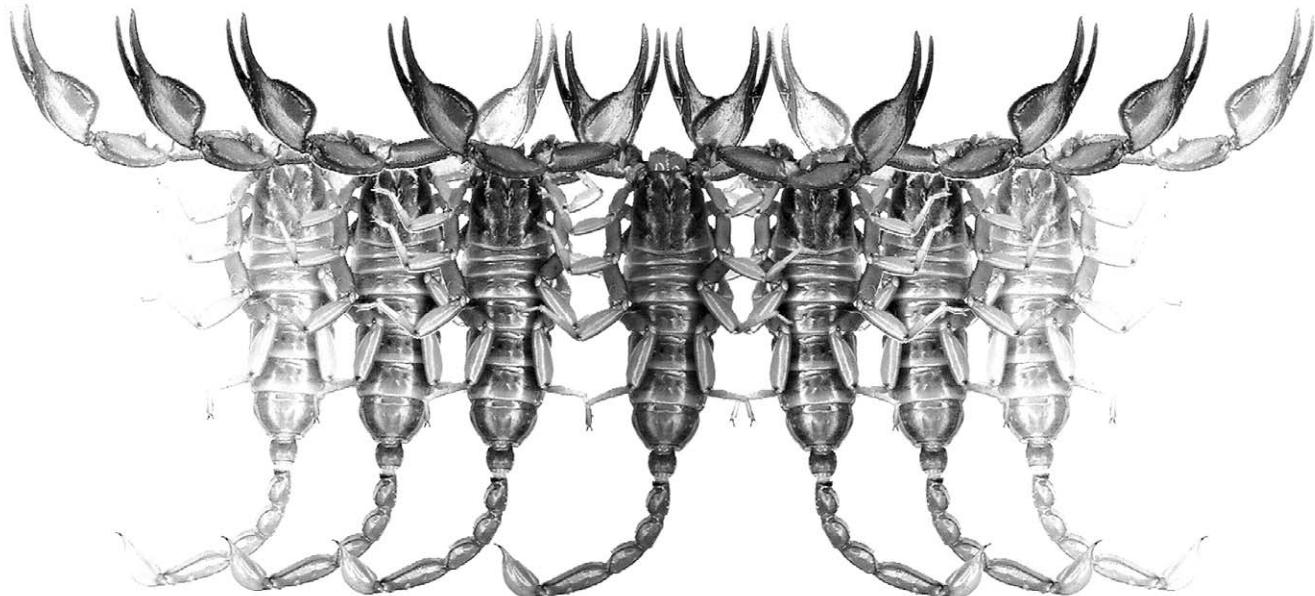


Euscorpius

Occasional Publications in Scorpiology



**Revision of the Central Asian Scorpion Genus *Anomalobuthus*
Kraepelin, 1900, with Descriptions of Three New Species and a
Generic Synonymy (Scorpiones: Buthidae)**

Rolando Teruel, František Kovařík & Victor Fet

October 2018 – No. 270

Euscorpius

Occasional Publications in Scorpiology

EDITOR: Victor Fet, Marshall University, 'fet@marshall.edu'
ASSOCIATE EDITOR: Michael E. Soleglad, 'msoleglad@gmail.com'

Euscorpius is the first research publication completely devoted to scorpions (Arachnida: Scorpiones). ***Euscorpius*** takes advantage of the rapidly evolving medium of quick online publication, at the same time maintaining high research standards for the burgeoning field of scorpion science (scorpiology). ***Euscorpius*** is an expedient and viable medium for the publication of serious papers in scorpiology, including (but not limited to): systematics, evolution, ecology, biogeography, and general biology of scorpions. Review papers, descriptions of new taxa, faunistic surveys, lists of museum collections, and book reviews are welcome.

Derivatio Nominis

The name ***Euscorpius*** Thorell, 1876 refers to the most common genus of scorpions in the Mediterranean region and southern Europe (family Euscorpiidae).

Euscorpius is located at: <http://www.science.marshall.edu/fet/Euscorpius>

(Marshall University, Huntington, West Virginia 25755-2510, USA)

ICZN COMPLIANCE OF ELECTRONIC PUBLICATIONS:

Electronic ("e-only") publications are fully compliant with ICZN ([International Code of Zoological Nomenclature](#)) (i.e. for the purposes of new names and new nomenclatural acts) when properly archived and registered. All ***Euscorpius*** issues starting from No. 156 (2013) are archived in two electronic archives:

- **Biotaxa**, <http://biotaxa.org/Euscorpius> (ICZN-approved and ZooBank-enabled)
- **Marshall Digital Scholar**, <http://mds.marshall.edu/euscorpius/>. (This website also archives all *Euscorpius* issues previously published on CD-ROMs.)

Between 2000 and 2013, ICZN did not accept online texts as "published work" (Article 9.8). At this time, ***Euscorpius*** was produced in two identical versions: online (ISSN 1536-9307) and CD-ROM (ISSN 1536-9293) (laser disk) in archive-quality, read-only format. Both versions had the identical date of publication, as well as identical page and figure numbers. Only copies distributed on a CD-ROM from ***Euscorpius*** in 2001-2012 represent published work in compliance with the ICZN, i.e. for the purposes of new names and new nomenclatural acts.

In September 2012, ICZN Article 8. *What constitutes published work*, has been amended and allowed for electronic publications, disallowing publication on optical discs. From January 2013, ***Euscorpius*** discontinued CD-ROM production; only online electronic version (ISSN 1536-9307) is published. For further details on the new ICZN amendment, see <http://www.pensoft.net/journals/zookeys/article/3944/>.

Publication date: 23 October 2018

<http://zoobank.org/urn:lsid:zoobank.org:pub:9D0AA0A5-38D9-49DB-B2FB-380550213399>

Revision of the Central Asian scorpion genus *Anomalobuthus* Kraepelin, 1900, with descriptions of three new species and a generic synonymy (Scorpiones: Buthidae)

Rolando Teruel^{1,2}, František Kovařík³ & Victor Fet⁴

¹ Grupo de Sistemática y Ecología de Artrópodos Caribeños, Calle 200 # 3759, e/ 37 y 45, Reparto Versalles, La Lisa, La Habana 13500, Cuba; teruelrolando6@gmail.com

² Instituto de Ecología y Sistemática (Subdirección de Colecciones Zoológicas), Carretera de Varona # 11835, e/ Oriente y Lindero, Reparto Calabazar, Boyeros, La Habana 11900, Cuba

³ P. O. Box 27, CZ - 145 01 Praha 45, Czech Republic; www.scorpio.cz

⁴ Department of Biological Sciences, Marshall University, Huntington, WV, 25755, USA; fet@marshall.edu

<http://zoobank.org/urn:lsid:zoobank.org:pub:9D0AA0A5-38D9-49DB-B2FB-380550213399>

Summary

We revise the Central Asian endemic genus *Anomalobuthus* Kraepelin, 1900, which was considered monotypic for more than 100 years until the recent addition of a second species from Iran (Teruel et al., 2014). We redefine the generic diagnosis of *Anomalobuthus* and reveal that it is composed of no less than six species, three of which are described as new: *A. krivochatskyi*, sp. n. (central Uzbekistan and extreme southern Kazakhstan), *A. lowei*, sp. n. (southeastern Kazakhstan), and *A. pavlovskyi*, sp. n. (south-central Kazakhstan and extreme northern Turkmenistan). The monotypic genus *Psammobuthus* Birula, 1911 (described from the Ferghana Valley at the border of Uzbekistan and Tajikistan) is synonymized under *Anomalobuthus*; its single species is transferred as *Anomalobuthus zarudnyi* (Birula, 1911), comb. n. We also clarify the type locality of the type species *A. rickmersi* Kraepelin, 1900, from accurate data published by its collector Rickmer Rickmers (1913) but overlooked since its very original description: it is Baljuvon in Tajikistan. Occurrence of *A. rickmersi* in southern and southeastern Turkmenistan is confirmed. All available species are fully illustrated with color photos of habitus and morphologically diagnostic characters, and a key covering all six recognized species of *Anomalobuthus* is included.

Introduction

A rare genus *Anomalobuthus* (Scorpiones: Buthidae) was described by Karl Kraepelin (1900) with its type species *A. rickmersi* based on a single type specimen, currently housed at Zoologisches Museum Hamburg, Germany (below, ZMUH). The specimen was captured in “Bucharei”, i.e., the Emirate of Bukhara (then a protectorate of the Russian Empire) by the famous German explorer Willi Rickmer Rickmers (1873–1965) who visited Central Asia several times. Later, *Anomalobuthus rickmersi* Kraepelin, 1900 was recorded in many deserts of Central Asia (Fet, 1989).

Sand desert scorpions of Central Asia, including *A. rickmersi*, were discussed by Fet et al. (1998) who noted high parallelism in the adaptive features allowing psammophily (life in sand). Recently, a phylogeographic mo-

del based on DNA markers, including *A. rickmersi* and a co-distributed convergent psammophile *Liobuthus kessleri* Birula, 1898, was offered by Graham et al. (2012) who also noted a phylogenetic structure between known populations of *Anomalobuthus*.

The genus *Anomalobuthus* remained monotypic until the recent discovery of a second, new species in eastern Iran, *A. talebii* (Teruel, et al., 2014). Further revisionary work of our research group has revealed that the populations assigned in literature to “*A. rickmersi*” in fact include at least four species, three of which are described below as new ones. Our study shows the presence of at least six species in the genus *Anomalobuthus*, found in five countries: Iran (one species), Kazakhstan (three species), Tajikistan (first record; two species), Turkmenistan (two species), and Uzbekistan (two species).

Methods & Material

Nomenclature and measurements follow Stahnke (1971), Kovařík (2009), and Kovařík & Ojanguren Afilastro (2013), except for trichobothriotaxy (Vachon, 1974), metasomal carinae (Francke, 1977), pedipalp chela carinae (Acosta et al., 2008, as interpreted by Armas et al., 2011), and sternum (Soleglad & Fet, 2003a). In the text, the redescription of the type species is presented first and the descriptions of the three new species follow ordered alphabetically; a shorter description of the species transferred to this genus is given last, taken from the original description because the types (only known specimens) were not available for study.

Scanning Electron Microscopy was performed by Jan Štundl at Charles University, Prague, Czech Republic, and Victor Fet (with the expert help of David Neff, Kelly Anne Daniel, and Jacqueline Aisling) at Marshall University, West Virginia, USA.

Specimens studied herein are preserved in 80% ethanol and deposited in the following collections: Naturhistorisches Museum Wien, Vienna, Austria (NHMW); National Museum of Natural History, Prague, Czech Republic (NMPC); National Museum of Natural History, Bulgarian Academy of Sciences, Sofia, Bulgaria (SOFM); Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia (ZISP); Zoological Museum, Moscow State University, Moscow, Russia (ZMSU); Centrum für Naturkunde (CeNak); Center of Natural History Universität Hamburg, Zoological Museum, Germany (ZMUH); Zoologische Sammlung der Universität, Rostock, Germany (ZSRO); and personal collections of Rolando Teruel (RTOC), František Kovařík (FKCP), Victor Fet (VFPC), and Graeme Lowe (GLPC).

Systematics

Family Buthidae C. L. Koch, 1837

Genus *Anomalobuthus* Kraepelin, 1900

Figures 1–141

Anomalobuthus Kraepelin, 1900: 1–11, figs. 4–7; Birula, 1917: 55; Werner, 1934: 272; Vachon, 1974: 908, fig. 37; Fet, 1989: 80; Sissom, 1990: 37, 46, 48–51, 101, 120, figs. 3.17h, m; Fet & Lowe, 2000: 75 (includes full list of references before 1998); Capes & Fet, 2001: 300–301; Fet et al., 2001: 183–185, tab. 1; Fet et al., 2003: 4; Fet et al., 2005: 2–3, 6–7, 10–11, 13, 22, 24–25, figs. 10, 23–25, tab. 1; Lourenço, 2005: 111; Volschenk et al., 2008: 652, 654, 659–660, Fig. 1I; Graham et al., 2012: 96; Teruel et al., 2014: 1–10, figs. 1–24, tabs. 1–2. *Nec Lourenço, 2001: 15–20* [misidentification].

Psammobuthus Birula, 1911a: 69–74; Werner, 1934: 271; Fet, 1989: 119; Sissom, 1990: 50, 52; Fet & Lowe, 2000: 214 (includes full list of references before 1998); Fet et al., 2001: 183, 185, tab. 1. **New synonym.**

DIAGNOSIS. Adult size small for the family (males 22–34 mm, females 23–37 mm). Adults slightly dimorphic: males smaller and slenderer, with pectines larger and with higher tooth counts. Cheliceral dentition modified from most common buthid pattern (Vachon, 1963): both fixed and movable finger ventrally with a single denticle. Pedipalps very slender, with chelae narrower than patella; trichobothrial pattern A-β, varying from apparently orthobothriotaxic to clearly neobothriotaxic (femoral d_2 and chelal Et , V_1 , and esb trichobothria absent to rudimentary), patellar trichobothrium d_3 located between dorsomedian and dorsointernal carinae; fingers without lobe/notch combination, with 8–11 principal rows of denticles (division of basalmost rows usually poorly defined), all arranged in a straight line, external accessory denticles entirely absent, internal accessory denticles absent from basalmost rows, movable finger with 1–2 accessory denticles basal to the terminal denticle. Carapace essentially without carinae, with anterior margin convex; median eyes very large and raised, five pairs of much smaller lateral eyes (three same-sized and aligned along each anterolateral corner, plus two tiny and offset above the former). Tergites I–VI vestigially to obsoletely tricarinate. Sternum type 1, relatively small, and triangular to subpentagonal in shape; posterior depression very large and deep. Pectines very large, with 22–27 teeth in males and 19–26 in females; fulcra well developed; lamellae and basal plate unmodified. Legs very long and slender, adapted to psammophily: tibia and tarsi of I–III short, curved, flat, and paddle-like, with setation heavily modified into bristlecombs, telotarsi with two rows of long setae on ventral surface, claws very long, asymmetrical, and weakly curved; tibial spurs highly variable, from fully developed to entirely absent (usually highly reduced), tarsal spurs well-developed but with complex armature (bifurcate, with setae and spines). Sternites with spiracles slit-like; V without a well-defined smooth patch. Metasoma slender, with carination highly reduced; dorsal lateral and lateral supramedian carinae of segments I–IV with 1–2 conspicuously enlarged posterior terminal denticles; ventral lateral carinae of segment V evenly flared, with sharp to round denticles; intercarinal spaces with some coarse punctuations on IV–V, each surrounding the base of a macroseta and usually along carinae. Telson elongate, subaculear tubercle absent.

DISTRIBUTION (Fig. 141): Iran, Kazakhstan, Tajikistan, Turkmenistan, and Uzbekistan.

Description of several distinct species of *Anomalobuthus* attests to differentiation of this psammophile genus in isolated pockets of Central Asian sand deserts, a biogeographic process well documented in other animal groups (see below in Biogeography section). The genus *Anomalobuthus* is found from eastern Iran, at 33°20'49.45"N, to Kazakhstan, at 44°20'37"N (Baigakum). Thus its range spans over 10 degrees (>1,100 km) from north to south across the great deserts of Central Asia and Iran. From west to east, it spans over 23 degrees (>2,600 km) from Kheles, Turkmenistan, at 53°24'E, to Kapchagay, Kazakhstan, at 77°05'E (Teruel et al., 2014).

The presence of *Anomalobuthus* in Afghanistan, Kyrgyzstan, and China has never been documented, but it can be predicted to occur there in continuous or similar habitats since at least four species occur very near to their borders: *A. lowei* sp. n., *A. rickmersi*, *A. talebii*, and *A. zarudnyi* comb. n. (Fig. 141).

ECOLOGY. Almost all species are ultra-psammophiles, which inhabit exclusively the vast sand dune systems of the various Central Asian deserts. The single exception is the type species *A. rickmersi*, a widespread psammophile that also reaches the upper clay taluses of the Kyzylsu Valley.

NOTES.

1. The genus *Psammobuthus* Birula, 1911, was described based on two specimens from the sands of the Fergana Valley, in the boundary of modern Uzbekistan and Tajikistan. It was never collected again and Fet et al. (2005: 13) quoted an earlier opinion of A. V. Gromov (pers. comm., 2002) that it could be a junior synonym of *Anomalobuthus*. The present study of abundant material of the latter, confirmed this suspicion: all characters used to diagnose *Psammobuthus* by Birula (1911a) are distributed within the variability range now known for the entire genus. Thus, the following synonymy is established herein: *Anomalobuthus* Kraepelin, 1900 = *Psammobuthus* Birula, 1911, **new synonym**.

2. Uzbekistan has been traditionally listed as a country record for the genus *Anomalobuthus*, based on the incorrect assumption that the holotype of *A. rickmersi* originated from this country (see below, in the section pertinent to this species). In fact, the first published specimens originating actually from Uzbekistan (modern Bukhara Province) were collected only in 2002 by V. Fet and A. V. Gromov, and first studied by Soleglad & Fet (2003a, 2003b) and Fet et al. (2005).

3. Lourenço (2001) published a “revised diagnosis” of the genus, allegedly based upon the holotype of *A. rickmersi*. However, it is entirely wrong because the specimen examined by Lourenço was not the actual

holotype and apparently not even a member of *Anomalobuthus* (see below, in the Notes section of that species).

SUBORDINATE TAXA. *Anomalobuthus rickmersi* Kraepelin, 1900 (Turkmenistan, Tajikistan), *A. krivochatskyi* Teruel, Kovářík et Fet, sp. n. (Uzbekistan, Kazakhstan), *A. lowei* Teruel, Kovářík et Fet, sp. n. (Kazakhstan), *A. pavlovskyi* Teruel, Kovářík et Fet, sp. n. (Kazakhstan, Turkmenistan), *A. talebii* Teruel, Kovářík, Navidpour et Fet, 2014 (Iran), *A. zarudnyi* (Birula, 1911), comb. n. (Uzbekistan, Tajikistan).

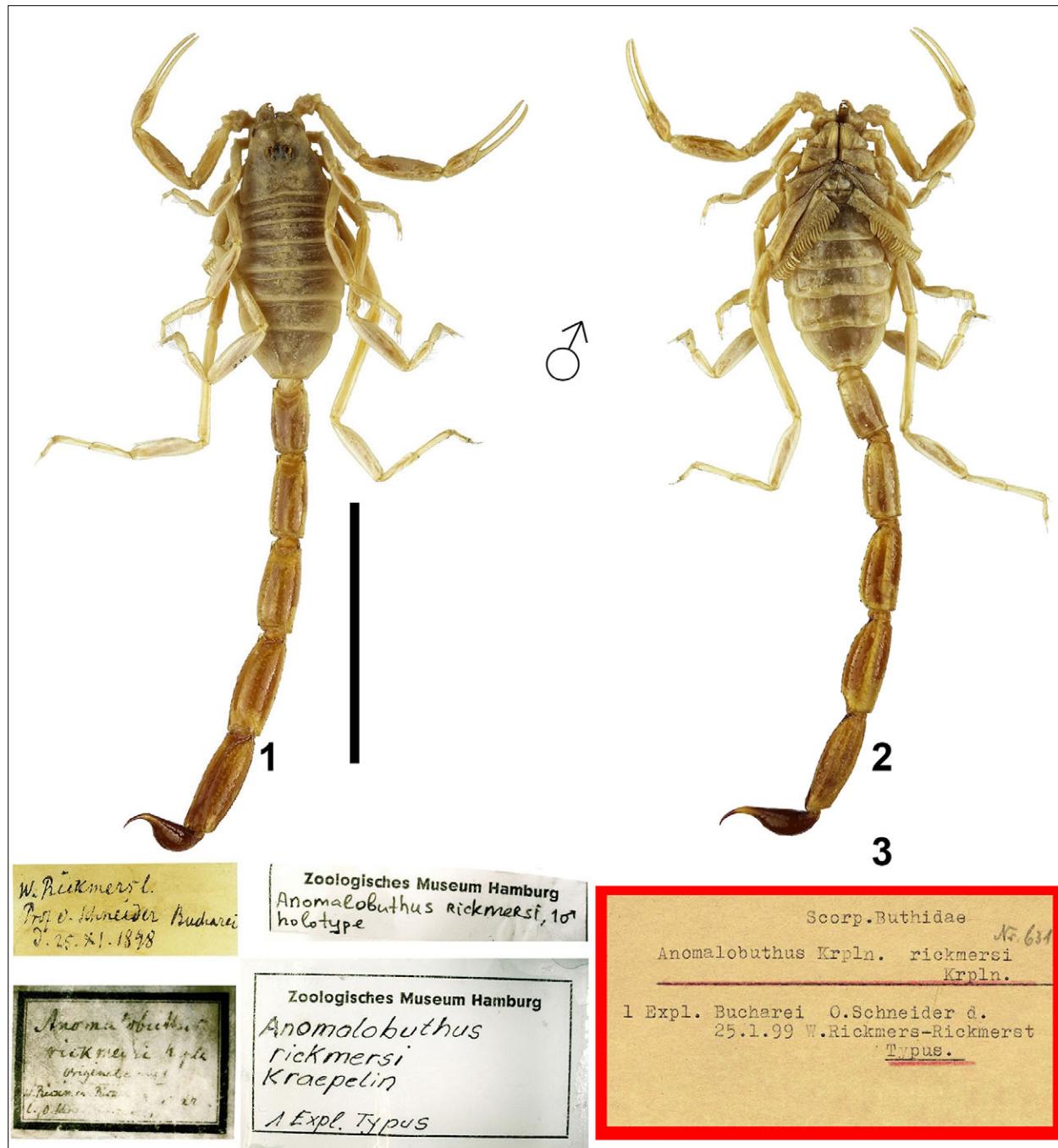
Anomalobuthus rickmersi Kraepelin, 1900

Figures 1–33, 117–119, 126–127, 137, 141; Tables 1, 4–5

Anomalobuthus rickmersi Kraepelin, 1900: 1–11, figs. 4–7; Birula, 1904: 32; Birula, 1905: 449 (in part); Birula, 1911a: 73–74 Birula, 1911b: 171 (in part); Rickmer Rickmers, 1913: 442; Birula, 1917: 112 (in part); Pavlovsky, 1934: 201 (in part). Werner, 1934: 272; fig. 341; Weidner, 1959: 98; Stahnke, 1972: 122 (in part), fig. 3; Vachon, 1974: 908, fig. 37; Fet, 1980: 224 (in part); Fet, 1989: 80 (in part); Sissom, 1990: 37, 46, 48–51, 96, 101, 120, figs. 3.17h, m; Fet, 1994: 531 (in part); Gromov & Kopdykbaev, 1994: 20 (in part); Fet et al., 1998: 613 (in part), fig. 6 [specimen from Repetek]; Fet & Lowe, 2000: 75 (in part, includes full list of references before 1998); Fet et al., 2001: 183–185, tab. 1 (in part). Fet et al., 2003: 4 (in part); Fet et al., 2005: 2–3, 6–7, 10–11, 13, 22, 24–25, figs. 10, 23–25, tab. 1 (in part); Graham et al., 2012: 95–96 (in part); Warburg, 2013: 96, 102 (in part); Teruel et al., 2014: 1, 4, 6–7, 9, fig. 20, tabs. 1–2 (in part). Nec Lourenço, 2001: 15–20 [misidentification, see below in Remarks section].

HOLOTYPE ♂ (ZMUH, examined). **Tajikistan**, Khatlon Province, Kyzylsu River valley, near Baljuvon (= Bal'dzhuvon or Baljuan), early summer 1896, leg. W. Rickmer Rickmers. See discussion below, in Remarks section.

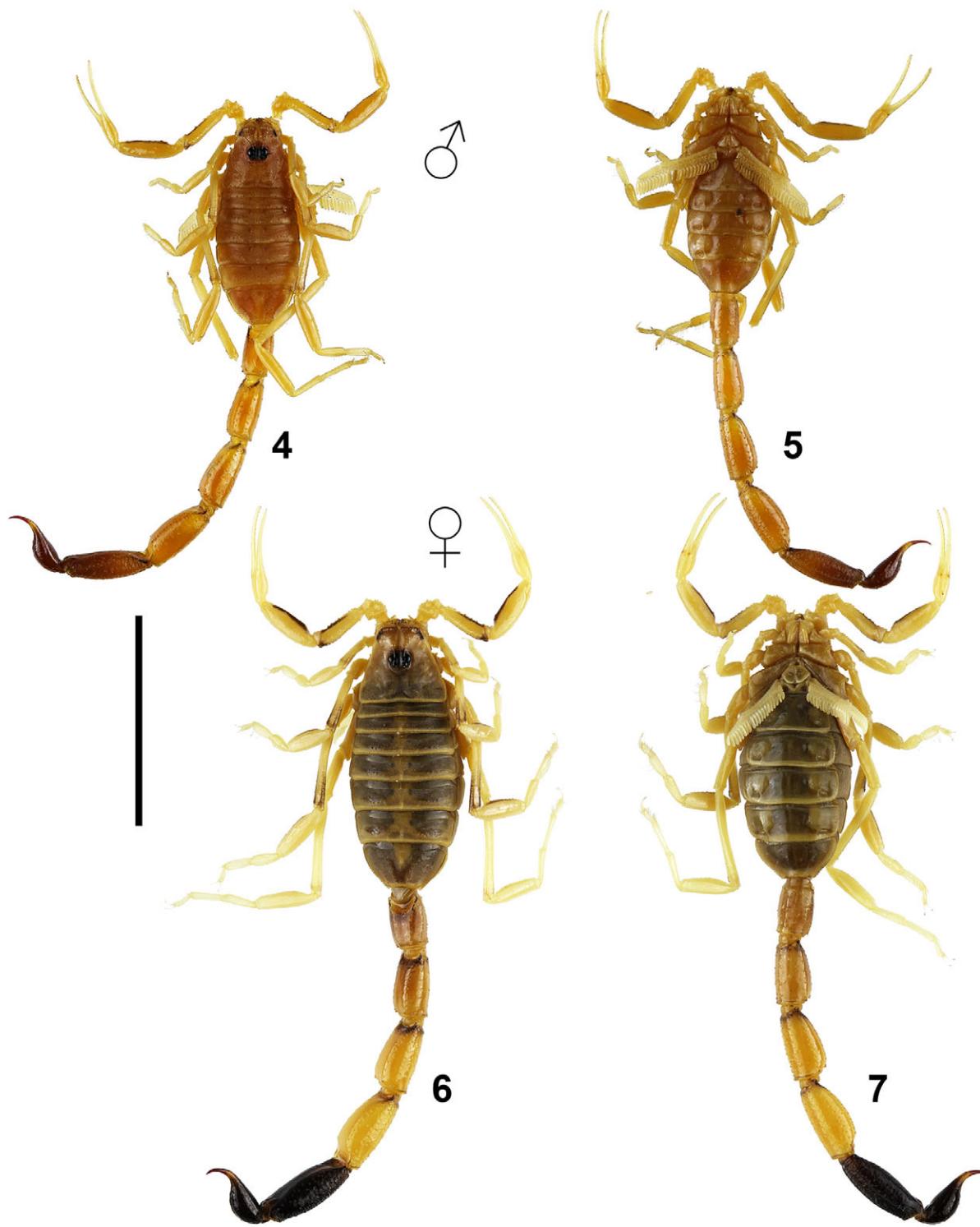
OTHER MATERIAL EXAMINED. **Turkmenistan**, Karakum Desert, Lebap (=Chardzhou) Province, Repetek Nature Reserve, 38°33'54"N 63°10'51"E, 201 m a.s.l., 21 July 1985, leg. V. Fet, 2♂♂ (NHMW), 5♂♂, 1 juvenile (VFPC); same data except 29 April 1967, leg. V. I. Kuznetsov, 1♂ (ZSRO Sc-1249); same data except 15 April 2002, leg. V. Fet, 1 juvenile (VFPC); Karakum Desert, Akhal Province, Tejen (= Tedzhen, Tedschen), 37°22'39"N 60°29'52"E, 188 m a.s.l., 10–24 July 1904 [23 July–6 August], leg. K. Aris, 1♂ (ZISP 809); Mary Province, Serkhetabad District, Badghyz Plateau, Chainury, 35°40'52"N 62°01'34"E, 458 m a.s.l., 6 April 2002, leg. V. Fet & A. V. Gromov, 1♀ (FKCP), 1♀ (NMPC).



Figures 1–3: *Anomalobuthus rickmersi*, adult male holotype: full-body views, dorsal (1) and ventral (2), plus original labels (3). Scale bar = 10 mm (1–2). The red inset at bottom right shows the label of the specimen examined by Lourenço (2001), demonstrating it was not the actual Rickmers's type specimen.

DIAGNOSIS (emended). Adult size 30–34 mm in males, 32–37 mm in females. Coloration light yellow, essentially immaculate, only with some regular blackish spots on pedipalps and metasoma (darker and more extended in female); metasomal segment V and telson reddish brown (male) to black (female). Pedipalp fingers with 9–10 principal rows of denticles and 7–9 internal

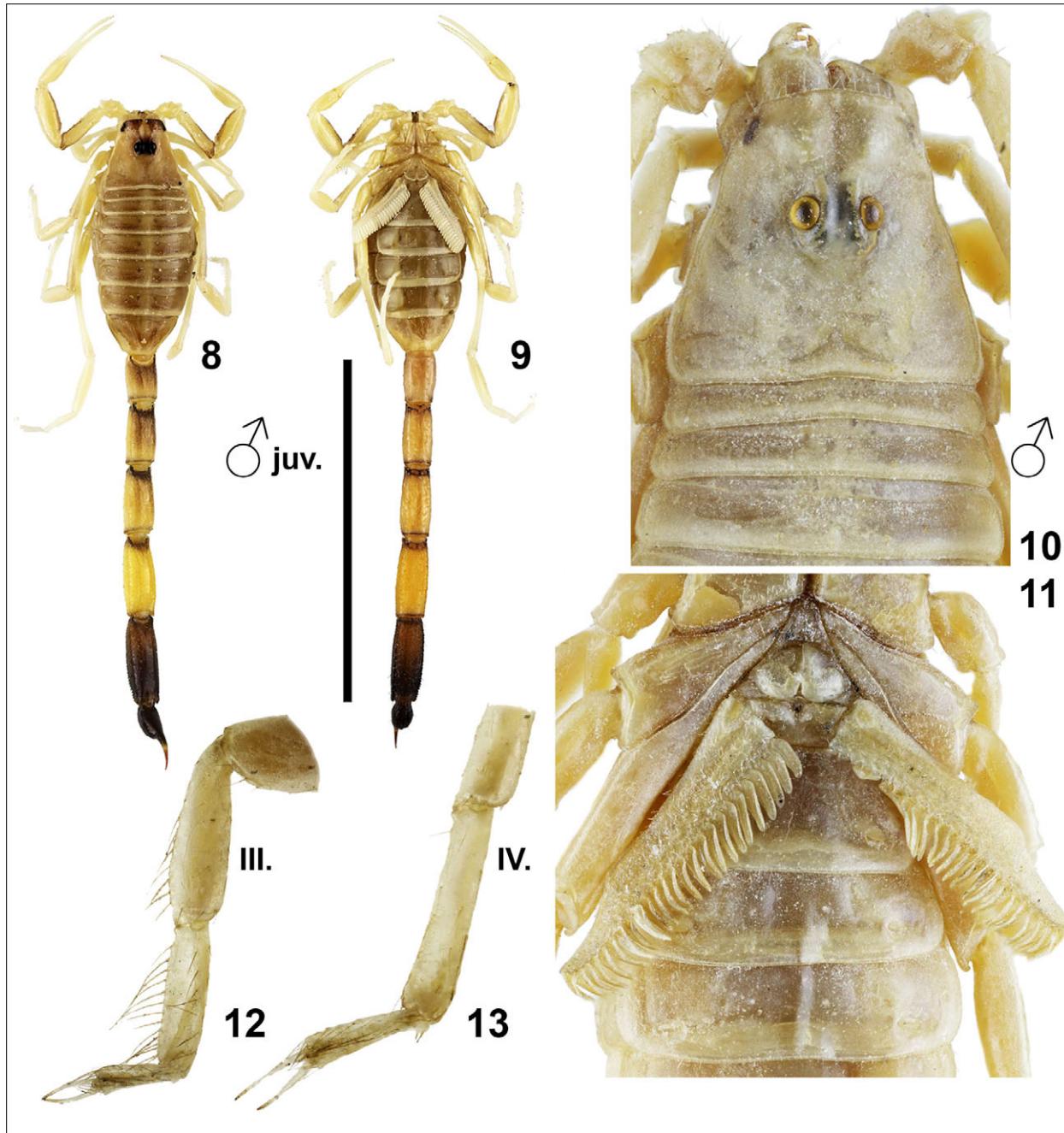
accessory denticles. Pectines with 23–27 teeth in males and 20–23 in females. Tibial spur variable from absent (specimens from Turkmenistan) to present but very small on leg IV only (male holotype from Tajikistan). Metasoma conspicuously attenuate, with most carinae obsolete to vestigial; ventral lateral carinae of segment V composed of denticles narrowly conical (male) to nar-



Figures 4–7: *Anomalobuthus rickmersi* from Turkmenistan: adult male from Repetek (4–5) and adult female from Chainury (6–7), full-body views, dorsal (4, 6) and ventral (5, 7). Scale bar = 10 mm.

rowly lobate (female), dorsal lateral and lateral supra-median carinae of segments I–IV with terminal dent-

icle enlarged; intercarinal spaces essentially smooth on segments I–III, sparsely granulose on ventral and lat-



Figures 8–13: *Anomalobuthus rickmersi*. **Figures 8–9.** Juvenile male from Repetek, Turkmenistan: full-body views, dorsal (8) and ventral (9). Scale bar = 10 mm. **Figures 10–13.** Adult male holotype: chelicerae, carapace and tergites I–III, dorsal (10), sternopectinal region and sternites III–V, ventral (11), distal part of left leg III, internal (12), distal part of left leg IV, internal (13).

eral areas of IV and very densely granulose on ventral and lateral areas of V (granulation sparser in female). Telson vesicle elongate oval and sparsely setose.

REDESCRIPTION (adult male holotype). **Coloration** (Figs. 1–2) moderately faded and translucent due to long preservation, but still reliably traceable. Base light yel-

lowish; in general, the base color is paler on pedipalp chelae, legs, and pectines. Chelicerae immaculate, except for dark brown finger teeth. Pedipalp femur and patella with internal surface infuscate; chela immaculate, only with finger denticles dark brown. Carapace immaculate, only with a blackish spot under every ocular group. Tergites immaculate. Coxosternal region and

genital operculum immaculate. Pectines pale yellowish, immaculate. Sternites immaculate. Legs essentially immaculate; claws with distal half dark brown. Metasoma not conspicuously bicolor, only becoming progressively darker and redder distally, segments I–IV with a diffusely annulated appearance (basal and distal parts of each segment faintly infuscate as thin brown rings, which become larger and more diffuse dorsally) and segment V faintly infuscate, becoming progressively darker and redder distally; carinae not infuscate nor underlined with dark pigment. Telson vesicle reddish brown, aculeus with basal half yellowish and distal half dark brown.

Chelicerae (Fig. 10). With dentition typical for the genus, as described for *A. krivochatskyi* sp. n. (see below).

Pedipalps (Figs. 14–22). Relatively short but very slender, essentially bare. Femur subtly curved inwards, with carinae weak, granulose to subdenticulate; intercarinal tegument smooth and glossy. Patella straight, with carinae obsolete to absent, smooth except on internal surface where vestigially denticulate; intercarinal tegument smooth and glossy. Chela elongate and very slender; manus conspicuously narrower than patella (ratio 0.79), subcylindrical (1.80 times longer than wide, 1.07 times wider than deep), with carinae weak to moderate, smooth; intercarinal tegument smooth and glossy; fingers very long (movable finger 2.44 times longer than underhand), only subtly curved and with 10 principal rows of denticles (the two basalmost rows are moderately well-defined), basal lobe/notch combination absent, external accessory denticles absent, internal accessory denticles very large and claw-like (increasing in size distally), numbering eight on both fixed and movable fingers, movable finger with one claw-like accessory denticle basal to the very large terminal denticle.

Carapace (Fig. 10). Very strongly trapezoidal (much narrower anteriorly) and wider than long; anterior margin shallowly convex, with 5–6 pairs of thin macrosetae and some very short microsetae. Carination essentially absent: the only carinae present are the superciliaries, which are smooth. Furrows: anterior median, median ocular, central median, posterior median and posterior marginal fused, wide and moderately deep; lateral oculars, lateral centrals, central transverse, and posterior laterals long, narrow and shallow. Tegument very finely and densely granulose, with a few small to medium-sized granules scattered all over.

Sternum (Fig. 11). Standard for the genus, relatively small and widely triangular in shape.

Genital operculum (Fig. 11). Slightly damaged. Relatively large, each half roundly subtriangular in shape. Genital papillae present.

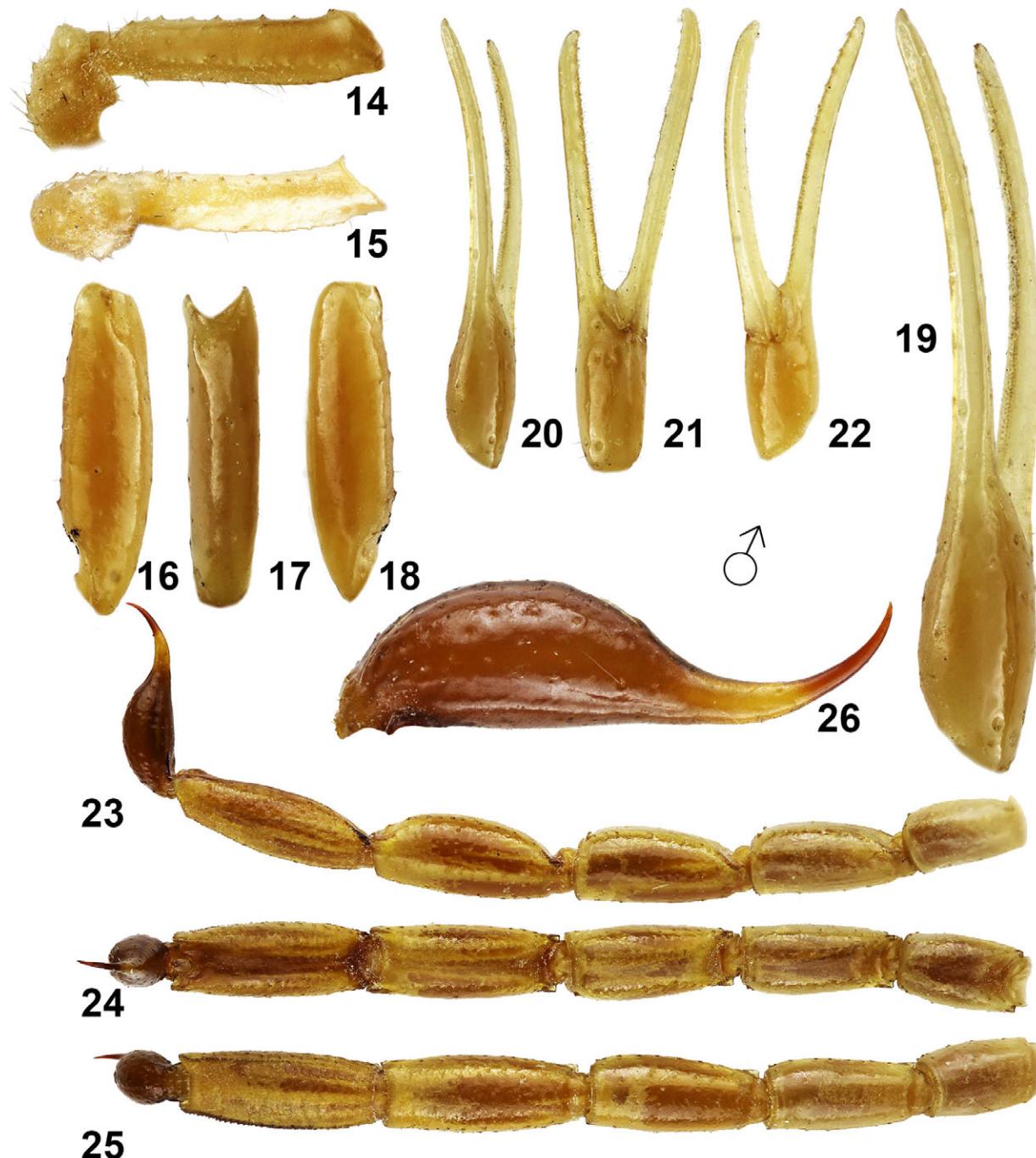
Pectines (Fig. 11). Standard-sized for the genus: very long, extending beyond leg IV coxa-trochanter joint), subrectangular and densely setose. Tooth count 25/25. Basal plate heavily sclerotized, much wider than long, anterior margin with a very deep, narrow antero-median furrow, posterior margin very shallowly convex.

Legs (Figs. 12–13). Very slender, with all carinae weak and subgranulose to subcostate; intercarinal tegument smooth and glossy. Tibial spurs entirely absent on legs III, reduced to a sinuous remnant on legs IV.

Mesosoma (Figs. 10–11). Tergites with the same sculpture as on carapace; I–VI irregularly tricarinate: the median longitudinal carina is weak, short, and formed by irregular medium-sized granules that do not project beyond posterior margin, but the submedian carinae are defined only by few coarse granules irregularly aligned; tergite VII with five well-defined carinae: the median carina is very short but strongly subserrate, the submedians and laterals are long, strong and finely serrate to denticulate. Sternites sparsely setose; III–VI glossy and with very subtle vestiges of smooth submedian carinae, spiracles relatively short and slit-like, almost transversely arranged (not strongly oblique), V with smooth patch absent; VII with two pairs of carinae: the submedians are long and finely crenulate to subcostate and the laterals are very short and subcrenulate, intercarinal tegument coriaceous to minutely granulose.

Metasoma (Figs. 23–25). Elongated and slightly wider subdistally; with 10/10/10/8/5 complete to almost complete carinae, almost all obsolete to vestigial and smooth, with coarse punctations scattered: dorsal laterals very weak on I–III (with one terminal denticle enlarged), obsolete to vestigial as rounded ridges on IV, absent on V; lateral supramedians very weak on I–III (with one terminal denticle enlarged), obsolete to vestigial as rounded ridges on IV–V; lateral inframedians obsolete on I–III, absent on IV–V; ventral laterals obsolete on I–IV, weak to moderate on V, where become progressively stronger and somewhat flared distally, formed by sharply serrate, subequal denticles; ventral submedians obsolete on I–IV, absent on V; ventral median absent on I–IV, weak to moderate on V. Intercarinal tegument smooth and glossy, with minute but sharp granulation on lateral and ventral surfaces, which become much denser towards distal segments. Dorsal furrow obsolete on all segments. Setation sparse, mostly represented by 5–8 dark macrosetae over every carina.

Telson (Figs. 26). Sparsely setose, with a few setae scattered on dorsal and lateral surfaces. Vesicle elongate oval (2.50 times longer than wide, 0.95 times wider than deep), tegument smooth and glossy, with vestiges of coarse granules arranged into three obsolete longitudinal carinae (ventral median and ventral submedians), and ventrally with some coarse punctations. Subaculear tub-



Figures 14–26: *Anomalobuthus rickmersi*, adult male holotype: right pedipalp trochanter and femur, dorsal (14) and ventral (15), right pedipalp patella, dorsal (16), external (17) and ventral (18), right pedipalp chela, dorsal (19–20), external (21) and ventrointernal (22), metasoma and telson, lateral (23), dorsal (24) and ventral (25), telson, lateral (26).

ercle absent. Aculeus conspicuously shorter than vesicle, thick and shallowly curved.

FEMALE (Chainury, Turkmenistan). Very similar to male, sexual dimorphism evident by: 1) size comparatively larger inside each size-class; 2) coloration

darker and much more sharply patterned, e.g., pedipalp femur with a conspicuous blackish spot on dorsodistal apex, which diffusely continues as a broad stripe over almost all internal surface, patella with internal surface blackish, carapace with anterior margin deeply infuscate, metasomal segment V and telson black; 3) mesosoma



Figures 27–33: *Anomalobuthus rickmersi* from Turkmenistan, adult male from Repetek (27–30) and adult female from Chainury (31–33): metasoma and telson, lateral (27, 31), dorsal (28, 32) and ventral (29, 33), telson, lateral (30).

and metasoma slightly less slender; 4) genital papillae absent; 5) pectines smaller, with consistently lower tooth counts; 6) metasomal segment V with lateral intercarinal tegument less granulose. See Figs. 6–7, 31–33 and Tabs. 1, 4–5.

VARIATION. Adult size varied from 30.4–34.1 mm in males and 32.1–36.5 mm in females.

Pectinal tooth count varied as follows: 23–27 teeth in males and 20–23 in females, without clearly defined mode in either sex (Tab. 5).

Males from Repetek are virtually identical to the holotype in all diagnostic characters. The only exception is that the tibial spurs are usually entirely absent. This

character alone is inappropriate to separate both populations taxonomically, especially when only a single specimen from Tajikistan is available. In addition, the male from Tejen (ZISP 809) has tibial spurs on both legs IV as noted already by Birula (1905: 450).

COMPARISON. Adults of *A. rickmersi* can be very easily distinguished by the greater slenderness of the metasoma, especially in males (Figs. 1–2, 4–7, 117; Tabs. 1, 4); even to unaided eye, most other congeners are more robust (Figs. 34–45, 65–66, 79–82, 90–91, 107, 110, 113–114; Tabs. 2–4). For example, see the following male ratios: metasoma + telson length / carapace length = 7.76 vs. 6.26–7.14, metasomal segments length

/ width = 1.74 vs. 1.02–1.35 (I), 2.13 vs. 1.35–1.82 (II), 2.20 vs. 1.39–1.88 (III), 2.56 vs. 1.75–2.23 (IV) and 2.71 vs. 1.85–2.38 (V).

Moreover, this species is the only one that has metasomal segment V and telson light reddish-colored in adult males (Figs. 1–2, 4–5, 23–25, 27–29, 117); in all other *Anomalobuthus* spp., it is blackish, entirely or at least in its distal half (Figs. 34–35, 38–39, 59–61, 79–80, 84–86).

DISTRIBUTION (Fig. 141). Widespread in southern Central Asia, from the sands of the Karakum Desert (eastern Turkmenistan), to the loess soils of the Kyzylsu River valley (southwestern Tajikistan). See further details below, in Remarks section.

ECOLOGY. According to the personal data of the collector (Rickmer Rickmers, 1913: 442), the holotype was collected in early summer, from crevices or cracks of fine alluvial soil (“*loess crannies*”). Populations from the Karakum Desert inhabit sand dunes but tend not to occupy loose sands where two other sympatric ultrasammophiles are found, *Liobuthus kessleri* and *Pectinibuthus birulai* Fet, 1984. Detailed ecological information from Repetek was published by Fet (1980).

NOTES. The holotype of *A. rickmersi* remains the single specimen known from Tajikistan. Its collecting site was reported by Kraepelin (1900) as Bukhara (“Bucharei”, see the original museum label in Fig. 3) and interpreted by all subsequent authors as originating from the city, the capital of the homonymous Bukhara Khanate, located in modern Uzbekistan. In addition, Birula (1911b: 171) erroneously stated that the type specimen of *A. rickmersi* originated from “westlichen Buchara” (i.e. western part of the Bukhara Emirate).

This specimen was collected by the famous German mountain explorer Willi Rickmer Rickmers (1873–1965) who repeatedly visited the Bukhara Emirate, then a protectorate of the Russian Empire, which included part of modern Uzbekistan and Tajikistan (Rickmer-Rickmers, 1899; Rickmer-Rickmers, 1913). During preparation of the present revision, we discovered that Rickmer Rickmers (1913: 442) himself actually published unequivocal information on the precise collection locality and date of the holotype, which we reproduce below *verbatim*:

“On the way to Baljuan I noticed that many poplar trees were pitted with wormholes bored by that stately Capricorn beetle the *Pachydissus Sartus*. In the early summer of 1896 the loess crannies around had yielded up to my collection new specimens of poisonous spider and scorpion, *Gylippus Rickmersi* and *Anomalobuthus Rickmersi*. I feel highly gratified that such vicious creatures should bear my name.”

By the way, the “poisonous spider” mentioned by the impressed collector is a solpugid, also described by Kraepelin (1899). It is a member of the Gylippidae family, currently regarded as a junior synonym of *Gylippus ferganensis* Birula, 1893 (see Harms & Dupérré, 2018). As all solpugids, it is indeed “vicious” but not “poisonous”.

Baljuan (also spelled Baldzhuan, now Baljuvon or Bal'dzhuvon) is a well-known town in modern Tajikistan, in the valley of Kyzylsu River, a tributary of the larger Panj River (= Pyandzh, Piandj), itself a tributary of the great Amudarya (the ancient Oxus). Baljuvon stands on the Silk Road, not far from the ancient Bactra (now Balkh in northern Afghanistan), and was last time noted as the place where Enver Pasha, a rival of the Turkish leader Mustafa Kemal (Ataturk), was killed in 1922 in a skirmish with the Soviet troops.

In more peaceful times, Rickmer-Rickmers (1899) published a map of his fourth travel to the Bukhara Emirate, conducted in 1898 (the 1896 trip was his third travel). We can see that he followed the same and (then) only route from Dushanbe (now the capital of Tajikistan) to Khovaling, via Baljuvon. Baljuvon lies very far to the southeast from the former Emirate's capital city of Bukhara (modern Uzbekistan) and is isolated by several mountain ranges from the lowland deserts of Uzbekistan.

Although quite active zoological research was conducted in Central Asia by numerous Russian (and then Soviet) researchers, very few scorpions have been collected in the remote valleys of northern tributaries of Amu Darya in modern Uzbekistan and Tajikistan. It is not surprising, therefore, that no other specimens of *A. rickmersi* have been collected in this area since 1896; in fact, no other scorpion collections we know of originate from Baljuvon. Moreover, another, much more amazing scorpion from the same area was not discovered until the 1990s: the relict *Pseudochactas ovchinnikovi* Gromov, 1998 (Pseudochactidae). Its type locality lies in the Surkhandarya River valley, which separates modern Uzbekistan from Tajikistan (Gromov, 1998; Fet et al., 2004).

The first known specimen from Turkmenistan (then the Transcaspian Region of the Russian Empire) was reported by Birula (1904: 32, 35). It was a female collected next to the railway station of Repetek in the East Karakum, the future site of the famed Repetek Natural Reserve, by the coleopterologist Eduard Nikolaevich Fischer in February 1904 (ZISP 808). The second specimen was also published by Birula (1905: 449–450); it was a male from Tejen (= Tedzhen, Tedshen) in Akhal Province, collected by K. Aris in June 1904 (ZISP 809). Further collections from Turkmenistan published by Fet (1989), included a series of more than 20 specimens from Repetek (ZISP, ZMMSU). In addition, two males from Repetek are housed in

Dimensions (mm)		TJK, Baljuvon	TKM, Chainury	
		♂ holotype (ZMUH)	♀ (FKCP)	♀ (FKCP)
Carapace	L / Wp	3.05 / 3.80	3.67 / 4.30	3.55 / 4.03
Mesosoma	L	7.70	9.40	7.10
Tergite VII	L / W	2.15 / 3.50	2.35 / 4.10	1.79 / 4.18
Metasoma + Telson	L	23.38	23.41	21.48
Segment I	L / W / D	2.80 / 1.61 / 1.43	2.80 / 1.95 / 1.79	2.50 / 1.75 / 1.43
Segment II	L / W / D	3.40 / 1.60 / 1.58	3.48 / 1.78 / 1.85	3.00 / 1.63 / 1.58
Segment III	L / W / D	3.80 / 1.73 / 1.73	3.85 / 1.85 / 1.90	3.43 / 1.68 / 1.73
Segment IV	L / W / D	4.43 / 1.73 / 1.74	4.35 / 1.88 / 1.95	4.05 / 1.75 / 1.74
Segment V	L / W / D	4.55 / 1.68 / 1.50	4.78 / 1.97 / 1.72	4.45 / 1.78 / 1.50
Telson	L	4.40	4.15	4.05
Vesicle	L / W / D	2.63 / 1.05 / 1.10	2.65 / 1.40 / 1.30	2.60 / 1.30 / 1.20
Aculeus	L	1.77	1.50	1.45
Pedipalp	L	11.08	11.15	10.65
Femur	L / W	3.03 / 0.65	2.95 / 0.75	2.75 / 0.70
Patella	L / W	3.40 / 0.95	3.40 / 1.08	3.25 / 1.00
Chela	L	4.65	4.80	4.65
Manus	L / W / D	1.35 / 0.75 / 0.70	1.35 / 0.86 / 0.85	1.11 / 0.75 / 0.75
Movable finger	L	3.30	3.45	3.54
Total	L	34.13	36.48	32.13

Table 1: Measurements of three adults of *Anomalobuthus rickmersi*. Abbreviations: length (L), width (W), posterior width (Wp), depth (D).

NHMW and one in R. Kinzelbach's collection (ZSRO). Some of these specimens are illustrated here in Figs. 4–5, 27–30, 103–115. A few specimens from northern Turkmenistan (Kunya-Urgench, ZISP 1699; Shakhs-enem, ZMMSU Tb-374), published by Fet (1989) as *A. rickmersi*, actually correspond to a different species (*A. pavlovskyi* sp. n., see below).

It is clear from A. Birula's publications that he never studied the holotype of *A. rickmersi*; however, it was seen and its trichobothrial pattern sketched by Vachon (1974: 908, fig. 37). On the other hand, Lourenço (2001) claimed to have examined it; however, it is obvious that the specimen he received on loan from ZMUH was not Kraepelin's original holotype, but a misidentified and wrongly labeled juvenile of maybe even another genus. Lourenço (2001) declared this specimen as an immature with a total length of 13–14 mm [sic], pectinal tooth count 24–26, and textually wrote: "... cutting edge of the movable finger with 6 series of granules [...] the basal-most extending onto more than half the length of the finger. [...] Pectinal Fulcra almost vestigial and flat..." [originally in French, English translation and bracketed text added by us].

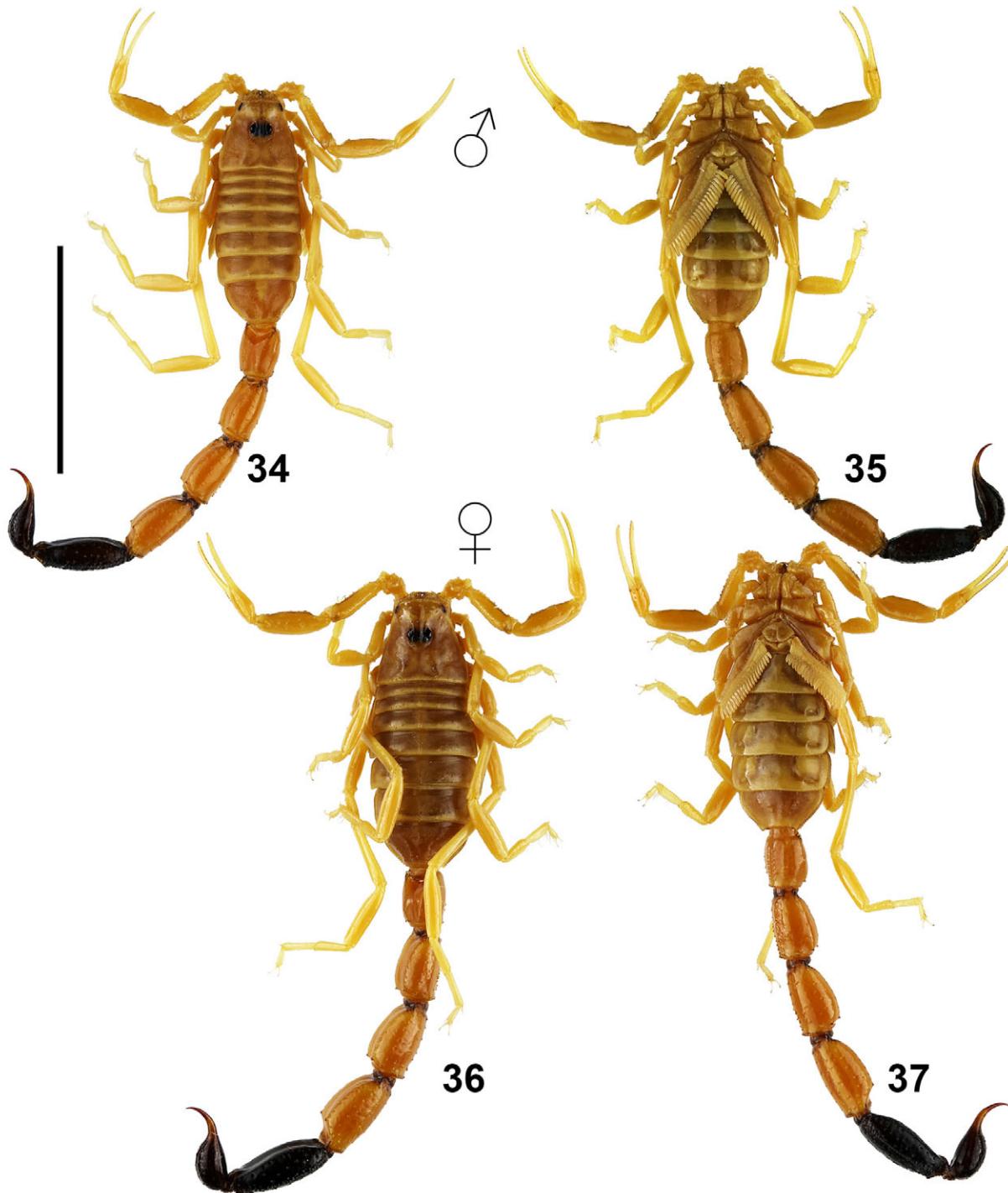
None of these crucial characters match the holotype of *A. rickmersi* and clearly contradict the original description and illustrations published by Kraepelin (1900), which were confirmed by our own examination of the true type: it is a large adult male with a total length of 34 mm, pectinal tooth count 25/25, fingers with 10 rows of primary denticles of which the basal-most extends onto less than one-third of finger, and fulcra normally developed and pearl-like. Finally, a photo of the label of the specimen examined by Lourenço (2001), provided by himself to V.F. in 2009, does not correspond to any of those accompanying the actual holotype (Fig. 3).

***Anomalobuthus krivochatskyi* Teruel, Kovářík et Fet, sp. n.**

Figures 34–64, 120–125, 128–133, 134–136, 138–141.
Tables 2, 4–5

<http://zoobank.org/urn:lsid:zoobank.org:act:3936A68B-96D5-461C-9568-5077BEA67488>

Anomalobuthus rickmersi: Soleglad & Fet, 2003a: 5, fig. 4 (in part; Bukhara); Soleglad & Fet, 2003b: 7, 59,

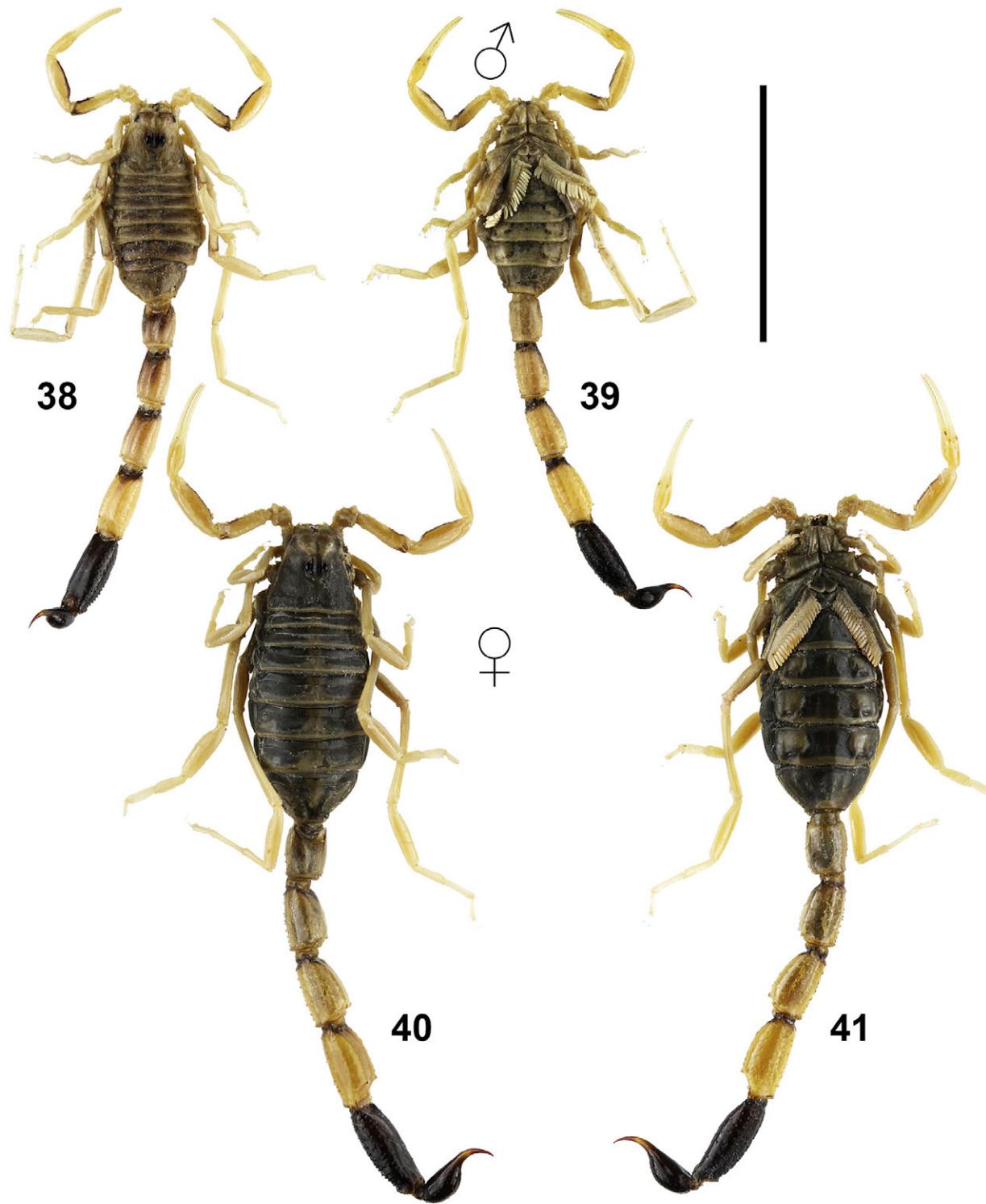


Figures 34–37: *Anomalobuthus krivochatskyi* sp. n., adult male holotype (34–35) and adult female paratotype (36–37): full-body views, dorsal (34, 36) and ventral (35, 37). Scale bar = 10 mm.

156, tab. 2 (in part; Bukhara); Fet et al., 2005: 2, 6, 11; fig. 10 (in part; Bukhara); Fet et al., 2006: 2, 10, tab. 3; Graham et al., 2012: 95–106, figs. 1–2, 6 (in part; between Bukhara and Gazli); Loria & Pren-

dini, 2014: S1: 2, S2: 2; Teruel et al., 2014: 1, 4, 6–7, 9, fig. 20, tabs. 1–2 (in part; Uzbekistan).

HOLOTYPE ♂ (FKCP). **Uzbekistan**, Navoiy Province, Tamdy (=Tomdi) District, 1–2 km SSE of



Figures 38–41: *Anomalobuthus krivochatskyi* sp. n., adult male (38–39) and adult female paratypes (40–41) from between Bukhara and Gazli, Uzbekistan: full-body views, dorsal (38, 40) and ventral (39, 41). Scale bar = 10 mm.

Zarafshan, 41°32'N 64°12'E, 18–28 April 1998, leg. A. V. Gromov.

PARATYPES. Same data as holotype, 1♂, 5♀ (FKCP), 1♂, 1♀ (RTOC: Sco-0233). **Uzbekistan**, Kizylkum Desert, Bukhara Province, between Bukhara and Gazli, 40°05'N 64°04'E, 206 m a.s.l., 11 May 2002, leg. V. Fet, 1♂, 1♀, 4 juveniles (NMPC), 1 juvenile (ZMUH), 1 juvenile (SOFM), 1♀ (RTOC: Sco-0208); Bukhara, 30 April 1979, leg. Antuš, 1♀ (FKCP). **Kazakhstan**, South Kazakhstan Province, 5 km west of Chardara, 41°16'14"N 67°53'02"E, 250 m a.s.l., 23–24 May 2016, leg. P. Kučera, 1♀, 1 juvenile (FKCP).

ETYMOLOGY. We are pleased to name this species after our colleague, Viktor Anatolyevich Krivochatsky (b. 1954) (St. Petersburg, Russia), an entomologist, a specialist in ant-lions (Neuroptera: Myrmeleontidae) and an old friend of V.F. from the time of their work in the natural reserves of Turkmenistan in the 1970s–1980s. Since 1991, Dr. Krivochatsky works in ZISP and is in charge of the famed scorpion collection of Alexei Birula.

DIAGNOSIS. Adult size 23–32 mm in males, 23–37 mm in females. Coloration orange yellow, essentially immaculate, only with some regular blackish spots on pedipalps and metasoma (slightly darker and more extended in female); metasomal segment V and telson blackish. Pedipalp fingers with 9–11 principal rows of denticles and 6–7 internal accessory denticles. Pectines with 22–25 teeth in males and 19–22 in females. Tibial spur in males absent, in females present in legs III–IV. Metasoma slightly attenuate, with most carinae weak; ventral lateral carinae of segment V composed of narrowly conical (males) to broadly lobate (females) denticles, dorsal lateral and lateral supramedian carinae of segments I–IV with terminal denticle enlarged; intercarinal areas essentially smooth, except sparsely granulose on ventrodistal and ventrolateral areas of segment V. Telson vesicle oval and densely setose.

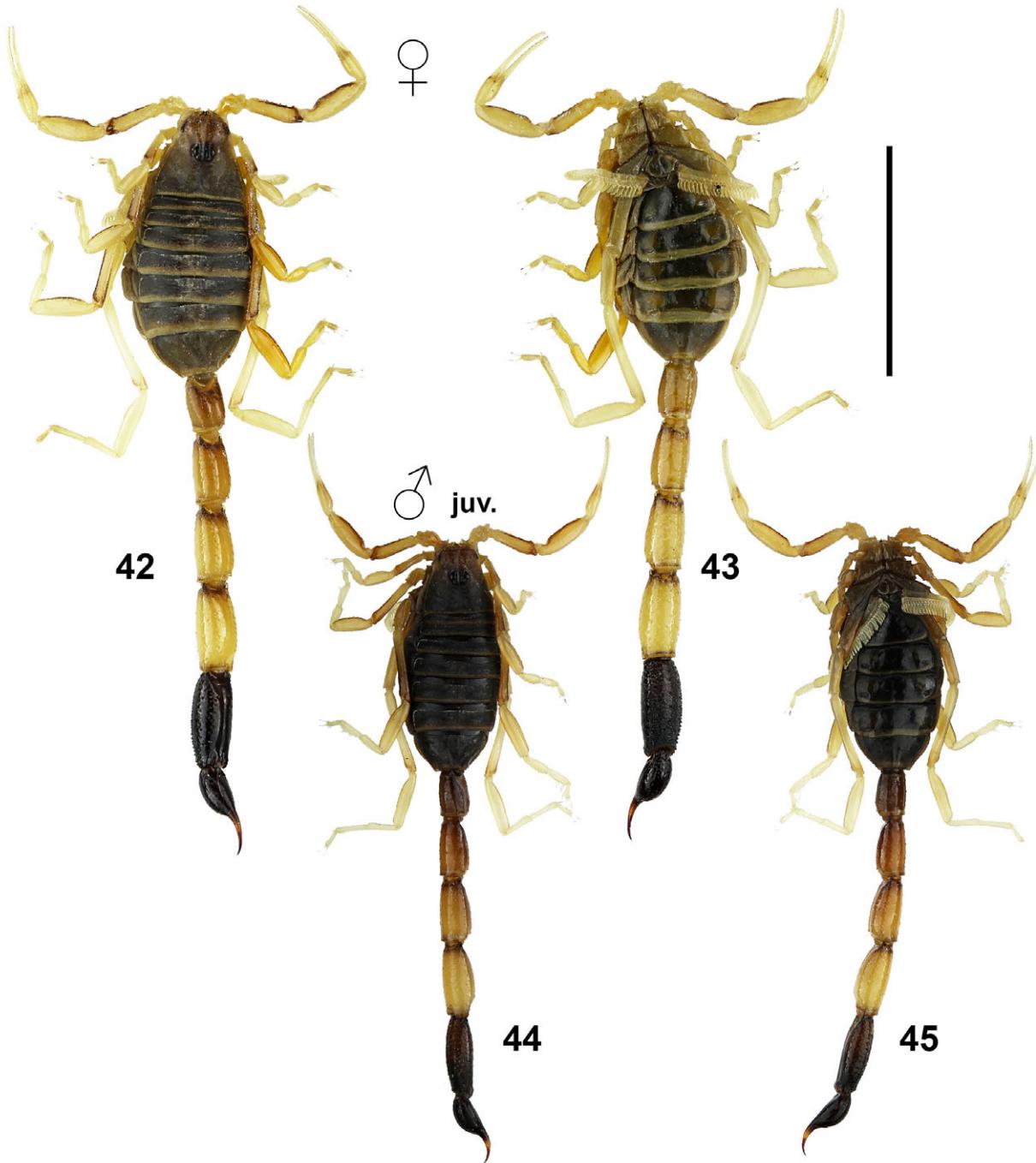
DESCRIPTION (adult male holotype). **Coloration** (Figs. 34–35) base very vivid yellow, with an orange shade; in general, the base color is paler on pedipalp chelae, legs, and pectines. Chelicerae immaculate, except for blackish finger teeth. Pedipalp femur with a conspicuous blackish spot on dorsodistal apex, which diffusely continues as a broad stripe over almost all internal surface; patella with internal surface blackish; chela immaculate, only with finger denticles blackish. Carapace immaculate, only with a blackish spot under every ocular group. Tergites immaculate. Coxosternal region and genital operculum immaculate. Pectines pale yellowish, immaculate. Sternites immaculate. Legs immaculate; claws with distal half dark brown to blackish. Metasoma conspicuously bicolor: segments I–IV yellow

with a diffuse annulated appearance (basal and distal parts of each segment infuscate in the shape of thin blackish rings, which become somewhat larger and more diffuse dorsally and basally), segment V entirely blackish; carinae not infuscate nor underlined with dark pigment, except for darkened terminal denticles on dorsal laterals and lateral supramedians. Telson vesicle blackish, similar to metasomal segment V; aculeus with basal half brownish and distal half blackish.

Chelicerae (Fig. 46). Manus smooth and shiny, dorsodistal portion with some weak granules arranged transversally, defining a depressed area; setation very dense ventrally but essentially lacking dorsally, except for many rigid macrosetae on fixed finger and a few around depressed area of manus. Fixed finger of size, shape and curvature ordinary for the family, dorsally with the four standard denticles: single *d* very large, sharp and falcate, single *sd* large, sharp and falcate, single *m* and *b* large, sharp, triangular and fused into a subrectangular bicusp; ventrally with a single denticle, which is medium-sized and placed at a level between dorsal denticles *m* and *b*. Movable finger of size, shape and curvature ordinary for the family, dorsally with the five standard denticles: single *ed* very large, sharp, falcate and placed at the same level of *id*, both closely opposable to fixed finger distal denticle, single *sd* large, sharp, triangular, single *m* very large, sharp, triangular, two *ed* small (basalmost smaller), sharp, triangular and adjacent to each other and *m*; ventrally with a single denticle which is medium-sized, small, placed at the level of dorsal denticle *sd* and raises from a conspicuous, translucent lamella.

Pedipalps (Figs. 34–35). Relatively short but very slender, essentially bare. Femur subtly curved inwards, with carinae weak, granulose to subdenticulate; intercarinal tegument smooth and glossy. Patella somewhat curved inwards, with carinae obsolete to vestigial, smooth; intercarinal tegument smooth and glossy. Chela elongate and very slender; manus conspicuously narrower than patella (ratio 0.78), cylindrical (2.14 times longer than wide, as wide as deep), with carinae obsolete to vestigial, smooth; intercarinal tegument smooth and glossy; fingers very long (movable finger 2.20 times longer than underhand), only subtly curved and with 9–10 principal rows of denticles (the two basalmost rows are poorly defined), basal lobe/notch combination absent, external accessory denticles absent, internal accessory denticles very large and claw-like (increasing in size distally), numbering seven and six on fixed and movable fingers, respectively, movable finger with one claw-like accessory denticles basal to the very large terminal denticle.

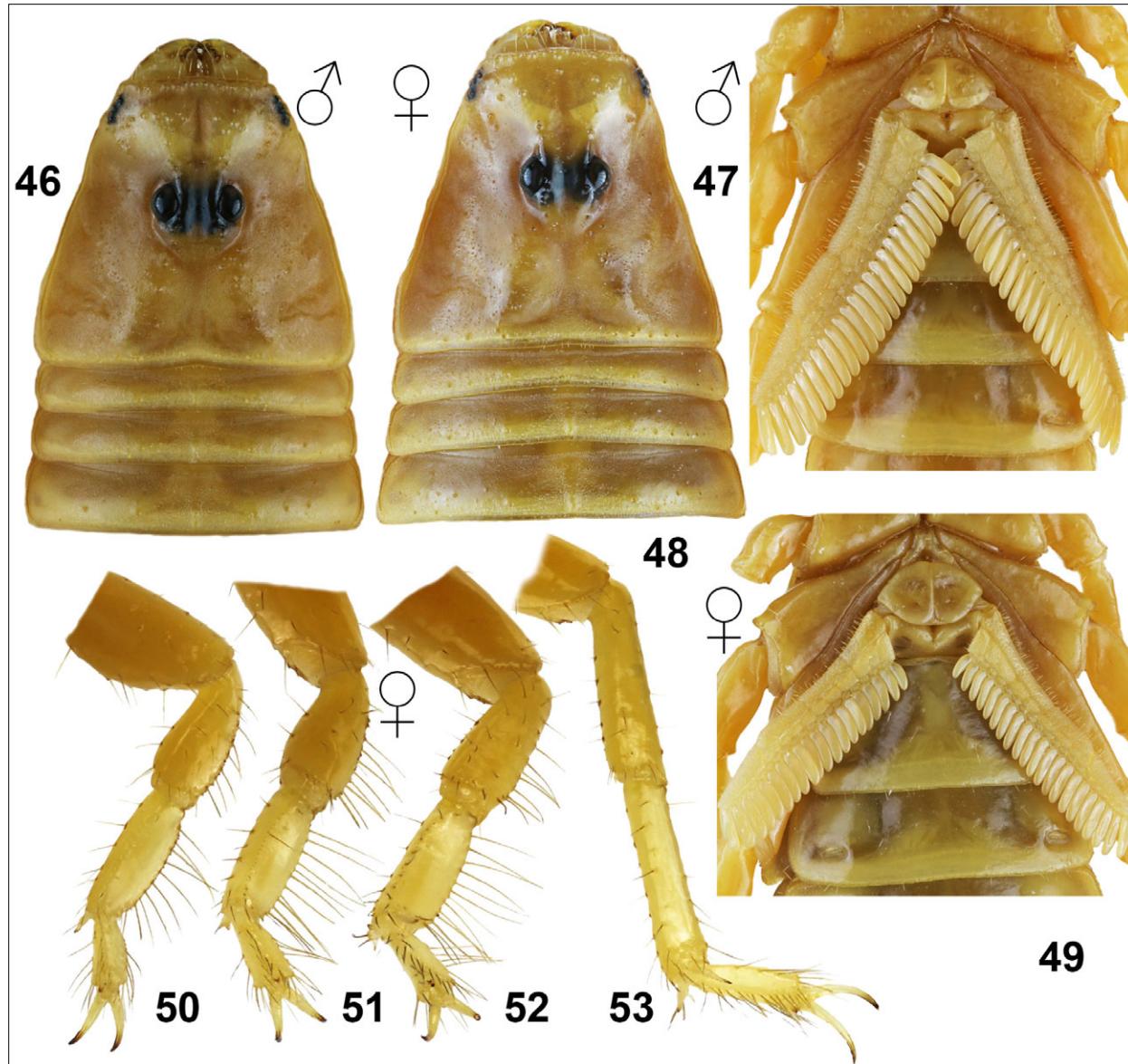
Carapace (Fig. 46). Very strongly trapezoidal (much narrower anteriorly) and wider than long; anterior margin shallowly convex, with 6–7 pairs of thin macrosetae and some very short microsetae. Carination



Figures 42–45: *Anomalobuthus krivochatskyi* sp. n., adult female (42–43) and juvenile male paratypes (44–45) from Chardara, Kazakhstan: full-body views, dorsal (42, 44) and ventral (43, 45).

essentially absent: the only carinae present are the superciliaries, which are weakly granulose to smooth. Furrows: anterior median, median ocular, central median, posterior median and posterior marginal fused, wide and moderately deep; lateral oculars, lateral cen-

trals, central transverse, and posterior laterals long, narrow and shallow. Tegument very finely and densely granulose, with many small to medium-sized granules scattered all over except on both sides of median axis, where the granules are coarser and glossy.



Figures 46–53: *Anomalobuthus krivochatskyi* sp. n., adult male holotype (46–47) and adult female paratopotype (48–53): chelicerae, carapace and tergites I–III, dorsal (46, 48), sternopectinal region and sternites III–V, ventral (47, 49), distal part of right legs I–IV, internal (50–53).

Sternum (Fig. 47). Standard for the genus, relatively small and widely triangular in shape, with two pairs of inconspicuous macrosetae.

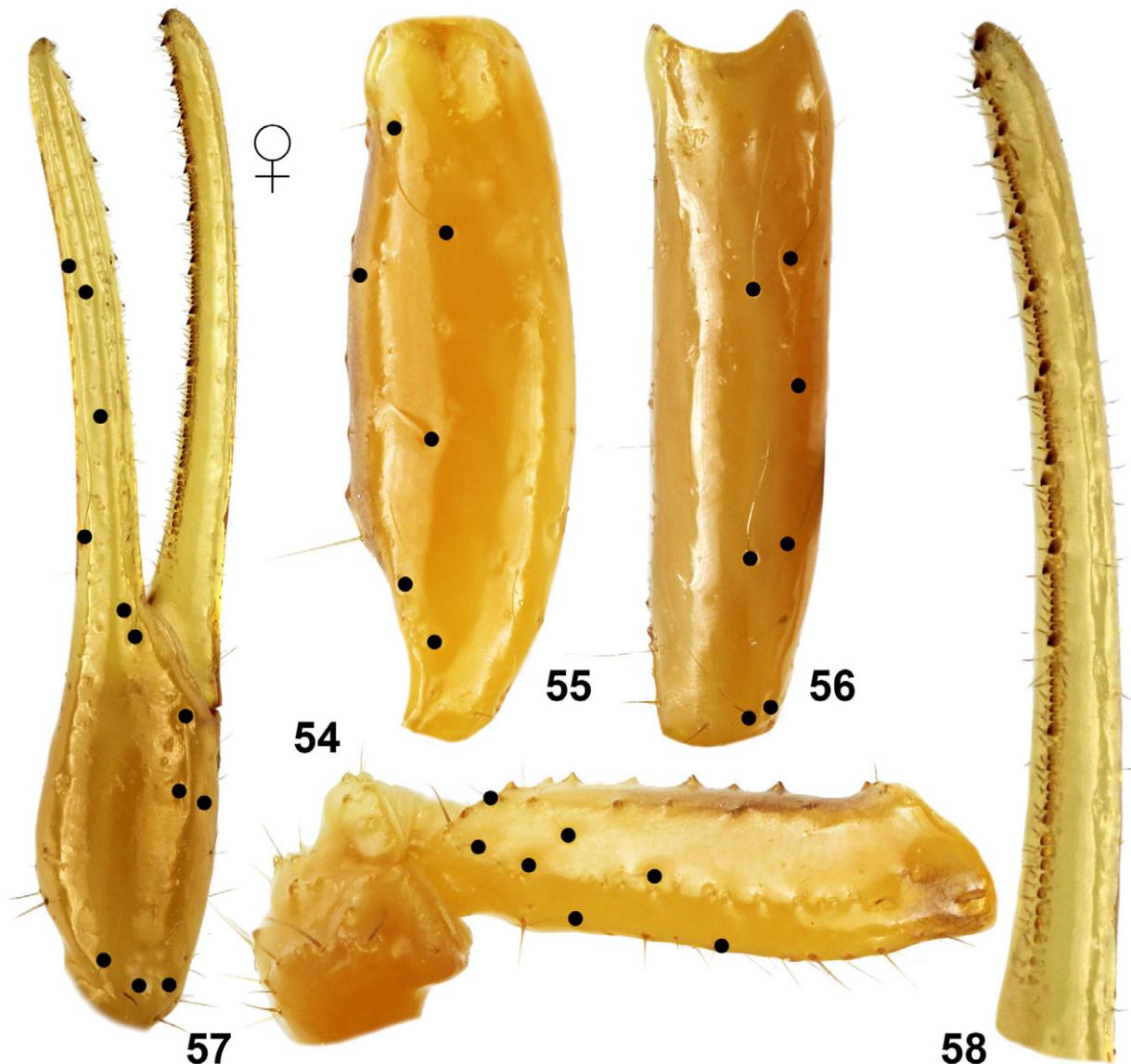
Genital operculum (Fig. 47). Relatively large, each half roundly subtriangular in shape, with three pairs of inconspicuous macrosetae, plus a few short microsetae. Genital papillae present.

Pectines (Fig. 47). Standard-sized for the genus: very long, extending beyond leg IV coxa-trochanter joint), subrectangular and densely setose. Tooth count 22/22. Basal plate heavily sclerotized, much wider than long, anterior margin with a very deep, narrow an-

teromedian furrow, posterior margin very shallowly convex.

Legs (Figs. 34–35). Very slender, with all carinae weak to obsolete and subgranulose to smooth; intercarinal tegument smooth and glossy. Tibial spur absent.

Mesosoma (Figs. 46–47). Tergites with the same sculpture as on carapace; I–VI irregularly tricarinate: the median longitudinal carina is moderately strong, short, and formed by irregular medium-sized granules that do not project beyond posterior margin, but the submedian carinae are undefined on I–IV, very irregular on V, and well defined only on VI; tergite VII with five well-

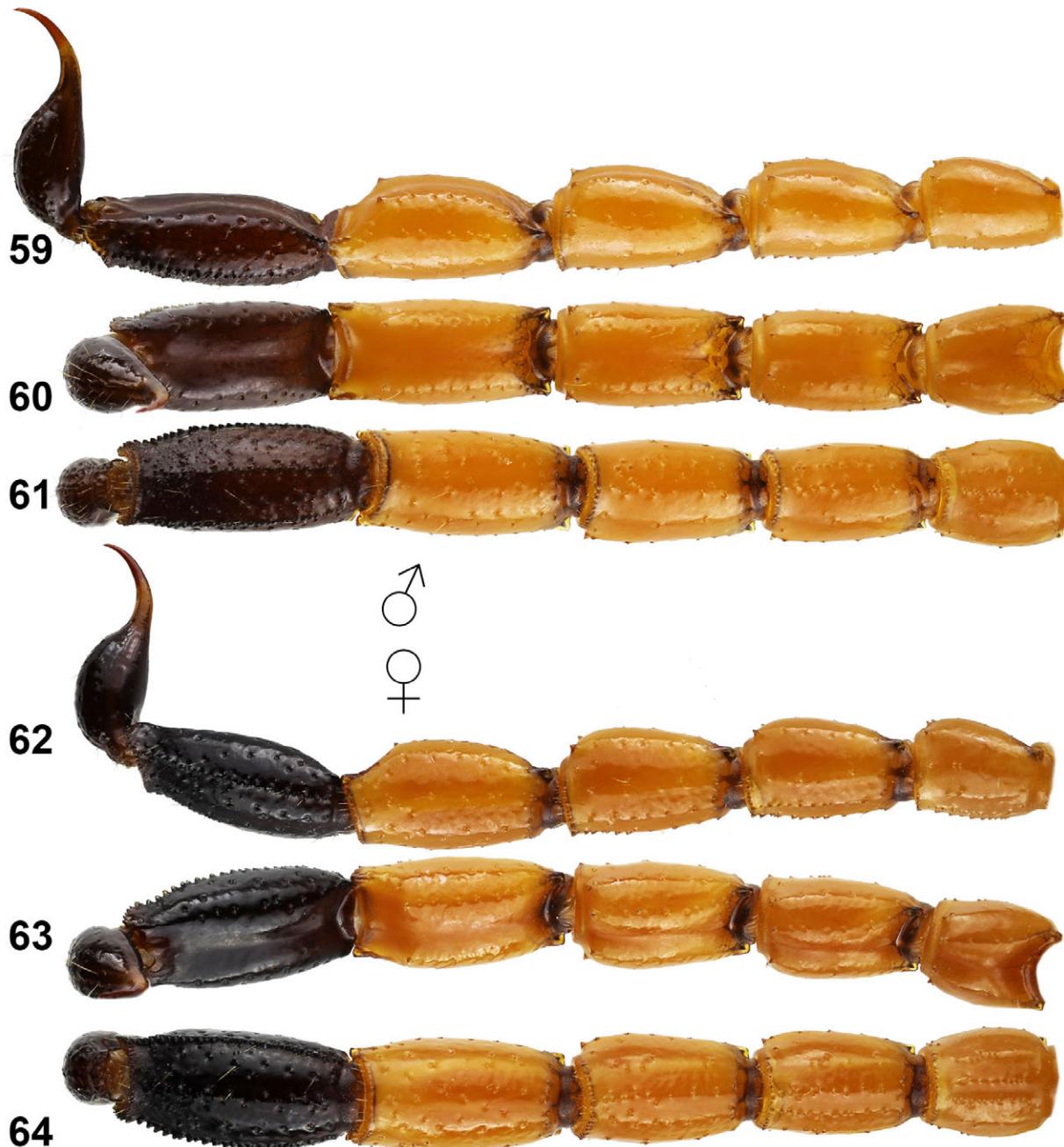


Figures 54–58: *Anomalobuthus krivochatskyi* sp. n., adult female paratotype: right pedipalp trochanter and femur, dorsal (54), right pedipalp patella, dorsal (55) and external (56), right pedipalp chela, dorsoexternal (57), right pedipalp movable finger, dorsoexternal (58). Black dots depict trichobothria.

defined carinae (median, submedians and laterals), which are long, strong and finely serrate to crenulate. Sternites essentially bare; III–VI glossy and with subtle vestiges of a pair of smooth submedian carinae, spiracles relatively short and slit-like, transversely arranged (not oblique), V with smooth patch absent; VII with two pairs of carinae (submedians and laterals) which are long and finely crenulate to serrate, intercarinal tegument coriaceous to minutely granulose.

Metasoma (Figs. 59–61). Somewhat elongated and slightly wider both basally and distally; with 10/10/10/8/5 complete to almost complete carinae, almost all formed by conspicuously isolated, sharply serrate to

denticulate granulation: dorsal laterals obsolete to vestigial on I–IV (with one terminal denticles enlarged), absent on V; lateral supramedians obsolete to vestigial on I–IV (with 1–2 terminal denticles enlarged), vestigial as rounded ridges on V; lateral inframedians obsolete to vestigial on I–III, absent on IV–V; ventral laterals obsolete to vestigial on I–IV, moderate to strong on V, where become progressively stronger and somewhat flared distally, formed by sharp, subequal denticles; ventral submedians moderate on I–II, weak on III, obsolete on IV, absent on V (indicated by somewhat raised tegument and irregular granulation on basal half); ventral median absent on I–IV, moderate on V. Inter-



Figures 59–64: *Anomalobuthus krivochatskyi* sp. n., adult male holotype (59–61) and adult female paratotype (62–64): metasoma and telson, lateral (59, 62), dorsal (60, 63) and ventral (61, 64).

carinal tegument smooth and glossy, with sparse granulation of different sizes ventrally. Dorsal furrow wide and shallow on all segments. Setation sparse, mostly represented by 4–7 dark macrosetae over every carina.

Telson (Figs. 59–61). Moderately setose, with many setae scattered all over dorsal and lateral surfaces. Vesicle short oval (1.92 times longer than wide, 0.92 times wider than deep), tegument smooth and glossy,

with vestiges of coarse granules arranged into three obsolete longitudinal carinae (ventral median and ventral submedians), and some coarse punctations ventrally. Subaculear tubercle absent, but subtly suggested by a vestigial granule. Aculeus conspicuously shorter than vesicle, thick and shallowly curved.

FEMALE (paratotype). Very similar to described male, sexual dimorphism evident by: 1) size compara-

Dimensions (mm)		UZB, Zarafshan			UZB, Bukhara to Gazli
		♂ holotype (FKCP)	♂ paratype (RTO: Sco-0233)	♀ paratype (RTO: Sco-0233)	♀ paratype (RTO: Sco-0208)
Carapace	L / Wp	3.30 / 3.70	3.40 / 3.80	3.80 / 4.60	3.00 / 3.40
Mesosoma	L	7.00	6.80	9.50	7.00
Tergite VII	L / W	2.22 / 3.40	2.00 / 3.60	2.20 / 4.60	1.80 / 3.70
Metasoma + Telson	L	21.90	21.30	23.30	18.40
Segment I	L / W / D	2.60 / 1.93 / 1.60	2.40 / 1.90 / 1.62	2.50 / 2.30 / 1.96	2.10 / 1.70 / 1.47
Segment II	L / W / D	3.13 / 1.78 / 1.55	3.00 / 1.70 / 1.70	3.30 / 2.20 / 2.00	2.60 / 1.60 / 1.48
Segment III	L / W / D	3.45 / 1.85 / 1.65	3.30 / 1.80 / 1.77	3.60 / 2.20 / 2.07	2.90 / 1.70 / 1.50
Segment IV	L / W / D	4.04 / 1.89 / 1.60	4.00 / 1.90 / 1.75	4.40 / 2.40 / 2.11	3.40 / 1.80 / 1.51
Segment V	L / W / D	4.48 / 1.92 / 1.42	4.40 / 1.90 / 1.55	4.80 / 2.40 / 1.80	3.80 / 1.80 / 1.41
Telson	L	4.20	4.20	4.70	3.60
Vesicle	L / W / D	2.75 / 1.28 / 1.26	2.30 / 1.20 / 1.30	2.70 / 1.50 / 1.40	2.10 / 1.20 / 1.10
Aculeus	L	1.45	1.90	2.00	1.50
Pedipalp	L	10.51	11.00	11.40	9.50
Femur	L / W	2.78 / 0.68	2.80 / 0.70	3.10 / 0.90	2.50 / 0.70
Patella	L / W	3.33 / 0.93	3.40 / 0.90	3.60 / 1.10	2.90 / 0.90
Chela	L	4.40	4.80	4.70	4.10
Manus	L / W / D	1.22 / 0.71 / 0.75	1.50 / 0.70 / 0.70	1.40 / 0.80 / 0.90	1.20 / 0.70 / 0.70
Movable finger	L	3.18	3.30	3.30	2.90
Total	L	32.20	31.50	36.60	28.40

Table 2: Measurements of four types of *Anomalobuthus krivochatskyi* sp. n. Abbreviations: length (L), width (W), posterior width (Wp), depth (D).

tively larger inside each size-class; **2**) mesosoma and metasoma slightly less slender; **3**) genital papillae absent; **4**) pectines smaller, with consistently lower tooth counts; **5**) tibial spur small, sharp and sinuose, present at least on both legs IV (sometimes also on one leg III); **6**) metasomal segment V with ventral intercarinal tegument less granulose. See Figs. 36–37, 40–43, 48–58, 62–64, 134–136, 138–140 and Tabs. 2, 4–5.

VARIATION. Adult size varied from 31.5–32.2 mm in males and 28.4–36.6 mm in females.

Count of teeth per pecten varied as follows (Tab. 5): in males 22 (3), 23 (1), 24 (3), 25 (3), and in females 19 (2), 20 (7), 21 (6), 22 (3). No significant differences detected among specimens from the localities examined by us.

The tibial spur is always absent in males, but in females it is present always on both leg IV and occasionally also in leg III of one side only (Figs. 130–132, 134).

Specimens from Chardara and Bukhara to Gazli are identical to those from the type locality in all diagnostic characters. They only differ by being slightly smaller and darker, with better-marked dark patterns (Figs. 38–45). These differences are minor and attributable to standard variation between different populations.

COMPARISON. Adults of *A. krivochatskyi* sp. n. can be very easily distinguished by the almost absolute smoothness of the metasomal intercarinal spaces, especially in males (Figs. 59–64, 121); almost all other congeners have at least the ventral and lateral surfaces of segments IV–V moderately to densely granulose (Figs. 23–25, 27–29, 31–33, 69, 75–78, 84–89).

The single exception is *A. talebii*, which is similarly smooth (Figs. 98–100), but the only female known has much higher pectinal tooth count (26/26 vs. 20–23) and several quite distinct morphometric ratios (see Tab. 4 and Comparison section of that species).

DISTRIBUTION (Fig. 137). Sands of the Kizylkum Desert, from central Uzbekistan through adjacent southern edge of Kazakhstan.

NOTES. The Bukhara Province (between Bukhara and Gazli) specimens of this new species were included (under *A. rickmersi*) in a DNA phylogeographic study by Graham et al. (2012), which demonstrated a derived position of this taxon within the genus.

Anomalobuthus lowei Teruel, Kovařík et Fet, sp. n.
Figures 65–78, 141; Tables 3–5

<http://zoobank.org/urn:lsid:zoobank.org:act:F416B15C-4E36-4D73-ABCC-DCCE1A6E9DB9>

Anomalobuthus rickmersi: Gromov & Kopdykbaev, 1994: 20 (in part); Gromov, 2005: 39 (in part); Gromov & Kazenas, 2006: 39 (in part); Mityaev et al., 2005: 39 (in part); Gromov, 2006: 44–45 (in part); Kamenz & Prendini, 2008: 6, 8, 40, 56–57, fig. 15a, tabs. 1–2.

HOLOTYPE ♀ (GLPC). Kazakhstan, Almaty Province, Kapchagay [43°53'N, 77°05'E], Ili River, 75 km north of Almaty, 17 May 1993, leg. A. Feodorov.

ETYMOLOGY. We are pleased to name this species after our friend and colleague, Graeme Lowe (Philadelphia, USA), who contributed greatly to the knowledge of the Palearctic desert scorpions. His assistance to the present paper was crucial, by selflessly spending his scarce free time in exhausting photographic sessions providing all the images of the holotype of *A. lowei* (Figs. 65–78).

DIAGNOSIS (based on one adult female). Adult size 35 mm. Coloration yellow, essentially immaculate, only with some irregular blackish spots on carapace, tergites, pedipalps, legs, and metasoma; metasomal segment V deeply infuscate, telson blackish. Pedipalp fingers with 7–8 principal rows of denticles and 6–7 internal accessory denticles. Pectines with 21/20 teeth. Tibial spur on leg IV only, small. Metasoma robust, with most carinae moderately developed; ventral lateral carinae of segment V composed of narrowly lobate denticles, dorsal lateral and lateral supramedian carinae of segments I–IV with terminal denticle greatly enlarged; intercarinal spaces essentially smooth on dorsal areas of all segments, densely granulose on ventral and lateral areas of I and V, sparsely granulose on ventral and lateral areas of II–IV. Telson vesicle short oval and sparsely setose.

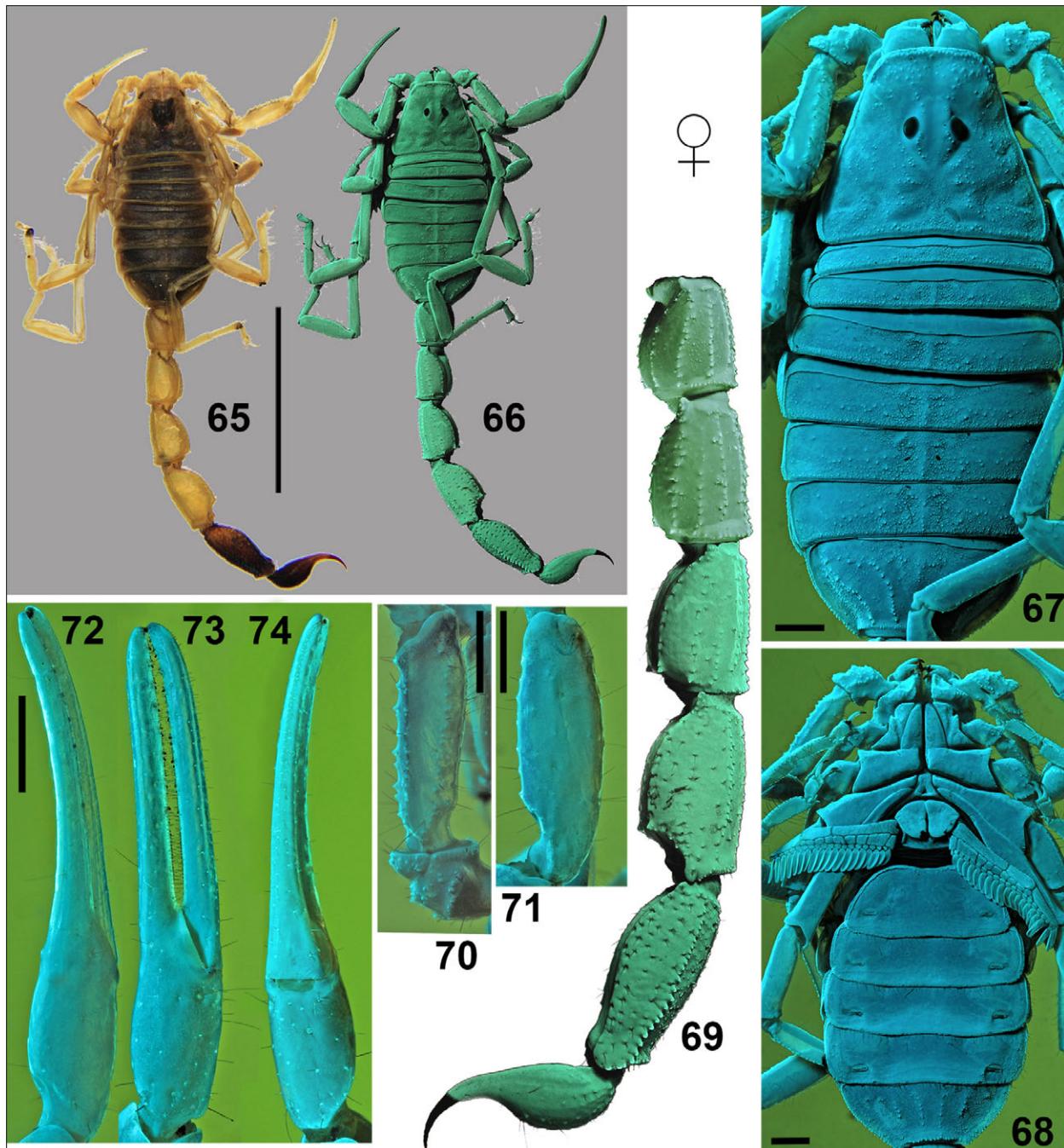
DESCRIPTION (adult female holotype). Coloration (Fig. 65) base light yellow, somewhat translucent due to

non-optimal preservation. Chelicerae immaculate, except for blackish finger teeth. Pedipalp femur with a conspicuous blackish spot on dorsodistal apex, which diffusely continues as a broad stripe over almost all internal surface; patella with internal surface blackish; chela with internal surface diffusely reticulate with dark brown, finger denticles blackish. Carapace with a large blackish spot that widely surrounds median ocular tubercle and extends to anterior margin and also diffusely to every group of lateral eyes. Tergites diffusely marbled with dark brown. Coxosternal region and genital operculum immaculate. Pectines pale yellowish, immaculate. Sternites immaculate. Legs spotted with dark brown, more densely on trochanter and femur of I–III; claws with distal third dark brown to blackish. Metasoma bicolor, segments I–IV yellow with a diffuse annulated appearance (basal and distal parts of each segment infuscate in the shape of thin blackish rings, which become somewhat larger and more diffuse dorsally and basally) and segment V very densely reticulated with blackish brown, becoming gradually paler and sparser towards basal half; carinae not infuscate nor underlined with dark pigment. Telson vesicle blackish, aculeus with basal half brownish and distal half blackish.

Chelicerae (Fig. 67). With dentition typical for the genus, as described for *A. krivochatskyi* sp. n. (see above).

Pedipalps (Figs. 70–74). Relatively short but slender, essentially bare. Trichobothrial pattern A-β neobothriotoxic, with the following trichobothria missing: femoral d_2 and chelal esb (both pedipalps), chelal Ei and chelal V_1 (right pedipalp). Chelal it in subdistal position, midway between second and third enlarged principal denticle from tip (left chela) or just distal to third enlarged principal denticle from tip (right chela). Femur essentially straight, with carinae weak to moderate, granulose to subdenticulate; intercarinal tegument smooth and glossy. Patella essentially straight, with carinae obsolete to absent, smooth; intercarinal tegument smooth and glossy. Chela elongate and slender; manus conspicuously narrower than patella (ratio 0.70), cylindrical (1.94 times longer than wide, 1.13 times deeper than wide), with carinae obsolete to absent, smooth; intercarinal tegument smooth and glossy; fingers long (movable finger 2.31 times longer than underhand), only subtly curved and with 8–9 principal rows of denticles (the two basalmost rows are poorly defined), basal lobe/notch combination absent, external accessory denticles absent, internal accessory denticles very large and claw-like (increasing in size distally), numbering seven and six on fixed and movable fingers, respectively, movable finger with two claw-like accessory denticles basal to the very large terminal denticle.

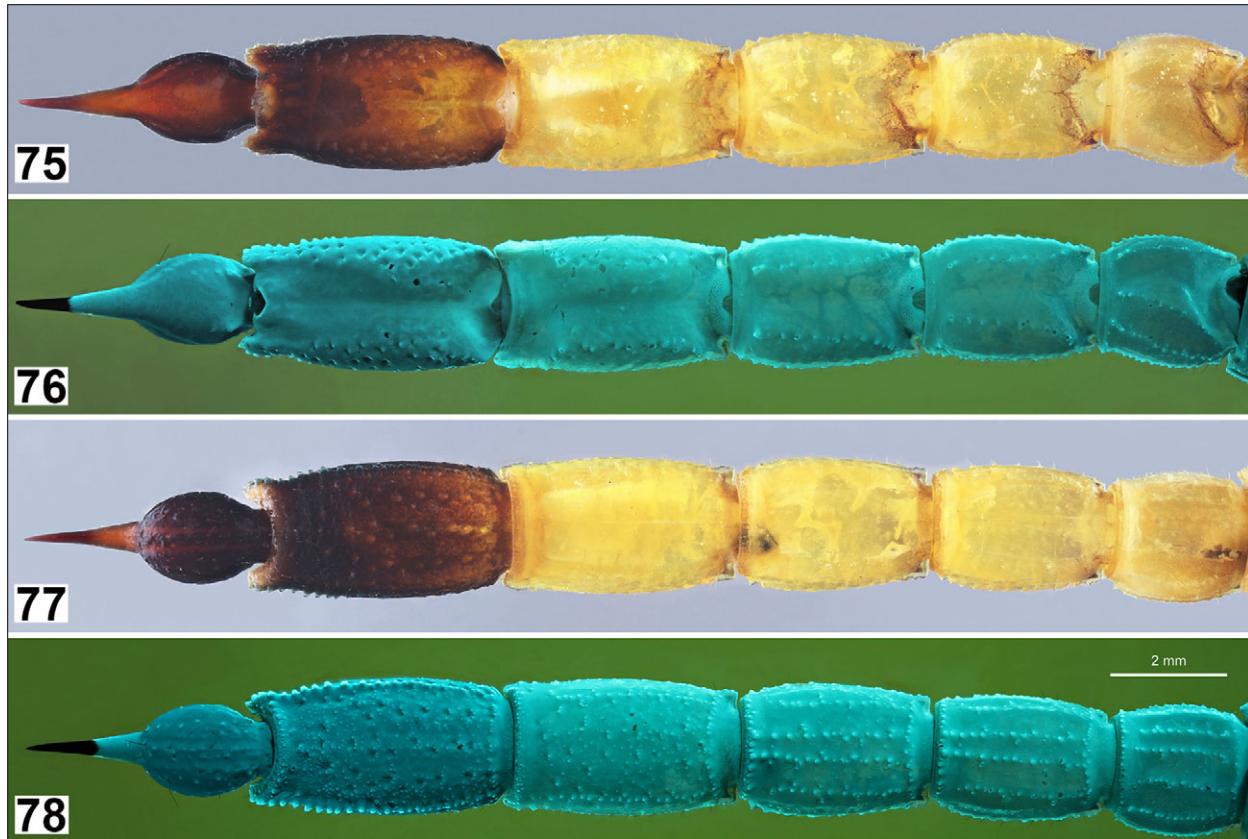
Carapace (Fig. 67). Very strongly trapezoidal (much narrower anteriorly) and wider than long; anterior margin shallowly convex, with 5–6 pairs of thin macro-



Figures 65–74: *Anomalobuthus lowei* sp. n., adult female holotype. **Figures 65–66.** full-body dorsal views, under white light (65) and under UV light (66). **Figures 67–68.** Mesosoma dorsal (67) and ventral (68) under UV light. **Figure 69.** Metasoma and telson under UV light, lateral. **Figures 70–74.** Pedipalp under UV light: right pedipalp trochanter and femur, dorsal (70), right pedipalp patella, dorsal (71), right pedipalp chela, dorsal (72), external (73) and ventral (74). Scale bars = 10 mm (65–66) and 1 mm (67–68, 70–74). Photographs courtesy Graeme Lowe.

setae and some very short microsetae. Carination essentially absent: the only carinae present are the superciliaries, which are vestigially granulose to smooth. Fur-

rows: anterior median, median ocular, central median, posterior median and posterior marginal fused, wide and very shallow; lateral oculars, lateral centrals, central



Figures 75–78: *Anomalobuthus lowei* sp. n., adult female holotype. **Figures 75–76.** Metasoma and telson, dorsal, under white light (75) and under UV light (76). **Figures 77–78.** Metasoma and telson, ventral, under white light (77) and under UV light (78). Scale bar = 2 mm. Photographs courtesy Graeme Lowe.

transverse, and posterior laterals long, narrow and shallow. Tegument very finely and densely granulose, with many small to medium-sized granules scattered all over except on ocular triangle, where the granules are coarser and glossy.

Sternum (Fig. 68). Standard for the genus 1, very small, and narrowly pentagonal in shape, with two pairs of macrosetae.

Genital operculum (Fig. 68). Very large, each half widely crescent-shaped, with 3–4 pairs of inconspicuous macrosetae, plus a few short microsetae. Genital papillae absent.

Pectines (Fig. 68). Somewhat small for the genus (just reaching leg IV coxa-trochanter joint), subrectangular and densely setose. Tooth count 21/20 (terminal tooth of right pecten missing, but base remains allows unequivocal count). Basal plate heavily sclerotized and densely granulose, much wider than long, anterior margin with a very deep, narrow anteromedian furrow, posterior margin very shallowly convex.

Legs (Figs. 65–66). Very slender, with all carinae weak to obsolete and subgranulose to smooth; intercarinal tegument smooth and glossy. Tibial spurs absent

from both legs III and right leg IV, but moderate-sized on left leg IV.

Mesosoma (Figs. 67–68). Tergites with the same sculpture as on carapace; I–VI essentially monocarinate: the median longitudinal carina is moderately strong, long, and formed by irregular medium-sized granules that do not project beyond posterior margin and the submedian carinae are undefined on I–VI, although suggested by a few slightly coarser, irregular granules; tergite VII with five well-defined carinae (median, submedians and laterals), which are long, strong and serrate to denticulate. Sternites essentially bare except on posterior margin, which is conspicuously setose; III–VI acarinate, glossy but with posterior and lateral margins finely and densely granulose, spiracles relatively short and slit-like, transversely arranged (not oblique), V with smooth patch absent; VII with two pairs of carinae: the submedians are long and finely denticulate and the laterals are short and coarsely denticulate, intercarinal tegument very densely granulose.

Metasoma (Figs. 69, 75–78). Robust and slightly wider both basally and distally; with 10/10/10/8/5 complete to almost complete carinae, all except dorsal

laterals and laterals supramedians, formed by contiguous, sharply serrate to denticulate granulation: dorsal laterals moderate on I, strong on II–III, moderate on IV (with terminal denticle greatly enlarged as a coarse, conical tubercle), absent on V; lateral supramedians moderately strong on I, weak on II–III, obsolete to very weak on IV (with 1–2 terminal denticles enlarged), vestigial as rounded ridges on V; lateral inframedians strong on I, moderate on II (undefined on basal 1/4), weak on III (undefined on basal 1/3), absent on IV–V; ventral laterals strong on I–II, moderate on III–IV, very strong on V, where become progressively stronger and somewhat flared distally, formed by round, subequal denticles; ventral submedians very strong on I–III, strong on III, moderate on IV, absent on V; ventral median absent on I–IV, moderate on V (poorly defined from intercarinal granulation). Intercarinal tegument smooth and glossy, with fine granules scattered all over except dorsally on I–IV, on V such granules are restricted to ventral surface but are much denser. Dorsal furrow wide and moderately deep on all segments. Setation moderately dense, mostly represented by 6–8 dark macrosetae over every carina. Setae on lateral surfaces of IV and V, and ventral surface of V arising from anterior edges of shallow pits or depressions. Lateral anal margins of V with 3 lobes, ventral anal arc heavily granulated.

Telson (Figs. 69, 75–78). Moderately setose, with some setae scattered over dorsal and lateral surfaces. Vesicle short oval (1.47 times longer than wide, 1.13 times wider than deep), tegument smooth and glossy, with vestiges of coarse granules arranged into five vestigial longitudinal carinae (ventral median, ventral submedians, and ventral laterals), and some coarse punctations ventrally. Subaculear tubercle absent. Aculeus shorter than vesicle, thick and moderately curved.

MALE. Unknown.

VARIATION. Unknown, no other specimens available to us.

COMPARISON (females only). *A. lowei* sp. n. can be very easily distinguished from all other *Anomalobuthus* spp. by its very robust appearance, well evident in its many unique morphometric proportions (Tab. 4). For example, it is the only species of this genus with metasomal segment I about as long as wide (ratio = 1.02 vs. 1.09–1.44 in all other congeners), it has the shortest metasoma + telson when compared to carapace length (ratio = 5.40 vs. 5.68–6.38), the shortest metasomal segment V (length/depth ratio = 1.85 vs. 2.00–2.50) and the deepest telson vesicle (length/depth ratio = 1.66 vs. 1.89–2.17).

DISTRIBUTION (Fig. 141). Sands of the Ili River valley in southeastern Kazakhstan. It is the easternmost species of *Anomalobuthus*, occurring at the northern piedmont of the Tian Shan Range.

NOTES. Based on geographical occurrence, the male recorded by Kamenz & Prendini (2008) as *A. rickmersi* most likely corresponds to *A. lowei* sp. n.

***Anomalobuthus pavlovskyi* Teruel, Kovářík et Fet, sp. n.**

Figures 79–89, 107–116, 141; Tables 3–5

<http://zoobank.org/urn:lsid:zoobank.org:act:D8B0A76D-BF70-426C-B822-D9E9C00A96C5>

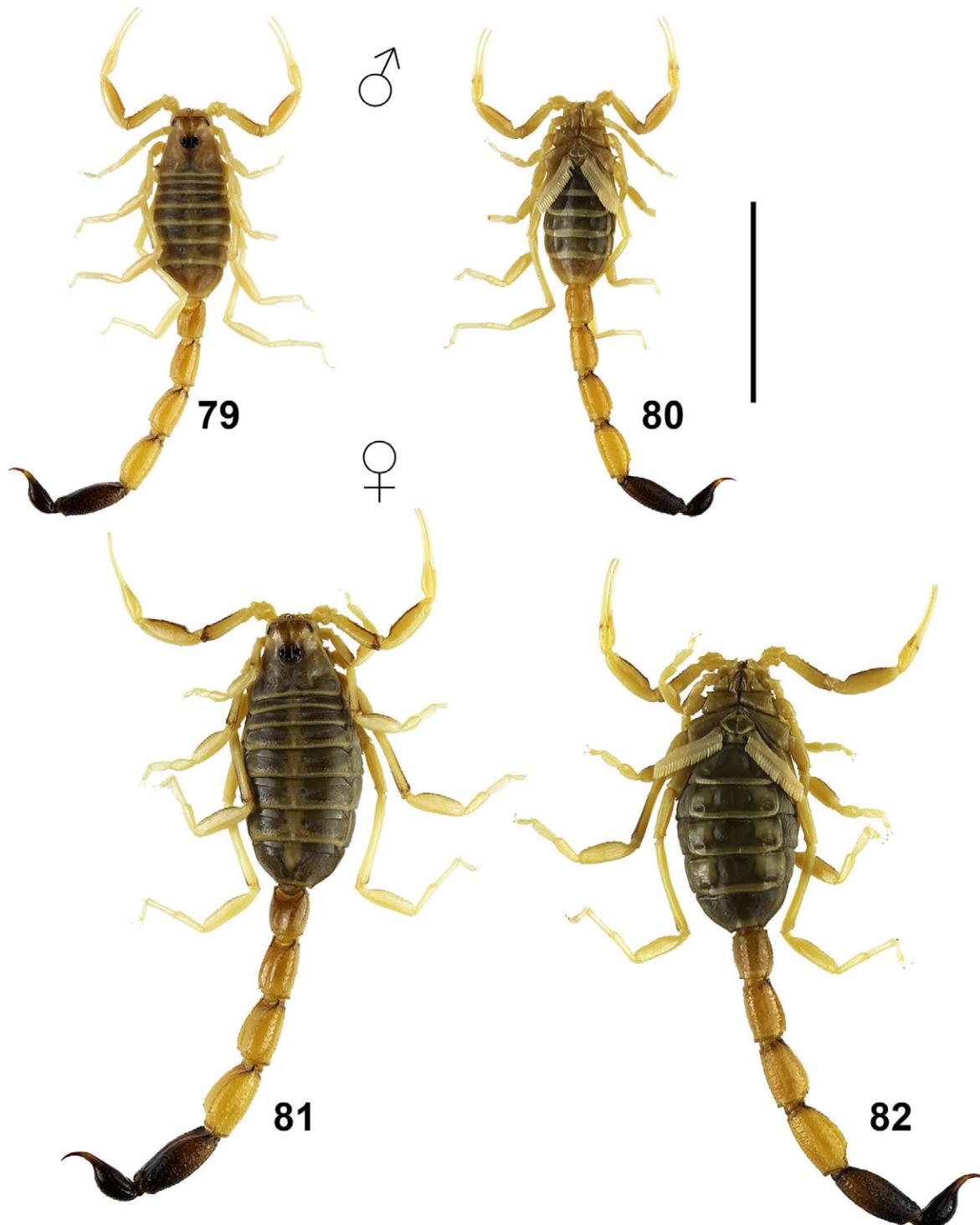
Anomalobuthus rickmersi: Birula, 1911b: 171 (in part; “Baigakum” [=Baigakum]); Pavlovsky, 1916a: 35 (in part; Dzhulek); Pavlovsky, 1916b: 243, fig. 1 (in part; Dzhulek); Fet, 1989: 80, unnumbered figure in page 138 (in part; Dzhulek and Kunya-Urgench); Gromov & Kopdykbaev, 1994: 20 (in part; Dzhulek); Gromov, 2005: 39 (in part); Mityaev et al., 2005: 39 (in part); Gromov, 2006: 44–45 (in part); Graham et al., 2012: 95–106, figs. 1–2, 6 (in part; Baigakum).

HOLOTYPE ♂ (RTOC: Sco-0476). **Kazakhstan**, Kizylkum Desert, Kyzyl-Orda Province, Chiili District, ca 2.5 km NW of Baigakum (=Djulek or Dzhulek), 44°20'37" to 44°20'29"N, 66°27'09" to 66°27'07"E, 127–143 m a.s.l., 25 May 2002, leg. V. Fet & A. V. Gromov.

PARATYPES. Same data as holotype, 2♂♂, 2♀♀ (FKCP), 1♂ (ZMUH), 1♂ (SOFM), 1♂ (NMPC), 3♀♀ (RTOC: Sco-0476). Same data as holotype except 6–21 June [19 June–4 July] 1907, leg. D. Glazunov, 2♂♂ (ZISP 810, one examined by Max Vachon and bearing his handwritten code VA-1667). **Turkmenistan**, Daşoguz (=Tashauz), Province, Köneürgenç (=Kunya-Urgench), 42°23'18"N 59°16'14"E, 3 June 1972, leg. G. S. Medvedev, 1♂, 1♀ (ZISP 1699).

OTHER MATERIAL. **Turkmenistan**, Daşoguz (=Tashauz) Province, Shakhsemem [old fortress ruins], 8 October 1983, leg. O. Soyunov, 1♀ (ZMMSU Tb-374).

ETYMOLOGY. We dedicate this species to the memory of the famous Russian zoologist Evgenii Nikanorovich Pavlovsky (1884–1965), who produced many well-known contributions to scorpion anatomy and histology. He was also the Director of ZISP for 20 years (after Alexei Birula was arrested in 1931 during the purges), and was the first one to observe and collect this species at the type locality, more than 100 years ago (Pavlovsky, 1916a, 1916b).



Figures 79–82: *Anomalobuthus pavlovskyi* sp. n., adult male (79–80) and adult female paratotypes (81–82): full-body views, dorsal (79, 81) and ventral (80, 82). Scale bar = 10 mm.

DIAGNOSIS. Adult size 22–30 mm in males, 23–36 mm in females. Coloration light yellow, essentially immaculate, only with some regular blackish spots on pedipalps and metasoma (darker and more extended in

female); metasomal segment V bicolor, blackish with yellowish red basal third (male) to basal half (female), telson blackish. Pedipalp fingers with 8–9 principal rows of denticles and 7–8 internal accessory denticles. Pec-

tines with 24–27 teeth in males and 22–23 in females. Tibial spur in males entirely absent to present only in leg IV, in females absent to present in legs III–IV. Metasoma moderately robust, with most carinae obsolete to vestigial; ventral lateral carinae of segment V composed of narrowly conical denticles, dorsal lateral and lateral supramedian carinae of segments I–IV with terminal denticle enlarged; intercarinal areas of segments I–IV with granulation sparse ventrally (male) to dense ventrally and laterally (female), of segment V moderately dense ventrally (male) to very dense ventrally and laterally (female). Telson vesicle elongate oval and sparsely setose.

DESCRIPTION (adult male holotype, except figures of adult male paratotype). **Coloration** (Figs. 79–80) base light yellowish, with a subtle orange shade; in general, the base color is paler on pedipalp chelae, legs, and pectines. Chelicerae subtly reticulate with dark brown, finger teeth blackish. Pedipalp femur with a conspicuous brown spot on dorsodistal apex, which diffusely continues as a broad stripe over almost all internal surface; patella with internal surface brown; chela immaculate, only with finger denticles blackish. Carapace largely immaculate, only with a blackish spot under every ocular group and interocular triangle moderately infuscate. Tergites immaculate. Coxosternal region and genital operculum immaculate. Pectines pale yellowish, immaculate. Sternites immaculate. Legs immaculate; claws with distal half dark brown. Metasoma bicolor, segment V blackish with basal third yellowish red, I–IV yellow with a diffuse annulated appearance: basal and distal parts of each segment infuscate in the shape of thin blackish rings, which become somewhat larger and more diffuse dorsally and basally; carinae not infuscate nor underlined with dark pigment, except for darkened terminal denticles on dorsal laterals and lateral supramedians. Telson blackish, with basal half of aculeus yellowish.

Chelicerae. With dentition typical for the genus, as described for *A. krivochatskyi* sp. n. (see above).

Pedipalps (Fig. 83). Relatively short but very slender, essentially bare. Femur subtly curved inwards, with carinae weak, granulose to subdenticulate; intercarinal tegument smooth and glossy. Patella straight, with carinae vestigial to weak, smooth; intercarinal tegument smooth and glossy. Chela elongate and very slender; manus conspicuously narrower than patella (ratio 0.71), cylindrical (2.00 times longer than wide, 1.20 times deeper than wide), with carinae vestigial to weak, smooth; intercarinal tegument smooth and glossy; fingers very long (movable finger 2.40 times longer than underhand), only subtly curved and with 8/9 principal rows of denticles (the two basalmost rows are poorly defined on movable finger), basal lobe/notch combination absent, external accessory denticles absent,

internal accessory denticles very large and claw-like (increasing in size distally), numbering eight and seven on fixed and movable fingers, respectively, movable finger with three claw-like accessory denticles basal to the very large terminal denticle.

Carapace. Very strongly trapezoidal (much narrower anteriorly) and wider than long; anterior margin straight, with 5–6 pairs of thin macrosetae and some very short microsetae. Carination essentially absent: the only carinae present are the superciliaries, which are weakly granulose. Furrows: anterior median, median ocular, central median, posterior median and posterior marginal fused, wide and moderately deep; lateral oculars, lateral centrals, central transverse, and posterior laterals long, narrow and moderately deep. Tegument very finely and densely granulose, with several small to medium-sized granules scattered all over

Sternum. Standard for the genus, relatively small and widely triangular in shape, with one pair of inconspicuous macrosetae.

Genital operculum. Relatively large, each half roundly subtriangular in shape, without macrosetae but with a few short microsetae. Genital papillae present.

Pectines. Standard-sized for the genus: long, extending beyond leg IV coxa-trochanter joint), subrectangular and densely setose. Tooth count 26/27. Basal plate heavily sclerotized, much wider than long, anterior margin with a very deep, narrow anteromedian furrow, posterior margin very shallowly convex.

Legs (Figs. 79–80). Very slender, with all carinae weak to obsolete and subgranulose to smooth; intercarinal tegument smooth and glossy. Tibial spurs present only on right leg IV.

Mesosoma (Figs. 79–80). Tergites with the same sculpture as on carapace; I–VI irregularly tricarinate: the median longitudinal carina is moderately strong, short, and formed by irregular medium-sized granules that do not project beyond posterior margin, but the submedian carinae are poorly defined on I–VI; tergite VII with five well-defined carinae (median, submedians and laterals), which are long, strong and finely serrate. Sternites essentially bare; III–VI glossy and with a pair of weak, smooth submedian carinae, spiracles relatively short and slit-like, transversely arranged (not oblique), V with smooth patch absent; VII with two pairs of carinae (submedians and laterals) which are long and finely crenulate, intercarinal tegument coriaceous to minutely granulose.

Metasoma (Figs. 84–86). Slightly elongated and essentially parallel-sided; with 10/10/10/8/5 complete to almost complete carinae, most formed by conspicuously isolated, sharply serrate to denticulate granulation: dorsal laterals vestigial on I–III, obsolete on IV (with 1–2 terminal denticle slightly enlarged), absent on V; lateral supramedians vestigial to obsolete on I–IV (with 1–2 terminal denticles slightly enlarged), vestigial as round-



Figures 83–89: *Anomalobuthus pavlovskyi* sp. n., adult male (83–86) and adult female paratotypes (87–89): right pedipalp (83), metasoma and telson, lateral (84, 87), dorsal (85, 88) and ventral (86, 89).

ed ridges on V; lateral inframedians weak on I, obsolete to vestigial on II–III, absent on IV–V; ventral laterals weak on I–IV, moderate to strong on V, where become progressively stronger and somewhat flared distally,

formed by sharp, subequal denticles; ventral submedians weak on I–III, vestigial on IV, absent on V (indicated by somewhat raised tegument and irregular granulation on basal half, but largely obscured by intercarinal gran-

DIMENSIONS (MM)		<i>A. lowei</i> sp. n.	<i>A. pavlovskyi</i> sp. n. (RTO: Sco-0476)		
		♀ holotype	♂ holotype	♀ paratype	♀ paratype
Carapace	L / Wp	3.88 / 4.75	2.10 / 2.90	2.60 / 3.00	3.88 / 4.47
Mesosoma	L	10.03	5.50	5.60	9.68
Tergite VII	L / W	2.41 / 4.79	1.60 / 2.08	1.50 / 2.80	2.30 / 4.28
Metasoma + Telson	L	20.97	15.00	15.00	22.02
Segment I	L / W / D	2.41 / 2.37 / 1.92	1.70 / 1.30 / 1.13	1.70 / 1.30 / 1.17	2.41 / 1.98 / 1.68
Segment II	L / W / D	3.02 / 2.23 / 1.95	2.10 / 1.20 / 1.18	2.20 / 1.20 / 1.19	3.13 / 1.80 / 1.83
Segment III	L / W / D	3.25 / 2.33 / 2.06	2.30 / 1.30 / 1.20	2.40 / 1.30 / 1.20	3.48 / 1.87 / 1.88
Segment IV	L / W / D	4.08 / 2.33 / 2.14	2.90 / 1.30 / 1.21	2.80 / 1.30 / 1.28	4.10 / 2.00 / 2.00
Segment V	L / W / D	4.33 / 2.34 / 1.84	3.10 / 1.30 / 1.19	3.00 / 1.30 / 1.27	4.50 / 2.08 / 1.73
Telson	L	4.08	2.90	2.90	4.40
Vesicle	L / W / D	2.33 / 1.58 / 1.40	1.70 / 0.90 / 0.80	1.70 / 0.90 / 0.80	2.50 / 1.51 / 1.20
Aculeus	L	1.67	1.20	1.20	1.90
Pedipalp	L	12.01	7.90	8.00	11.44
Femur	L / W	3.17 / 0.92	2.00 / 0.50	2.00 / 0.60	2.90 / 0.81
Patella	L / W	3.58 / 1.17	2.50 / 0.70	2.50 / 0.80	3.50 / 1.10
Chela	L	5.26	3.40	3.50	5.04
Manus	L / W / D	1.59 / 0.82 / 0.93	1.00 / 0.50 / 0.60	1.00 / 0.60 / 0.60	1.42 / 0.73 / 0.90
Movable finger	L	3.67	2.40	2.50	3.62
Total	L	34.88	22.60	23.20	35.58

Table 3: Measurements of the types of two new species of *Anomalobuthus*. Abbreviations: length (L), width (W), posterior width (Wp), depth (D).

ulation); ventral median absent on I–IV, moderate on V but largely obscured by intercarinal granulation. Intercarinal tegument smooth and glossy, with sparse granulation of different sizes ventrally. Dorsal furrow wide and shallow on all segments. Setation moderately dense, represented by 6–9 mostly pale macrosetae over every carina.

Telson (Figs. 84–86). Sparsely setose, with some setae scattered all over dorsal and lateral surfaces. Vesicle short oval (2.00 times longer than wide, 0.83 times wider than deep), tegument smooth and glossy, with vestiges of coarse granules arranged into three obsolete longitudinal carinae (ventral median and ventral submedians), some also on dorsal surface, and some coarse punctations all over. Subaculear tubercle absent, but subtly suggested by a vestigial granule. Aculeus conspicuously shorter than vesicle, thick and shallowly curved.

FEMALE (paratotype). Very similar to described male, sexual dimorphism evident by: 1) size comparatively larger inside each size-class; 2) mesosoma

and metasoma slightly less slender; 3) genital papillae absent; 4) pectines smaller, with consistently lower tooth counts; 5) metasomal segments with ventral and lateral intercarinal tegument much more densely granulose. See Figs. 81–82, 87–89, 114 and Tabs. 3–5

VARIATION. Adult size varied from 22.6–25.5 mm in males and 23.2–35.6 mm in females.

Pectinal tooth count varied as follows (Tab. 5): in males 25 (5), 26 (5), 27 (2), and in females 22 (5) and 23 (3). No significant differences detected among specimens from the localities examined by us.

The tibial spur is highly variable amongst paratypes: it is entirely absent from all legs (one male), present on a single leg IV (three males including holotype, two females), present on each leg III–IV of the same side (left, one female), or present on both legs IV (two males, one female). In all cases where it is present, it is small to vestigial.

COMPARISON. *A. pavlovskyi* sp. n. can be very easily distinguished by having intercarinal spaces of

metasoma much more densely granulose in females than in males (Figs. 84–89); in all other *Anomalobuthus* spp., the metasomal segments are mostly sparsely granulated to smooth and glossy in females (*A. krivochatskyi* sp. n., *A. lowei* sp. n. and *A. talebii*, see Figs. 62–64, 69, 75–78, 98–100), or more densely granulose in males (*A. rickmersi*, see Figs. 23–25, 27–29, 31–33).

Moreover, this species and *A. lowei* sp. n. are the only that still retain as adult a typically juvenile character: the segment V with basal third yellowish red (Figs. 84–89); in all other congeners it is entirely reddish or blackish, or only subtly faded to dark reddish brown at its extreme base (Figs. 1–2, 4–5, 8–9, 23–45, 59–64, 90–91, 98–100). But *A. lowei* sp. n. is very different in many morphometric ratios (see Tab. 4 and Comparison section of that species).

DISTRIBUTION (Fig. 141). Lowland sands of the Aral Basin (Kizylkum Desert), from south-central Kazakhstan through extreme northern Turkmenistan.

NOTES.

1. The first specimens of this species were recorded by Birula (1911b) as *A. rickmersi*; all were collected from Baigakum Sands (Dzhulek) in 1907 by Dmitri Konstantinovich Glazunov (1869–1914), a Russian entomologist and brother of the composer Alexander K. Glazunov.
2. The pioneering observations of Pavlovsky (1916b) in Dzhulek (now Baigakum) remain the only data on this species' biology and behavior.
3. The Baigakum specimens of this new species were included (under *A. rickmersi*) in a DNA phylogeographic study by Graham et al. (2012), which demonstrated a derived position of this taxon within the genus.

Anomalobuthus talebii Teruel, Kovařík,
Navidpour et Fet, 2014
Figures 90–106, 141. Tables 3–5

Anomalobuthus talebii Teruel, Kovařík, Navidpour & Fet, 2014: 1–10, figs. 1–24, tabs. 1–2.

HOLOTYPE. ♀ (FKCP). **Iran**, South Khorasan Province, Hemmatabad (=Hemmatābād) Desert, 33°20'49.45"N 60°25'56.86"E, close to the Afghanistan border, 17 April 2013, leg. A. Talebi Gol.

DIAGNOSIS (updated, based on one adult female). Adult size 35 mm. Coloration yellow, with irregular blackish spots on carapace, tergites, pedipalps, legs, and metasoma; tergites with two faint submedian dark

stripes; metasomal segment V and telson blackish. Pedipalp fingers with 10–11 principal rows of denticles and 6–7 internal accessory denticles. Pectines with 26/26 teeth. Tibial spur absent. Metasoma slightly attenuate, with most carinae moderately developed; ventral lateral carinae of segment V composed of narrowly conical denticles, dorsal lateral and lateral supramedian carinae of segments I–IV with terminal denticle greatly enlarged; intercarinal spaces essentially smooth on all segments, except for very few sparse granules on ventrodistal area of V. Telson vesicle short oval and sparsely setose.

DESCRIPTION. See Teruel et al. (2014).

MALE. Unknown.

VARIATION. Unknown, single specimen known.

COMPARISON (females only). *A. talebii* can be unequivocally distinguished by its much higher pectinal tooth count of 26/26, while all other *Anomalobuthus* spp. do have 19–23 teeth (Tab. 5). Also, it has some unique morphometric proportions, e.g., the slenderest telson vesicle (length/width ratio = 2.18 vs. 1.47–2.00 in the other species) and the shortest pedipalp movable finger when compared to manus length (ratio = 2.26 vs. 2.31–3.18 in all other congeners); see Tab. 4.

It is the only species of *Anomalobuthus* known to occur south of the impressive Kopet Dagh mountain range, the natural boundary between Turkmenistan and Iran (Fig. 141).

DISTRIBUTION (Fig. 141). Sands of the Dasht-e-Lut Desert, in eastern Iran.

ECOLOGY. See Teruel et al. (2014).

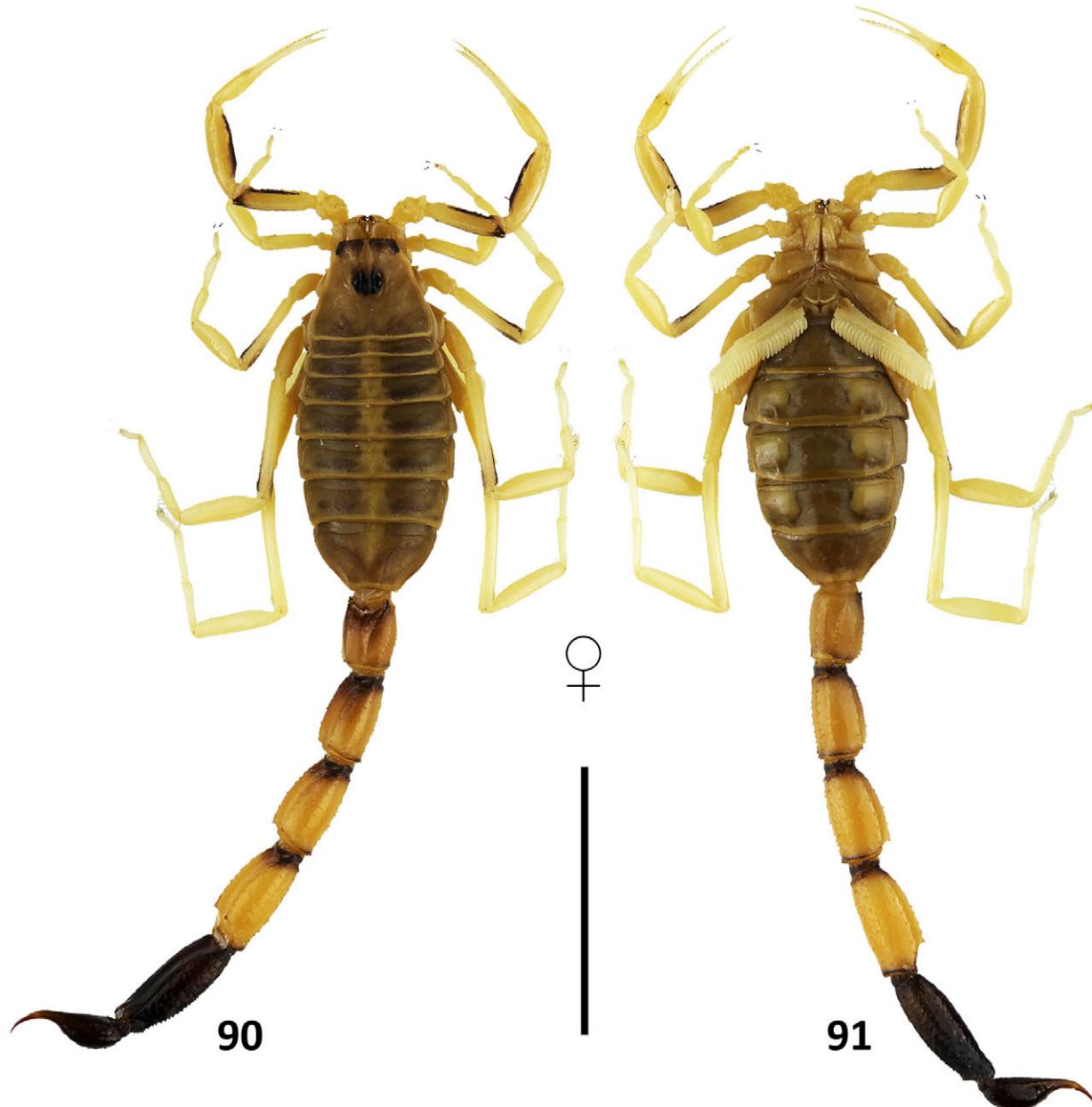
NOTES. See Teruel et al. (2014).

Anomalobuthus zarudnyi (Birula, 1911), comb. n.
Figure 141

Psammobuthus zarudnyi Birula, 1911a: 69–74; Birula, 1911b: 172; Birula, 1917: 131–132, 150, 166; Fet, 1989: 119; Fet & Lowe, 2000: 214 (includes full list of references before 1998); Capes & Fet, 2001: 300–301; Fet et al., 2001: 184.

LECTOTYPE ♂ (ZISP 615, herein designated). **Uzbekistan**, Andijon Province, Mingbulak, 40°51'56"N 71°39'55"E, 13 [26] August 1909, leg. N. Zarudny.

PARALECTOTYPE. ♀ (ZISP 616). **Tajikistan**, Khu-jand Province, Kairakkum, 40°15'39"N 69°47'57"E, 28–31 May [10–13 June] 1908, leg. N. Zarudny.

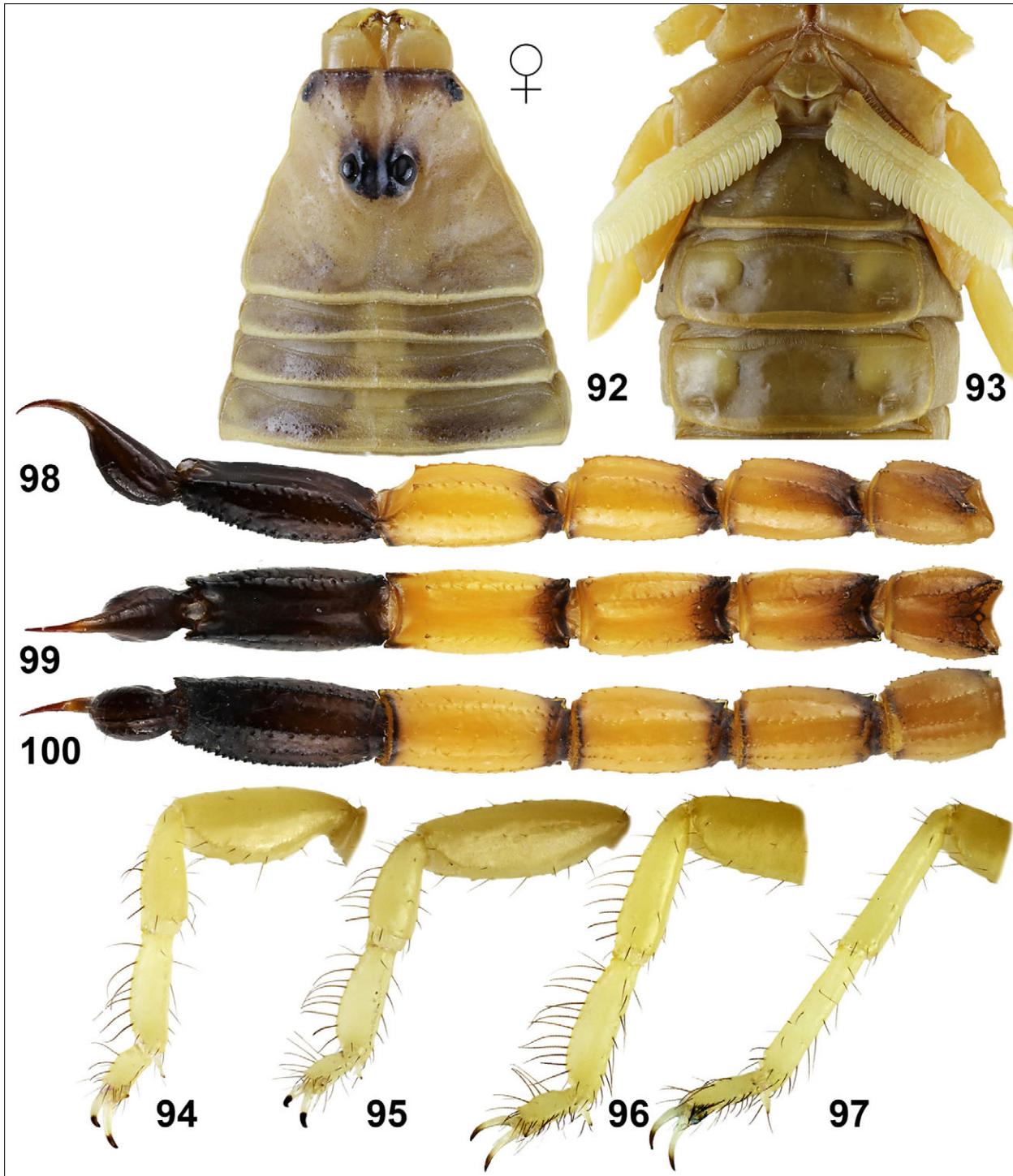


Figures 90–91: *Anomalobuthus talebii*, adult female holotype: full-body views, dorsal (90) and ventral (91).

DIAGNOSIS (updated, based on one adult pair). Adult size standard for the genus (male 29 mm, female 30 mm). Coloration yellow, with irregular blackish spots and reticulations on carapace, tergites, pedipalps, legs, and metasoma; tergites with two conspicuous submedian dark stripes; metasomal segment V and telson reddish. Pedipalp fingers with 10–11 principal rows of denticles and 8 internal accessory denticles. Pectines with 24/26 teeth in male, 20/20 in female. Tibial spur present in legs III–IV (weaker in female leg III). Metasoma with most carinae moderately developed; ventral lateral carinae of

segment V composed of sharply lobate denticles, dorsal lateral and lateral supramedian carinae of segments I–IV with terminal denticle enlarged; intercarinal areas mostly smooth, with granulation sparse ventrally and laterally, of segment V dense ventrally and sparse laterally. Telson vesicle elongate oval.

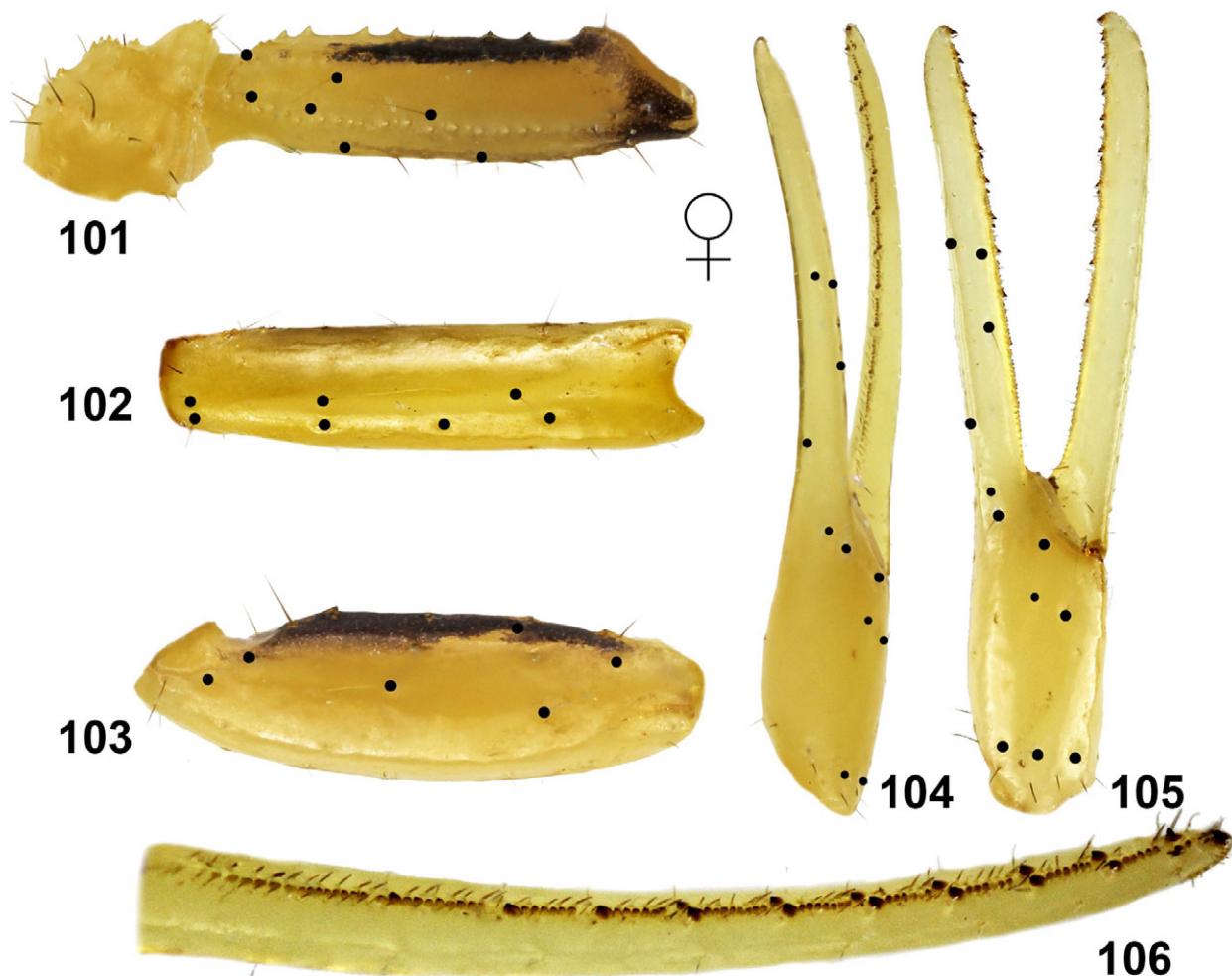
DESCRIPTION (adult male lectotype, translated and updated from Birula, 1911a). **Coloration** base pale to brownish yellow. Pedipalp femur with dorsal surface infuscate; patella with internal surface infuscate. Cara-



Figures 92–100: *Anomalobuthus talebii*, adult female holotype: chelicerae, carapace and tergites I–III, dorsal (92), sternopectinal region and sternites III–V, ventral (93), distal part of right legs I–IV, internal (94–97), metasoma and telson, lateral (98), dorsal (99) and ventral (100).

pace with an anterior V-shaped, broad blackish spot from median ocular tubercle through frontal margin, plus three large, transverse blackish spots: one behind median ocular tubercle and two laterally along posterior

margin. Tergites each with two large dark spots, that form a pair of broad lateral bands. Legs essentially immaculate, only with femur of II–III infuscate. Metasoma not conspicuously bicolor, but becoming progressively



Figures 101–106: *Anomalobuthus talebii*, adult female holotype: right pedipalp trochanter and femur, dorsal (101), right pedipalp patella, dorsal (102) and external (103), right pedipalp chela, dorsal (104) and external (105), right pedipalp movable finger, dorsal (106). Black dots depict trichobothria.

darker distally, with a diffuse annulated appearance: basal part of each segment infuscate in the shape of dark rings, which become larger and reticulate both dorsally and ventrally.

Pedipalps. Relatively short but very slender. Femur with carinae granulose; intercarinal tegument smooth and glossy. Patella with carinae vestigial, smooth; intercarinal tegument smooth and glossy. Chela elongate and slender; manus somewhat wider than patella (ratio 1.50), somewhat flattened (1.07 times longer than wide, 1.67 times wider than deep), without carinae; intercarinal tegument smooth and glossy; fingers long (movable finger 2.00 times longer than underhand), only subtly curved and with 10–11 principal rows of denticles (the three basalmost rows are poorly defined), basal lobe/notch combination absent, external accessory denticles absent, internal accessory denticles large and

numbering eight on both fingers, movable finger with one accessory denticle basal to the terminal denticle.

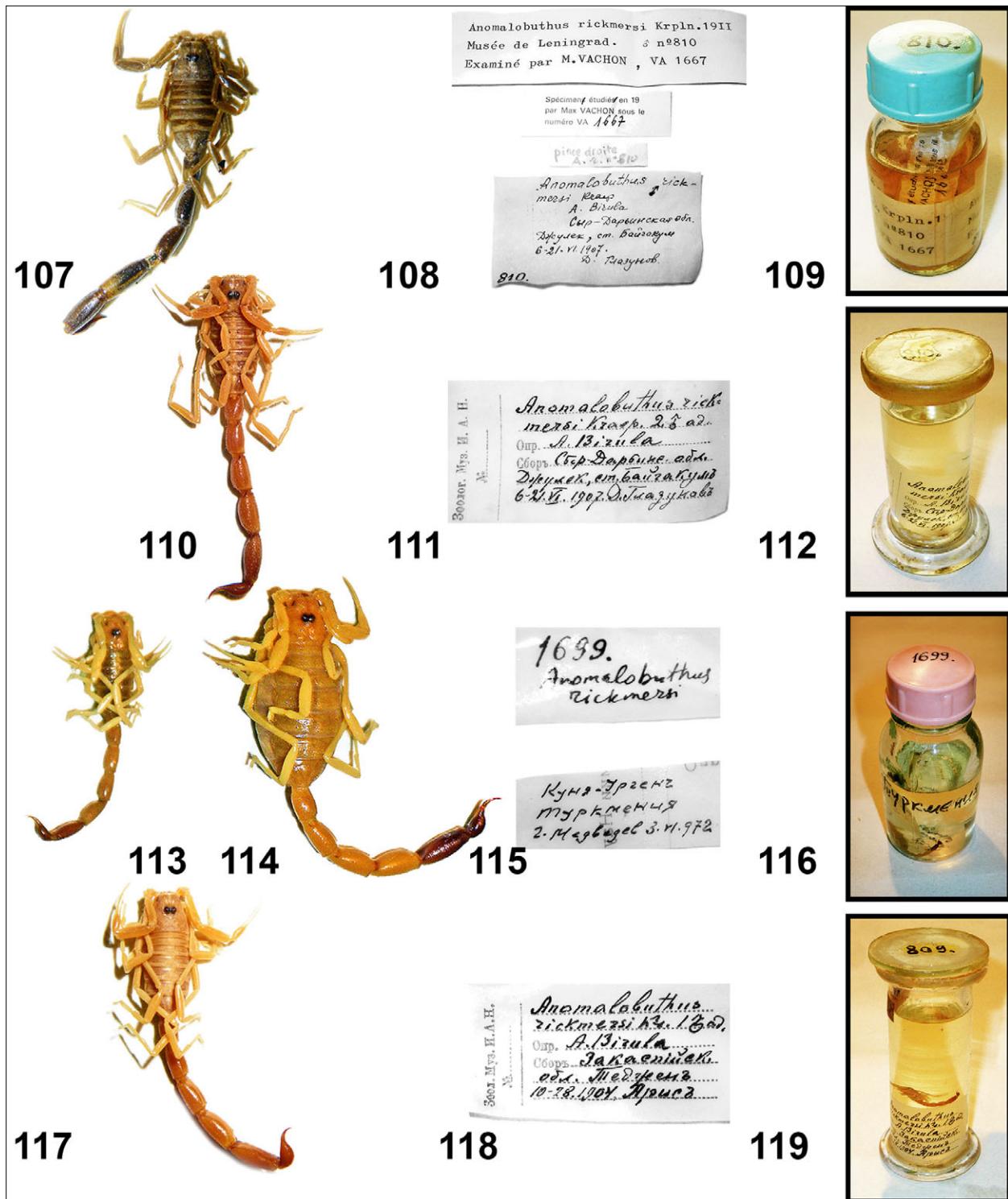
Carapace. Anterior margin straight to shallowly convex. Carination essentially absent: the only carinae present are the superciliaries, which are strongly granulose. Tegument very finely and densely granulose, with coarser granules scattered all over.

Sternum. Standard for the genus, relatively small and wide.

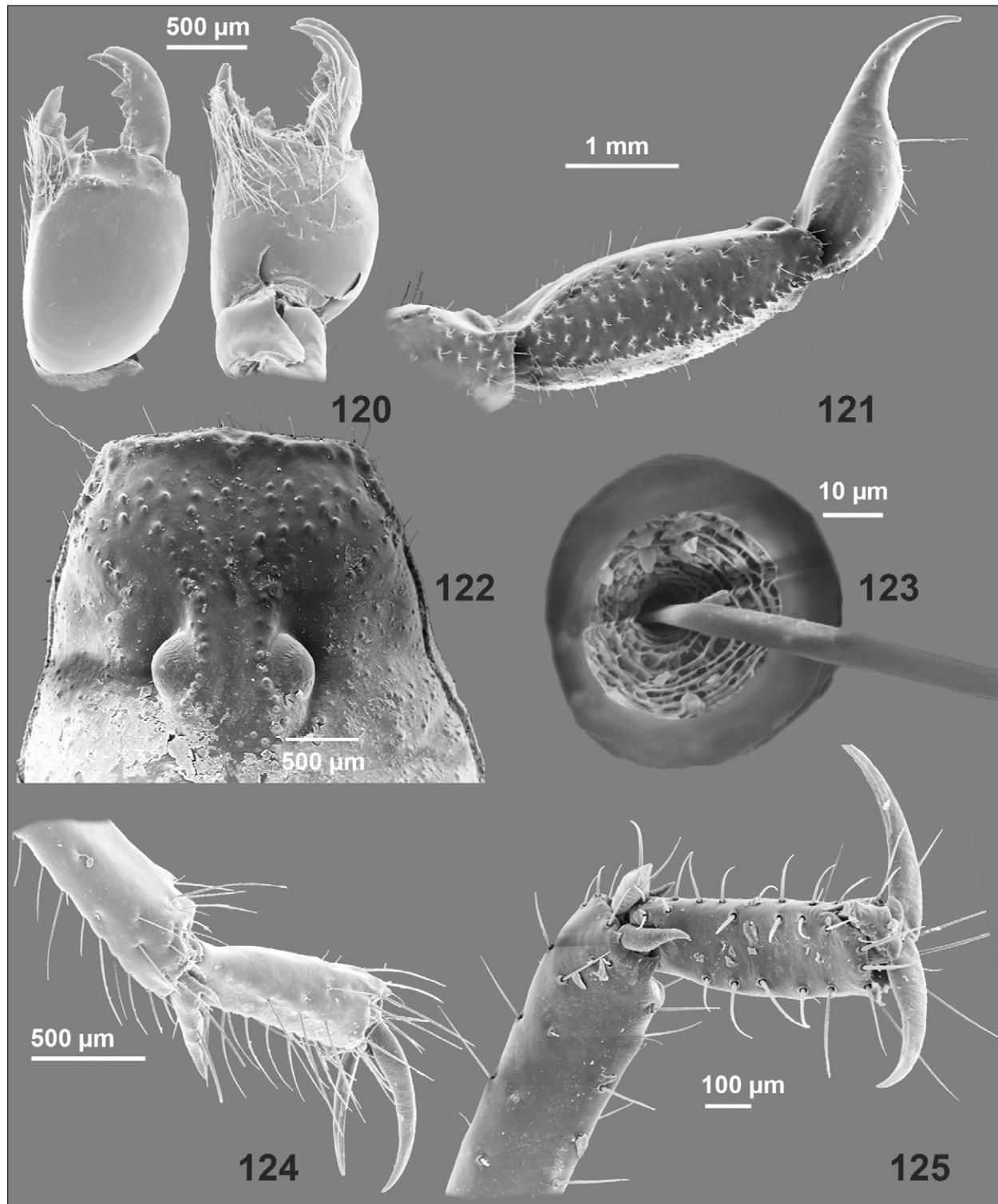
Genital operculum. Each half roundly subtriangular in shape.

Pectines. Standard-sized for the genus: very long, extending to posterior margin of sternite IV, subrectangular. Tooth count 24/26.

Legs. Very slender, with all carinae weak and subgranulose to subcostate; intercarinal tegument smooth and glossy. Tibial spurs well-developed on legs III–IV.



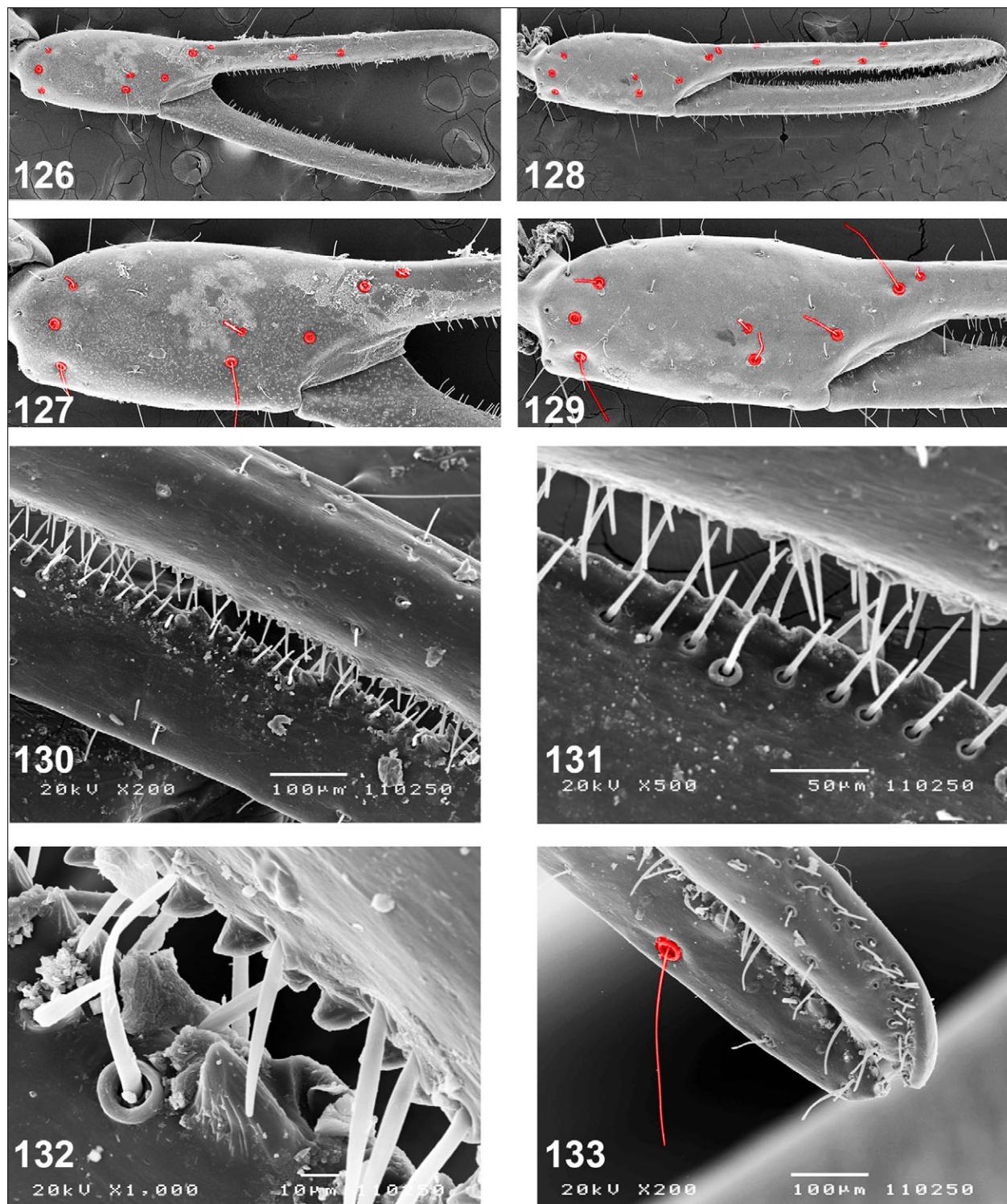
Figures 107–119: *Anomalobuthus* spp., from ZISP historical collection: adult male topotypes of *A. pavlovskyi* sp. n. (107–112), full-body dorsal views (107, 110), labels (108, 111) and bottles (109, 112); adult male (113) and adult female (114) *A. pavlovskyi* sp. n. from Kunya-Urgench, Turkmenistan, full-body dorsal views (113, 114), labels (115) and bottle (116); adult male *A. rickmersi* from Tejen, Turkmenistan (117–119), full-body dorsal view (117), labels (118) and bottle (119). Photographs courtesy Alexander Koval.



Figures 120–125: *Anomalobuthus krivochatskyi* sp. n., adult male paratotype: SEM views of chelicerae, dorsal and ventral (120), metasoma V and telson, lateral (121); anterior half of carapace, dorsal (122); close-up of trichobothria (123); left leg IV basitarsus and telotarsus, ventrointernal (124); left leg IV basitarsus and telotarsus, external (125). Images courtesy Jan Štundl.

Ratios	<i>A. lowei</i> sp. n.	<i>A. krivochatskyi</i> sp. n.	<i>A. pavlovskyi</i> sp. n.	<i>A. rickmersi</i>		<i>A. talebii</i>		
	♀ HT	♂♂ HT, PT	♀♀ PT	♂ HT	♀♀ PT	♂ HT	♀♀	♀ HT
Pedipalp chela (L/W)	6.41	6.20–6.86	5.86–5.87	6.80	5.83–6.90	6.20	5.58–6.20	6.29
Pedipalp chela (L) / movable finger (L)	1.43	1.38–1.45	1.41–1.42	1.42	1.39–1.40	1.41	1.31–1.39	1.44
Pedipalp movable finger (L) / manus (L)	2.31	2.20–2.61	2.42–2.50	2.40	2.50–2.55	2.44	2.55–3.18	2.26
Metasoma + Telson (L) / Carapace (L)	5.40	6.26–6.37	6.12–6.13	7.14	5.68–5.77	7.67	6.05–6.38	6.34
Metasomal segment I (L/W)	1.02	1.26–1.35	1.09–1.23	1.31	1.22–1.31	1.74	1.43–1.44	1.30
Metasomal segment II (L/W)	1.35	1.76–1.77	1.50–1.62	1.75	1.74–1.83	2.13	1.84–1.96	1.82
Metasomal segment III (L/W)	1.39	1.83–1.86	1.64–1.71	1.77	1.85–1.86	2.20	2.04–2.08	1.88
Metasomal segment IV (L/W)	1.75	2.11–2.14	1.83–1.89	2.23	2.05–2.15	2.56	2.30–2.31	2.23
Metasomal segment V (L/W)	1.85	2.32–2.33	2.00–2.11	2.38	2.16–2.31	2.71	2.42–2.50	2.34
Telson vesicle (L/W)	1.47	1.92–2.15	1.75–1.80	1.89	1.66–1.89	2.50	1.89–2.00	2.18
Telson vesicle (L/D)	1.66	1.77–2.18	1.91–1.93	2.12	2.08–2.12	2.39	1.89–2.17	2.14

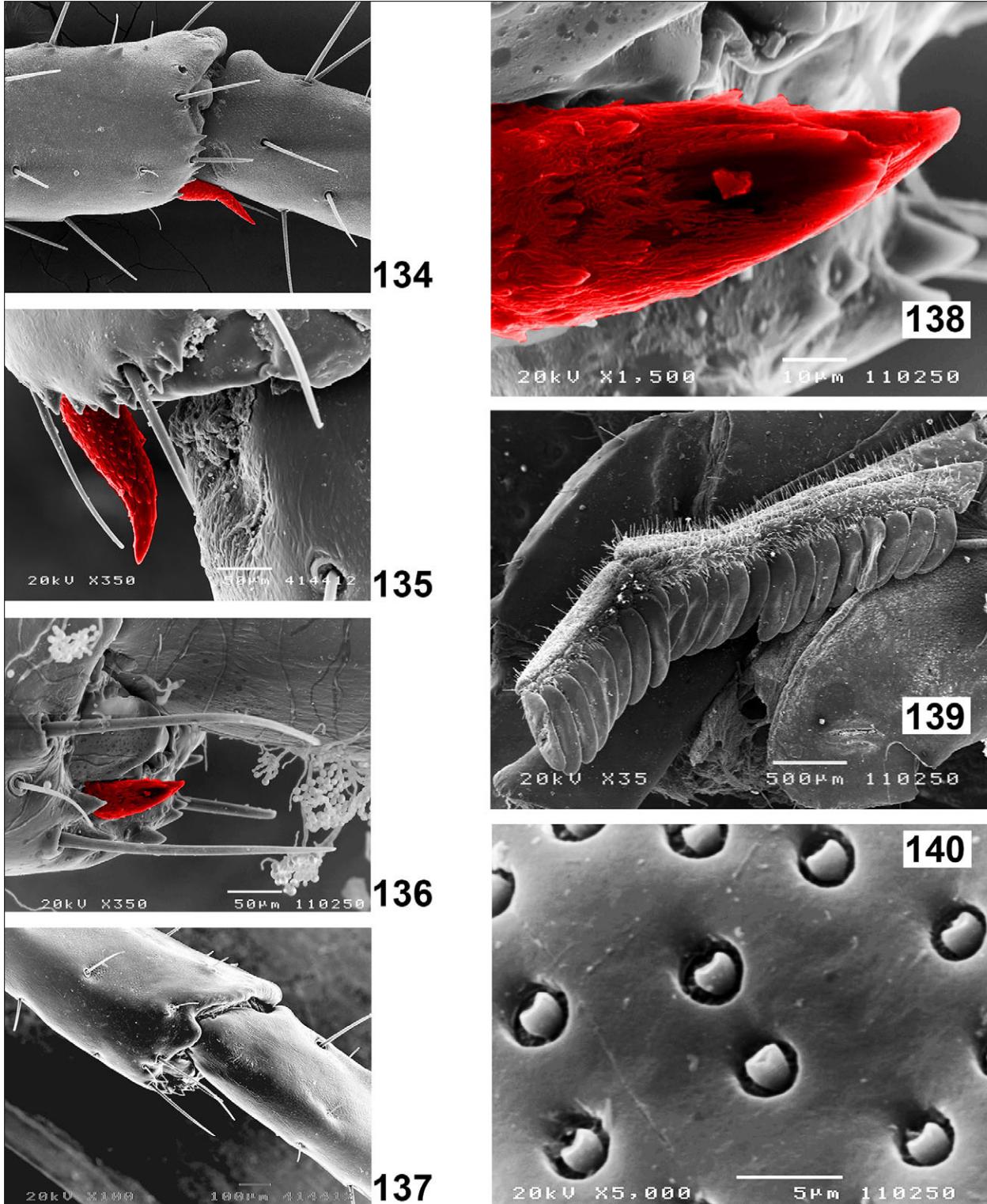
Table 4: Comparison between five species of *Anomalobuthus* based upon selected morphometric ratios. Abbreviations: length (L), width (W), depth (D), holotype (HT), paratypes (PT).



Figures 126–133: *Anomalobuthus* spp., SEM views of right pedipalp of adult male *A. rickmersi* from Repetek (126–127) and adult male paratotype *A. krivochatskyi* sp. n. (128–133): chela (126, 128), close-up of manus (127, 129), three ventrointernal magnified views of mid part of both fingers in consecutive figures (130–132, movable finger on top), ventrointernal close-up of fingertips (133, movable finger on top). See trichobothria highlighted in red.

Mesosoma. Tergites very finely and densely granulose, with subtle vestiges or coarser granules scattered; I–VI irregularly tricarinate: the median longitudinal

carina is weak and the submedian carinae are poorly defined by 2–3 coarse granules only. Sternites III–VI smooth and glossy; VII with two pairs of carinae: the



Figures 134–140: *Anomalobuthus* spp., SEM views showing size variation of leg IV tibial spur (highlighted in red): large in paratotype female *A. krivochatskyi* sp. n. (134), moderately large in paratype female *A. krivochatskyi* sp. n. from Bukhara (135), small in paratotype female *A. krivochatskyi* sp. n. (136), absent in male *A. rickmersi* from Repetek (137), close-up of a medium-sized leg IV tibial spur of a paratotype female *A. krivochatskyi* sp. n. from Zarafshan (138), see spinulate and striate sculpture. *Anomalobuthus krivochatskyi* sp. n., adult female paratotype: SEM views of right pecten and adjacent parts of leg coxae and sternite III (139), peg sensilla of tooth from same pecten (140).

Species	Sex	N	Pectinal Teeth									Ave.	SD
			19	20	21	22	23	24	25	26	27		
<i>A. krivochatskyi</i> sp. n.	♂♂	8				3	1	3	1			23.25	± 1.09
	♀♀	16	2	7	4	3						20.50	± 0.94
<i>A. lowei</i> sp. n.	♀♀	2		1	1							20.50	± 0.50
<i>A. pavlovskyi</i> sp. n.	♂♂	15						2	6	5	2	25.47	± 0.88
	♀♀	12				8	4					22.33	± 0.47
<i>A. rickmersi</i> sp. n.	♂♂	22			2	1	3	4	4	7	6	24.82	± 1.15
	♀♀	9					3				1	21.78	± 1.13
<i>A. talebii</i>	♀♀	2									2	26.00	± 0.00
<i>A. zarudnyi</i> comb. n.	♂♂	2			2						1	25.00	± 1.00
	♀♀	2										20.00	± 0.00

Table 5: Pectinal tooth count variation in all known species of *Anomalobuthus*. Abbreviations: number of pectines (N), average (Ave.), standard deviation (SD). This includes counts taken from sources with precise and reliable geographic data (Birula, 1905, 1910).

submedians are smooth and the laterals are granulose, intercarinal tegument very finely and densely granulose except smooth medially.

Metasoma. Moderately elongated and slightly narrower distally; with 10/8/8/8/5 complete to almost complete, serrate carinae: dorsal laterals very strong on I, strong on II–III with terminal denticles enlarged on the latter, moderate on IV, absent on V; lateral supramedians very strong on I, irregular on II–III with terminal denticles enlarged on the latter, weak on IV, smooth on V; lateral inframedians very strong on I, undefined to absent on II–V; ventral laterals strong on I, strong on II–III, obsolete on IV, strong on V, where become progressively stronger and somewhat flared distally, formed by sharp, subequal denticles; ventral submedians very strong on I, strong on II–III, obsolete on IV, absent on V; ventral median absent on I–IV, finely denticulate and distally bifurcate on V. Intercarinal tegument smooth and glossy, with many granules of different sizes scattered all over lateral and ventral surfaces, which become progressively denser and coarser towards segment V. Dorsal furrow moderately deep on all segments. Setation sparse over carinae.

Telson. Vesicle elongate oval (2.00 times longer than wide, 0.77 times wider than deep), tegument smooth and glossy, with coarse granules arranged into longitudinal carinae. Subaculear tubercle absent. Aculeus shorter than vesicle.

FEMALE (paralectotype, data extracted from Birula, 1911a). Very similar to male, sexual dimorphism evident by: 1) size slightly larger; 2) metasoma somewhat less slender; 3) tergites I–VI with median carina more strongly and regularly developed; 4) pectines with consistently lower tooth count (20/20); 5) tibial spur highly reduced on leg III.

VARIATION. Unknown, only one adult of each sex have been collected.

COMPARISON. According to Birula (1911a), the extensively dark-patterned coloration and the strong development of ventral lateral and ventral submedian carinae on metasomal segments II–III, both seem to distinguish this species clearly from all its other congeners. Moreover, it is the only species of *Anomalobuthus* known to occur in the sands of the Ferghana Valley.

DISTRIBUTION (Fig. 141). Isolate sands of the Ferghana Valley in the border region between Uzbekistan and Tajikistan.

NOTES.

1. The only known two specimens of this species were collected in 1908 and 1909 by the famous Russian ornithologist and traveler Nikolay Alekseevich Zarudny (1859–1919) who also brought numerous scorpions for A. Birula's ZISP collection, including many new species from the previously unexplored areas of Iran.
2. The unavailability of the types and lack of additional specimens of *A. zarudnyi* comb. n. prevents us from doing a deeper analysis of its true taxonomic status within the genus. Until any counterevidence appears, it seems more appropriate to retain it as a valid species. Moreover, two points seem to support the present assumption: the strikingly contrasting coloration (Birula, 1911a) that does not match any of the populations of *Anomalobuthus* studied during this revision, and its isolated distribution inside the Ferghana Valley (Fig. 137).
3. In the last 100 years, the Ferghana Valley sands have all but disappeared due to irrigation. On 18–20 May

2002, our field expedition (VF and A.V. Gromov) visited the remaining sand massifs of the modern Ferghana Province, Uzbekistan (Kairakkum Sands in Besharyk District, 40.4735°N 70.4503°E , and “Karakalpak Steppe” in Yazyavan District, 40.6580°N 71.5072°E). We did not find *A. zarudnyi*, while psammophilic *Mesobuthus gorelovi* Fet et al., 2018 was abundant and active.

Key to the species of *Anomalobuthus* Kraepelin, 1900

1. Coloration with the dark pattern very dense all over, tergites with two conspicuous submedian stripes *A. zarudnyi*
- Coloration with the dark pattern inconspicuous to essentially absent on carapace, legs and metasoma (except for segment V blackish to reddish), tergites immaculate to at most with two faint submedian stripes 2
2. Tergites with two faint submedian dark stripes. Female (single sex known) with 26 pectinal teeth *A. talebii*
- Tergites without submedian dark stripes. Female with 19–23 pectinal teeth 3
3. Habitus very robust in female (single sex known), see the following ratios: metasoma + telson length/carapace length = 5.40, metasomal segment I length/width = 1.02, metasomal segment V length/width = 1.85, telson vesicle length/depth = 1.66 *A. lowei* sp. n.
- Habitus remarkably slenderer in female, see the following ratios: metasoma + telson length/carapace length = 5.68–6.38, metasomal segment I length/width = 1.09–1.44, metasomal segment V length/width = 2.00–2.50, telson vesicle length/depth = 1.89–2.17 4
4. Adult metasoma with intercarinal spaces much more densely granulose in female than in male; basal third of segment V yellowish red *A. pavlovskyi* sp. n.
- Adult metasoma with intercarinal spaces either smooth and glossy in female, or more densely granulose in male; segment V entirely reddish to blackish, at most only subtly paler at its extreme base 5
5. Adult male habitus very slender: metasoma + telson length/carapace length ratio = 7.67. Adult metasoma with ventral and lateral intercarinal spaces sparsely granulose on segment IV and very densely granulose on V, especially in male; segment V reddish in adult male *A. rickmersi*
- Adult male habitus less slender: metasoma + telson length/carapace length ratio = 6.26–6.37. Adult metasoma with intercarinal spaces almost smooth in both sexes; segment V blackish in adult male *A. krivochatskyi* sp. n.

Discussion

Morphology

Trichobothria. The trichobothria of the genus *Anomalobuthus* present a very peculiar problem. Even though the trichobothrial pattern is clearly A-β, some trichobothria are either absent or very reduced and difficult to distinguish from the surrounding setae under ordinary white/UV light microscopy, e.g., femoral d_2 and chelal Et , V_1 , and esb . This is because most ordinary pedipalpal setae are hypertrophied, having a very large and heavily socketed base and a thick shaft, too closely resembling true trichobothria which also have shaft thicker than usual (Figs. 72–74, 122–129). Despite this, its current placement in the “*Buthus* group” by Fet et al (2005) stands correct, based on two important diagnostic characters: trichobothrial pattern beta, with patellar d_3 trichobothrium located internal to dorsal median carina.

Tibial spurs. Fet et al. (2005) reviewed the importance of tibial spur on legs III–IV as a character in scorpion systematics, in particular in buthoid scorpions. In parvorder Buthida (*sensu* Soleglad & Fet, 2003b), tibial spurs are completely absent (lost) in New World genera (a major synapomorphy) but their presence is variable within the Old World members (Fet et al., 2005, Table 1).

In his original diagnosis of the male holotype of *A. rickmersi*, Kraepelin (1899) reported that the tibial spur was absent on legs III, and present but reduced (to a very small size, represented by a sinuous remnant) on legs IV. His important text is translated below:

“Recently I got from Professor O. Schneider a small scorpion collected in the Buchara by Mr. W. Rickmer Rickmers, which unfortunately contradicts with classification of Buthidae as established by myself, into the two subfamilies of Buthinae and Centrurinae because, although an undoubtedly genuine Buthine, a character feature of this group, a tibial spur of the third and fourth pairs of legs, in this scorpion is developed only at the fourth leg pair as a very tiny rudiment (Fig. 4), being completely absent on the third pair of legs. Since the structure of the rows on the cutting edge of pedipalp finger also does not match with any of the existing genera, I decided to establish a new genus *Anomalobuthus*, which I must attribute, despite its almost completely disappearing tibial spur, to the subfamily of Buthinae, as discussed below in more detail.”

Birula (1905) following Kraepelin made a connection between this reduction and the absence of tibial spurs in the New World buthids, thus questioning the relationship of *Anomalobuthus* with other Old World genera. Birula (1905: 449–450) who was the next to study *Anomalobuthus*, had only two specimens collected in the modern Turkmenistan. He observed that a male

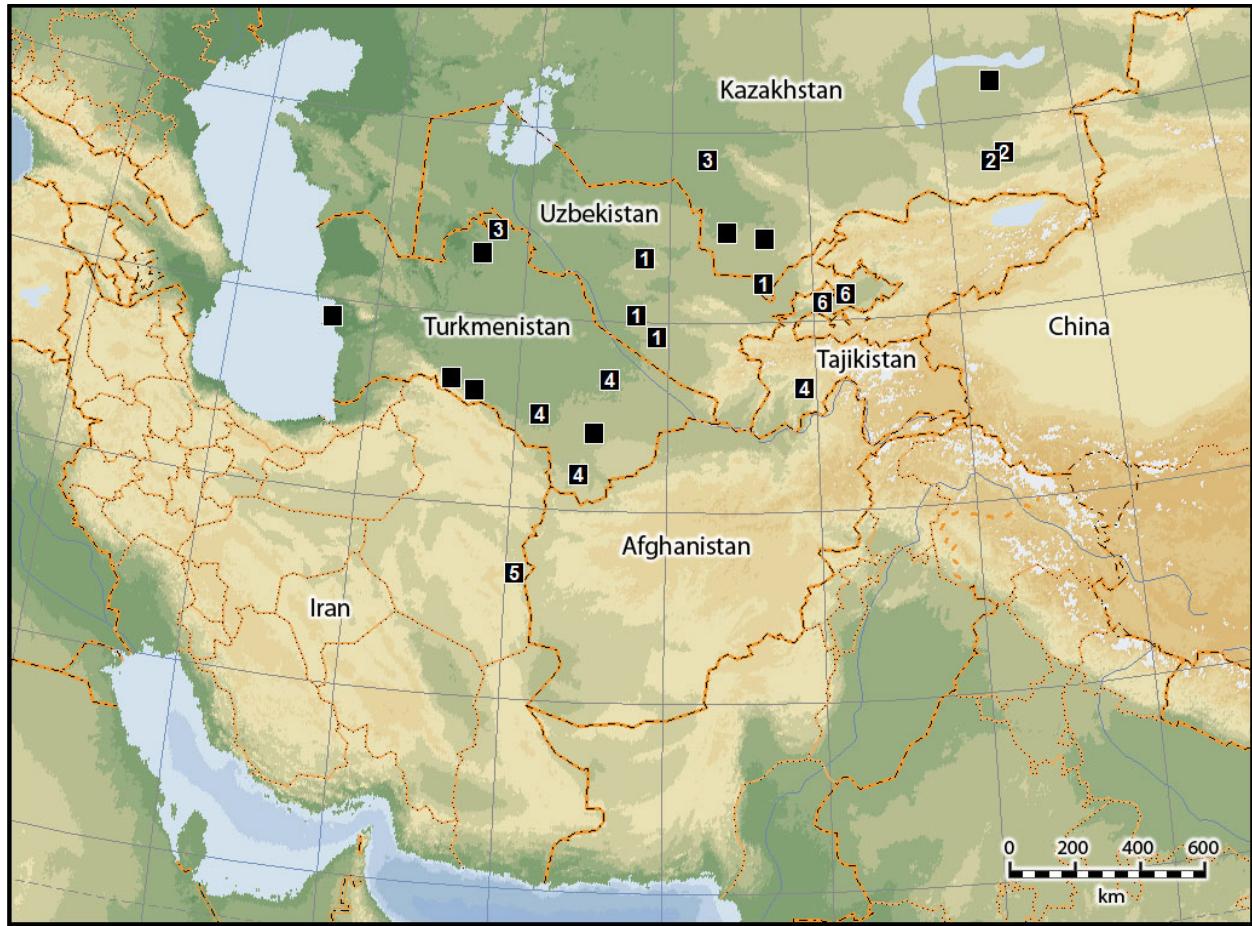


Figure 141: Distribution of the genus *Anomalobuthus*: *A. krivochatskyi* sp. n. (1), *A. lowei* sp. n. (2), *A. pavlovskyi* sp. n. (3), *A. rickmersi* (4), *A. talebii* (5), *A. zarudnyi* comb. n. (6), and literature records whose identification is pending (black squares). Data compiled from specimens studied herein and the following supplementary sources: Rickmer Rickmers (1913), Fet (1989, 1994), Gromov & Kopdykbaev (1994), Gromov (2006), Mityaev et al. (2008), and Graham et al. (2012).

from Tejen (ZISP 809, clearly diagnosable as a male by having 25 pectinal teeth, see our Figs. 113–115) had developed tibial spurs only on legs IV, while a female from Repetek (ZISP 808, 22 pectinal teeth) completely lacked tibial spurs. Later, Birula (1911a: 73) in describing the genus *Psammobuthus* Birula, 1911, from Ferghana (Uzbekistan) (which we here synonymize with *Anomalobuthus*) noted that it had well-developed tibial spurs on legs III and IV in males but rudimentary ones on legs III in females; and stated that “females in *Anomalobuthus* have no spurs on legs III and IV but males only have rudimentary tibial spurs on legs IV.” This was interpreted as a sexual dimorphism. Birula (1911b: 171) reported two more males from Baigakum (Kazakhstan), collected by D. Glazunov, but did not comment on their tibial spurs. Males in Baigakum (our *A. pavlovskyi* sp. n.), as we now know, have spurs in different degrees of development.

All subsequent genus-level keys of Buthidae (Werner, 1934; Stahnke, 1972, fig. 3; Sissom, 1990)

mentioned tibial spur reduction in *Anomalobuthus*. Sissom (1990: 96) stated that in this genus tibial spurs on legs III are absent, and on legs IV are “sometimes vestigial”. Note that Sissom (1990) only studied Turkmenistan specimens from Repetek, supplied by V. Fet. Later, Capes & Fet (2001) and Fet et al. (2001) stated that females of *Anomalobuthus* lack tibial spurs while males have them “occasionally present, but small, on leg IV.”

Our current study revealed a complex picture of interspecific, intraspecific, and intrapopulational variation in loss or reduction of tibial spurs across all six species of the genus *Anomalobuthus* (Figs. 130–134). This variation includes several stages of reduction, marked fluctuating asymmetry (presence on either left or right side), and possible sexual dimorphism. The tibial spur was usually absent in *A. rickmersi* from Turkmenistan (except the male from Tejen has it on both legs IV), and is absent in the only known female of *A. talebii* from Iran. In *A. krivochatskyi* sp. n., the tibial spur was

always absent in males, but in females it was present always on both legs IV, and sometimes also in leg III but only on one side. In *A. pavlovskyi* sp. n., the tibial spur development was highly variable among Baigakum specimens: it was either entirely absent from all legs (one male), or present asymmetrically on a single leg IV (three males including holotype, two females), or present asymmetrically on each leg III–IV of the same side (left, one female), or, finally, present on both legs IV (two males, one female); but in all cases where it was present, it was small to vestigial. In the only known female of *A. lowei* sp. n., tibial spur is absent from both legs III and right leg IV, but a moderate-sized spur is found on left leg IV. Finally, in *A. zarudnyi* sp. n., the only known male has tibial spurs well-developed on legs III–IV but in the only known female, they are highly reduced on legs III. These patterns suggest a clear trend within *Anomalobuthus* for developmental instability in exhibiting variable reduction or loss of an important morphological character.

Quite possibly, this trend is related to psammophilic adaptation of *Anomalobuthus* since it is also observed in other Old World sand desert scorpions. Various modifications of leg structures in psammophile buthids have been amply documented (Fet et al., 1998). Monotypic genera *Liobuthus* Birula, 1898 and *Pectinibuthus* Fet, 1984 (Central Asia) and *Plesiobuthus* Pocock, 1900 (Pakistan) completely lack tibial spurs (Capes & Fet, 2001; Fet et al., 2001, 2005). Tibial spurs are often reduced or missing, with asymmetry exhibited, in two Middle Eastern psammophile buthid genera, *Apistobuthus* Finnegan, 1932 and *Vachoniolus* Levy et al., 1973, which have been recently studied in detail. Graeme Lowe (pers. comm.) kindly summarized for us the available data. Already in her original description of *Apistobuthus pterygocercus*, Finnegan (1932) stated: "Tibial spurs absent on third pair of legs and present as a small weak spine on only one of the fourth pair of legs in two of the three specimens collected (text-fig. 8), absent from all the legs of the third specimen." Such asymmetric reduction or loss in this species was also reported by Vachon (1980). Navidpour & Lowe (2009) found that tibial spur loss or degeneration (to a very small vestigial spur ca 20% the length of a fully developed spur) was much more common in *A. pterygocercus* than in the congeneric *A. susanae*. "In a sample of $n = 20$ adults of *A. susanae*: 39 intact leg III tibia included 30/39 spurs present, 9/39 (23%) spurs lost; 38 intact leg IV tibiae included 34/38 spurs present, 4/39 (10%) spurs lost. In contrast, in a sample of $n = 31$ adults of *A. pterygocercus*: 60 intact leg III tibiae included 15/60 spurs present, 45/60 (75%) spurs lost; 60 intact leg IV tibiae included 36/60 spurs present, 24/60 (40%) spurs lost. The much higher frequency of degeneration or loss of tibial spurs in *A. pterygocercus* correlates to the ultrapsammophile habit of this species,

and we suggest that it represents a derived character state" (Navidpour & Lowe, 2009).

For another psammophile genus from the Arabian Peninsula, *Vachoniolus*, Lowe (2010) noted that, in *V. gallagheri*, "tibial spurs were either present or absent, and were absent more frequently on leg III than leg IV; of 30 leg III tibiae, spurs were present in 19 (63.3 %), and absent in 11 (36.7 %); of 29 leg IV tibiae, spurs were present in 25 (86.2 %), and absent in 4 (13.8 %)." The same trend was observed by Lowe (2010) in the congeneric *V. globimanus*: "Tibial spurs were either present or absent, or vestigial (< 20% of the length of fully formed spur), and were lost with similarly high frequencies on both legs III and IV: of 78 intact leg III tibiae, spurs were present in 39 (50.0 %), and absent or vestigial in 39 (50.0 %); of 77 intact leg IV tibiae, spurs were present in 43 (55.8 %), and absent or vestigial in 34 (44.2 %)."

Importantly, already the pilot DNA-based phylogeny of Fet et al. (2003) for 17 genera of Buthidae suggested the polyphyletic origin of psammophily among these genera; full or partial tibial spur loss is observed independently in at least three independent lineages which include (a) *Anomalobuthus*, (b) *Liobuthus*, and (c) *Vachoniolus* + *Apistobuthus*. We suspect therefore that this trend is an example of parallelism (convergent evolution) under selection toward psammophily.

Biogeography

The dynamic biogeographic history of Central Asian sand deserts is well-known, and likely had a profound impact on the diversification of psammophilic scorpions, including remarkable endemic genera *Anomalobuthus* and *Liobuthus*. The fauna, flora and geology of Kazakhstan, Uzbekistan, and Turkmenistan have been thoroughly studied but most of the literature was published in Russian, thus remaining largely inaccessible to the global research community. The most comprehensive biogeographic review was generated for Coleoptera (Kryzhanovsky, 1965), while the remaining data on the fauna and biogeography of Central Asia are scattered in Russian journals as dozens of papers covering specific taxa and regions. After the demise of the USSR in 1991, the former Soviet Central Asia was fragmented politically into five independent countries (Kazakhstan, Kyrgyzstan, Uzbekistan, Tajikistan, and Turkmenistan). Since then, the rate and quality of zoological research from the region has decreased markedly. Of these five countries, only a comprehensive review of the ecology and biogeography of Turkmenistan has been published in English (Fet & Atamuradov, 1994). Our research group and its collaborators were the first to use molecular phylogenetics (based on mitochondrial DNA sequence data) to study

the biogeography of scorpions from the Central Asian deserts (Gantenbein et al., 2003; Graham et al., 2012; Fet et al., 2018).

As with many animal and plant groups of Central Asia, speciation is clearly connected to the region's geomorphology; such as landscape fragmentation driven by mountain uplift and substrate modifications during the formation of sand and clay deserts. Furthermore, enclaves of sand desert within mountain valleys (such as the type locality of *A. rickmersi* in Tajikistan) contributed to local evolution of psammophilic fauna, with narrow endemics found at considerable altitude. In Central Asia, geological data emphasize two major types of late Cenozoic paleogeographical changes, mountain uplift and eustatic changes of the ancient Caspian Sea (a remnant of the Tethys Sea). The great alluvial deserts, primarily the Karakum and the Kizylkum, have been formed as a result of deposits by the Amudarya and Syrdarya Rivers (reviewed in Graham et al., 2012).

The largely psammophilic *Mesobuthus gorelovi* Fet et al., 2018., which spans most of the deserts of Central Asia, shows significant phylogeographic structure, with specimens from Turkmenistan forming a clade distinct from populations in Uzbekistan and Kazakhstan. *M. gorelovi* is one of the most common scorpion species in Central Asia, found widespread in the lowland deserts and exhibiting psammophilic adaptations such as sand combs. The distribution of *M. gorelovi* was likely affected by transgressions of the Caspian Sea, especially in Pliocene and further in Pleistocene, when it was divided by the Amudarya River, as found in other co-distributed buthids (Graham et al., 2012). Divergence within *M. gorelovi* was estimated to have occurred in this timeframe (5.2 – 1.4 Ma; mean = 3.1 Ma). The main clades within *M. gorelovi* occur on either side the Amudarya River, consistent with the hypothesis of Pliocene vicariance. Another psammophilic species, *Mesobuthus elenae* Fet et al. 2018, was found isolated in the Amudarya Valley of southwestern Tajikistan and Uzbekistan, broadly overlapping with the only known Tajikistan population of *A. rickmersi* (Baljuvon). The divergence of *M. elenae* from its sister species *M. parthorum* is also dated to the Pliocene (4.9 – 1.6 Ma; mean = 3.1 Ma).

Graham et al. (2012) have analyzed mtDNA markers in several specimens of *Anomalobuthus*, then placed under "*A. rickmersi*". As we demonstrate above on the basis of morphology, the material used by Graham et al. (2012) should be classified as three different species, namely *A. rickmersi* (Turkmenistan), *A. krivochatskyi* sp. n. (Uzbekistan) and *A. pavlovskyi* sp. n. (Kazakhstan). Although this molecular study did not include *A. lowei* sp. n., *A. talebii* Teruel et al., 2014, and *A. zarudnyi* (Birula, 1911), comb. n., its conclusions are very important in addressing the endemic speciation of *Anomalobuthus*. This first DNA-based analysis of

Graham et al. (2012) confirms that both great waterways of Central Asia, especially Amudarya and (in part) Syrdarya, acted as biogeographic boundaries in vicariant speciation of *Anomalobuthus*. They indicated also that "the levels of divergence within *Anomalobuthus*, *Lio-buthus*, and *Mesobuthus* are somewhat deep for intraspecific studies." Indeed, the most recent revision of the "*Mesobuthus caucasicus* complex" (Fet et al., 2018) revealed existence of diverse species across Central Asia.

The southern and southeastern Turkmenistan populations (Karakum Desert), which morphologically all belong to *A. rickmersi*, are clearly separated by the Amudarya River from the Uzbekistan/southern Kazakhstan populations (Kizylkum Desert), which are now demonstrated to belong to a morphologically distinct *A. krivochatskyi* sp. n. A more complex picture emerges regarding the vicariant distribution of *A. krivochatskyi* sp. n., limited to the southern Kizylkum (40-41°N) and *A. pavlovskyi* sp. n., found in the sands of the Aral Basin (42-44°N), from extreme northern Turkmenistan (Kunya Urgench) to south-central Kazakhstan (Baigakum, or Dzhulek on Syrdarya River); in addition, we describe the northernmost Kazakhstan species *A. lowei* sp. n. from the Ili River valley (Kapchagay). sp. n.. The DNA data of Graham et al. (2012) indicate that *A. krivochatskyi* sp. n. forms a sister clade to *A. pavlovskyi* sp.n, as compared to an outgroup *A. rickmersi*. An approximate divergence time between two new species is estimated from 16S mtDNA data (M. R. Graham, pers. comm.) between 5.34 and 1.62 Ma, with a mean estimate of 3.41 Ma (Pliocene), which corresponds well to the above listed *Mesobuthus* divergence estimates. Early to Middle Pliocene has been the time of diversification in many taxa in the deserts and mountains of Central Asia, followed by the Caspian Sea transgressions and cooling of the climate in the late Pliocene (Atamuradov, 1994; Kazenas & Baishashov, 1999).

Allopatric distribution of species-level, uniquely adapted psammophile endemics in the alluvial sands of the Karakum, Kizylkum, and the Aral Basin has been studied in many examples of invertebrate and vertebrate fauna (Kryzhanovsky, 1965). As one of the most recent studies, we can quote a comprehensive molecular and morphological work on the psammophilic toad agama *Phrynocephalus mystaceus* (Agamidae) (Solovyova et al., 2018), which sampled many of the same desert localities as our work on scorpions. We are glad to report that *Anomalobuthus* follows the classical pattern of vicariant speciation in these great sand deserts of Central Asia.

Acknowledgments

The 2002 field mission to Central Asia (Kazakhstan, Turkmenistan, and Uzbekistan) that provided many of

the studied specimens was supported by the National Geographic Society (USA) Research and Exploration Fund (grant 7001–0001 to VF). Alexander Gromov provided a great help during the field work across Central Asia in March–May 2002. Collection permits were granted by the ministries of natural resources of Kazakhstan, Turkmenistan, and Uzbekistan. We are grateful to Dzhamshid Dzhuraev, Aliya Gromova, Gochmyrat Gutlyev, Alexander and Elena Kreuzberg, Viktor Lukarevsky, Sergei Morozov, Shukhrat Shakhnazarov, and Alexander Tarabrin for their hospitality and help in field logistics.

We also thank everyone who helped to obtain and describe rare specimens in field and from the museum collections over many years, including but not limited to: Yuri Balashov, Matt Braunwalder, Michelle Capes, Hieronymus Dastych, Andrei Feodorov, Yuri Galaktionov, Yuri Gorelov, Alexander Gromov, Jürgen Gruber, Danilo Harms, Christoph Hörweg, Ragnar Kinzelbach, Viktor Krivochatsky, Pavel Kučera, Gennady Kuznetsov, Yuri Marusik, Gleb Medvedev, Kirill Mikhailov, Vladimir Ovtsharenko, W. David Sissom, Oraz Soyunov, Verena Stagl, and Andreas Wessel, and Sergei Zonstein.

We are grateful to Graeme Lowe for his great help in taking exquisite images of the rare *A. lowei* sp. n. We especially thank Alexander Koval, Andrei Ovchinnikov, and Anastasia Ovchinnikova (St. Petersburg, Russia) for taking the images of the ZISP specimens, and Kirill Mikhailov, Elena Temereva, and Roman Nazarov (Moscow, Russia) for the images of the ZMMSU specimens; and Jan Štundl for several scanning electron microscope (SEM) images (Figs. 116–121). We thank Matthew R. Graham, Viktoria Oláh-Hemmings, and Joshua Greenwood for the DNA analysis that allowed the first insight into *Anomalobuthus* phylogeny and biogeography (Graham et al., 2012). David Neff, Michael Brewer, Matthew R. Graham, Jacqueline Aisling (Webb), Kelly Anne Daniel, and Kelsey Longe greatly helped VF with SEM imaging (Figs. 122–136). Shakhrokh Navidpour brought to our attention (Teruel et al., 2014) the only known Iranian species, which was collected by the late Amir Talebi Gol (1980–2014).

Finally, VF would like also to thank his late mentors, Gary A. Polis (1946–2000) (California, USA) and Oleg L. Kryzhanovsky (1918–1997) and Yaroslav I. Starobogatov (1932–2004), both of St. Petersburg, Russia) for their great support of his studies in the sand deserts of Central Asia.

We are grateful to Michael Soleglad and two anonymous reviewers for their valuable comments.

References

ACOSTA, L. E., D. M. CANDIDO, E. H. BUCKUP & A. D. BRESCOVIT. 2008. Description of *Zabius*

gaucho (Scorpiones, Buthidae), a new species from southern Brazil, with an update about the generic diagnosis. *The Journal of Arachnology*, 36: 491–501.

ARMAS, L. F. DE, R. TERUEL & F. KOVAŘÍK. 2011. Redescription of *Centruroides granosus* (Thorell, 1876) and identity of *Centrurus granosus simplex* Thorell, 1876 (Scorpiones: Buthidae). *Euscorpius*, 127: 1–11.

ATAMURADOV, KH. I. 1994. Paleogeography of Turkmenistan. Pp. 49–64 in: Fet, V. & Kh. I. Atamuradov (eds.). *Biogeography and Ecology of Turkmenistan*. Kluwer Academic Publishers, Dordrecht.

BIRULA, A. A. 1904. Miscellanea Scorpilogica. VII. Synopsis der russischen Skorpione. *Annuaire du Musée Zoologique de l'Académie Impériale des Sciences de St. Pétersbourg*, 9: 28–38.

BIRULA, A. A. 1905. 4. Skorpilogische Beiträge, 1.–3. *Microbuthus littoralis* (Pavesi), *Anomalobuthus rickmersi* Kraepelin und *Buthus zarudnianus* n. nom. *Zoologischer Anzeiger*, 29(1–4): 445–450.

BIRULA, A. A. 1911a. Skorpilogische Beiträge. 7.–8. *Psammobuthus* g. n. *Zoologischer Anzeiger*, 37(3–4): 69–74.

BIRULA, A. A. 1911b. Miscellanea Scorpilogica. IX. Ein Beitrag zur Kenntnis der Skorpionenfauna des Russischen Reiches und der angrenzenden Länder. *Annuaire du Musée Zoologique de l'Académie Impériale des Sciences de St. Petersburg*, 16: 161–179.

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

CAPES, E. M. & V. FET. 2001. A redescription of the scorpion genus *Plesiobuthus* Pocock, 1900 (Scorpiones: Buthidae) from Pakistan. *Entomologische Mitteilungen aus dem Zoologischen Museum Hamburg*, 13(164): 295–304.

- FET, V. 1980. Ecology of the scorpions (Arachnida, Scorpiones) of the Southeastern Kara-Kum. *Revue d'Entomologie de l'URSS*, 59(1): 223–228 (in Russian). English translation: *Entomological Review*, 1981, 59(1): 223–228.
- FET, V. 1989. A catalogue of scorpions (Chelicerata: Scorpiones) of the USSR. *Rivista del Museo Civico di Scienze Naturali "Enrico Caffi"*, Bergamo, 13: 73–171.
- FET, V. 1994. Fauna and zoogeography of scorpions (Arachnida: Scorpiones) in Turkmenistan. Pp. 525–534 in: Fet, V. & K. I. Atamuradov (eds.). *Biogeography and Ecology of Turkmenistan. Monographiae Biologicae*, 72. Dordrecht, The Netherlands: Kluwer Academic Publishers.
- FET, V. & K. I. ATAMURADOV (eds.). 1994. *Biogeography and Ecology of Turkmenistan. Monographiae Biologicae* 72. Dordrecht, The Netherlands: Kluwer Academic Publishers.
- FET, V., E. M. CAPES & W. D. SISSOM. 2001. *Polisius*, a new scorpion genus from Iran (Scorpiones: Buthidae). Pp. 183–190 in: Fet, V. & P. A. Selden (eds.) *Scorpions 2001. In Memoriam Gary A. Polis*. Burnham Beeches, Bucks: British Arachnological Society, xi + 404 pp.
- FET, V., B. GANTENBEIN, A. V. GROMOV, G. LOWE & W. R. LOURENÇO. 2003. The first molecular phylogeny of Buthidae (Scorpiones). *Euscorpius*, 4: 1–10.
- FET, V., F. KOVÁŘÍK, B. GANTENBEIN, R. C. KAISER, A. K. STEWART & M. R. GRAHAM. 2018. Revision of *Mesobuthus caucasicus* complex from Central Asia, with descriptions of six new species (Scorpiones: Buthidae). *Euscorpius*, 255: 1–77.
- FET, V. & G. LOWE. 2000. Family Buthidae. Pp. 54–286 in: Fet, V., W. D. Sissom, G. Lowe & M. E. Braunwalder (eds.). *Catalog of the Scorpions of the World (1758–1998)*. New York: New York Entomological Society, v + 690 pp.
- FET, V., G. A. POLIS & W. D. SISSOM. 1998. Life in sand: the scorpion model. *Journal of Arid Environments*, 39: 609–622.
- FET, V., M. E. SOLEGLAD & M. S. BREWER. 2006. Laterobasal aculear serrations (LAS) in scorpion family Vaejovidae (Scorpiones: Chactoidea). *Euscorpius*, 45: 1–19.
- FET, V., M. E. SOLEGLAD & A. V. GROMOV. 2004. The platypus of a scorpion: the genus *Pseudochactas* Gromov, 1998 (Scorpiones: Pseudochactidae). *Euscorpius*, 17: 61–48.
- FET, V., M. E. SOLEGLAD & G. LOWE. 2005. A new trichobothrial character for the high-level systematics of Buthoidea (Scorpiones: Buthidae). *Euscorpius*, 23: 1–40.
- FRANCKE, O. F. 1977. Scorpions of the genus *Diplocentrus* Peters from Oaxaca, Mexico. *The Journal of Arachnology*, 4: 145–200.
- FINNEGAR, S. 1932. Report on the scorpions collected by Mr. Bertram Thomas in Arabia. *Journal of the Linnaean Society (Zoology)*, 38: 91–98.
- GRAHAM, M. R., V. OLÁH-HEMMINGS & V. FET. 2012. Phylogeography of co-distributed dune scorpions identifies the Amu Darya River as a long-standing component of Central Asian biogeography (Scorpiones: Buthidae). *Zoology in the Middle East*, 55: 95–110.
- GROMOV, A. V. 1998. [A new family, genus, and species of scorpion (Arachnida, Scorpiones) from the southern part of Central Asia]. *Zoologicheskii Zhurnal*, 77(9): 1003–1008 (in Russian, English summary). English translation (same title): *Russian Journal of Zoology*, 1998, 2(3): 409–413.
- GROMOV, A. V. 2005. [Rickmers' Scorpion. *Anomalobuthus rickmersi*]. P. 39 in: *Udivitel'nyi mir espozvonochnykh. [A Remarkable World of Invertebrates]*. Almaty. (in Russian).
- GROMOV, A. V. 2006. *Anomalobuthus rickmersi* Kraepelin, 1900. Pp. 44–45 in: Mityaev, I. D. (ed.) *Qazaqstannyň Qyzyl Kitaby. Krasnaya kniga Kazakhstana. Red Data Book of Kazakhstan. Vol. 1. Zhanuarlar. Zhivotnye. Animals. Part 2. Omytrqasyzdar. Bespozvonochnye. [Invertebrates]*. Almaty: Oner, 232 pp. (parallel text in Kazakh and Russian).
- GROMOV, A. V. & V. L. KAZENAS. 2006. *Anomalobuthus rickmersi* Kraepelin, 1900. Pp. 24–25 in: *Almaty Oblysynnyň Qyzyl Kitaby (Zhanuarlar). Krasnaya kniga Almatinskoi oblasti (Zhivotnye). The Red Data Book of Almaty District (Animals)*. Almaty: Oner, 520 pp. (parallel text in Kazakh and Russian).
- GROMOV, A. V. & Y. Y. KOPDYKBAEV. 1994. [The fauna of the scorpions and solpugids (Arachnida: Solpugida) of Kazakhstan]. *Zoologicheskii Zhurnal*, 73(10): 10–16 (in Russian).

- Scorpiones, Solifugae) in Kazakhstan]. *Selevinia*, 2(2): 19–23 (in Russian).
- HARMS, D. & N. DUPÉRRÉ. 2018. An annotated type catalogue of the camel spiders (Arachnida: Solifugae) held in the Zoological Museum Hamburg. *Zootaxa*, 4375(1): 1–58.
- KAMENZ, C. & L. PRENDINI. 2008. An atlas of book lung fine structure in the order Scorpiones (Arachnida). *Bulletin of the American Museum of Natural History*, 316: 1–359.
- KAZENAS, V. L. & B. U. BAISHASHOV. 1999. [The geological history and faunogenesis of Kazakhstan and adjacent territories at the time of evolution of mammals and anthropophilic insects]. *TETHYS Entomological Research*, 1: 5–46 (in Russian).
- KOVARÍK, F. 2009. *Illustrated catalog of scorpions. Part I. Introductory remarks; keys to families and genera; subfamily Scorpioninae with keys to Heterometrus and Pandinus species*. Prague: Clairon Production, 170 pp.
- KOVARÍK, F. & A. A. OJANGUREN AFFILASTRO. 2013. *Illustrated catalog of scorpions. Part II. Bothriuridae; Chaerilidae; Buthidae I. Genera Compsobuthus, Hottentotta, Isometrus, Lychas, and Sassanidotus*. Prague: Clairon Production, 400 pp.
- KRAEPELIN, K. 1899. Zur Systematik der Solifugen. *Mitteilungen aus dem Naturhistorischen Museum in Hamburg*, 16: 197–259.
- KRAEPELIN, K. 1900. Über einige neue Glieder-spinnen. *Abhandlungen aus dem Gebiete der Naturwissenschaften. Herausgegeben vom Natur-wissenschaftlichen Verein in Hamburg*, 16, 1(4): 1–17.
- KRYZHANOVSKY, O. L. 1965. [The composition and origin of the terrestrial fauna of Middle Asia.] Moscow & Leningrad: Nauka, 419 pp. (in Russian; English translation: New Delhi, 1980).
- LORIA, S.F. & L. PRENDINI. 2014. Homology of the lateral eyes of Scorpiones: a six-ocellus model. *PLoS ONE*, 9(12): e112913. <https://doi:10.1371/journal.pone.0112913>.
- LOURENÇO, W. R. 2001. Un nouveau genre de Buthidae, probable vicariant géographique d'*Anomalobuthus* Kraepelin (Chelicerata, Scorpiones). *Biogeographica*, 77(1): 15–20.
- LOURENÇO, W. R. 2005. A new genus and species of scorpion from Afghanistan (Scorpiones, Buthidae). *Bonner Zoologische Beiträge*, 53(2004): 111–114.
- LOWE, G. 2010. The genus *Vachoniolus* (Scorpiones: Buthidae) in Oman. *Euscorpius*, 100: 1–37.
- MITYAEV, I. D., R. V. YASHCHENKO & V. L. KAZENAS. 2005. *Po stranitsam Krasnoj knigi Kazakhstana. Bespozvonochnye* [Through the Pages of the Red Book of Kazakhstan. Invertebrates]. Almaty: OAO Almaty, 116 pp. (parallel text in Kazakh and Russian).
- NAVIDPOUR, S. & G. LOWE. 2009. Revised diagnosis and redescription of *Apistobuthus susanae* (Scorpiones, Buthidae). *Journal of Arachnology*, 37(1): 45–59.
- PAVLOVSKY, E. N. 1916a. [Dzhulek, of Perovsky District, Syr-Darya Province, and some biological observations in its environs]. *Trudy Imperatorskago Petrogradskago Obshchestva Yestestvoispytatelei* [Travaux de la Société impériale des Naturalistes de Petrograd], 47(1): 27–68 (in Russian).
- PAVLOVSKY, E. N. 1916b. Quelques observations biologiques sur les scorpions de la famille des Buthidae. *Comptes rendus de la Société biologique* [Petrograd], 81: 243–246.
- PAVLOVSKY, E. N. 1934. [Some data on the poisonous animals of Turkmenia]. Pp. 191–204 in: *Trudy Kara-Kalinskoi i Kzyl-Atrekskoi parazitologicheskoi ekspeditsii 1931 goda i materialy po faune Turkmenii* [Transactions of the 1931 Kara-Kala and Kzyl-Atrek Parasitological Expedition, with contributions to the fauna of Turkmenia]. Leningrad: Ed. Acad. Sci. USSR and Narkomzdrav of Turkmenia (in Russian).
- RICKMER-RICKMERS, W. 1899. Travels in Bokhara. *Geographical Journal*, 14: 596–620.
- RICKMER-RICKMERS, W. 1913. *The Duab of Turkestan, a Physiographic Sketch and Account of Some Travels*. Cambridge, UK: Cambridge University Press, 546 pp.
- SISSOM, W. D. 1990. Systematics, biogeography and paleontology. Pp. 64–160 in: Polis, G. A. (ed.). *Biology of Scorpions*. Stanford, California: Stanford University Press, 587 pp.

- SOLEGLAD, M. E. & V. FET. 2003a. The scorpion sternum: structure and phylogeny (Scorpiones: Orthosterni). *Euscorpius*, 5: 1–34.
- SOLEGLAD, M. E. & V. FET. 2003b. High-level systematics and phylogeny of the extant scorpions (Scorpiones: Orthosterni). *Euscorpius*, 11: 1–175.
- SOLOVYOVA, E. N., E. N. DUNAYEV, R. A. NAZAROV, M. RADJABIZADEH & N.A. POYARKOV, JR. 2018. Molecular and morphological differentiation of Secret Toad-headed Agama, *Phrynocephalus mystaceus*, with the description of a new subspecies from Iran (Reptilia, Agamidae). *ZooKeys*, 748: 97–129. <https://doi.org/10.3897/zookeys.748.20507>
- STAHNKE, H. L. 1971. Scorpion nomenclature and mensuration. *Entomological News*, 81: 297–316.
- STAHNKE, H. L. 1972. A key to the genera of Buthidae (Scorpionida). *Entomological News*, 83(5): 121–133.
- TERUEL, R., F. KOVÁŘÍK, S. NAVIDPOUR & V. FET. 2014. The first record of the genus *Anomalobuthus* Kraepelin, 1900 from Iran, with description of a new species (Scorpiones: Buthidae). *Euscorpius*, 192: 1–10.
- VACHON, M. 1963. De l'utilité, en systématique, d'une nomenclature des dents de chélicères chez les scorpions. *Bulletin du Muséum National d'Histoire Naturelle*, Paris, (2), 35 (2): 161–166.
- VACHON, M. 1974. Études des caractères utilisés pour classer les familles et les genres des scorpions (Arachnides). 1. La trichobothriatxie en arachnologie. Sigles trichobothriaux et types de trichobothriatxie chez les Scorpions. *Bulletin du Muséum national d'Histoire naturelle*, 3e série, 140 (Zoologie, 104): 857–958.
- VACHON, M. 1980. Scorpions du Dhofar. The scientific results of the Oman flora and fauna survey 1977 (Dhofar). Scorpions du Dhofar. *Journal of the Oman Studies, Special Report*, 2: 251–263.
- VOLSCHENK, E. S., C. I. MATTONI & L. PRENDINI. 2008. Comparative anatomy of the mesosomal organs of scorpions (Chelicerata, Scorpiones), with implications for the phylogeny of the order. *Zoological Journal of the Linnean Society*, 154: 651–675.
- WARBURG, M. R. 2013. The locomotory rhythmic activity in scorpions: with a review. *Arthropods*, 2(3): 95–104.
- WEIDNER, H. 1959. Die Entomologischen Sammlungen des Zoologischen Staatsinstituts und Zoologischen Museums Hamburg, I. Teil, Pararthropoda und Chelicera I. *Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut*, 57: 89–142.
- WERNER, F. 1934. Scorpiones, Pedipalpi. Pp. 1–316 in: Bronns, H. G. (ed.). *Klassen und Ordnungen des Tierreichs*. Akademische Verlag Gesellschaft, Leipzig, 5, IV, 8, Lief. 1–2 (Scorpiones), 316 pp.