.35	1.33	1.40	1.28	1.19	1.15	1.13	1.08
	Posterior width	1.05	1.55	1.63	1.45	1.45	1.43	1.23	1.25	1.34	1.13
Leg coxa II	Length	1.09	1.60	1.68	1.58	1.65	1.54	1.40	1.38	1.38	1.25
Leg coxa III	Length	1.05	1.59	1.70	1.63	1.69	1.55	1.40	1.43	1.48	1.26
Leg coxa IV	Length	1.63	2.70	2.86	2.73	2.75	2.60	2.41	2.34	2.28	2.08
Pectines	Total length	1.70	2.20	1.95	2.00	2.20	1.90	1.80	1.70	1.70	1.50
	Length along dentate margin	1.50	1.95	1.55	1.70	1.70	1.55	1.40	1.30	1.40	1.20
	Tooth count (left/right)	11/10	11/10	10/10	10/11	11/11	11/11	10/11	11/11	11/11	11/10
Sternite VII	Length	1.20	2.20	1.90	1.65	1.90	1.70	1.60	1.50	1.50	1.50
	Width	1.95	3.50	3.35	3.00	3.35	2.95	2.65	2.60	2.60	2.40
Metasoma	Total length[e]	11.40	18.25	17.00	16.25	16.90	–	13.90	13.90	12.80	12.10
Metasoma I	Length	1.05	1.70	1.40	1.20	1.30	1.30	1.30	1.20	1.00	1.10
	Width	1.30	2.20	2.20	2.00	2.20	1.85	1.75	1.70	1.65	1.55
	Height	1.09	1.75	1.65	1.55	1.63	1.48	1.45	1.31	1.30	1.25
Metasoma II	Length	1.20	1.90	1.80	1.60	1.70	1.60	1.40	1.40	1.20	1.30
	Width	1.20	1.90	1.90	1.75	1.90	1.65	1.60	1.50	1.45	1.40
	Height	1.09	1.65	1.65	1.48	1.58	1.40	1.36	1.28	1.29	1.20
Metasoma III	Length	1.30	2.20	2.00	1.90	2.00	1.90	1.50	1.60	1.50	1.40
	Width	1.20	1.90	1.90	1.70	1.90	1.65	1.50	1.45	1.40	1.30
	Height	1.04	1.60	1.65	1.50	1.73	1.40	1.30	1.25	1.25	1.16
Metasoma IV	Length	1.70	2.70	2.50	2.40	2.50	2.30	2.00	2.00	1.80	1.70
	Width	1.10	1.75	1.90	1.70	1.70	1.50	1.45	1.40	1.35	1.25
	Height	1.00	1.50	1.60	1.43	1.44	1.33	1.21	1.18	1.18	1.05
Metasoma V	Length	3.00	4.60	4.30	4.20	4.30	4.00	3.50	3.60	3.40	3.10
	Width	1.10	1.75	1.85	1.60	1.60	1.50	1.35	1.35	1.30	1.15
	Height	0.95	1.40	1.50	1.35	1.40	1.25	1.18	1.15	1.15	0.98
Telson	Total length	3.15	5.15	5.00	4.95	5.10	4.03[c]	4.20	4.10	3.90	3.50
	Aculeus length	0.70	1.50	1.50	1.40	1.50	–	1.20	1.20	1.10	1.05
	Vesicle length	2.10	3.60	3.50	3.40	3.50	3.30	3.00	2.80	2.70	2.30
	Vesicle width	1.20	2.00	2.10	1.90	2.00	1.80	1.50	1.60	1.50	1.30
	Vesicle height	1.10	1.80	1.85	1.60	1.85	1.70	1.40	1.50	1.30	1.10

Measurements follow Stahnke (1970), except those for the coxosternal region, which follow Soleglad and Fet (2003a).
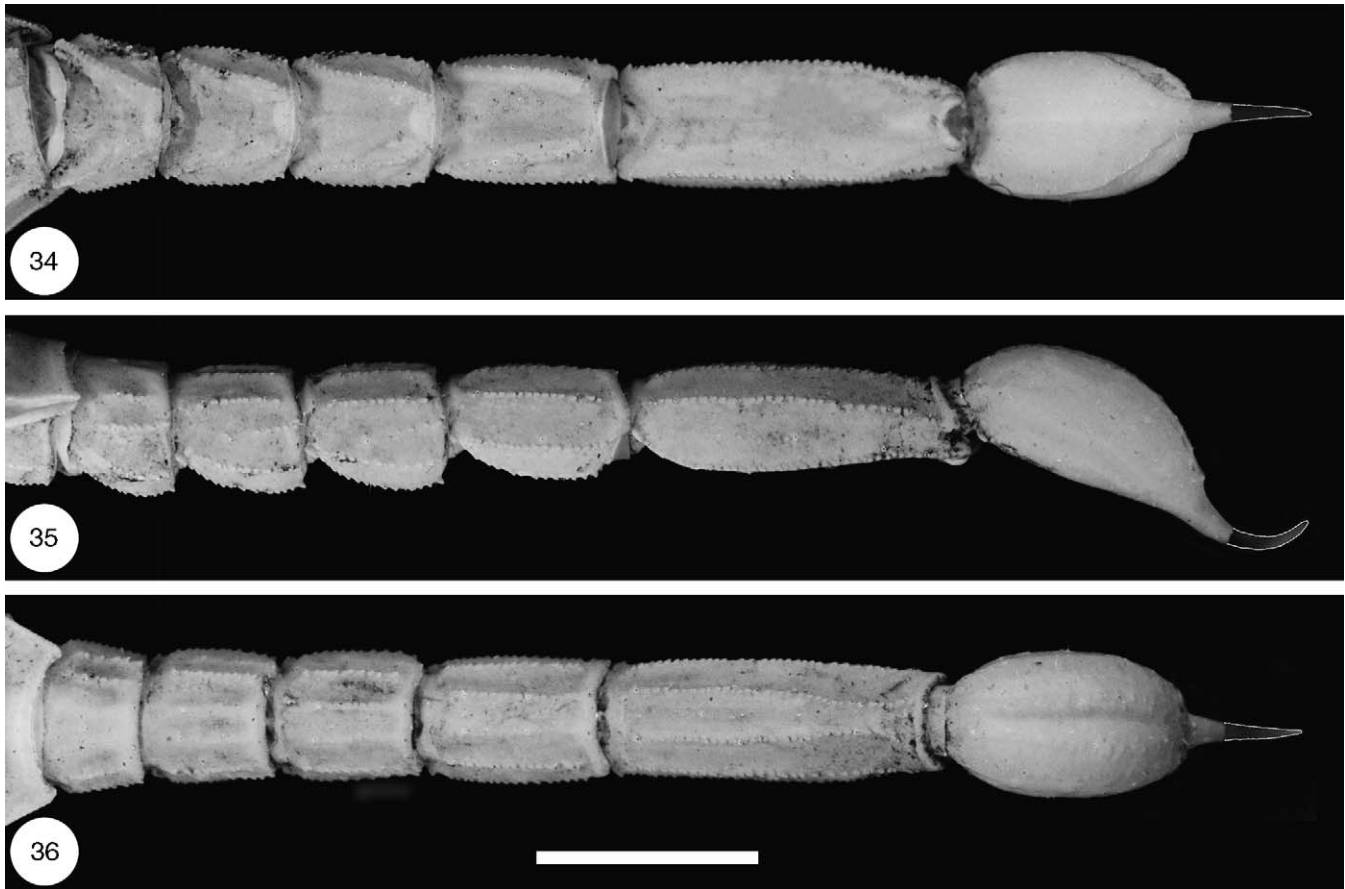[a]Sum of carapace, tergites I–VII, metasomal segments I–V, and telson.
[b]Measured from base of condyle to tip of fixed finger.
[c]Damaged.
[d]Sum of tergites I–VII.
[e]Sum of metasomal segments I–V and telson.

Figs. 34–36. *Pseudochactas ovchinnikovi* Gromov, 1998, metasoma and telson of ♀ (AMNH). (**34**) Dorsal aspect. (**35**) Lateral aspect. (**36**) Ventral aspect. Scale bar = 10 mm.

granules laterally and ventrally; aculeus without a subaculear tubercle ventrally. Venom glands thin-walled, simple and unfolded, confirming the observations of Soleglad and Fet (2003b, p. 60, Fig. 108) (Figs. 37–40).

Male reproductive organs: Paraxial organs and hemi-spermatophore unlike those of any other scorpion (Figs. 41–44), extremely small (1.45 mm long and 0.45 mm wide), associated with a single glandular structure. Hemispermatophore comprising a shaft, connecting distally to a thick, ring-like structure, here considered homologous to the flagellum (the flagellum of buthid scorpions and the distal lamella of nonbuthid scorpions are also considered homologous). The flagellum possesses fine ribbing and is folded into a horseshoe shape. A poorly sclerotised cuticular lobe is observed ventral to the flagellar area (Figs. 42 and 43). Our understanding of the capsule area is still incomplete but there appear to be several lobes and a large cuticular process (Fig. 44), the latter, based on its placement in the capsule, most likely being homologous with the structure usually referred to as the basal lobe in buthid hemispermatophores. The reason previous authors were

unable to locate the hemispermatophore appears to be due to the fact that (1) most of the specimens purported to be adult males are, in fact, subadults and (2) the hemispermatophore is extremely small and not easily recognized (Fig. 45).

Female reproductive organs: Most authors recognise two types of ovariuterine anatomy in scorpions (Birula 1917; Pavlovsky 1924, 1925; Werner 1934; Millot and Vachon 1949; Mathew 1956; Francke 1982c; Stockwell 1989; Hjelle 1990; Sissom 1990; Prendini 2000a; Soleglad and Fet 2003b). Buthidae possess an eight-celled ovariuterus, with five transverse ovarian tubes (or anastomoses, the connections between longitudinal and transverse tubes), whereas the nonbuthid families possess a six-celled ovariuterus with four transverse ovarian tubes. A third condition is reported from several species in the buthid genus *Tityus*, in which only the anterior and posterior transverse ovarian tubes are present, forming a two-celled ovariuterus (de Toledo-Piza 1939a, b; Matthiesen 1970). An alternative interpretation for the condition observed in *Tityus* is that the transverse ovarian tubes are lacking, the 'cells' being formed by the longitudinal tubes alone (Francke in

Table 6. Comparison of the pectinal peg sensillae of several scorpion species with *Pseudochactas* Gromov, 1998

	Overall length	Distal end width	Distal shape	Ornamentation
Buthidae *s.l.*				
Ananteris balzanii Thorell, 1891	Moderately elongated	Slightly expanded distally	Round	Absent
Birulatus israelensis Lourenço, 2002	Short	Cylindrical	Square	Absent
Grosphus ankarafantsika Lourenço, 2003	Short	Cylindrical	Square	Absent
Lychasioides amieti Vachon, 1974	Elongated	Tapering	Round	Absent
Mesobuthus eupeus (C.L. Koch, 1839)	Short, stout	Cylindrical	Square	Absent
Microananteris minor Lourenço, 2003	Elongated	Tapering	Round	Absent
Microcharmus fischeri Lourenço, 1998	Elongated	Tapering	Round	Absent
Heteroscorpionidae				
Heteroscorpion goodmani Lourenço, 1996	Moderately elongated	Slightly tapered	Round	Absent
Heteroscorpion magnus Lourenço, 2002	Moderately elongated	Slightly tapered	Round	Absent
Heteroscorpion opisthacanthoides (Kraepelin, 1896)	Moderately elongated	Slightly tapered	Round	Absent
Liochelidae				
Opisthacanthus madagascariensis Kraepelin, 1894	Moderately elongated	Cylindrical	Square	Absent
Palaeocheloctonus pauliani Lourenço, 1996	Moderately elongated	Cylindrical to slightly expanded	Square	Absent
Pseudochactidae				
Pseudochactas ovchinnikovi Gromov, 1998	Short to slightly elongated	Expanded distally	Square	Pair of laterodistal processes

Data from Ivanov (1981, Figs. 45–47) and Lourenço (2002a, Figs. 8–10; 2002b, Figs. 29, 32, 33, 36, 37, 41, 45–47; 2003a, Figs. 3, 4, 7, 8, 11, 12, 15, 16; 2003b, Figs. 20, 21).

Hjelle 1990). The scorpion taxa in which the ovariuterine anatomy has been documented are summarised in Table 7 for comparison with *Pseudochactas*. The ovariuterus of *Pseudochactas* comprises a reticulate mesh of six cells (Figs. 46 and 47), as in most nonbuthid scorpions. Oocytes are contained in sessile follicles directly contacting the ovaruterine tubes. Development is therefore apoikogenic (Laurie 1896).

3.3.5. Geographic variation
No significant variation.

3.3.6. Ontogenetic variation
Juvenile and subadult *Pseudochactas* are paler in color and less sclerotized than adults, and usually exhibit a distinctly distended mesosoma containing a large mass of hepatopancreas, when dissected. Males and females closely resemble one another externally until the final instar. However, juveniles and subadults 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 during this study. Upon dissection, none of these specimens possessed gonads or hemispermatophores, and we conclude that they 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) than most of the other males examined. More adult male specimens must be collected to determine whether penultimate instars are larger than sexually mature males, or the sole confirmed adult male specimen is simply a small adult.

3.3.7. Sexual dimorphism
The genital papillae, visible the entire length and thus completely separating the two sclerites of the genital operculum (Figs. 12 and 17), are the characters of primary external sexual dimorphism in the male. The two sclerites of the genital operculum are also separated for most of their length in the female, although genital papillae are absent (Figs. 14 and 18). Few secondary sexual characters are observed in the only confirmed adult male, compared with adult females and juveniles of both sexes. The most obvious are the slightly better developed pectines, the teeth of which are somewhat larger, although similar in number (Figs. 17 and 18;
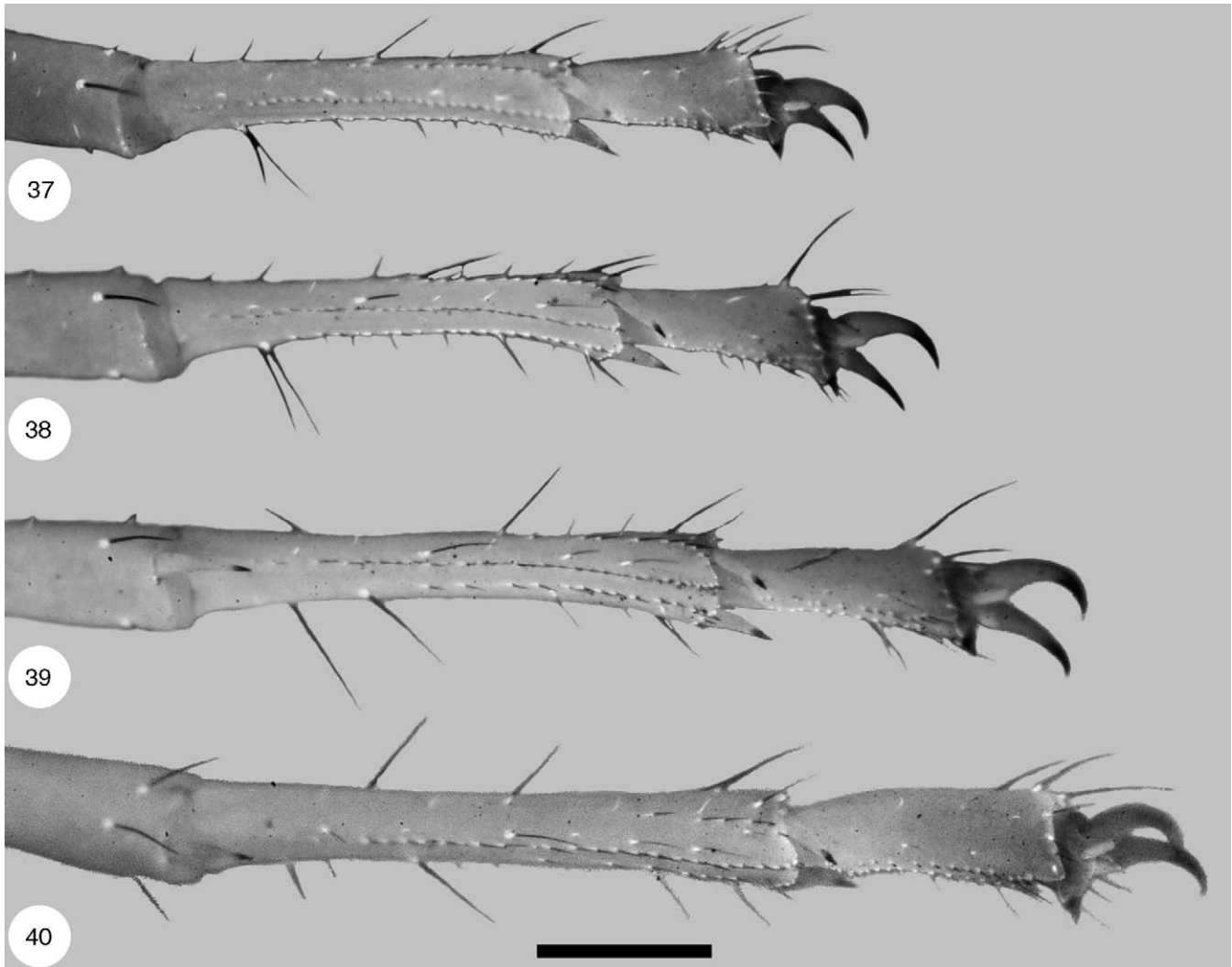
Figs. 37–40. *Pseudochactas ovchinnikovi* Gromov, 1998, sinstral legs I–IV, basitarsus and telotarsus of ♀ (AMNH). (**37**) Leg I, prolateral aspect. (**38**) Leg II, prolateral aspect. (**39**) Leg III, prolateral aspect. (**40**) Leg IV, prolateral aspect. Scale bar = 1 mm.

Table 5). In addition, the adult male is proportionally more slender (Figs. 11 and 12), with a slightly longer metasoma and telson, slightly longer fingers on the pedipalp chela, and slightly more pronounced granulation on the carapace, pedipalps, and tergites, than the adult female (Figs. 13 and 14).

3.3.8. Distribution

Pseudochactas is presently known from only a few localities in the Babatag mountain range of southeastern Uzbekistan and a single locality in the Aruktau mountain range of southwestern Tajikistan. The localities in Uzbekistan are separated from the locality in Tajikistan by the Kofirnixon River (Fig. 3). Most of the specimens originate from Dikhana Canyon, on the eastern slopes of the Babatag range (Figs. 4–7). All the known locality records occur at fairly low altitude (720–1010 m) in a semi-arid savanna dominated by

sparse grasses, xerophile perennials and Pistachio trees (Gromov 1998).

3.3.9. Ecology

Pseudochactas is a lapidicolous species (Prendini 2001b) that inhabits the cracks and crevices of near-vertical mud walls on steep, eroded riverbanks and gullies (Figs. 6 and 7). 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 2003b; Fet et al. 2004). During the 2003 expedition, specimens were found to be more abundant on humid nights, especially following convectional thunderstorms that occurred during the late afternoon. Several specimens were found very close to the edge of a small stream, sitting on moist mud banks, suggesting a requirement for high humidity. It is not
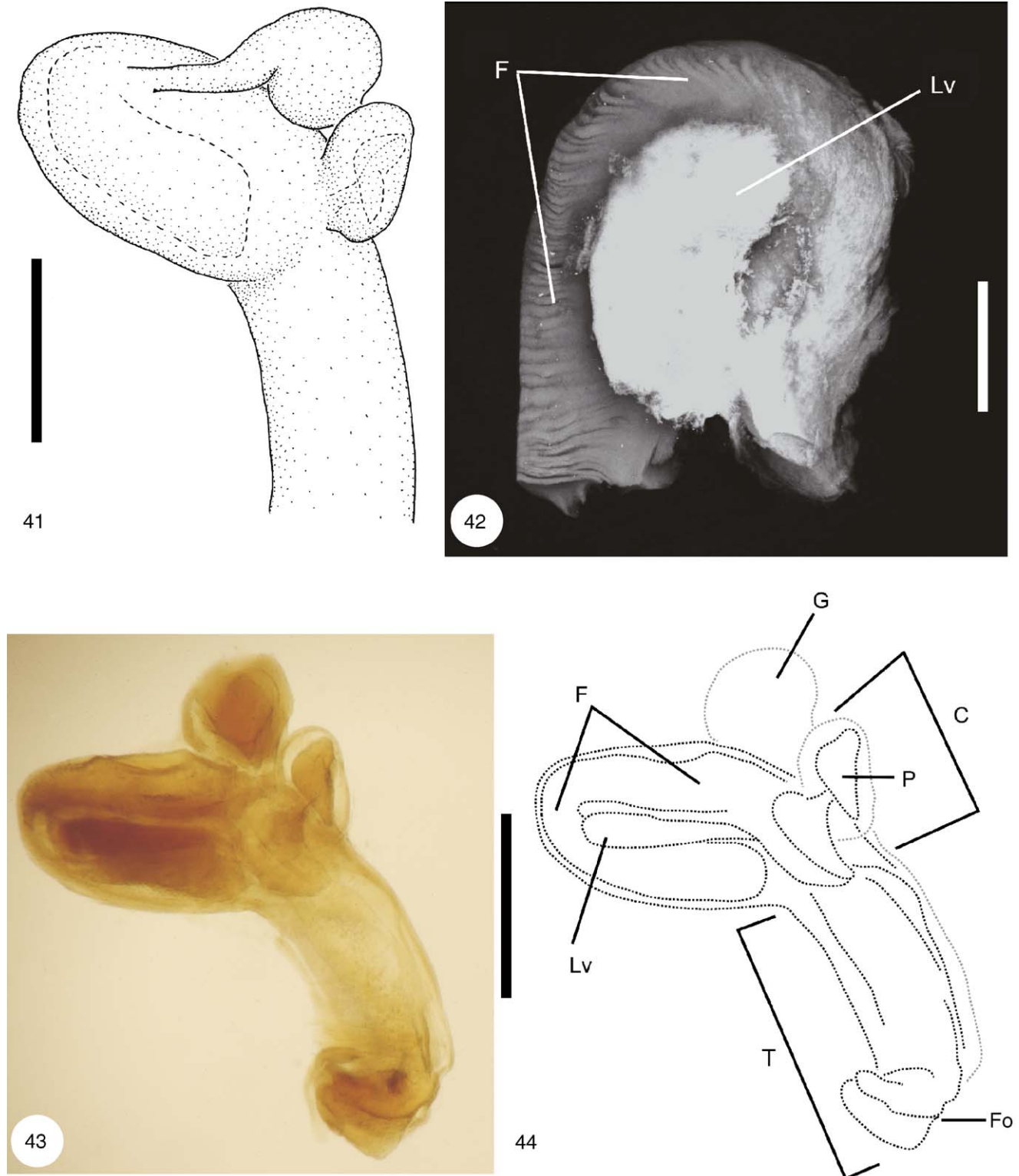
Figs. 41–44. *Pseudochactas ovchinnikovi* Gromov, 1998, paraxial organ and hemispermatophore of ♂ (AMNH). (**41**). Paraxial organ and dextral hemispermatophore, ental aspect. (**42**) Confocal 3D-reconstruction of flagellar region of sinstral hemispermatophore, ventral aspect. (**43**) Dextral paraxial organ, cleared in clove oil, ental aspect. (**44**) Hemispermatophore outline (black), indicating capsule region (C), flagellum (F), foot (Fo), gland (G), ventral lobe (Lv), process (P), and trunk (T). Scale bars = 50 μm (41, 43, 44), 25 μm (**42**).
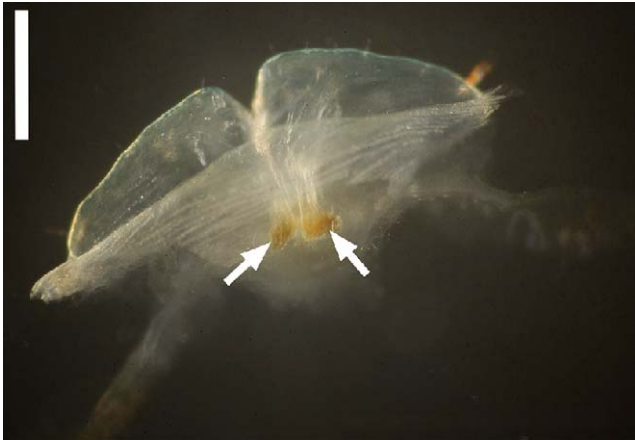
Fig. 45. *Pseudochactas ovchinnikovi* Gromov, 1998, genital operculum and genital plugs of ♀ (AMNH), slide mounted in 85% lactic acid (arrows indicate two genital plugs). Scale bar = 50 μm.

known whether *Pseudochactas* spends most of the dry season in hibernation, as suggested by Soleglad and Fet (2003b) and Fet et al. (2004). Specimens were observed to be actively moving on the mud faces, suggesting that 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, *Pseudochactas* was collected in sympatry with three other scorpion species, all buthids: *Mesobuthus eupeus* (C.L. Koch, 1839), *Mesobuthus* cf. *tamulus* (Fabricius, 1798), and *Orthochirus scrobiculosus* (Grube, 1873). The much larger *M.* cf. *tamulus* was common in the cracks and crevices of the mud walls inhabited by *Pseudochactas*, 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.

3.3.10. Conservation status

Despite the low agricultural potential of the semi-arid savanna in which *Pseudochactas* occurs, the habitat is heavily utilised 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 (Figs. 4–7). The impact of this habitat degradation on *Pseudochactas* is unknown but presumed to be negative. The threat of habitat degradation, taken together with the very restricted distributional range, which is completely unprotected, and the biological importance of this species as a monotypic family and basal lineage of extant scorpions, warrants its assignment to the Endangered Category of the IUCN Red List. This

species is characterised 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 activities) 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.

4. Discussion

The following discussion, summarised in Appendix A, evaluates the evidence supporting three hypotheses thus far proposed to account for the phylogenetic position of *Pseudochactas*, and a fourth hypothesis not previously considered. The discussion concludes with an assessment of the implications of alternative hypotheses for the historical biogeography of *Pseudochactas*.

### 4.1. Non-evidence: autapomorphies and uninformative characters

Gromov (1998) noted or illustrated six characters of *Pseudochactas* that he considered to be unique among Recent scorpions: a single pair of lateral ocelli; a pair of circumocular sutures with a U-shaped configuration; the absence of basal teeth on the dorsal edge of the cheliceral movable finger; a pair of ventrosubmedian rows of spinules on the telotarsi; a pair of ventrosubmedian carinae on metasomal segment V; the trichobothrial pattern. Soleglad and Fet (2003b), followed by Fet et al. (2004), confirmed Gromov's (1998) observations, as have we, and cited three of them (the Type D trichobothrial pattern; the absence of basal teeth; the paired ventrosubmedian rows of spinules) as diagnostic 'synapomorphies' of *Pseudochactas*. The unique laterodistal processes on the pectinal peg sensillae, newly documented in the present study, might be added to this list.

To the extent that they are autapomorphic, the U-shaped circumocular sutures and single pair of lateral ocelli are uninformative about the phylogenetic position of *Pseudochactas*. The absence of basal teeth, which also occurs in the superstitioniid, *Typhlochactas mitchelli* Sissom, 1988, presumably evolved independently in both taxa, and is probably autapomorphic and uninformative regarding the phylogenetic position of *Pseudochactas*. Some uncertainty exists as to whether the paired ventrosubmedian rows of spinules are autapomorphic or plesiomorphic in *Pseudochactas* (Soleglad and Fet

Table 7. Comparison of the number of 'cells' in the ovariuterus of several scorpion species with *Pseudochactas* Gromov, 1998 with original citations

Eight-celled	Buthidae *s. l.*	*Androctonus australis* (Linnaeus, 1758)	Pavlovsky 1924, 1925
		Anomalobuthus rickmersi Kraepelin, 1900	Pavlovsky 1924, 1925
		Babycurus buettneri Karsch, 1886	Pavlovsky 1924, 1925
		Buthus occitanus (Amoureux, 1789)	Pavlovsky 1924, 1925
		Centruroides elegans (Thorell, 1876)	Pavlovsky 1924, 1925
		Centruroides margaritatus (Gervais, 1841)	Pavlovsky 1924, 1925
		Compsobuthus acutecarinatus (Simon, 1882)	Pavlovsky 1924, 1925
		Grosphus madagascariensis (Gervais, 1843)	Pavlovsky 1924, 1925
		Hottentotta eminii (Pocock, 1890)	Pavlovsky 1924, 1925
		Hottentotta hottentotta (Fabricius, 1787)	Pavlovsky 1924, 1925
		Hottentotta judaicus (Simon, 1872)	Pavlovsky 1924, 1925
		Hottentotta saulcyi (Simon, 1880)	Pavlovsky 1924, 1925
		Isometrus maculatus (DeGeer, 1778)	Pavlovsky 1924, 1925
		Leiurus quinquestriatus (Ehrenberg, 1828)	Pavlovsky 1924, 1925
		Liobuthus kessleri Birula, 1898	Pavlovsky 1924, 1925
		Lychas marmoreus (C.L. Koch, 1844)	Pavlovsky 1924, 1925
		Lychas mucronatus (Fabricius, 1798)	Pavlovsky 1924, 1925
		Lychas tricarinatus (Simon, 1884)	Pavlovsky 1924, 1925; Mathew 1962
		Lychas variatus (Thorell, 1876)	Pavlovsky 1924, 1925
		Mesobuthus caucasicus (Nordmann, 1840)	Pavlovsky 1924, 1925
		Mesobuthus eupeus (C.L. Koch, 1839)	Pavlovsky 1924, 1925
		Odonturus dentatus Karsch, 1879	Pavlovsky 1924, 1925
		Orthochirus scrobiculosus (Grube, 1873)	Pavlovsky 1924, 1925
		Parabuthus leiosoma (Ehrenberg, 1828)	Pavlovsky 1924, 1925
		Parabuthus planicauda (Pocock, 1889)	Pavlovsky 1924, 1925
		Rhopalurus rochai Borelli, 1910	Matthiesen 1970
		Tityus bolivianus Kraepelin, 1895	Pavlovsky 1924, 1925
		Tityus cambridgei Pocock, 1897[a]	Pavlovsky 1924, 1925
		Uroplectes fischeri (Karsch, 1879)	Pavlovsky 1924, 1925
		Uroplectes formosus Pocock, 1890	Pavlovsky 1924, 1925
		Uroplectes lineatus (C.L. Koch, 1844)	Pavlovsky 1924, 1925
		Uroplectes triangulifer (Thorell, 1876)	Pavlovsky 1924, 1925
Six-celled	Bothriuridae	*Bothriurus bonariensis* (C.L. Koch, 1842)	Pavlovsky 1924, 1925
		Brachistosternus intermedius Lönnberg, 1902	Pavlovsky 1924, 1925
	Chactidae	*Broteochactas gollmeri* (Karsch, 1879)	Pavlovsky 1924, 1925
		Brotheas subgranosus Pocock, 1898	Pavlovsky 1924, 1925
		Teuthraustes witti (Kraepelin, 1896)	Pavlovsky 1924, 1925
	Chaerilidae	*Chaerilus variegatus* Simon, 1877	Pavlovsky 1924, 1925
	Euscorpiidae	*Euscorpiops montanus* Karsch, 1879	Pavlovsky 1924, 1925
		Euscorpius flavicaudis (DeGeer, 1778)	Pavlovsky 1924, 1925
		Scorpiops leptochirus Pocock, 1893	Pavlovsky 1924, 1925
	Iuridae	*Hadrurus arizonensis* Ewing, 1928	Sissom 1990
		Iurus dufoureius (Brullé, 1832)	Pavlovsky 1924, 1925
	Liochelidae	*Iomachus politus* Pocock, 1896	Pavlovsky 1924, 1925
		Liocheles australasiae (Fabricius, 1775)	Pavlovsky 1924, 1925
	Pseudochactidae	*Pseudochactas ovchinnikovi* Gromov, 1898	Here
	Scorpionidae	*Heterometrus cyaneus* (C.L. Koch, 1836)	Pavlovsky 1924, 1925
		Heterometrus scaber (Thorell, 1876)	Mathew 1956
		Scorpio maurus Linnaeus, 1758	Millot and Vachon 1949
	Vaejovidae	*Uroctonus mordax* Thorell, 1876	Pavlovsky 1924, 1925
		Vaejovis cristimanus Pocock, 1898	Pavlovsky 1924, 1925
		Vaejovis spinigerus (Wood, 1863)	Pavlovsky 1924, 1925
Two-celled	Buthidae *s. l.*	*Tityus bahiensis* (Perty, 1833)	de Toledo-Piza 1939b; Matthiesen 1970
		Tityus cambridgei Pocock, 1897	Matthiesen 1970
		Tityus serrulatus Lutz and Mello, 1922	de Toledo-Piza 1939a; Matthiesen 1970
		Tityus stigmurus (Thorell, 1876)	Matthiesen 1970

[a]Note that Pavlovsky's (1924, 1925) observations on *T. cambridgei* are contradicted by later authors.
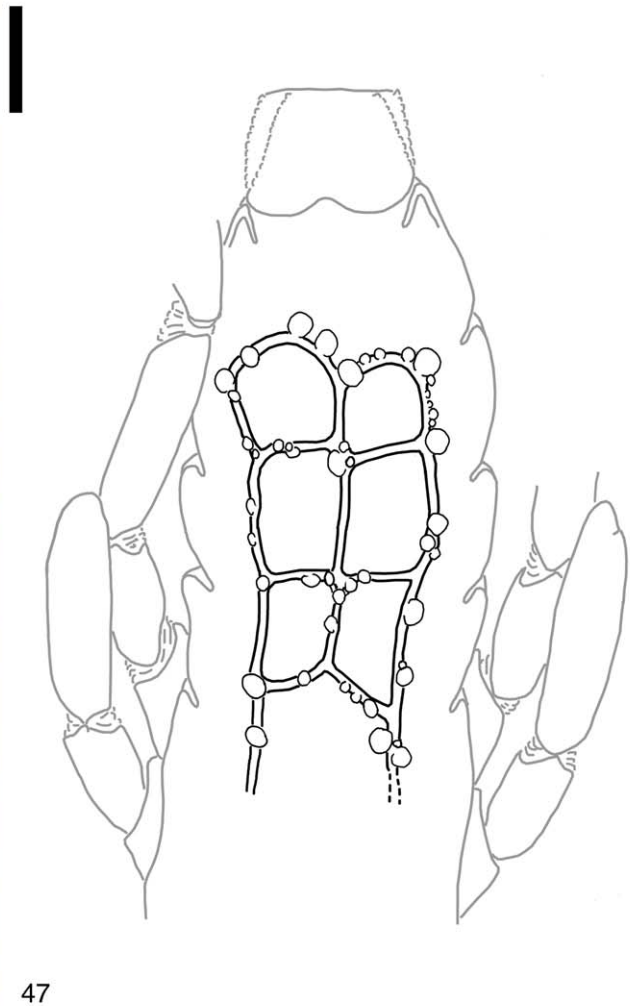
Figs. 46–47. *Pseudochactas ovchinnikovi* Gromov, 1998, ovariuterus of ♀ (AMNH). (**46**) Actual dissection. (**47**) Outline (black) of ovariuterine tubules. Scale bar = 1 mm.

2003b, p. 18). The condition in the relevant fossil taxa, e.g. the Carboniferous *Palaeopisthacanthus*, is equivocal and the character therefore ambiguous regarding the placement of *Pseudochactas*. The polarity of the pectinal peg sensillar processes of *Pseudochactas* likewise cannot be determined in the absence of evidence from the fossils hence this character is uninformative as well.

Concerning the trichobothrial pattern, we agree with Soleglad and Sissom (2001) and Soleglad and Fet (2001) that trichobothrial homology statements should be made at the level of individual trichobothria, rather than at the level of pedipalp segments or surfaces (e.g., as gross counts), although we recognise significant practical difficulties in doing so (Lamoral 1979; Francke and Soleglad 1981; Francke 1982a, b; Stockwell 1989; Sissom 1990; Prendini 2000a; Prendini and Wheeler 2005). We therefore reject the 'Type D' trichobothrial pattern as a statement of homology *per se* and, consequently, as an autapomorphy for *Pseudochactas* (Soleglad and Fet 2003b; Fet et al. 2004).

We see no evidence for the transverse anterior carinae on metasomal segments I–III reported to be 'synapomorphic' in *Pseudochactas* by Soleglad and Fet (2003b, p. 87) and Fet et al. (2004, p. 61), yet presumed to be plesiomorphic based on their occurrence in *Palaeopisthacanthus* (Jeram 1994; Soleglad and Fet 2003b, p. 144). Nor do we consider the small size and oval shape of the respiratory spiracles to be autapomorphic or diagnostic for *Pseudochactas* (Soleglad and Fet 2003b, p. 87; Fet et al. 2004, p. 61). Small, oval spiracles are o(bserved in many other scorpions, e.g., Chaerilidae (Stockwell 1989; Soleglad and Fet 2003b).

4.2. Evidence for Hypothesis 1: Sister group of other Recent scorpions

According to Soleglad and Fet (2003b), the pair of ventrosubmedian carinae on metasomal segment V is plesiomorphic in *Pseudochactas*, based on its occurrence

in *Palaeopisthacanthus* (Jeram 1994), and places *Pseudochactas* basal to other extant scorpions. Although we tentatively accept the polarity of this character as plesiomorphic, we reject the underlying homology statement. Our observation, in some *Pseudochactas* specimens, of a weak medial row of granules between the ventrosubmedian carinae of segment V, consistent with the position of the ventromedian carina observed in most other extant scorpions, refutes Soleglad and Fet's (2003b, p. 13) suggestion that the ventrosubmedian carinae of segment V 'are in the process of becoming single' and represent an intermediate state between the paired condition in *Palaeopisthacanthus* and the single (ventromedian) condition of other scorpions. We have also observed pairs of ventrosubmedian carinae, coincident with a single ventromedian carina, on metasomal segment V in other scorpions, e.g., *Bothriurus* and *Parabuthus* (e.g., see Prendini 2004), questioning whether the ventrosubmedian carinae of *Pseudochactas* are homologous with the ventromedian carina of other scorpions.

Besides the presence of a pair of ventrosubmedian carinae on metasomal segment V, the following characters placed *Pseudochactas* basal to other Recent scorpions in the analysis by Soleglad and Fet (2003b): sternum Type 1, without horizontal compression; femoral trichobothria d_3 and d_4 in the same axis, parallel and closer to the dorsoexternal carina than to d_1; hemispermatophore morphology 'unknown, primitive' (i.e., not flagelliform or fusiform). None of these characters can be unequivocally demonstrated to be plesiomorphic in *Pseudochactas*, however.

Although the sternal morphology of *Pseudochactas* is allegedly similar to that illustrated for *Palaeopisthacanthus* by Kjellesvig-Waering (1986), the sternum of *Palaeopisthacanthus* was not actually observed by Soleglad and Fet (2003b), much less dissected to study its internal structure. As such, the putative sternal similarities among these taxa are mere speculation.

Soleglad and Fet's (2003b, p. 143) distinction between the unknown, but presumably 'primitive' hemispermatophore of *Pseudochactas* (to which a 'null state' was assigned in their phylogenetic analysis), and those of other extant scorpions must likewise be dismissed as conjecture. While we have demonstrated significant (probably autapomorphic) differences between the hemispermatophore of *Pseudochactas* and those of other scorpions, we have also demonstrated possible synapomorphies with the hemispermatophores of Buthidae *s. l.*, as discussed further below.

The relative positions of femoral trichobothria d_3 and d_4 of *Pseudochactas*, which appear similar to those portrayed in the original and subsequent (Soleglad and Fet 2001, 2003b) descriptions of the Cretaceous fossil *Archaeobuthus* Lourenço, 2001, are also observed in some extant buthids, e.g. *Liobuthus* Birula, 1898

(Vachon 1974), according to the reinterpretation proposed here (Table 4). If this interpretation is accepted, the character provides a potential synapomorphy for a group containing *Pseudochactas*, *Archaeobuthus* and Buthidae *s. l.* (Appendix A), rather than a plesiomorphy placing *Pseudochactas* basal to all other scorpions.

In contrast, the absence of two trichobothria on the pedipalp chela and one on the pedipalp patella (Tables 3 and 4; Appendix A) potentially support the basal position of *Pseudochactas*. The identity of these trichobothria is open to interpretation, however, and their putative absence in Palaeozoic scorpions, e.g. *Palaeopisthacanthus*, on which the character polarity depends, relies on the confidence with which they can be considered 'absent' in the fossils in question. The absence of trichobothria in a fossil might be nothing more than an artefact of its preservation, given the difficulty with which trichobothria are generally observed in fossils, especially those preserved in rock (Jeram 1994; Lourenço and Weitschat 1996, 2000, 2001; de Carvalho and Lourenço 2001; Lourenço 2001, 2003c; Prendini and Wheeler 2005). Therefore, following Prendini and Wheeler (2005), we maintain that the absence of trichobothria in fossil taxa should be scored 'unknown' (?), rather than definitively absent (cf. Soleglad and Fet 2001, 2003b). It follows that the absence of the three trichobothria would also be autapomorphic in *Pseudochactas* and thus uninformative about its phylogenetic position.

In summary, we consider Hypothesis 1 to be potentially supported by at most five characters, only one of which, the presence of a pair of ventrosubmedian carinae on metasomal segment V, would unambiguously place *Pseudochactas* basal to other Recent scorpions (Appendix A), but even this character depends on a questionable interpretation of homology. Three of the other characters, the absence of two trichobothria on the pedipalp chela and one on the pedipalp patella, rely on the putative absence of trichobothria in fossils that cannot be established with certainty. The fifth character, configuration of femoral trichobothria d_3 and d_4 in the same axis, parallel and closer to the dorsoexternal carina than to d_1, occurs in at least one buthid according to the reinterpretation proposed here (Table 4), and is potentially synapomorphic for a group containing *Pseudochactas*, *Archaeobuthus* and Buthidae *s. l.*, rather than plesiomorphic in *Pseudochactas*.

4.3. Evidence for Hypothesis 2: Sister group of Buthidae *s. l.*

Gromov (1998) noted or illustrated five characters of *Pseudochactas* that might support a sister-group relationship with Buthidae *s. l.*, all of which were observed by Soleglad and Fet (2001, 2003b), Fet et al. (2004), and

us: a pair of anterosubmedial lyriform carinae, anterior to the median ocular tubercle, on the carapace; more than 10 trichobothria on the pedipalp femur (including three trichobothria on the external surface and four on the internal surface); absence of trichobothria on the ventral surface of the pedipalp patella; oblique orientation of the granular subrows of the median denticle row on the fixed and movable fingers of the pedipalp chela; tibial spurs on legs III and IV.

Anterosubmedial lyriform carinae on the carapace are characteristic of many buthids and otherwise unknown outside that family (Sissom 1990), thus representing a potentially unambiguous synapomorphy with *Pseudochactas*. In contrast, the presence of tibial spurs on legs III and IV is probably plesiomorphic in *Pseudochactas*, based on their occurrence in some Carboniferous fossil scorpions, e.g., *Pulmonoscorpius* Jeram, 1994, as well as the extant iurid genus *Calchas* Birula, 1899 (Jeram 1994; Soleglad and Fet 2003b). The oblique orientation of the dentition on the pedipalp chela fingers, characteristic of most Buthidae *s. l.*, also occurs in the nonbuthid families Chaerilidae, Iuridae Thorell, 1876 and Superstitioniidae Stahnke, 1940 (Stockwell 1989; Soleglad and Fet 2003b), suggesting that it is also plesiomorphic in *Pseudochactas*.

The trichobothrial pattern of *Pseudochactas* presents several potential synapomorphies with Buthidae *s. l.* (Tables 3 and 4; Appendix A). The first of these, the absence of trichobothria on the ventral surface of the pedipalp patella, is considered by some (e.g., Stockwell 1989; Soleglad and Fet 2001, 2003b) to be plesiomorphic based on its occurrence in *Palaeopisthacanthus* and *Archaeobuthus*. If, however, the missing trichobothria of these fossil taxa were scored unknown, the character (loss of the ventral trichobothria) might provide a potential synapomorphy for *Pseudochactas* and Buthidae *s. l.* A more convincing potential synapomorphy, however, is the presence in *Pseudochactas* of patellar trichobothrium d_3, unknown outside of Buthidae *s. l.* and, contingent on interpretation, *Archaeobuthus* (Tables 1, 3, and 4).

The presence of more than one trichobothrium on the internal surface of the pedipalp femur is also unknown outside Buthidae *s. l.* and *Archaeobuthus*. All other nonbuthid scorpions display a single internal trichobothrium (Table 1). If each trichobothrium were considered a separate character, as recommended by Soleglad and Sissom (2001) and Soleglad and Fet (2001), the three additional trichobothria might constitute three synapomorphies for a group comprising *Pseudochactas*, Buthidae *s. l.* and *Archaeobuthus*. In addition, three (or more) trichobothria on the external surface of the pedipalp femur are observed in some neobothriotaxic buthids, e.g. *Buthiscus* Birula, 1905 and *Liobuthus* (Vachon 1974; Sissom 1990), but these taxa are generally considered derived within Buthidae *s. l.*, based on other characters, implying that their additional trichobothria were acquired independently of *Pseudochactas*. Buthids

deviating from the orthobothriotaxic Type A pattern are listed in Table 4.

Another three potential synapomorphies with Buthidae *s. l.*, or with a group comprising *Pseudochactas*, Buthidae *s. l.* and *Archaeobuthus*, emerge from our reexamination and reinterpretation of the trichobothria of *Pseudochactas*, presented here. The 'petite' condition of chela manus trichobothrium Eb_3 and femoral trichobothrium d_2, newly documented in the present study, are unknown outside Buthidae *s. l.* (the condition of these trichobothria in *Archaeobuthus* is equivocal), providing two potential synapomorphies with the latter (Appendix A). Our reinterpretation of the relative positions of trichobothria on the dorsal surface of the femur provides a potential synapomorphy for a group comprising *Pseudochactas*, Buthidae *s. l.* and *Archaeobuthus* (Table 4 and Appendix A).

Our studies of the internal anatomy of *Pseudochactas* provide a further two potential synapomorphies with Buthidae *s. l.* The first of these is the folded nature of the hemispermatophore flagellum, typical of buthid hemispermatophores (Lamoral 1980; Stockwell 1989; Sissom 1990; Prendini 2000a; Soleglad and Fet 2003b). All nonbuthid hemispermatophores possess a straight and unfolded flagellum, i.e., the distal lamella. No buthids are known to possess the large, heavily sclerotised and ribbed flagellum seen in *Pseudochactas*, but this may be autapomorphic and therefore uninformative, or plesiomorphic, relative to Buthidae *s. l.* The second probable homologue is the basal lobe, a structure seen in Buthidae *s. l.* but absent in Chaerilidae and other nonbuthid scorpions. The male reproductive system of *Pseudochactas* thus seems most similar to that of the buthids. The female reproductive system, however, in which the ovariuterus is divided into six 'cells' by one longitudinal and four transverse ovarian tubes, as in most nonbuthid scorpions (Stockwell 1989; Hjelle 1990; Sissom 1990; Soleglad and Fet 2003b), appears to be plesiomorphic.

In light of this new evidence, we consider Hypothesis 2, supported by at least 10 potential synapomorphies (Appendix A), to be more plausible than the alternatives. The evidence does not suggest that *Pseudochactas* is a buthid, however. At least five trichobothrial characters (Tables 3 and 4), two characters pertaining to cheliceral dentition, and characters from the hemispermatophore and tarsal armature (Appendix A) unambiguously exclude *Pseudochactas* from the Buthidae *s. l.*, or a a group comprising *Pseudochactas*, Buthidae *s. l.* and *Archaeobuthus* (Hypothesis 2b).

4.4. Evidence for Hypothesis 3: Sister group of Chaerilidae

Characters noted or illustrated by Gromov (1998) that might support a sister-group relationship with the

nonbuthid scorpion families, and especially with Chaerilidae, were also observed by Soleglad and Fet (2001, 2003b) and by us: dentition on the ventral surfaces of the fixed and movable fingers of the chelicera; pentagonal sternum; a single trichobothrium on the ventral surface of the pedipalp chela manus; two trichobothria on the internal surface of the fixed finger of the pedipalp chela; the habitus, which resembles 'chactoid' scorpions (and was the incentive for the generic name, *Pseudochactas*).

Soleglad and Fet (2003a) considered the pentagonal sternum of *Pseudochactas* to be a plesiomorphic condition of the Type 1 sternum (also recognised in Buthidae *s. l.* and Chaerilidae), and perhaps the most plesiomorphic sternum of any extant scorpion. The pentagonal sternum of *Pseudochactas* does not support a sister-group relationship with the nonbuthid scorpions in general, or Chaerilidae in particular.

The presence of two trichobothria on the internal surface of the fixed finger (*it* and *ib*), observed in most nonbuthids and widely considered to be plesiomorphic (Lamoral 1980; Stockwell 1989; Soleglad and Fet 2001, 2003a, b), cannot be regarded as synapomorphic for *Pseudochactas* and Chaerilidae, although it could potentially be synapomorphic for *Pseudochactas* and all other nonbuthids (discussed below). In this study, we identified a third, petite trichobothrium on the internal surface of the fixed finger of *Pseudochactas* (Fig. 31), apparently yet another autapomorphy for this taxon.

The dentition on the ventral surfaces of the fixed and, to a lesser extent, movable fingers of the chelicera, though similar in *Pseudochactas* and Chaerilidae, is apparently also shared with the fossil *Palaeopisthacanthus* (Jeram 1994; Soleglad and Fet 2003b) and thus probably plesiomorphic. The 'chactoid' habitus, which we do not regard as a character *per se*, is nevertheless probably also plesiomorphic. *Pseudochactas* lacks another synapomorphy of Chaerilidae: the distal edges of maxillary lobes (coxapophyses) I are not expanded (Lamoral 1980; Stockwell 1989; Sissom 1990; Prendini 2000a; Soleglad and Fet 2003b).

Both *Pseudochactas* and *Chaerilus* display similar, but not exact numbers of external trichobothria on the pedipalp femur (three in *Pseudochactas* and four in *Chaerilus*) and chela manus (four in *Pseudochactas* and five in Chaerilidae). Compared with the two external trichobothria on the femur of most buthids, the third external trichobothrium could be synapomorphic for *Pseudochactas* and *Chaerilus* (and the fourth autapomorphic for Chaerilidae), but this would not be an unambiguous synapomorphy because, as mentioned above, at least two buthids (*Buthiscus* and *Liobuthus*) also possess more than two external trichobothria. In contrast, the femoral d_4 trichobothrium which, according to the interpretation proposed here (Table 4), occurs in *Pseudochactas*, *Chaerilus*, some buthids (e.g. *Liobuthus*), and *Archaeobuthus*, is more likely to be plesiomorphic in these taxa than synapomorphic for *Pseudochactas* and Chaerilidae. Only one potential synapomorphy supports Hypothesis 3, i.e., the presence of a single trichobothrium (V_1) on the ventral surface of the pedipalp chela manus (alternatively phrased as the loss of trichobothrium V_2), a character otherwise restricted to Chaerilidae and *Archaeobuthus* (in which its absence has not been demonstrated with certainty). It is plausible, though less parsimonious, that the presence of a single trichobothrium is symplesiomorphic in *Pseudochactas*, the Chaerilidae, and perhaps *Archaeobuthus*, and that additional ventral trichobothria were gained independently in Buthidae *s. l.* and the rest of the non-buthid families. Alternatively, if the single ventral trichobothrium on the manus of *Pseudochactas* is interpreted as being homologous with V_2, rather than with V_1, of Buthidae, which is reasonable based on their similar positions, this would provide a potential synapomorphy with Buthidae *s. l.* and perhaps *Archaeobuthus*, rather than with Chaerilidae. Based on our conclusions that only three characters support Hypothesis 3 (Appendix A), and all are ambiguous in this regard, we consider this to be the least plausible of the alternatives.

4.5. Evidence for Hypothesis 4: Sister group of Nonbuthids

Two potentially unambiguous synapomorphies lend support for a hypothesis not previously proposed in the literature, i.e., *Pseudochactas* as the sister group of a monophyletic group comprising all other nonbuthids (including Chaerilidae): the presence of an *ib* trichobothrium (designated ib_1 in the present study) on the chela manus, and the position of trichobothrium *it* at the base of the chela fixed finger. Both characters are observed only in nonbuthid scorpions. The evidence supporting Hypothesis 4 is nevertheless overwhelmed by the evidence supporting Hypothesis 2, that *Pseudochactas* is the sister group of Buthidae *s. l.*

4.6. Biogeographical conjectures

Available data suggest that *Pseudochactas* is restricted to a small area in the Babatag and Aruktau mountain ranges of the Tajik Depression, Central Asia (Fig. 3), a region of relatively mild climate surrounded by desert at lower altitudes (Gromov 1998; Soleglad and Fet 2003b; Fet et al. 2004). Given its restricted geographical range and basal phylogenetic position, we regard *Pseudochactas* as a palaeoendemic, a relict of an earlier, probably mesic scorpion fauna that existed before climate change (e.g., the onset of increased aridity and/or seasonality) eliminated most other members of its lineage. The

modern climate in the Tajik Depression is apparently one of the mildest in Central Asia, with the longest frost-free period (Korzhenevsky 1960; Bogdanova et al. 1968), one of several factors that could have contributed to the survival of this relict scorpion (Soleglad and Fet 2003b; Fet et al. 2004).

According to Fet et al. (2004, p. 63), the discovery of *Pseudochactas* confirms that four, rather than three scorpion lineages survived the K-T extinctions, and is supported by evidence of modern scorpion superfamilies from the Upper Cretaceous of Burma, e.g., Chaeriloidea (Santiago-Blay et al., 2004) and Brazil, e.g., Scorpionoidea (de Carvalho and Lourenço 2001). Soleglad and Fet (2003b) and Fet et al. (2004) speculated about a possible Pangaean origin (Permian–Triassic time) for the pseudochactid lineage, along with three other extant scorpion lineages, which they named 'parvorders'. Two of these, Buthidae *s. l.* and Soleglad and Fet's (2003b) 'Iurida' (the nonbuthid families with a Type C trichobothrial pattern, i.e., excluding Pseudochactidae and Chaerilidae) are broadly, if discontinuously, distributed on all continents except Antarctica. In contrast, Pseudochactidae and Chaerilidae, each with a single relict genus, *Pseudochactas* and *Chaerilus*, currently survive only in Central and Southern Asia.

The pseudochactid lineage is represented by a single extant species and there are no fossil representatives. The conclusion that *Pseudochactas* diverged from all other scorpion lineages 'well before the Triassic' (more than 250 Ma) or even that it diverged more than 200 Ma (Soleglad and Fet 2003b; Fet et al. 2004, p. 63, 64) therefore rests solely on the confirmation of its phylogenetic position as the sister group of all other Recent scorpions (Hypothesis 1). If, however, *Pseudochactas* were the sister group of Buthidae *s. l.* (Hypothesis 2), its divergence could be more recent. A more recent divergence accords better with the suggestions by Soleglad and Fet (2003b) and Fet et al. (2004) that *Pseudochactas* may represent a remnant of a littoral or insular fauna of the Tethys Sea, that evolved towards the end of the Cretaceous and became elevated by mountain uplift during the Tertiary, surviving the onset of aridification in Central Asia as a consequence thereof. During the Cretaceous, the modern Kyzylkum desert of Central Asia was underwater, the southwestern part of the Tajik Depression was a coastal landscape comprising numerous lagoons and river deltas, seasonality was moderate, and mountains were low (Kryzhanovsky 1965). The major tectonic unheaval that created the Pamiro-Alai began later in the Neogene (late Eocene) and precipitated the onset of aridification and marked seasonality (Sinitsyn 1962; Atamuradov 1994; Kazenas and Bayshashov 1999). It is during this time that many of the taxa that evolved on islands or in the littoral zone of the Tethys Sea, when climatic conditions were moderate, would have become extinct. Only those taxa sheltered in climatic refuges, such as the low mountain ranges inhabited by *Pseudochactas*, would have survived. Other relict taxa inhabiting the low mountain ranges of Uzbekistan and Tajikistan are similarly thought to have evolved on islands or in the littoral zone of the eastern Tethys Sea during the Upper Cretaceous or Lower Tertiary and survived due to the sheltered climate in the mountains (Kryzhanovsky 1965; Kamelin 1979).

4.7. Conclusions and future directions

The aim of the study presented here was not to determine the phylogenetic position of *Pseudochactas*, but to undertake a comprehensive, fully-documented reexamination and, where necessary, reinterpretation, of its external morphology and internal anatomy, within the limits of available material. Our observations and interpretations offer fresh insights on the debate concerning the phylogenetic position of this remarkable and enigmatic scorpion. The weight of evidence (Appendix A) supports a sister-group relationship with the extant family Buthidae *s. l.*, or perhaps with a monophyletic group comprising Buthidae *s. l.* and the Cretaceous *Archaeobuthus* and its relatives. These hypotheses await rigorous testing in a phylogenetic analysis, however. Such an analysis should include all relevant ingroup and outgroup taxa, sampled using multiple sources of character evidence (external morphology, internal anatomy, and DNA sequences from multiple loci in the nuclear and mitochondrial genomes), analysed simultaneously under a variety of parameter sets. No analysis remotely approximating these criteria has thus far been presented, and the question will remain unresolved until it has.

Appendix A

Evidence for alternative hypotheses for the phylogenetic position of *Pseudochactas* Gromov, 1998, their proponents (G = Gromov, 1990; S&F = Soleglad and Fet, 2001, 2003b; Fea = Fet et al., 2004; here, interpretations 1–4), and distribution in extinct and extant scorpions.

Evidence for Hypothesis 1: Sister group of other Recent scorpions (at most five characters):

(1) Pedipalp chela, absence of two trichobothria: proposed: Eb_3, *esb* (S&F, Fea), *Est*, *esb* (here 1), Et_1, *esb* (here 2), *eb*, *esb* (here 3), *est*, *et* (here 4, preferred); distribution: extinct scorpions: *Archaeobuthus* (equivocal), extant scorpions: *Pseudochactas*; comments: depends on interpretation of trichobothrial homology, absence unconfirmed in fossil.

(2) Pedipalp patella, absence of em_1 trichobothrium: proposed: S&F, Fea, here; distribution: extinct scorpions: *Archaeobuthus* (equivocal), extant scorpions: *Pseudochactas*; comments: depends on interpretation of trichobothrial homology, absence unconfirmed in fossil.

(3) Pedipalp femur, trichobothria d_3 and d_4 in same axis, parallel: proposed: S&F, Fea; distribution: extinct scorpions: *Archaeobuthus*, extant scorpions: *Pseudochactas*; comments: depends on interpretation of trichobothrial homology.

(4) Metasomal segment V, pair of ventrosubmedian carinae: proposed: S&F, Fea, here; distribution: extinct scorpions: *Palaeopisthacanthus*, extant scorpions: *Pseudochactas*.

Evidence for Hypothesis 2: Sister group of Buthidae *s. l.* (at least 10 characters):

(1) Pedipalp patella, presence of d_3 trichobothrium: proposed: S&F, Fea, here; distribution: extinct scorpions: *Archaeobuthus*, extant scorpions: *Pseudochactas*, Buthidae *s. l.*; comments: depends on interpretation of trichobothrial homology.

(2) Pedipalp femur, presence of four trichobothria: proposed: d_2, i_2, i_3, i_4 (G, S&F, Fea); d_5, i_2, i_3, i_4 (here 1); d_2, d_5, i_2, i_4 (here 2, preferred); distribution: extinct scorpions: *Archaeobuthus*, extant scorpions: *Pseudochactas*, Buthidae *s. l.*; comments: depends on interpretation of trichobothrial homology.

(3) Pedipalp chela manus, Eb_3 trichobothrium, petite condition: proposed: here; distribution: extinct scorpions: unknown, extant scorpions: *Pseudochactas*, Buthidae *s. l.*; comments: depends on interpretation of trichobothrial homology.

(4) Pedipalp femur, d_2 trichobothrium, petite condition: proposed: here 2; distribution: extinct scorpions: unknown, extant scorpions: *Pseudochactas*, Buthidae *s. l.*; comments: depends on interpretation of trichobothrial homology.

(5) Pedipalp femur, trichobothria d_3 and d_4 in same axis, parallel: proposed: here; distribution: extinct scorpions: *Archaeobuthus*, extant scorpions: *Pseudochactas*, some buthids (e.g. *Liobuthus*), similar in Chaerilidae; comments: depends on interpretation of trichobothrial homology.

(6) Hemispermatophore, folded flagellum: proposed: here; distribution: extinct scorpions: unknown, extant scorpions: *Pseudochactas*, Buthidae *s. l.*

(7) Hemispermatophore, basal lobe: proposed: here; distribution: extinct scorpions: unknown, extant scorpions: *Pseudochactas*, Buthidae *s. l.*

(8) Carapace, anterosubmedial lyriform carinae: proposed: G, here; distribution: extinct scorpions: unknown, extant scorpions: *Pseudochactas*, Buthidae *s. l.*

Evidence for Hypothesis 2b: *Pseudochactas* excluded from Buthidae *s. l.* (at least 14 characters):

(1) Pedipalp chela, absence of two trichobothria: proposed: Eb_3, *esb* (S&F, Fea); *Est*, *esb* (here 1); Et_1, *esb* (here 2); *eb*, *esb* (here 3), *est*, *et* (here 4, preferred); distribution: extinct scorpions: *Palaeopisthacanthus* (equivocal), *Archaeobuthus* (equivocal), extant scorpions: *Pseudochactas*; comments: depends on interpretation of trichobothrial homology, absence unconfirmed in fossils.

(2) Pedipalp chela manus, presence of ib_1 trichobothrium: proposed: G, here; distribution: extinct scorpions: unknown, extant scorpions: *Pseudochactas*, other nonbuthids.

(3) Pedipalp chela, position of *it* trichobothrium, base of fixed finger: proposed: here; distribution: extinct scorpions: unknown, extant scorpions: *Pseudochactas*, many other nonbuthids, excluding Chaerilidae and iurids (e.g. *Iurus*, *Calchas*); comments: depends on interpretation of trichobothrial homology.

(4) Pedipalp chela manus, absence of ventral trichobothrium V_2: proposed: here; distribution: extinct scorpions: *Archaeobuthus* (equivocal), extant scorpions: *Pseudochactas*, Chaerilidae; comments: depends on interpretation of trichobothrial homology, absence unconfirmed in fossil.

(5) Pedipalp patella, absence of d_4, d_5 and em_1 trichobothria: proposed: here; distribution: extinct scorpions: *Palaeopisthacanthus* (equivocal),

Archaeobuthus (equivocal), extant scorpions: *Pseudochactas*, Chaerilidae, other nonbuthids; comments: depends on interpretation of trichobothrial homology, absence unconfirmed in fossils.

(6) Pedipalp femur, trichobothria d_3 and d_4 in same axis, parallel: proposed: S&F, Fea; distribution: extinct scorpions: *Archaeobuthus*, extant scorpions: *Pseudochactas*; comments: depends on interpretation of trichobothrial homology.

(7) Metasomal segment V, pair of ventrosubmedian carinae: proposed: S&F, Fea, here; distribution: extinct scorpions: *Palaeopisthacanthus*, extant scorpions: *Pseudochactas*, absent.

(8) Extremely reduced hemispermatophore, with large, heavily sclerotised, ribbed flagellum: proposed: here; distribution: extinct scorpions: unknown, extant scorpions: *Pseudochactas*, absent.

(9) Telotarsi, paired ventrosubmedian rows of spinules: proposed: G, S&F, Fea, here; distribution: extinct scorpions: equivocal, extant scorpions: *Pseudochactas*, absent.

(10) Cheliceral fixed finger, ventral edge, 4–5 denticles: proposed: G; distribution: extinct scorpions: *Palaeopisthacanthus*, extant scorpions: *Pseudochactas*, Chaerilidae.

(11) Cheliceral movable finger, ventral edge, crenulated: proposed: G; distribution: extinct scorpions: *Palaeopisthacanthus*, extant scorpions: *Pseudochactas*, Chaerilidae.

Evidence for Hypothesis 3: Sister group of Chaerilidae (at most three characters):

(1) Pedipalp chela manus, absence of ventral trichobothrium V_2: proposed: G, S&F, Fea; distribution: extinct scorpions: *Archaeobuthus* (equivocal), extant scorpions: *Pseudochactas*, Chaerilidae; comments: depends on interpretation of trichobothrial homology, absence unconfirmed in fossil.

(2) Pedipalp femur, presence of d_4 trichobothrium: proposed: here; distribution: extinct scorpions: *Archaeobuthus*, extant scorpions: *Pseudochactas*, Chaerilidae, some Buthidae *s. l.* (e.g. *Liobuthus*); comments: depends on interpretation of trichobothrial homology.

(3) Pedipalp femur, presence of e_3 trichobothrium: proposed: here; distribution: extinct scorpions: unknown, extant scorpions: *Pseudochactas*, Chaerilidae, some Buthidae *s. l.* (e.g. *Buthiscus*, *Liobuthus*); comments: depends on interpretation of trichobothrial homology.

Evidence for Hypothesis 4: Sister group of Nonbuthids, including Chaerilidae (at most two characters):

(1) Pedipalp chela manus, presence of ib_1 trichobothrium: proposed: G, here; distribution: extinct scorpions: unknown, extant scorpions: *Pseudochactas*, other nonbuthids.

(2) Pedipalp chela, position of *it* trichobothrium, base of fixed finger: proposed: here; distribution: extinct scorpions: unknown, extant scorpions: *Pseudochactas*, many other nonbuthids, excluding Chaerilidae and iurids (e.g. *Iurus*, *Calchas*); comments: depends on interpretation of trichobothrial homology.

Probable autapomorphies:

(1) Pedipalp chela manus, presence of petite ib_2 trichobothrium: proposed: here; distribution: extinct scorpions: unknown, extant scorpions: *Pseudochactas*.

(2) Extremely reduced hemispermatophore, with large, heavily sclerotised, ribbed flagellum: proposed: here; distribution: extinct scorpions: unknown, extant scorpions: *Pseudochactas*.

(3) Single pair of lateral ocelli: proposed: G, S&F, Fea, here; distribution: extinct scorpions: absent, extant scorpions: *Pseudochactas*.

(4) Pair of circumocular sutures with U-shaped configuration: proposed: G, here; distribution: extinct scorpions: unknown, extant scorpions: *Pseudochactas*, absent.

(5) Cheliceral movable finger, dorsal edge, absence of basal teeth: proposed: G, S&F, Fea, here; distribution: extinct scorpions: equivocal, extant scorpions: *Pseudochactas*, also in *Typhlochactas mitchelli* (Superstitioniidae).

(6) Pectinal peg sensillae, pair of laterodistal processes: proposed: here; distribution: extinct scorpions: unknown, extant scorpions: *Pseudochactas*, absent in limited sample of buthids and nonbuthids, unknown in Chaerilidae.

(7) Telotarsi, paired ventrosubmedian rows of spinules: proposed: G, S&F, Fea, here; distribution: extinct scorpions: equivocal, extant scorpions: *Pseudochactas*.

Probable plesiomorphies:

(1) Small, oval respiratory spiracles: proposed: S&F, Fea; distribution: extinct scorpions: variable; extant scorpions: *Pseudochactas*, many buthids and nonbuthids.

(2) Pedipalp patella, ventral surface, absence of trichobothria: proposed: G; distribution: extinct scorpions: *Palaeopisthacanthus*, *Archaeobuthus*, extant scorpions: *Pseudochactas*, Buthidae *s. l.*; comments: absence unconfirmed in fossils.

(3) Pedipalp chela finger dentition, oblique orientation of granular rows: proposed: G; distribution: extinct scorpions: *Palaeopisthacanthus*, *Archaeobuthus*, extant scorpions: *Pseudochactas*, Buthidae *s. l.*, Chaerilidae, Iuridae, Superstitioniidae.

(4) Legs III and IV, tibial spurs: proposed: G; distribution: extinct scorpions: some, extant scorpions: *Pseudochactas*, Buthidae *s. l.*, *Calchas* (Iuridae).

(5) Pentagonal sternum: proposed: G; distribution: extinct scorpions: some, extant scorpions: *Pseudochactas*, many buthids, most nonbuthids.

(6) Ovariuterine tubules, six 'cells', oocytes sessile: proposed: here; distribution: extinct scorpions: unknown, extant scorpions: *Pseudochactas*, most other nonbuthids.

(7) Pedipalp chela with eight carinae: proposed: S&F; distribution: extinct scorpions: equivocal, extant scorpions: *Pseudochactas*, Buthidae *s. l.*, Chaerilidae, Iuridae (e.g. *Calchas*, *Iurus*).

Characters rejected:

(1) Unique trichobothrial pattern 'Type D': proposed: G, S&F, Fea; distribution: extinct scorpions: equivocal, extant scorpions: *Pseudochactas*; comments: not a character.

(2) Metasomal segments I–III, transverse anterior carinae: proposed: S&F, Fea; distribution: extinct scorpions: *Palaeopisthacanthus*, extant scorpions: *Pseudochactas*; comments: no evidence in *Pseudochactas*.

(3) Chactoid habitus: proposed: G; distribution: extinct scorpions: most extant scorpions: *Pseudochactas*, other nonbuthids; comments: not a character.

(4) Sternum Type 1: proposed: S&F, Fea; distribution: extinct scorpions: equivocal, extant scorpions: *Pseudochactas*, buthids, chaerilids; comments: not a character.

(5) Sternum without horizontal compression: proposed: S&F, Fea; distribution: extinct scorpions: equivocal, extant scorpions: *Pseudochactas*, buthids, chaerilids.

(6) 'Primitive' hemispermatophore: proposed: S&F, Fea; distribution: extinct scorpions: unknown, extant scorpions: *Pseudochactas*; comments: not observed.

References

Atamuradov, K.I., 1994. Paleogeography of Turkmenistan. In: Fet, V., Atamuradov, K.I. (Eds.), Biogeography and Ecology of Turkmenistan. Kluwer Academic Publishers, Dordrecht, pp. 49–64.

(Birula, A.A.) Byalynitskii-Birulya, A.A., 1917. Faune de la Russie et des pays limitrophes fondee principalement sur les collections du Musée Zoologique de l'Académie des Sciences de Russie. Arachnides (Arachnoidea). 1: xx, 227pp., Petrograd [Russian; English translation: Byalynitskii-Birulya, A.A., 1965. Fauna of Russia and Adjacent Countries. Arachnoidea. vol. I. Scorpions. Israel Program for Scientific Translations, Jerusalem, xix, 154pp.].

Bogdanova, N.M., Murzaev, E.M., Chupakhin, V.M., 1968. [Central Asian mountains and plateaus] pp. 368–392 in: [Central Asia]. Nauka, Moscow, 484pp. (in Russian).

Bradley, R., 1988. The behavioural ecology of scorpions—a review. In: Austin, A.D., Heather, N.W. (Eds.), Australian Arachnology. Australian Entomological Society Miscellaneous Publication 5. Watson, Ferguson & Co., Brisbane, pp. 23–36.

de Carvalho, M.G.P., Lourenço, W.R., 2001. A new family of fossil scorpions from the Early Cretaceous of Brazil. C.R. Acad. Sci. Paris Earth Planet. Sci. 332, 711–716.

Coddington, J.A., Giribet, G., Harvey, M.S., Prendini, L., Walter, D.E., 2004. Arachnida. In: Cracraft, J., Donoghue, M. (Eds.), Assembling the Tree of Life. Oxford University Press, Oxford, pp. 296–318.

Fet, V., 2000a. Family Chaerilidae Pocock, 1893. In: Fet, V., Sissom, W.D., Lowe, G., Braunwalder, M.E. (Eds.), Catalog of the Scorpions of the World (1758–1998). New York Entomological Society, New York, pp. 323–328.

Fet, V., 2000b. Family Pseudochactidae Gromov, 1998. In: Fet, V., Sissom, W.D., Lowe, G., Braunwalder, M.E. (Eds.), Catalog of the Scorpions of the World (1758–1998). New York Entomological Society, New York, p. 426.

Fet, V., Gantenbein, B., Gromov, A.V., Lowe, G., Lourenço, W.R., 2003. The first molecular phylogeny of Buthidae (Scorpiones). Euscorpius 4, 1–10 Available at: 〈http://www.science.marshall.edu/fet/euscorpius/〉.

Fet, V., Soleglad, M.E., Gromov, A.V., 2004. The platypus of a scorpion: the genus *Pseudochactas* Gromov, 1998 (Scorpiones: Pseudochactidae). Euscorpius 17, 61–68 Available at: 〈http://www.science.marshall.edu/fet/euscorpius/〉.

Francke, O.F., 1982a. Studies of the scorpion subfamilies Superstitioninae and Typhlochactinae, with description of a new genus (Scorpiones, Chactoidea). Bull. Assoc. Mex. Cave Stud. 8, 51–61.

Francke, O.F., 1982b. Studies of the scorpion subfamilies Superstitioninae and Typhlochactinae, with description of a new genus (Scorpiones, Chactoidea). Bull. Texas Mem. Mus. 28, 51–61.

Francke, O.F., 1982c. Parturition in scorpions (Arachnida, Scorpiones): a review of the ideas. Rev. Arachnol. 4, 27–37.

Francke, O.F., Soleglad, M.E., 1981. The family Iuridae Thorell (Arachnida, Scorpiones). J. Arachnol. 9, 233–258.

Gromov, A.V., 1998. [A new family, genus and species of scorpions (Arachnida, Scorpiones) from southern Central Asia]. Zool. Zh. 77, 1003–1008 ([in Russian, English summary]. English translation: (1998): Russ. J. Zool. 2, 409–413).

Hjelle, J.T., 1990. Anatomy and morphology. In: Polis, G.A. (Ed.), The Biology of Scorpions. Stanford University Press, Stanford, CA, pp. 9–63.

Honetschlager, L.D., 1965. A new method for hunting scorpions. Turtox News 43, 69–70.

International Union for the Conservation of Nature (IUCN), 2001. IUCN Red List Categories and Criteria: Version 3.1. IUCN Species Survival Commission. IUCN, Gland, Switzerland Available at: 〈http://www.iucn.org/themes/ssc/redlists/RLcats2001booklet.html〉.

Ivanov, V.P., 1981. [Sensory organs of scorpions (Scorpiones)]. Proc. Zool. Inst. Acad. Sci. USSR 106, 4–33 (in Russian).

Jeram, A., 1994. Carboniferous Orthosterni and their relationship to living scorpions. Palaeontology 37, 513–550.

Kamelin, R.V., 1979. The Kuhistan District of montane Central Asia, a botanical geographical analysis. Komarov Read. 31, 1–116 (in Russian).

Kazenas, V.L., Bayshashov, B.U., 1999. [Geological history and genesis of fauna of Kazakhstan and adjacent territories in epochs of development of mammals and anthophilous insects]. In: Yashchenko, R.V. (Ed.), Tethys Entomological Research, vol. 1, pp. 5–46 (in Russian).

Khatoon, S., 1999. Scorpions of Pakistan (Arachnida: Scorpionida). Proc. Pakistan Congr. Zool. 19, 207–225.

Kjellesvig-Waering, E.N., 1986. A restudy of the fossil Scorpionida of the world. Palaeontogr. Am. 55, 1–287 (organized for publication by A.S. Caster & K.E. Caster, Ithaca, New York).

Klaus, A.V., Kulasekera, V.L., Schawaroch, V., 2003. Three-dimensional visualisation of insect morphology using confocal laser scanning microscopy. J. Microsc. 212, 107–121.

Korzhenevsky, N.L., 1960. The nature of Central Asia. Izdatelstvo SAMGU, Tashkent, (211pp. [in Russian]).

Kovařík, F., 2000. Revision of family Chaerilidae (Scorpiones), with descriptions of three new species. Serket 7, 38–77.

Kovařík, F., 2004. Revision and taxonomic position of genera Afghanorthochirus Lourenço and Vachon, Baloorthochirus Kovařík, Butheolus Simon, Nanobuthus Pocock, Orthochiroides Kovařík, Pakistanorthochirus Lourenço and Asian Orthochirus Karsch, with descriptions of twelve new species (Scorpiones, Buthidae). Euscorpius 16, 1–33 Available at: ⟨http://www.science.marshall.edu/fet/euscorpius/⟩.

Kovařík, F., 2005. Two new species of the genus Chaerilus Simon, 1877 from Malaysia (Scorpiones: Chaerilidae). Euscorpius 26, 1–7 Available at: ⟨http://www.science.marshall.edu/fet/euscorpius/⟩.

Kryzhanovsky, O.L., 1965. The composition and origin of the terrestrial fauna of Middle Asia (based primarily on Coleopteran material). Nauka, Moscow, Leningrad, (420pp. [in Russian]. English translation: (1980): Smithsonian Institution Translation Program, New Delhi, India).

Lamoral, B.H., 1979. The scorpions of Namibia (Arachnida: Scorpionida). Ann. Natal Mus. 23, 497–784.

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

Laurie, M., 1896. Further notes on the anatomy and development of scorpions, and their bearing on the classification of the order. Ann. Mag. Nat. Hist. 18 (6), 121–133.

Lourenço, W.R., 2000. Panbiogeographie, les familles des scorpions et leur repartition geographique. Biogeographica (Paris) 76, 21–39.

Lourenço, W.R., 2001. A remarkable scorpion fossil from the amber of Lebanon. Implications for the phylogeny of Buthoidea. C. R. Acad. Sci. Paris Earth Planet. Sci. 332, 641–646.

Lourenço, W.R., 2002a. Further morphological considerations on the genus Birulatus Vachon (Scorpiones, Buthidae), with the description of a new species from Israel. Rev. Ibér. Aracnol. 6, 141–145.

Lourenço, W.R., 2002b. Scorpions from the Daraina region of northeastern Madagascar, with special reference to the family Heteroscorpionidae Kraepelin, 1905. Rev. Ibér. Aracnol. 6, 53–68.

Lourenço, W.R., 2003a. Humicolous buthoid scorpions: a new genus and species from French Guiana. C. R. Biol. 326, 1149–1155.

Lourenço, W.R., 2003b. New taxonomic considerations on some species of the genus Grosphus Simon, with description of a new species (Scorpiones, Buthidae). Rev. Suisse Zool. 110, 141–154.

Lourenço, W.R., 2003c. The first scorpion fossil from the Cretaceous amber of France. New implications for the phylogeny of Chactoidea. C. R. Palevol 2, 213–219.

Lourenço, W.R., Vachon, M., 1996. Complements to the phylogeny and biogeography of the genera Alayotityus Armas and Tityopsis Armas (Scorpiones, Buthidae). Biogeographica 72, 33–39.

Lourenço, W.R., Weitschat, W., 1996. More than 120 years after its description, the enigmatic status of the genus of the Baltic amber scorpion "Tityus eogenus" Menge, 1869 can finally be clarified. Mitt. Geol.-Paläont. Inst. Univ. Hamburg 79, 183–193.

Lourenço, W.R., Weitschat, W., 2000. New fossil scorpions from the Baltic amber – implications for Cenozoic biodiversity. Mitt. Geol.-Paläont. Inst. Univ. Hamburg 84, 247–260.

Lourenço, W.R., Weitschat, W., 2001. Description of another fossil scorpion from Baltic amber, with considerations on the evolutionary levels of Cenozoic Buthoidea. Mitt. Geol.-Paläont. Inst. Univ. Hamburg 85, 277–283.

Mathew, A.P., 1956. Embryology of Heterometrus scaber. Bull. Centr. Res. Inst. (Univ. Travancore) 1, 1–96.

Mathew, A.P., 1962. Reproductive biology of Lychas tricarinatus (Simon). Biol. Bull. 123, 344–350.

Matthiesen, F.A., 1970. Reproductive system and embryos of Brazilian scorpions. Ann. Acad. Brasil. Ciênc. 42, 627–632.

Millot, J., Vachon, M., 1949. Ordre des Scorpiones. In: Grassé, P.-P. (Ed.), Traité de zoologie, vol. 6. Masson, Paris, pp. 386–436.

Pawlowsky, E.N., 1924. Skorpiotomische Mitteilungen. III. Zur äusseren Morphologie der Scorpione. IV. Zur Morphologie der weiblichen Genitalorgane der Scorpione. Zool. Jahrb. Abt. Anat. Ontogenie 46, 473–508.

Pawlowsky, E.N., 1925. Zur Morphologie des weiblichen Genitalapparates und zur Embryologie der Skorpione. Ann. Mus. Zool. Acad. Sci. USSR 26, 137–205.

Polis, G.A., 1990. Ecology. In: Polis, G.A. (Ed.), The Biology of Scorpions. Stanford University Press, Stanford, CA, pp. 247–293.

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

Prendini, L., 2000b. A new species of Parabuthus Pocock (Scorpiones: Buthidae), and new records of Parabuthus

capensis (Ehrenberg), from Namibia and South Africa. Cimbebasia 16, 31–45.

Prendini, L., 2001a. Species or supraspecific taxa as terminals in cladistic analysis? Groundplans versus exemplars revisited. Syst. Biol. 50, 290–300.

Prendini, L., 2001b. Substratum specialization and speciation in southern African scorpions: the effect Hypothesis revisited. In: Fet, V., Selden, P.A. (Eds.), Scorpions 2001. *In Memoriam* Gary A. Polis. British Arachnological Society, Burnham Beeches, UK, pp. 113–138.

Prendini, L., 2004. The systematics of southern African *Parabuthus* Pocock (Scorpiones, Buthidae): revisions to the taxonomy and key to the species. J. Arachnol. 32, 109–186.

Prendini, L., 2005. Revision of *Karasbergia* Hewitt (Scorpiones: Buthidae), a monotypic genus endemic to southern Africa. J. Afrotrop. Zool. 1, 77–93.

Prendini, L., Wheeler, W.C., 2004. Assembling the scorpion tree of life: phylogeny of extant scorpions based on molecules, morphology and exemplars [Abstract]. Cladistics 20, 602–603.

Prendini, L., Wheeler, W.C., 2005. Scorpion higher phylogeny and classification, taxonomic anarchy, and standards for peer review in online publishing. Cladistics 21, 446–494.

Qui, J.-X., Zhu, M.-S., Lourenço, W.R., 2005. Eight new species of the genera *Scorpiops* Peters, *Euscorpiops* Vachon, and *Chaerilus* Simon (Scorpiones: Euscorpiidae, Chaerilidae) from Tibet and Yunnan, China. Euscorpius 32, 1–40 Available at: ⟨http://www.science.marshall.edu/fet/euscorpius/⟩.

Santiago-Blay, J.A., Fet, V., Soleglad, M.E., Anderson, S., 2004. A new genus and subfamily of scorpions from Cretaceous Burmese amber (Scorpiones: Chaerilidae). Rev. Ibér. Aracnol. 9, 3–14.

Sinitsyn, V.M., 1962. [Paleogeography of Asia]. Izdatelstvo AN SSSR, Moscow, Leningrad, (268pp. [in Russian]).

Sissom, W.D., 1990. Systematics, biogeography, and paleontology. In: Polis, G.A. (Ed.), The Biology of Scorpions. Stanford University Press, Stanford, CA, pp. 64–160.

Sissom, W.D., Polis, G.A., Watt, D.D., 1990. Field and laboratory methods. In: Polis, G.A. (Ed.), The Biology of Scorpions. Stanford University Press, Stanford, CA, pp. 445–461.

Smithe, F.B., 1974. Naturalist's color guide supplement. American Museum of Natural History, New York (xiii + 229pp.).

Smithe, F.B., 1975. Naturalist's color guide. American Museum of Natural History, New York (unpaginated).

Smithe, F.B., 1981. Naturalist's Color Guide. Part III. American Museum of Natural History, New York, (37pp.).

Soleglad, M.E., Fet, V., 2001. Evolution of scorpion orthobothriotaxy: a cladistic approach. Euscorpius 1, 1–38 Available at.

Soleglad, M.E., Fet, V., 2003a. The scorpion sternum: structure and phylogeny (Scorpiones: Orthosterni). Euscorpius 5, 1–34 Available at: ⟨http://www.science.marshall.edu/fet/euscorpius/⟩.

Soleglad, M.E., Fet, V., 2003b. High-level systematics and phylogeny of the extant scorpions (Scorpiones: Orthosterni). Euscorpius 11 ii + 1–175. Available at: ⟨http://www.science.marshall.edu/fet/euscorpius/⟩.

Soleglad, M.E., Sissom, W.D., 2001. Phylogeny of the family Euscorpiidae Laurie, 1896: a major revision. In: Fet, V., Selden, P.A. (Eds.), Scorpions 2001. *In Memoriam* Gary A. Polis. British Arachnological Society, Burnham Beeches, UK, pp. 25–111.

Stahnke, H.L., 1970. Scorpion nomenclature and mensuration. Entomol. News 81, 297–316.

Stahnke, H.L., 1972. UV light, a useful field tool. BioScience 22, 604–607.

Stockwell, S.A., 1989. Revision of the phylogeny and higher classification of scorpions (Chelicerata). Ph.D. Thesis, University of California, Berkeley, CA.

de Toledo-Piza Jr., S., 1939a. Estudos anatomicos em escorpioes brasileiros. I, O aparelho reproduto feminino e o inicio do desenvolvimento do embriao de *Tityus serrulatus*, compativamente a o que foi observado em *Tityus bahiensis*. J. Agro. Sao Paulo 2, 273–276.

de Toledo-Piza Jr., S., 1939b. Observaçoes sobre o aparelho reprodutor e a reprodeçao do *Tityus bahiensis* (Scorpiones: Buthidae, Isometrinae). J. Agro. Sao Paulo 2, 49–56.

Vachon, M., 1973 [1974]. Étude des caractères utilisés pour classer les familles et les genres de scorpions (Arachnides). 1. La trichobothriotaxie en arachnologie. Sigles trichobothriaux et types de trichobothriotaxie chez les scorpions. Bull. Mus. Natl. Hist. Nat. Paris Ser. 3 140, 857–958.

Werner, F., 1934. Scorpiones und Pedipalpi. In: H.G. Bronns Klassen und Ordnungen des Tierreichs. 5, IV, 8, Lief. 1–2 (Scorpiones). Akademische Verlaggesellschaft, Leipzig, pp. 1–136.