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Phylogeographic structure, distribution and morphological variability of *Mesobuthus bogdoensis* (Birula, 1896) (Scorpiones: Buthidae)

Филогеографическая структура, распространение и морфологическая изменчивость *Mesobuthus bogdoensis* (Birula, 1896) (Scorpiones: Buthidae)

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KEY WORDS: arachnids, scorpions, relic, genetics, COI mtDNA, morphometry, principal component analysis, median-joining network.

КЛЮЧЕВЫЕ СЛОВА: арахниды, скорпионы, реликт, генетика, COI мтДНК, морфометрия, анализ главных компонентов, медианная сеть.

ABSTRACT. Based on a study of a number of populations of *Mesobuthus bogdoensis*, the results of studying the phylogeographic structure and morphological variability are presented, and an analysis of the distribution of this species is carried out based on an analysis of the literature and our own data. An expanded diagnosis and morphological description for *M. bogdoensis* is presented. It has been proven that the indication in a number of literary sources of scorpions for the Guberlinsky Mountains (Orenburg Region, Russia) is a label error. In populations of *M. bogdoensis* from the right bank of the Volga River, a unique morphological character was identified — anal lobe divided in three parts; it is the first species of this genus to have two or three anal lobes; for other species the following combinations are known — two, three and three or four anal lobes. Principal component analysis (PCA) results based on comparative measurements of proportions indicate that the contribution of differences between different populations is less pronounced than the contribution of differences between males and females.

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РЕЗЮМЕ. На основе изучения ряда популяций *Mesobuthus bogdoensis* представлены результаты изучения филогеографической структуры и морфологической изменчивости, а также, проведен анализ распространения этого вида исходя из анализа литературных и собственных данных. Представлен расширенный диагноз и морфологическое описание для *M. bogdoensis*. Доказано, что указание в ряде литературных источников скорпионов для Губерлинских гор (Оренбургская область, Россия) это ошибка этикетки. У популяций *M. bogdoensis* с правого берега реки Волга выявлен уникальный морфологический признак — анальная лопасть разделена на три части; это первый вид этого рода, который имеет две или три анальные лопасти; для других видов известны следующие комбинации — две, три и три или четыре анальные лопасти. Результаты анализа главных компонентов (PCA) основанные на сравнительных измерениях пропорций показывают, что вклад различий между разными популяциями менее выражен, чем вклад различий между самцами и самками.

Introduction

Mesobuthus bogdoensis (Birula, 1896) (see Fig. 1) is one of 30 valid species of the Asian genus *Mesobuthus* Vachon, 1950 [Barahoei, 2022; Kovařík *et al*., 2022], which lives in the Precaspian lowland in Russia and Kazakhstan [Kovařík *et al*., 2022], and individual populations of this relict species represent the northernmost

Fig. 1. *Mesobuthus bogdoensis* (♀, *in situ*), near Shcherbatovka Vill., Volgograd Region, Russia (photo by Ivan Pristrem).
Рис. 1. *Mesobuthus bogdoensis* (♀, *in situ*), окр. с. Щербатовка, Волгоградская область, Россия (фото Иван Пристрем).

scorpion record in the Palearctic Realm and this could be also the northernmost boundary of the order Scorpiones worldwide [Poverennyi *et al*., 2022]. This species was first mentioned by the famous traveler Peter Simon Pallas [1776, 1799] without species name for three localities (see Suppl. Table 2). The species was first formaslly described by the famous arachnologist Alexei Birula [1896] as *Buthus eupeus* forma δ *bogdoënsis* Birula, 1896 from the Maloe Bogdo Hill (now the territory of Kazakhstan). Subsequently, Birula mentions (description not published) [Birula, 1917], and then describes [Birula, 1925] near Selitrennoe (now in Astrakhan Region, Russia) another subspecies, *Buthus eupeus volgensis* Birula, 1925. Vachon [1959] transferred these two subspecies from the genus *Buthus* Leach, 1815 to a new genus *Mesobuthus* [Vachon, 1950]. Until Kovařík [2019] elevated *M. bogdoensis* to species status, it was mentioned under various names from various localities (see Suppl. Table 2 for bibliography, species names and localities for details). The recent revision of the genus *Mesobuthus* [Kovařík *et al.*, 2022] provides a brief diagnosis for *M. bogdoensis* based on the study of syntypes (highlighted, ♂ lectotype and ♀ paralectotype); *M. e. volgensis*, based on the study of syntypes of this subspecies, is synonymized with *M. bogdoensis*. At the same time, Kovařík *et al*. [2022] provide phylogenetic analysis based on COI mtDNA for the genus *Mesobuthus* and the position of *M. bogdoensis* in the system of this genus, as well as an estimate of the time of divergence between species and groups of species of this genus.

From all of the above, we can conclude that since the original description was incomplete from a morphological point of view [Birula, 1896, 1925], only a brief diagnosis was given for this species based on a re-examination of the type series and its iconography [Kovařík *et al*., 2022], without actual study of morphological variability between individual populations. Also, there was no detailed analysis of the geographical distribution for this species in individual localities based on an in-depth analysis of scattered literature data and the study of the phylogeographic structure of various populations. Thus, we set ourselves the task of studying the phylogeographic structure, distribution and morphological variability of *M. bogdoensis* (including providing an expanded diagnosis and morphological description in accordance with generally accepted modern standards for order Scorpiones).

Material and methods

Sampling and deposited. Study of the phylogeographic structure and morphological variability of populations of the scorpion *Mesobuthus bogdoensis* was based on the material collected by the first author (private collection of Nikita M. Poverennyi, abbreviated as NMP), and also used material from the collection at the Zoological Institute of the Russian Academy of Sciences, Saint Petersburg, Russia (ZISP).

Molecular and phylogenetic study. Total DNA was extracted from metasoma *in vivo* in 96% ethanol. The total cellular DNA was isolated using an QIAamp UCP DNA Micro Kit (Germany). For an analysis of genetic variation, a fragment of the COI mtDNA locus was used. The study was conducted utilizing a full-length mtDNA fragment obtained through amplification with HCO2198 and LCO1490 primers [Folmer *et al*., 1994].

The homological sites of the sequences were tested for errors in FinchTV 1.4.0 [Rothgänger *et al*., 2006] and aligned using MEGA7 software [Kumar *et al*., 2016]. Haplotype networks were built using the Median Joining algorithm [Bandelt *et al*.,

Table 1. A list of the sampling sites and accession numbers of the COI mtDNA gene sequences for *Mesobuthus bogdoensis* included in this study. References are given for the sequences obtained from GenBank (NCBI).
Таблица 1. Список мест отбора проб и номеров доступа последовательностей генов мтДНК COI для *Mesobuthus bogdoensis*, включенных в это исследование. Ссылки даны на последовательности из GenBank (NCBI).

Russia, Saratov Region, Krasnoarmeisky Distr., near Nizhnyaya Bannovka (50°40′49.0″N 45°38′49.0″E)	PP439977 PP439978	This study
	OM905078	Kovařík *et al*. [2022]
Russia, Saratov Region, Krasnoarmeisky Distr., Danilovsky Ravine (50°34′47.0″N 45°41′26.0″E)	OM905079	Kovařík *et al*. [2022]
	OM905080	
Russia, Volgograd Region, Kamyshinsky Distr., near Shcherbatovka (50°29′56.0″N 45°41′03.0″E)	OM905081	Kovařík *et al*. [2022]
Russia, Astrakhan Region, Akhtubinsky Distr., Bogdo-Baskunchak Reserve (48°07′42.6″N 46°49′52.3″E)	PP439976	This study
	OM905077	Kovařík *et a*l. [2022]
Russia, Orenburg Region, Kuvandyksky Distr., near Aytuar (51°06′25.9″N 57°39′38.2″E)	PP439979	This study
	OM905082	Poverennyi *et al*. [2022]
Western Kazakhstan (without specifying the exact locality)	MT371782	Zhang *et al.* [2020]

1999] with help of the PopART 1.7 software [Leigh, Bryant, 2015]. The pairwise *p*-distances were calculated in MEGA7 with 1000 bootstrap replicates.

In addition to four COI sequences obtained in this study, seven COI sequences were added from the GenBank (published in Zhang *et al.* [2020], Kovařík *et al.* [2022] and Poverennyi *et al.* [2022]). A total set of eleven sequences of COI fragments with a length of 416 bp was used from six localities was examined (see Table 1).

Morphological studies. Nomenclature and measurements follow Stahnke [1971], Kovařík [2009], except for chelicerae [Vachon, 1963] and trichobothriotaxy [Vachon, 1974].

To study the morphometric variability of *Mesobuthus*, 14 specimens from four localities were used (four specimens indicated in this study for the locality "not Guberlinsky Mountains", are not related to *M. bogdoensis*), as well as measurement data for the lectotype and paralectotype of this species [Kovařík *et al*., 2022].

The photographs of habitus and morphological structures were taken with a Leica M165C stereo microscope on a Leica MC170 HD (12MPs) digital camera using the extended focus technology; the final image was compiled from multiple layers using Helicon Focus 7.7.4. Morphological drawings were processed using Adobe Photoshop CS6 (ver. 13.0.1.3).

The distribution map was created using Google Earth Pro (ver. 7.3.4.8248) and Adobe Photoshop CS6 (ver. 13.0.1.3).

The ratios of comparative measurements were statistically processed using MS Excel. The comparison of multiple samples was performed using the Kruskal-Wallis followed by the Dunn's post hoc test with Bonferroni correction (*rstatix* and *tidyverse* packages in R version 4.3.1). Principal component analysis (PCA) was performed using the *ggfortify* package.

Results

Genetic study (COI barcoding)

The results of phylogenetic analysis of studied populations of *Mesobuthus bogdoensis* are presented as the median-joining network of COI mtDNA haplotypes (Fig. 2). According to estimates of genetic *p*-distances (Suppl. Table 1), common haplotypes were identified for populations from the Bogdo-Baskunchak Reserve together with Danilovsky Ravine, as well as for near Nizhnyaya Bannovka together with near Shcherbatovka. Between these two groups of Lower Volga populations, *p*-distance is 0.005±0.003 (2 mutations of 416 bp). However, one of the haplotypes PP439977 from near Nizhnyaya Bannovka differs significantly from the Bogdo-Baskunchak Reserve/Danilovsky Ravine haplotype (0.022±0.007; 11 mutations on 416 bp) and the haplotype near Nizhnyaya Bannovka/near Shcherbatovka (0.017±0.006; 8 mutations on 416 bp). The differences between the populations from near Aytuar and Western Kazakhstan are 0.002±0.002 (1 mutation of 416 bp). At the same time, the differences near Aytuar from the bulk of the Lower Volga populations range from 0.012±0.005 (7 mutations of 416 bp) to 0.017±0.007 (10 mutations of 416 bp); and the differences from the unique haplotype from near Nizhnyaya Bannovka are 0.020±0.007 (10 mutations of 416 bp).

Distribution of *Mesobuthus bogdoensis*

Based on the analysis of literary data and author's collections, the distribution of *Mesobuthus bogdoensis* was analyzed. Over the entire period of the study, this species was mentioned under many different names. The results obtained are presented in Fig. 3 and in Suppl. Table 2. Thus, *M. bogdoensis* lives on both banks of the lower reaches of the Volga River (localities No. 1–15, see Fig. 3 and Suppl. Table 2), on the right bank of the Ural River in the lower reaches (localities No. 16– 18, see Fig. 3 and Suppl. Table 2) and on the left bank of the Urals in the upper reaches (localities No. 19–21, see Fig. 3 and Suppl. Table 2).

Regarding the indication of the location of *Mesobuthus bogdoensis* (listed as *M. eupeus thersites* (C.L. Koch, 1839)) on the right bank of the Ural River in the Guberlinsky Mountains, Orenburg Region, Russia (ca. 51°12′N 58°05′E) [Birula, 1904; Fet, 1989], this is a locality error. The morphological analysis showed that this is a different species of the genus and should be considered as *Mesobuthus* sp. from "not Guberlinsky Mountains" (for more details see the Morphological part and Discussion sections).

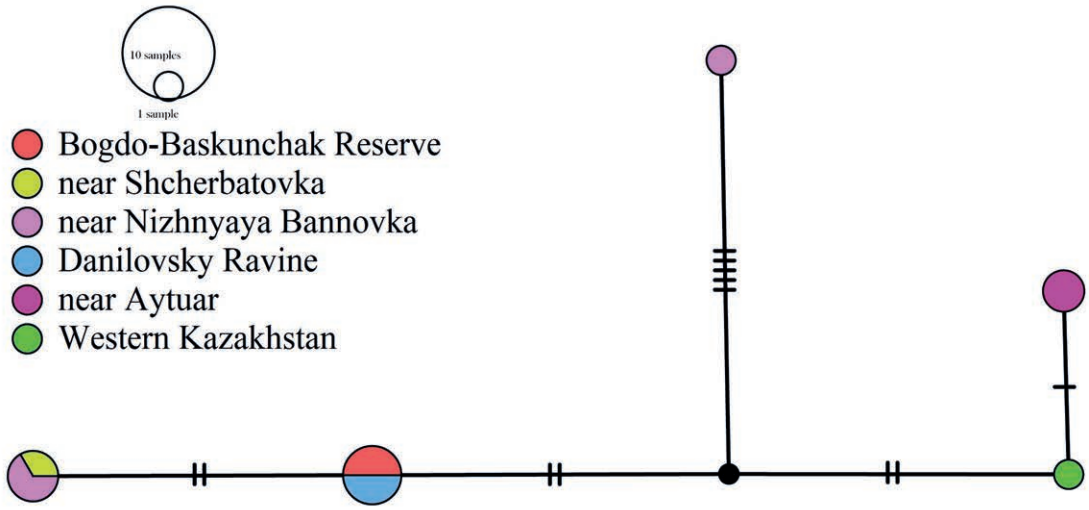

Fig. 2. Median-joining network of COI mtDNA haplotypes for study populations of *Mesobuthus bogdoensis*.
Рис. 2. Медианная сеть гаплотипов COI мтДНК для изученных популяций *Mesobuthus bogdoensis*.

Fig. 3. Distribution map of *Mesobuthus bogdoensis* based on analysis of literary and author's data. Numbers localities are designated in Suppl. Table 2.

Рис. 3. Карта распространения *Mesobuthus bogdoensis* на основе анализа литературных и авторских данных. Номера локалитетов обозначены в Дополнительной таблице 2.

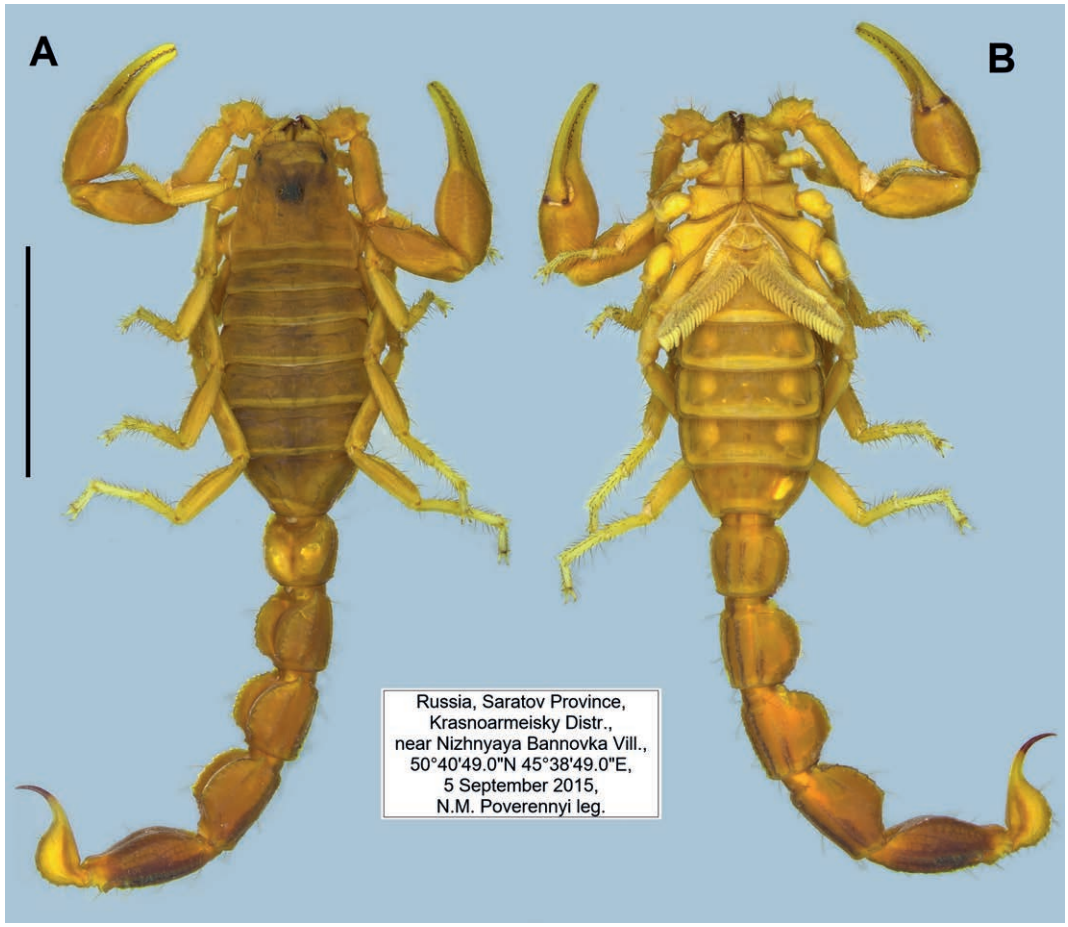

Fig. 4. Habitus of *Mesobuthus bogdoensis* (♂) from near Nizhnyaya Bannovka Vill., Saratov Region, Russia: A — dorsal view; B — ventral view. Scale bar: 10.0 mm.

Рис. 4. Общий вид *Mesobuthus bogdoensis* (♂) из окр. с. Нижняя Банновка, Саратовская область, Россия: A — вид сверху; B — вид снизу. Масштаб: 10,0 мм.

Finding scorpions listed as *Mesobuthus eupeus* on the left bank of the lower reaches of the Ural River [Fet, 1989; Gromov, 2001] requires a more detailed study. According to the results of the obtained molecular genetic data [Poverennyi, Anikin, 2023], species of the genus *Olivierus* Farzanpay, 1987 live in this region (for more details see the Discussion section).

Also, the exact locality for *Mesobuthus bogdoensis* indicated as *M. eupeus* by molecular genetic data for Kazakhstan remains unknown [Zhang *et al.*, 2020]. According to Dr Cheng-Min Shi (pers. comm.) this material was received from Dr A.V. Gromov with the label "Eop-46, W Kazakhstan, salty clay, 2012/5/14", and it is not possible to clarify a more precise locality.

Morphological part

Based on a detailed study of the morphology of *Mesobuthus bogdoensis* from several populations, an expanded diagnosis of this species is given (addition to Kovařík *et al.*, [2022]) and for the first time since the original description of this species, a detailed morphological description is provided. Based on the results of a morphological study of scorpions (a diagnosis and morphological description are given) from the Guberlinsky Mountains, Orenburg Region, Russia [Birula, 1904; Fet, 1989], it was shown that this is a different species of the genus, and this material should be considered as *Mesobuthus* sp. from "not Guberlinsky Mountains" (further as *Mesobuthus* sp.), due to a data error in the label (locality error).

Mesobuthus bogdoensis (Birula, 1896)
Figs 1, 4–9.

MATERIAL EXAMINED: 2 ♂♂, 2 ♀♀ (NMP), Russia, Saratov Region, Krasnoarmeisky Distr., near Nizhnyaya Bannovka Vill., 50°40′49.0″N 45°38′49.0″E, 5 September 2015, N.M. Poverennyi leg.; 3 ♂♂, 1 ♀ (NMP), Russia, Volgograd Region, Kamyshinsky Distr., near Shcherbatovka Vill., 50°29′56.0″N 45°41′03.0″E, 4 June 2017, N.M. Poverennyi leg.; 1 ♀ (NMP), Russia, Astrakhan Region, Akhtubinsky Distr., Bogdo-Baskunchak Reserve, 48°07′42.6″N 46°49′52.3″E, 9 September 2020, N.M. Poverennyi leg.; 3 ♂♂, 2 ♀♀ (NMP), Russia, Orenburg Region, Kuvandyksky Distr., near Aytuar Vill., 51°06′25.9″N 57°39′38.2″E, 13 August 2021, N.M. Poverennyi leg.

DIAGNOSIS. Total length of adult male 32.2–42.0 mm, female 31.0–45.5 mm. Trichobothrium *db* on the fixed finger of the pedipalp in males is located between trichobothria *est* and *esb*, near *est*, in females *db* is on the same level as *est*. Male has the fingers of chela proximally more twisted than female. Pedipalp chela length/width ratio 3.12–3.42 in male and 3.27–3.96 in female. Pectinal teeth number 21–27 in males, 17–25 in females.

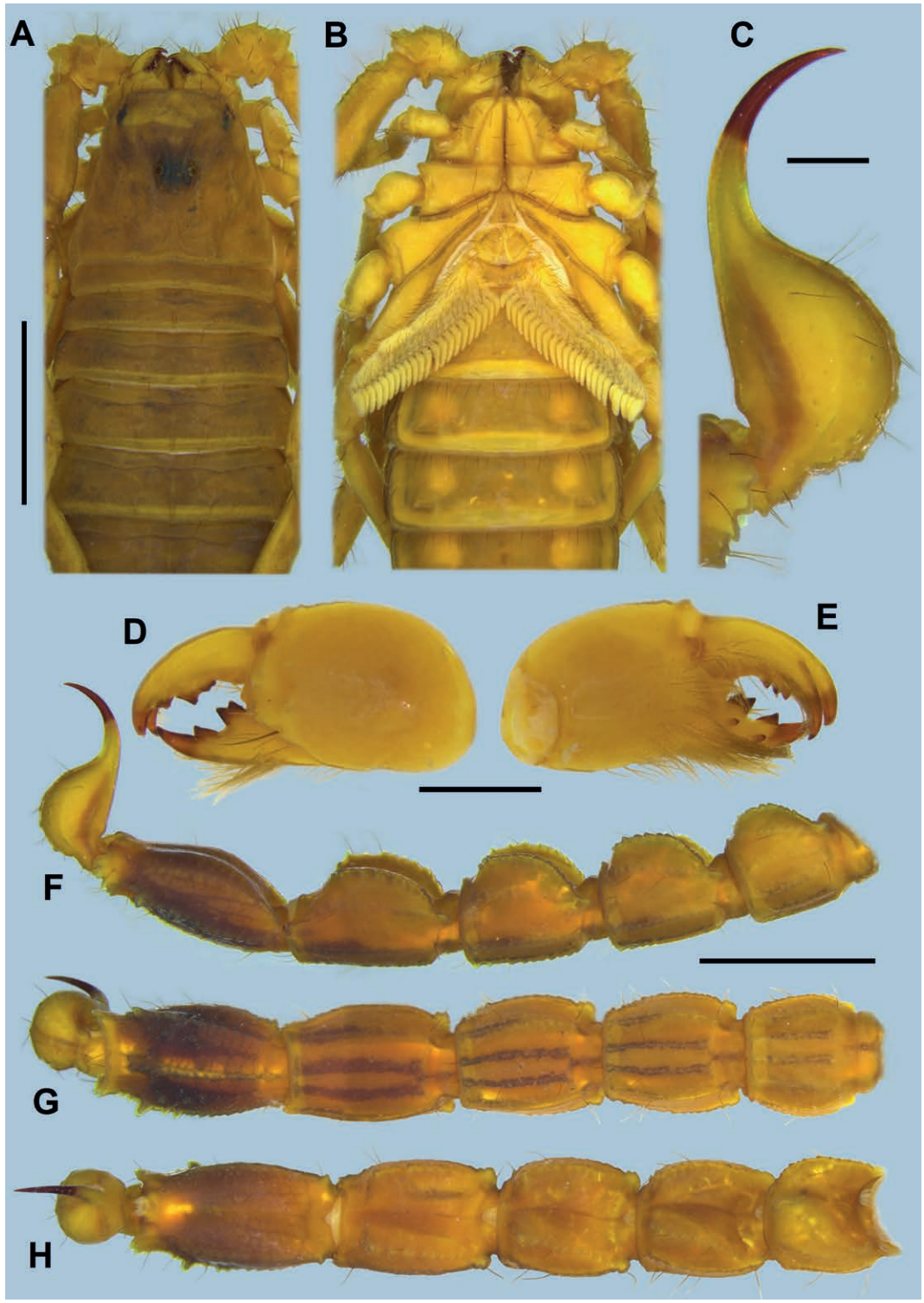

Fig. 5. *Mesobuthus bogdoensis* (♂) from near Nizhnyaya Bannovka Vill., Saratov Region, Russia: A — chelicerae, carapace and tergites I–V, dorsal view; B — chelicerae, coxae, sternopectinal region and sternites III–V, ventral view; C — telson, lateral view; D, E — right chelicera, dorsal (D) and ventral (E) views; F–H — metasoma and telson, lateral (F), dorsal (G) and ventral (H) views. Scale bars: 5.0 mm (A, B, F–H), 1.0 mm (C–E).

Рис. 5. *Mesobuthus bogdoensis* (♂) из окр. с. Нижняя Банновка, Саратовская область, Россия: A — хелицеры, карапакс и тергиты I–V, вид сверху; B — хелицеры, тазики, стерно-пектинальная область и стерниты III–V, вид снизу; C — тельсон, вид сбоку; D, E — правая хелицера, вид сверху (D) и снизу (E); F–H — метасома и тельсон, вид сбоку (F), сверху (G) и снизу (H). Масштаб: 5,0 мм (A, B, F–H), 1,0 мм (C–E).

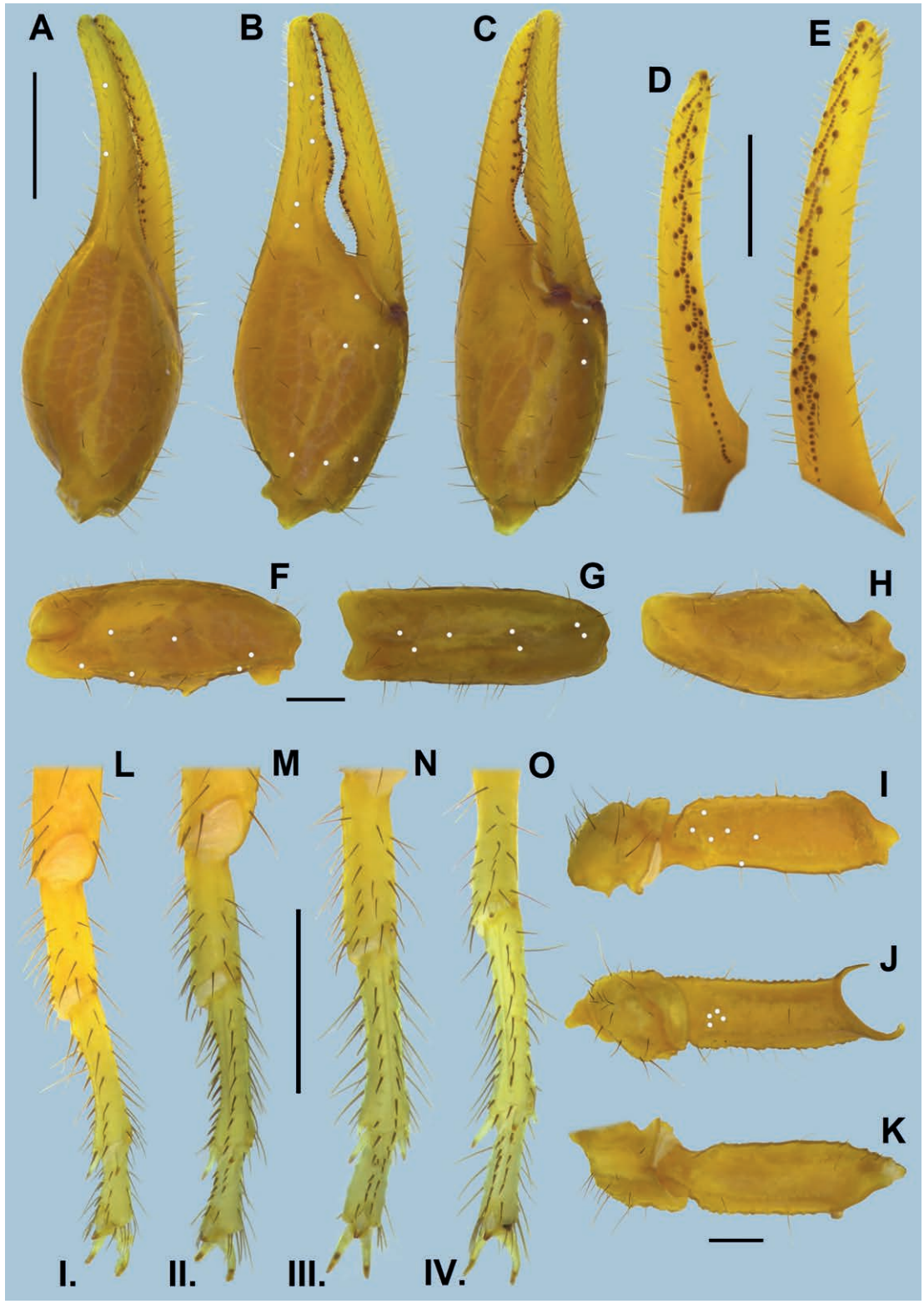

Fig. 6. *Mesobuthus bogdoensis* (♂) from near Nizhnyaya Bannovka Vill., Saratov Region, Russia: A–C — right chela, dorsal (A), external (B) and ventral (C) views; D — fixed chelal fingers, ventral view; E — movable chelal fingers, dorsal view; F–H — right patella, dorsal (F), external (G) and ventral (H) views; I–K — right femur and trochanter, dorsal (I), internal (J) and ventral (K) views; L–O — left legs I–IV, retrolateral aspect. Scale bars: 3.0 mm (A–C), 1.0 mm (D–K), 2.0 mm (L–O).

Рис. 6. *Mesobuthus bogdoensis* (♂) из окр. с. Нижняя Банновка, Саратовская область, Россия: A–C — правая хела, вид сверху (A), спереди (B) и снизу (C); D — фиксированный хелальный палец, вид снизу; E — подвижный хелальный палец, вид сверху; F–H — правое колено, вид сверху (F), спереди (G) и снизу (H); I–K — правые бедро и вертлуг, вид сверху (I), внутренний (J) и снизу (K); L–O — левые ноги I–IV, задне-боковой аспект. Масштаб: 3,0 мм (A–C), 1,0 мм (D–K), 2,0 мм (L–O).

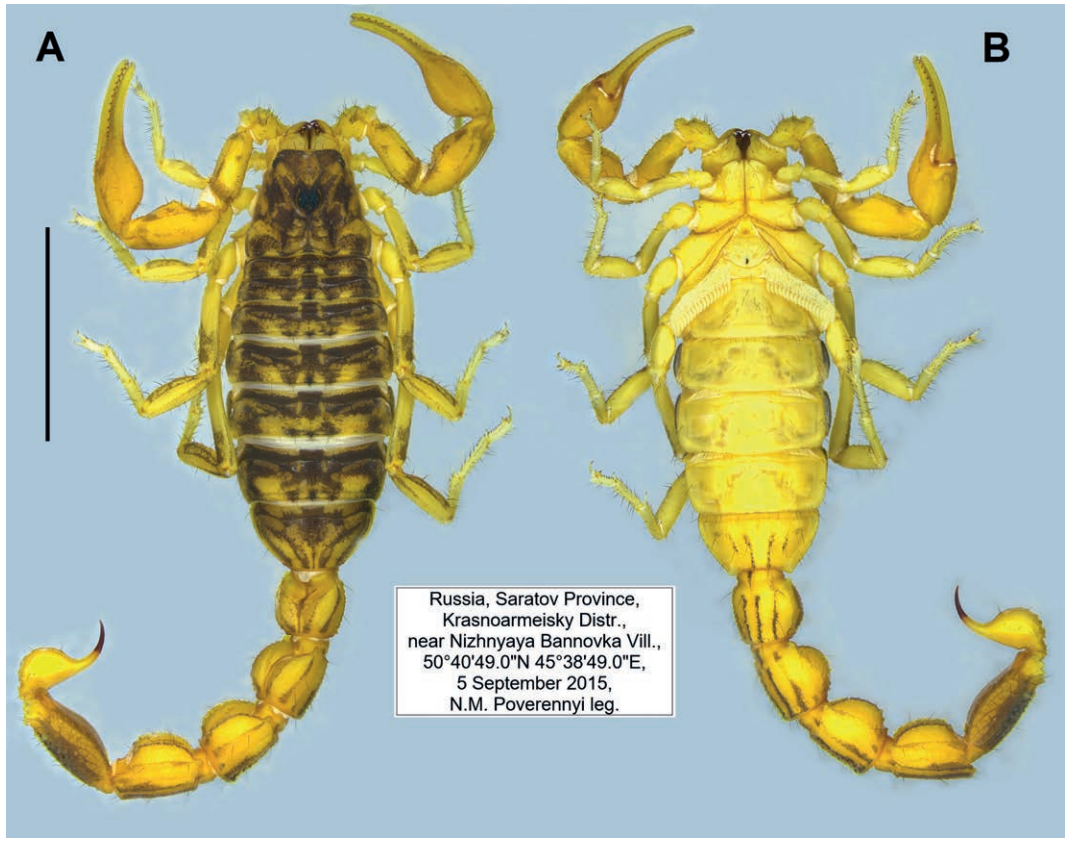

Fig. 7. Habitus of *Mesobuthus bogdoensis* (♀) from near Nizhnyaya Bannovka Vill., Saratov Region, Russia: A — dorsal view; B — ventral view. Scale bar: 10.0 mm.

Рис. 7. Общий вид *Mesobuthus bogdoensis* (♀) из окр. с. Нижняя Банновка, Саратовская область, Россия: A — вид сверху; B — вид снизу. Масштаб: 10,0 мм.

Chelicerae yellow, without reticulation. Denticle *m* of movable finger of chelicerae triangular, large. Pedipalps and metasoma very sparsely hirsute. Carapace, metasoma, telson, pedipalps and legs yellow to reddish brown with pigmentation reduced or black pigmentation. Femur of pedipalp with 4–5 granulate carinae. Patella with 8 granulated or smooth carinae. Chela lacks carinae. Movable fingers of pedipalps with 10–12 cutting rows of denticles and 5 terminal denticles. Central lateral and posterior lateral carinae of carapace not joined to form a continuous linear series of granules to posterior margin. Sternite VII with 4 well marked smooth carinae. Metasomal segment I with 10 carinae; second to fourth with 8 carinae, other two carinae are indicated by incomplete row of denticles on metasomal segments II and III; segment IV with 8 carinae; segment V with 5 carinae. Metasoma IV with lateromedian carina smooth, all other carinae granulated. Length to depth ratio of metasoma III 1.21–1.38 in male, 1.01–1.39 in female, metasoma IV 1.63–2.10 in male, 1.44–1.63 in female. Telotarsus III ventral setation represented by short and strong spiniform setae. Tarsi not densely hirsute, adults with 7–9 retroinferior macrosetae on basitarsus III. Pedal spurs of legs with solitary setae only. Telson elongated. Anal lobe divided in two or three parts.

DESCRIPTION. Total length of adult male 32.2–42.0 mm, female 31.0–45.5 mm. Trichobothrium *db* on the fixed finger of the pedipalp in males is located between trichobothria *est* and *esb*, near *est* (Fig. 6A, B), in females *db* is on the same level as *est* (Fig. 9A, B). Male has the fingers of chela proximally more twisted than female. Female has longer and very slightly narrower chela of pedipalps. For measurements, see Suppl. Table 3.

Coloration (Figs 1, 4, 7) is quite variable. Chelicerae yellow, without reticulation, the tips of teeth on cheliceral fingers are reddish brown. Carapace and tergites yellow to reddish brown with pigmentation reduced or black pigmentation. Sternites metasoma, telson, pedipalps and legs yellow to reddish brown with pigmentation reduced or no pigmentation.

Mesosoma and carapace (Figs 5A, B, 8A, B). Central lateral and posterior lateral carinae of carapace not joined to form a continuous linear series of granules to posterior margin; anterior median carinae are weakly expressed, almost do not reach the anterior margin of carapace. Tergites I–VI with three carinae, are sparsely granulated in males and are granulated, with some intercarinal granules small and others larger and rounded in females. Tergite VII is pentacarinate. Pectinal tooth count is 21–27 in males, 17–25 in females. Pectinal marginal tips extend to about one-fourth of the sternite V in males and one-fourth of the sternite IV in females. Pectines have three marginal lamellae and six to nine middle lamellae. Lamellae with numerous long setae, each fulcrum with three to five dark setae. All sternites smooth, sparsely hirsute. Sternite VII with four well marked, usually smooth carinae. Other sternites have two furrows.

Chelicerae (Figs 5D, E, 8D, E) with typical buthid dentition. Denticle *m* of movable finger triangular, large.

Pedipalps (Figs 6A–K, 9A–K). Pedipalps very sparsely hirsute and smooth, only femur is finely granulated dorsally. Femur has four to five granulated carinae, the middle carina on internal surface consists of strong irregular granules. Patella with 8 usually granulated or smooth carinae. Chela without carinae. Movable fingers of pedipalps have 10–12 cutting rows

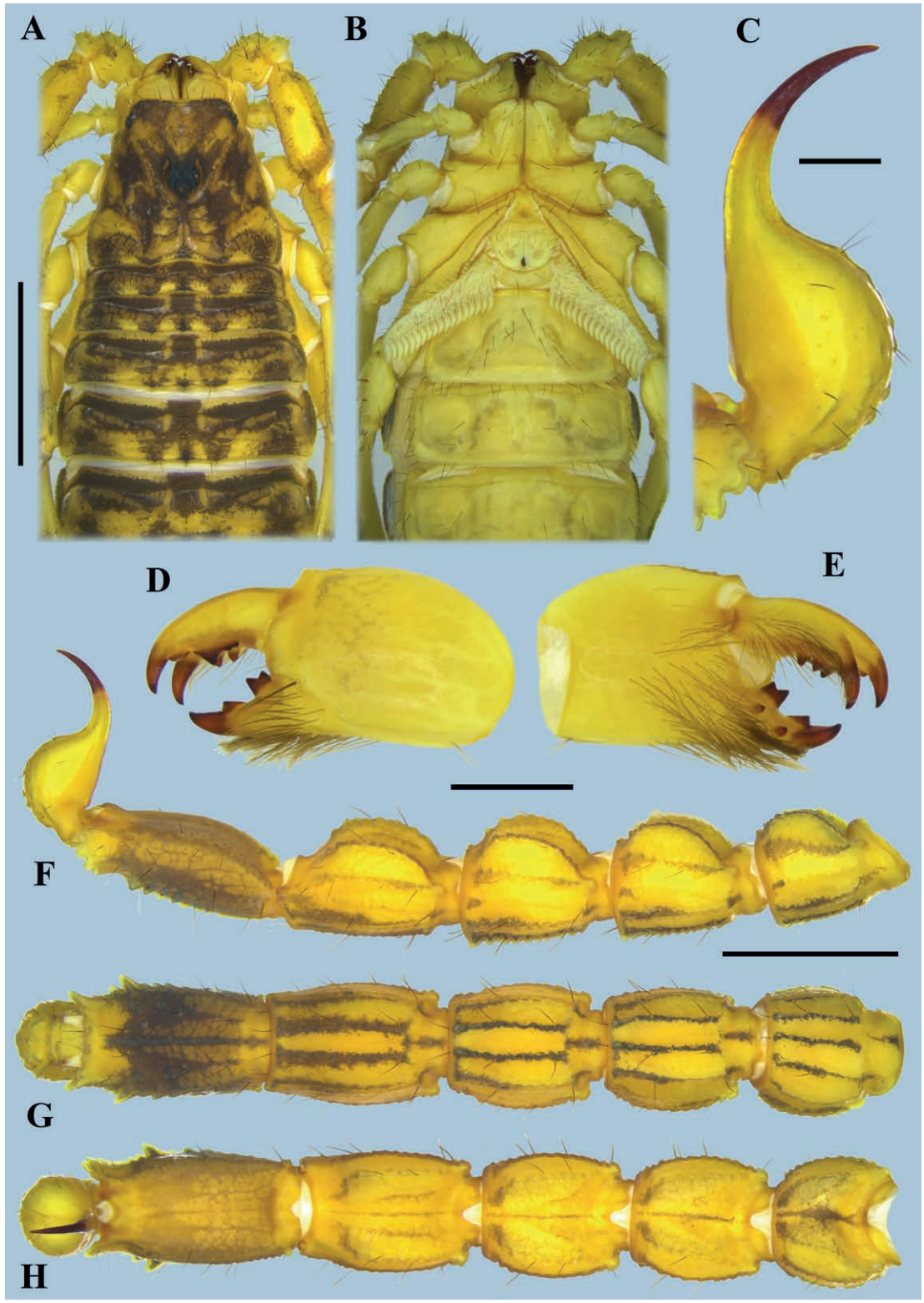

Fig. 8. *Mesobuthus bogdoensis* (♀) from near Nizhnyaya Bannovka Vill., Saratov Region, Russia: A — chelicerae, carapace and tergites I–V, dorsal view; B — chelicerae, coxae, sternopectinal region and sternites III–V, ventral view; C — telson, lateral view; D, E — right chelicera, dorsal (D) and ventral (E) views; F–H — metasoma and telson, lateral (F), dorsal (G) and ventral (H) views. Scale bars: 5.0 mm (A, B, F–H), 1.0 mm (C–E).

Рис. 8. *Mesobuthus bogdoensis* (♀) из окр. с. Нижняя Банновка, Саратовская область, Россия: A — хелицеры, карапакс и тергиты I–V, вид сверху; B — хелицеры, тазики, стерно-пектинальная область и стерниты III–V, вид снизу; C — тельсон, вид сбоку; D, E — правая хелицера, вид сверху (D) и снизу (E); F–H — метасома и тельсон, вид сбоку (F), сверху (G) и снизу (H). Масштаб: 5,0 мм (A, B, F–H), 1,0 мм (C–E).

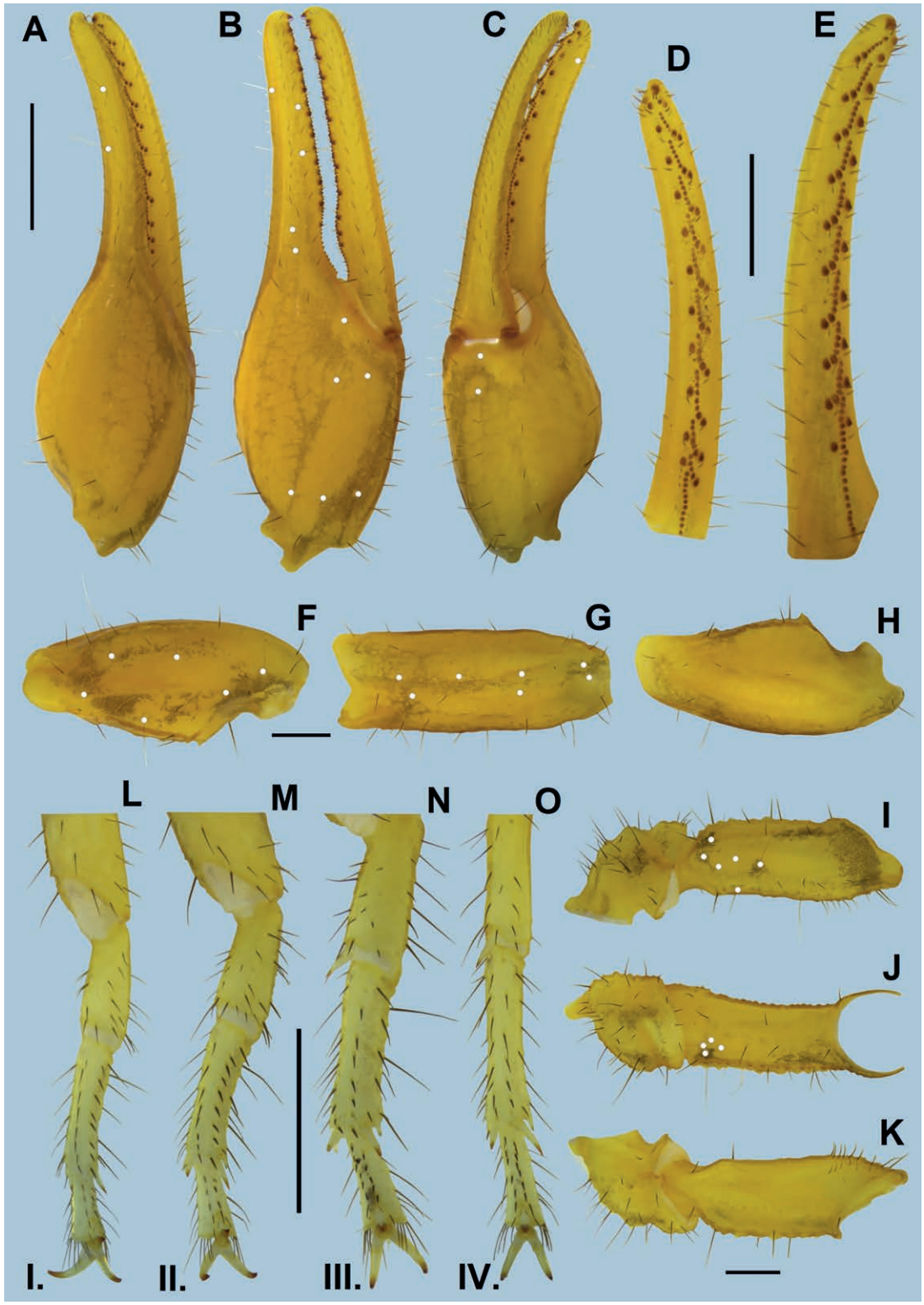

Fig. 9. *Mesobuthus bogdoensis* (♀) from near Nizhnyaya Bannovka Vill., Saratov Region, Russia: A–C — right chela, dorsal (A), external (B) and ventral (C) views; D — fixed chelal fingers, ventral view; E — movable chelal fingers, dorsal view; F–H — right patella, dorsal (F), external (G) and ventral (H) views; I–K — right femur and trochanter, dorsal (I), internal (J) and ventral (K) views; L–O — left legs I–IV, retrolateral aspect. Scale bars: 3.0 mm (A–C), 1.0 mm (D–K), 2.0 mm (L–O).

Рис. 9. *Mesobuthus bogdoensis* (♀) из окр. с. Нижняя Банновка, Саратовская область, Россия: A–C — правая хела, вид сверху (A), спереди (B) и снизу (C); D — фиксированный хелальный палец, вид снизу; E — подвижный хелальный палец, вид сверху; F–H — правое колено, вид сверху (F), спереди (G) и снизу (H); I–K — правые бедро и вертлуг, вид сверху (I), внутренний (J) и снизу (K); L–O — левые ноги I–IV, задне-боковой аспект. Масштаб: 3,0 мм(A–C), 1,0 мм (D–K), 2,0 мм (L–O).

Fig. 10. Habitus of *Mesobuthus* sp. (♀) from Guberlinsky Mountains, Orenburg Region, Russia (locality error): A — dorsal view; B — ventral view. Scale bar: 10.0 mm.

Рис. 10. Общий вид *Mesobuthus* sp. (♀) из Губерлинских гор, Оренбургская область, Россия (ошибка локалитета): A — вид сверху; B — вид снизу. Масштаб: 10,0 мм.

of denticles, each with external and internal denticles present, and five terminal denticles.

Legs (Figs 6L–O, 9L–O). Telotarsus III ventral setation represented by short and strong spiniform setae. Tarsi not densely hirsute, adults with 7–9 retroinferior macrosetae on basitarsus III. Femur and patella with carinae well developed. Tibial spurs present and moderate to strong on legs III and IV and absent on the other legs. Pedal spurs of legs with solitary setae only.

Metasoma and telson (Figs 5C, F–H, 8C, F–H). All metasomal segments are rather moderately hirsute with long setae. Metasomal segment I with 10 carinae; second to fourth with 8 carinae, other two carinae are indicated by incomplete row of denticles on metasomal segments II and III; segment IV with 8 carinae with lateromedian carina smooth, all other carinae granulated; segment V with 5 carinae. Intercarinal surfaces on metasoma smooth. Ventrolateral carinae of metasoma V posteriorly with several large lobate denticles. Telson only sparsely hirsute, elongated. Anal lobe divided in two or three parts.

REMARKS. A surprising feature of this species is the varying amount of anal lobe in different populations. Two anal lobes are characteristic of the following populations: Maloe Bogdo Hill, Bogdo-Baskunchak Reserve and near Aytuar. Three anal lobes in populations from near Shcherbatovka and near Nizhnyaya Bannovka. Between these populations there is a clear zoogeographic boundary — the Volga River. The results obtained are not consistent with the identification key of Kovařík *et al*. [2022]. This is the first species of this genus that has two or three anal lobes; for other species the following combinations are known — two, three and three or four [Kovařík *et al*., 2022].

Mesobuthus sp. from “not Guberlinsky Mountains” Figs 10–12.

Mesobuthus eupeus thersites: Birula, 1904: 29; Fet, 1989: 94.

MATERIAL EXAMINED: locality error — 4 ♀♀ (ZISP ARA_SCO_0000001), Russia, Orenburg Region, Kuvandyksky Distr., Guberlinsky Mountains, ca. 51°12′N 58°05′E, O. Herz leg.

DIAGNOSIS. Total length of adult female 39.3–48.2 mm. Trichobothrium *db* on the fixed finger of the pedipalp in females is on the same level as *est*. Pedipalp chela length/width ratio 3.40–4.20 in female. Pectinal teeth number 16–22 in females. Chelicerae reddish brown, without reticulation. Denticle *m* of movable finger of chelicerae flat, without pronounced elevation. Pedipalps and metasoma very sparsely hirsute. Carapace, tergites, pedipalps, metasoma and telson reddish brown with pigmentation reduced. Sternites and legs dark yellow with pigmentation reduced or no pigmentation. Femur of pedipalp with 4–5 granulate carinae. Patella with 8 granulated or smooth carinae. Chela lacks carinae. Movable fingers of pedipalps with 10–11 cutting rows of denticles and 5 terminal denticles. Central lateral and posterior lateral carinae of carapace joined to form a continuous linear series of granules to posterior margin. Sternite VII with weakly marked, usually smooth carinae. Metasomal segment I with 10 carinae; second to fourth with 8 carinae, other two carinae are indicated by incomplete row of denticles on metasomal segments II and III; segment IV with 8 carinae with lateromedian carina smooth, all other carinae granulated; segment V with 5 carinae. Length to depth ratio of metasoma III 1.02–1.28 and metasoma IV 1.26–1.75 in female. Telotarsus

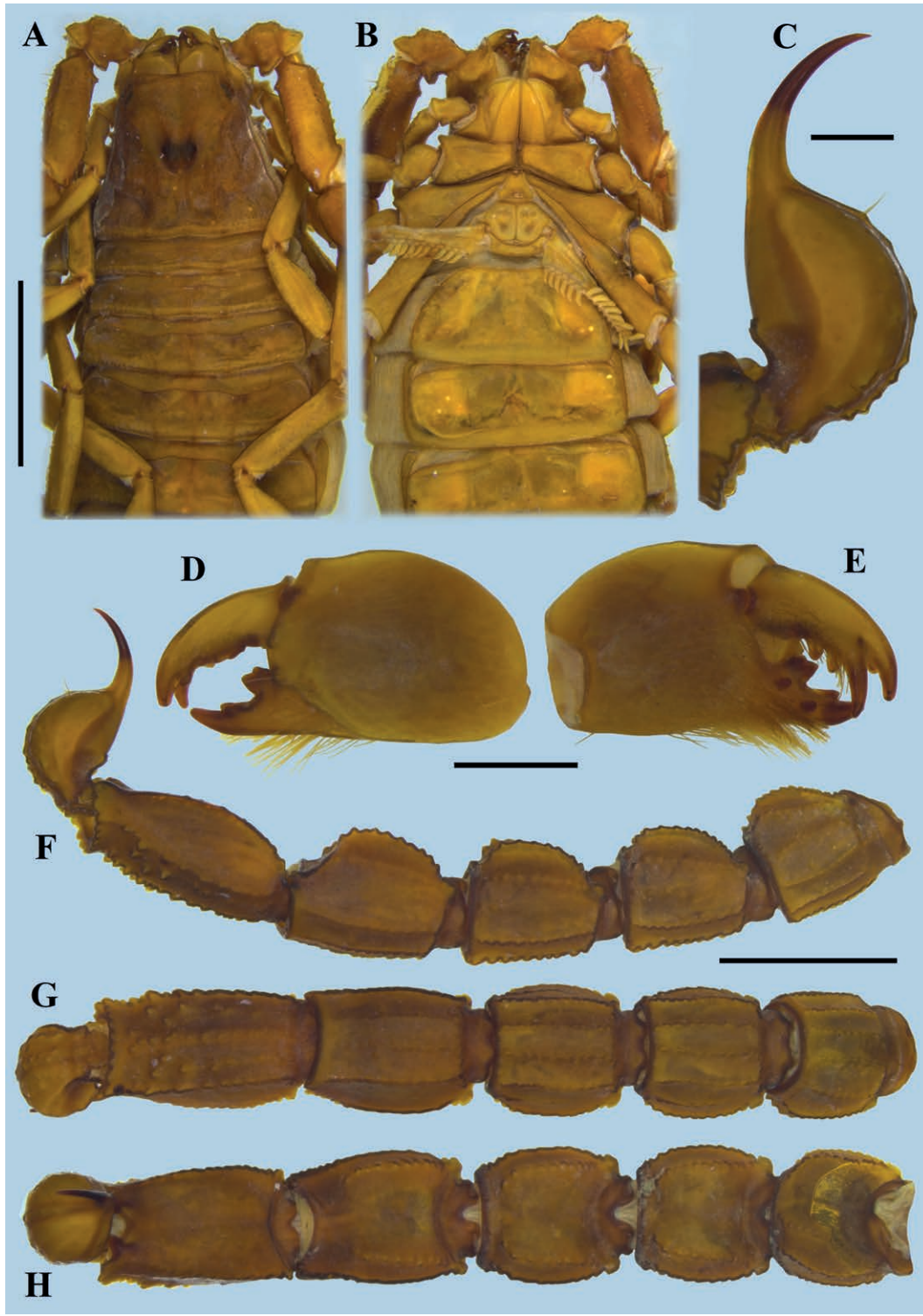

Fig. 11. Habitus of *Mesobuthus* sp. (♀) from Guberlinsky Mountains, Orenburg Region, Russia (locality error): A — chelicerae, carapace and tergites I–V, dorsal view; B — chelicerae, coxae, sternopectinal region and sternites III–V, ventral view; C — telson, lateral view; D, E — right chelicera, dorsal (D) and ventral (E) views; F–H — metasoma and telson, lateral (F), dorsal (G) and ventral (H) views. Scale bars: 5.0 mm (A, B, F–H), 1.0 mm (C–E).

Рис. 11. Общий вид *Mesobuthus* sp. (♀) из Губерлинских гор, Оренбургская область, Россия (ошибка локалитета): A — хелицеры, карапакс и тергиты I–V, вид сверху; B — хелицеры, тазики, стерно-пектинальная область и стерниты III–V, вид снизу; C — тельсон, вид сбоку; D, E — правая хелицера, вид сверху (D) и снизу (E); F–H — метасома и тельсон, вид сбоку (F), сверху (G) и снизу (H). Масштаб: 5,0 мм (A, B, F–H), 1,0 мм (C–E).

Fig. 12. *Mesobuthus* sp. (♀) from Guberlinsky Mountains, Orenburg Region, Russia (locality error): A–C — right chela, dorsal (A), external (B) and ventral (C) views; D — fixed chelal fingers, ventral view; E — movable chelal fingers, dorsal view; F–H — right patella, dorsal (F), external (G) and ventral (H) views; I–K — right femur and trochanter, dorsal (I), internal (J) and ventral (K) views; L–O — left legs I–IV, retrolateral aspect. Scale bars: 3.0 mm (A–C), 1.0 mm (D–K), 2.0 mm (L–O).

Рис. 12. *Mesobuthus* sp. (♀) из Губерлинских гор, Оренбургская область, Россия (ошибка локалитета): A–C — правая хела, вид сверху (A), спереди (B) и снизу (C); D — фиксированный хелальный палец, вид снизу; E — подвижный хелальный палец, вид сверху; F–H — правое колено, вид сверху (F), спереди (G) и снизу (H); I–K — правые бедро и вертлуг, вид сверху (I), внутренний (J) и снизу (K); L–O — левые ноги I–IV, задне-боковой аспект. Масштаб: 3,0 мм (A–C), 1,0 мм (D–K), 2,0 мм (L–O).

III ventral setation represented by short and strong spiniform setae. Tarsi not densely hirsute, adults with 5–7 retroinferior macrosetae on basitarsus III. Pedal spurs of legs with solitary setae only. Telson elongated. Anal lobe divided in two parts.

DESCRIPTION. Total length of adult female 39.3–48.2 mm. Trichobothrium *db* on the fixed finger of the pedipalp in females is on the same level as *est* (Fig. 12A, B). Chela of pedipalps in females is long and narrow. For measurements, see Suppl. Table 3.

Coloration (Fig. 10). Chelicerae reddish brown, without reticulation, the tips of teeth on cheliceral fingers are reddish brown. Carapace, tergites, pedipalps, metasoma and telson reddish brown with pigmentation reduced. Sternites and legs dark yellow with pigmentation reduced or no pigmentation.

Mesosoma and carapace (Fig. 11A, B). Central lateral and posterior lateral carinae of carapace joined to form a continuous linear series of granules to posterior margin; anterior median carinae are weakly expressed, almost do not reach the anterior margin of carapace. Tergites I–VI with three carinae, are sparsely granulated, with intercarinal granules small. Tergite VII is pentacarinate. Pectinal tooth count is 16–22 in females. Pectinal marginal tips extend to about one-fourth of the sternite IV in females. Pectines have three marginal lamellae and six to eight middle lamellae. Lamellae with numerous long setae, each fulcrum with three to five dark setae. All sternites smooth, sparsely hirsute. Sternite VII with weakly marked, usually smooth carinae. Other sternites have two furrows.

Chelicerae (Fig. 11D, E) with typical buthid dentition. Denticle *m* of movable finger flat, without pronounced elevation.

Pedipalps (Fig. 12A–K). Pedipalps very sparsely hirsute and smooth, only femur is finely granulated dorsally. Femur has four to five granulated carinae, the middle carina on internal surface consists of strong irregular granules. Patella with 8 usually granulated or smooth carinae. Chela without carinae. Movable fingers of pedipalps have 10–11 cutting rows of denticles, each with external and internal denticles present, and five terminal denticles.

Legs (Fig. 12L–O). Telotarsus III ventral setation represented by short and strong spiniform setae. Tarsi not densely hirsute, adults with 5–7 retroinferior macrosetae on basitarsus III. Femur and patella with carinae well developed. Tibial spurs present and moderate to strong on legs III and IV and absent on the other legs. Pedal spurs of legs with solitary setae only.

Metasoma and telson (Fig. 11C, F–H). All metasomal segments are quite rarely hirsute with long setae.

Metasomal segment I with 10 carinae; second to fourth with 8 carinae, other two carinae are indicated by incomplete row of denticles on metasomal segments II and III; segment IV with 8 carinae with lateromedian carina smooth, all other carinae granulated; segment V with 5 carinae. Intercarinal surfaces on metasoma smooth. Ventrolateral carinae of metasoma V posteriorly with several slightly rounded small lobate denticles. Telson elongated is sparsely hirsute, rather bulbous and smooth. Anal lobe divided in two parts.

REMARKS. *Mesobuthus* sp. is closest to *M. afghanus* (Pocock, 1889) from Afghanistan, Iran and Turkmenistan [Kovařík *et al*., 2022], but can be distinguished by the following characters: pedipalp chela length/width ratio 3.40–4.20 in females (*vs.* 3.22–3.30 in females in *M. afghanus*); central lateral and posterior lateral carinae of carapace joined (*vs*. not joined in *M. afghanus*). If these characters correspond to intraspecific variation, then the range of *M. afghanus* completely coincides with where the collector of these scorpions traveled (for more details see the Discussion section). However, we will refrain from exact species identification of this material.

More details about the differences between *M. bogdoensis* and *Mesobuthus* sp. see Discussion section.

Morphology comparison

To identify morphological variability between different populations of *Mesobuthus bogdoensis*, as well as to clarify the differences between *Mesobuthus* sp. from *M. bogdoensis*, we used the principal component analysis (PCA), for which 34 ratios of comparative measurements were selected (see Suppl. Table 4). The results obtained are presented in Fig. 13. PCA analysis for all specimens explained 38.12% of shape variations by the first two PC axes extracted from the variance-covariance matrix (PC1=22.63% and PC2=15.49%). The group located only on the positive side of PC1 is composed of specimens *Mesobuthus* sp. and *M. bogdoensis* from Bogdo-Baskunchak Reserve. The group situated on the negative side of PC1 comprises specimens *M. bogdoensis* from near Shcherbatovka and near Nizhnyaya Bannovka. Specimens *M. bogdoensis* from Maloe Bogdo Hill and near Aytuar are located in central part of PC1. Males of all studied specimens from different populations are on the negative side of PC1, while almost all females are on the positive side of PC1. For more details about the contribution of the most significant comparative measurements to PCA, see in Discussion.

Discussion

As shown by the results of morphological analysis, the material listed as *Mesobuthus eupeus thersites* for Guberlinsky Mountains, Orenburg Region, Russia [Birula, 1904; Fet, 1989] is a locality error and does not belong to *M. bogdoensis*. There is a number of other pieces of evidence to support this assertion. Firstly, in the collection of scorpions of the Zoological Institute of the Russian Academy of Sciences, Saint Petersburg, Russia there are other scorpions of the family Buthidae collected by O.F. Herz (1852–1905) with the label "Guberlinsky Mountains", previously identified as *M. caucasicus parthorum* (Pocock, 1889) (now, *Olivierus* sp.) and *Orthochirus scrobiculosus scrobiculosus* (Grube, 1873) (now, *Orthochirus* sp.). Both of these species do not live in Russia, but are found in Middle Asia [Fet *et al.*, 2018; Kovařík *et al*., 2020]. This error was also noted by Fet [1989], pointing out that this is a locality error for these two species. Secondly, based on Herz's collections from the Guberlinsky Mountains, Birula [1938] described the camel spiders *Rhagodes grimmi septentrionalis* Birula, 1938 (Solifugae: Rhagodidae). This material was subsequently synonymized with another Central Asian species, *R. melanochaetus* Heymons, 1902 [Gromov, 1989], and it was suggested that this was also a locality error. Thirdly, in the obituary dedicated to O.F. Herz [Kuznetsov, 1907] indicates that Herz had never been to the Guberlinsky Mountains (Orenburg Region, Russia), but in the period 1887–1897 he repeatedly visited Central Asia (modern Uzbekistan and Turkmenistan), northeastern Persia and southwestern Transcaucasia. At present, based on morphological data, it is difficult for us to attribute this material to any species of the genus *Mesobuthus*. Attempts to obtain DNA from this museum material for more accurate species identification were unsuccessful

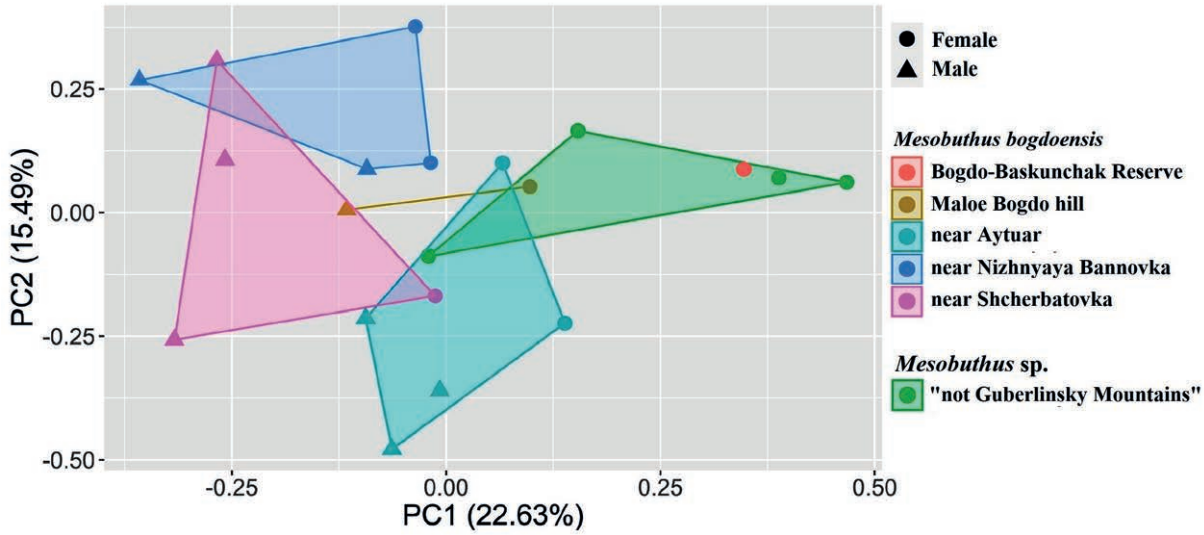

Fig. 13. PCA plot of the analysis of morphometric characteristics for study populations of *Mesobuthus bogdoensis* and *Mesobuthus* sp. from "not Guberlinsky Mountains" (locality error).

Рис. 13. График PCA анализа морфометрических характеристик исследуемых популяций *Mesobutus bogdoensis* и *Mesobuthus* sp. из «не Губерлинские горы» (ошибка локалитета).

due to its old age [Poverennyi, Anikin, 2022a]. Thus, the above proves that this is a locality error and this material should currently be considered *Mesobuthus* sp. from "not Guberlinsky Mountains".

Indication of *Mesobuthus eupeus* for two localities on the left bank of the lower reaches of the Ural River in near Inderbor and near Lake Inder (Atyrau Region, Kazakhstan) [Fet, 1989; Gromov, 2001], requires additional research. Firstly, according to the results of molecular genetic analysis [Poverennyi, Anikin, 2023] on the left bank of the Ural River in Dossor (Atyrau Region, Kazakhstan) *Olivierus longichelus* (Sun et Zhu, 2010) (referred to in the article as *O. gorelovi*) were collected. Secondly, the genus *Olivierus* was recently restored to the status of a valid genus [Kovařík, 2019], and most of its species were previously assigned to the genus *Mesobuthus*, which does not exclude confusion in definitions. Thus, detailed studies of scorpions in this region are necessary to clarify their taxonomic affiliation. And the previously obtained results [Poverennyi, Anikin, 2023] about the presence of *O. longichelus* near Dossor significantly expand to the northwest the range of this species, known from Kazakhstan and China [Tang *et al*., 2024].

As was shown earlier [Kovařík *et al*., 2022], divergence in the "*thersites* complex" clade occurred 8.31 Mya, while the divergence between sister species *M. barszczevskii* (Birula, 1904) and *M. bogdoensis* dates back to 6.37 Mya. Both species represent interesting, disjunct relicts whose ancestors could have been isolated on landmasses in the late Miocene while the Paratethys was receding: *M. barszczevskii* in the mountains of southern Central Asia, and northwestern *M. bodgoensis*, at the "paleo-Caspian" shores. These data indicate ancient speciation and range expansions in dating back to Miocene desiccations and recoveries of the Paratethys Sea [Palcu *et al*., 2021]. At the same time, the median crown age for *M. bogdoensis* is estimated at 0.97 Mya [Kovařík *et al*., 2022]. Thus, the time of divergence between populations of *M. bogdoensis* can be associated with numerous changes in the level of the Caspian Sea (transgressions and regressions) in the Pleitocene [Svitoch, 2014]. However, the unique haplotype PP439977 (see Fig. 2, Table 1) that we discovered near Nizhnyaya Bannovka (see Fig. 3, locality No. 1) may indicate two waves of *M. bogdoensis* colonization on the right bank of the Volga from the main range of the species, located in the interfluve of the Volga and the Urals (see Fig. 3). Most likely the unique haplotype PP439977 this is the first (more ancient) wave of settlement, and the other haplotypes PP439978, OM905078, OM905079, OM905080 and OM905081 from the right bank of the Volga are the second younger wave. This judgment is supported by the fact of the presence of a unique morphological character in populations of the right bank of the Volga River — anal lobe divided in three parts. Perhaps this morphological character comes from an older line that was isolated for a long time. Most likely, modern gene introgression and repeated intraspecific hybridization are taking place between these two lineages. To confirm this opinion, it is necessary to conduct molecular genetic studies using nuclear genes in the future.

According to the results of principal component analysis (PCA) by the first two PC axes (see Fig. 13), the ten of the most statistically significant ratios were identified for the studied populations of *Mesobuthus bogdoensis*. The following lists the minimum to maximum values between different populations of *M. bogdoensis* and compares these values with *Mesobuthus* sp. from "not Guberlinsky Mountains" (further as, *Mesobuthus* sp.): 1) total length/carapace width ratio from 6.37–7.68, mean 7.28 (n=4) in near Nizhnyaya Bannovka to 7.76–8.50, mean 8.02 (n=4) in near Shcherbatovka (*vs*. 7.13–7.99, mean 7.52 (n=4) in *Mesobuthus* sp.); 2) tergite VII length/width ratio from 0.46–0.52, mean 0.48 (n=4) in near Nizhnyaya Bannovka

to 0.51–0.65, mean 0.58 (n=5) in near Aytuar (*vs*. 0.42–0.54, mean 0.48 (n=4) in *Mesobuthus* sp.); 3) segment I length/depth ratio from 0.75 (n=1) in Bogdo-Baskunchak Reserve to 1.08–1.38, mean 1.19 (n=4) in near Nizhnyaya Bannovka (*vs*. 0.68–0.97, mean 0.85 in *Mesobuthus* sp.); 4) segment IV length/depth ratio from 1.45–1.66, mean 1.55 (n=2) in Maloe Bogdo Hill to 1.63–1.86, mean 1.71 (n=4) in near Shcherbatovka and 1.56–2.10, mean 1.71 (n=4) in near Nizhnyaya Bannovka (*vs*. 1.26–1.75, mean 1.52 (n=4) in *Mesobuthus* sp.); 5) segment III length/width ratio from 1.00 (n=1) in Bogdo-Baskunchak Reserve to 1.08–1.30, mean 1.17 (n=4) in near Nizhnyaya Bannovka (*vs*. 0.94–1.23, mean 1.10 (n=4) in *Mesobuthus* sp.); 6) metasoma+telson length/segment V length ratio from 4.02–4.77, mean 4.40 (n=5) in near Aytuar to 4.73–5.15, mean 4.94 (n=2) in Maloe Bogdo Hill (*vs*. 4.04–4.28, mean 4.17 (n=4) in *Mesobuthus* sp.); 7) total length/carapace length ratio from 8.54 (n=1) in Bogdo-Baskunchak Reserve to 9.10–9.59, mean 9.33 (n=4) in near Shcherbatovka (*vs*. 8.36–9.23, mean 8.67 (n=4) in *Mesobuthus* sp.); 8) segment I length/width ratio from 0.70 (n=1) in Bogdo-Baskunchak Reserve to 0.92–0.97 (n=2) in Maloe Bogdo Hill (*vs*. 0.69–0.80, mean 0.75 (n=4) in *Mesobuthus* sp.); 9) patella length/width ratio from 2.33 (n=1) in Bogdo-Baskunchak Reserve to 2.86–3.48, mean 3.16 (n=5) in near Aytuar (*vs*. 2.08–2.33, mean 2.24 (n=4) in *Mesobuthus* sp.); 10) carapace length/width ratio from 0.79–0.85, mean 0.82 (n=4) in near Nizhnyaya Bannovka to 0.87–0.90, mean 0.88 (n=2) in Maloe Bogdo Hill (*vs*. 0.84–0.90, mean 0.86 (n=4) in *Mesobuthus* sp.).

According to the results of principal component analysis (PCA) along the PC1 axis for *Mesobuthus bogdoensis* (see Fig. 13), differences between males (n=9) and females (n=7) were reliably revealed (this trend is supported by *Mesobuthus* sp., for which only females (n=4) are known). The most statistically significant following the ten ratios: 1) segment I length/depth ratio 1.00–1.32, mean 1.15 in males (*vs*. 0.75–1.38, mean 1.07 in females; 0.68–0.97, mean 0.85 in females *Mesobuthus* sp.); 2) segment IV length/depth ratio 1.58–2.10, mean 1.77 in males (*vs*. 1.44–1.63, mean 1.55 in females; 1.26–1.75, mean 1.52 in females *Mesobuthus* sp.); 3) segment III length/depth ratio 1.21–1.38, mean 1.32 in males (*vs*. 1.01–1.39, mean 1.17 in females; 1.02–1.28, mean 1.16 in females *Mesobuthus* sp.); 4) segment I length/width ratio 0.83–1.14, mean 0.96 in males (*vs*. 0.70–1.09, mean 0.92 in females; 0.69–0.80, mean 0.75 in females *Mesobuthus* sp.); 5) segment II length/width ratio 1.01–1.27, mean 1.09 in males (*vs*. 0.92–1.24, mean 1.05 in females; 0.92–1.13, mean 1.00 in females *Mesobuthus* sp.); 6) metasoma+telson length/segment I length ratio 6.82–8.67, mean 7.87 in males (*vs*. 7.34–9.96, mean 8.25 in females; 8.98–10.00 in females *Mesobuthus* sp.); 7) chela length/movable finger length ratio 1.50–1.73, mean 1.58 in males (*vs*. 1.56–1.72, mean 1.63 in females; 1.60–2.03, mean 1.77 in females *Mesobuthus* sp.); 8) total length/carapace length ratio 8.78–9.59, mean 9.2 in males (*vs*. 7.38–9.36, mean 8.64 in females; 8.36–9.23, mean 8.67 in females *Mesobuthus* sp.); 9) segment IV length/width ratio 1.34–1.58, mean 1.44 in males (*vs*. 1.21–1.61, mean 1.36 in females; 1.17–1.48, mean 1.32 in females *Mesobuthus* sp.); 10) total length/metasoma+telson length ratio 1.56–1.81, mean 1.66 in males (*vs*. 1.56–1.93, mean 1.71 in females; 1.71–1.81, mean 1.74 in females *Mesobuthus* sp.).

Based on the PCA results, it can be seen that the contribution of differences between different populations is less pronounced than the contribution between males and females.

Supplementary Issues

Supplementary Table 1. Estimates of the average value of pairwise sequence divergence (*p*-distances) of partial COI mtDNA gene (below diagonal) and standard errors (above diagonal) between studied *Mesobuthus bogdoensis* specimens from different populations.

Supplementary Table 2. Distribution of *Mesobuthus bogdoensis* based on analysis of literary and author's data. A number of coordinates from nearby points are combined into one locality.

Supplementary Table 3. Comparative measurements of studied populations of *Mesobuthus* (measurements lectotype and paralectotype of *M. bogdoensis* by Kovařík *et al*., [2022]).

Supplementary Table 4. Ratios on comparative measurements for *Mesobuthus* populations studied (ratios for lectotype and paralectotype of *M. bogdoensis* are derived from measurements from Kovařík *et al*., [2022]).

Compliance with ethical standards

CONFLICT OF INTEREST: The authors declare that they have no conflict of interest.

Ethical approval: No ethical issues were raised during our research.

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