

***Taniatrechus xeniae* sp. nov. (Coleoptera: Carabidae: Trechini), the second species of the most specialised troglobitic carabid genus of the Caucasus**

***Taniatrechus xeniae* sp. nov. (Coleoptera: Carabidae: Trechini) – второй вид наиболее специализированного троглобионтного рода жувелиц Кавказа**

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Abstract. *Taniatrechus xeniae* sp. nov., the second species of the genus, is described from Prostornaya Cave in the central part of the Bzyb Mountain Range, Abkhazia. A comparative study of all available specimens of the genus is carried out using both linear morphometrics (indices) and geometric morphometrics: generalised Procrustes analysis (GPA), principal component analysis (PCA), and canonical variate analysis (CVA). This study allowed us to estimate infraspecific variation in the external morphology of *T. setosus* Belousov et Dolzhansky, 1994, on the one hand, and to reveal reliable diagnostic features that distinguish between the two species, on the other. The diagnosis and description of the genus are completed to include the new species and variation found in the type species. Some characters were also described more accurately or corrected based on more abundant material. The major morphological features of *Taniatrechus* spp. are photographed, their geographic distribution is mapped, and new data on living conditions of the genus are provided. The members of the genus seem to be the most specialised hypogean Trechini in the Caucasus, with the deepest finding ever reported for Coleoptera (one specimen of *T. setosus* was found at a level of 1,800 m below the cave entrance). In view of recent discoveries in highlands, the subterranean layer suitable for living of hypogean insects may reach more than three km thick in intensively folded karst areas. Thus, the hypogean life is much more widespread than previously thought. Prostornaya Cave, the type locality of *T. xeniae* sp. nov., is described for the first time.

Резюме. *Taniatrechus xeniae* sp. nov., второй вид рода, описан из пещеры в центральной части Бзыбского хребта Абхазии. Сравнительное изучение всех доступных экземпляров рода было проведено с использованием как линейной морфометрии (индексов), так и геометрической морфометрии: обобщенного Прокрустова анализа (GPA), анализа главных компонент (PCA) и канонического вариационного анализа (CVA). Это позволило нам, с одной стороны, оценить внутривидовую изменчивость внешней морфологии *T. setosus* Belousov et Dolzhansky, 1994 и, с другой, – выявить надежные диагностические признаки между двумя известными видами. Диагноз и описание рода были дополнены с учетом включения второго вида и изменчивости, обнаруженной у типового вида. Некоторые признаки также были описаны более точно или исправлены на основе более обширного материала. Даны фотографии основных морфологических признаков *Taniatrechus* spp., нанесены на карту все известные местонахождения видов рода и представлены новые данные об условиях их жизни. Представители рода, по-видимому, являются наиболее специализированными гипогейными Trechini на Кавказе, с самым глубоким нахождением, о котором когда-либо сообщалось для Coleoptera (один экземпляр *T. setosus* был найден на глубине

1800 м от входа в пещеру). Таким образом, с учетом недавних открытий в высокогорьях, подземный слой, пригодный для обитания гипогейных насекомых, может достигать толщины более 3 км в областях с интенсивным развитием складчатого карстового рельефа. Эти данные показывают, что подземная жизнь распространена значительно шире, чем считалось ранее. Впервые описана пещера Просторная – типовое место *T. xeniae* sp. nov.

Key words: Western Caucasus, Abkhazia, Bzyb Mountain Range, Snezhnaya Cave System, Prostornaya Cave, troglobitic, hypogean, aphenopoid, deepest finding of cave Coleoptera, geometric morphometrics, Carabidae, Trechini, *Taniatrechus*, new species

Ключевые слова: Западный Кавказ, Абхазия, Бзыбский хребет, система пещеры Снежная, пещера Просторная, троглобионт, гипогейный, афенопсоид, самая глубокая находка пещерных Coleoptera, геометрическая морфометрия, Carabidae, Trechini, *Taniatrechus*, новый вид

ZooBank Article LSID: D376B26F-B407-49B7-A27D-F03D9E50D68B

Introduction

Along with species of the genus *Caucasaphaenops* Belousov 1999, members of the genus *Taniatrechus* Belousov et Dolzhansky 1994 are the rarest troglobitic trechines of the Caucasus. The type species of the genus, *Taniatrechus setosus* Belousov et Dolzhansky, 1994, was described based on a unique female specimen from Souvenir Cave (Abkhazia, Western Caucasus). In 2009, a male specimen of this species was collected allowing the authors of the present paper to complete the diagnosis of the genus with taxonomically important characters of the male protarsi and genitalia (Belousov & Koval, 2009). In a few following years, still some female specimens of the species were collected and became available for examination. All these individuals were collected in the type locality and its vicinity (the Snezhnaya Cave System) and largely match the holotype in all essential points with only slight variation in proportions (see Table 1) and some features of minor importance.

In 2011, one more female specimen belonging to this genus and apparently representing a new taxon was collected in pitfall traps exposed for nearly one year in a cave in the central part of the Bzyb Mountain Range outside the Razdelny Mountain Range, where all previously known specimens of the genus were found. This specimen differs from *T. setosus* in some characters, first of all, in three setiferous discal pores (apart from the preapical one) on the elytra *vs.* only two in all previously known specimens and in the shape of the head and

pronotum. Therefore, it is considered here to be an independent species. We waited over 10 years for additional material. However, the extreme rarity of genus members resulted in only two female specimens of *T. setosus* being collected during this time and one male and two females of the same species at the last moment, when the present paper had already been prepared. That is why we eventually decided to describe the new species based on a single female individual and to summarise all available information on *T. setosus* with a focus on variation in characters and revealing reliable diagnostic features at species and generic levels.

Thus, the main goal of the present paper is to introduce a new species and give new data on the distribution, morphology, and ecology of the genus members.

Material and methods

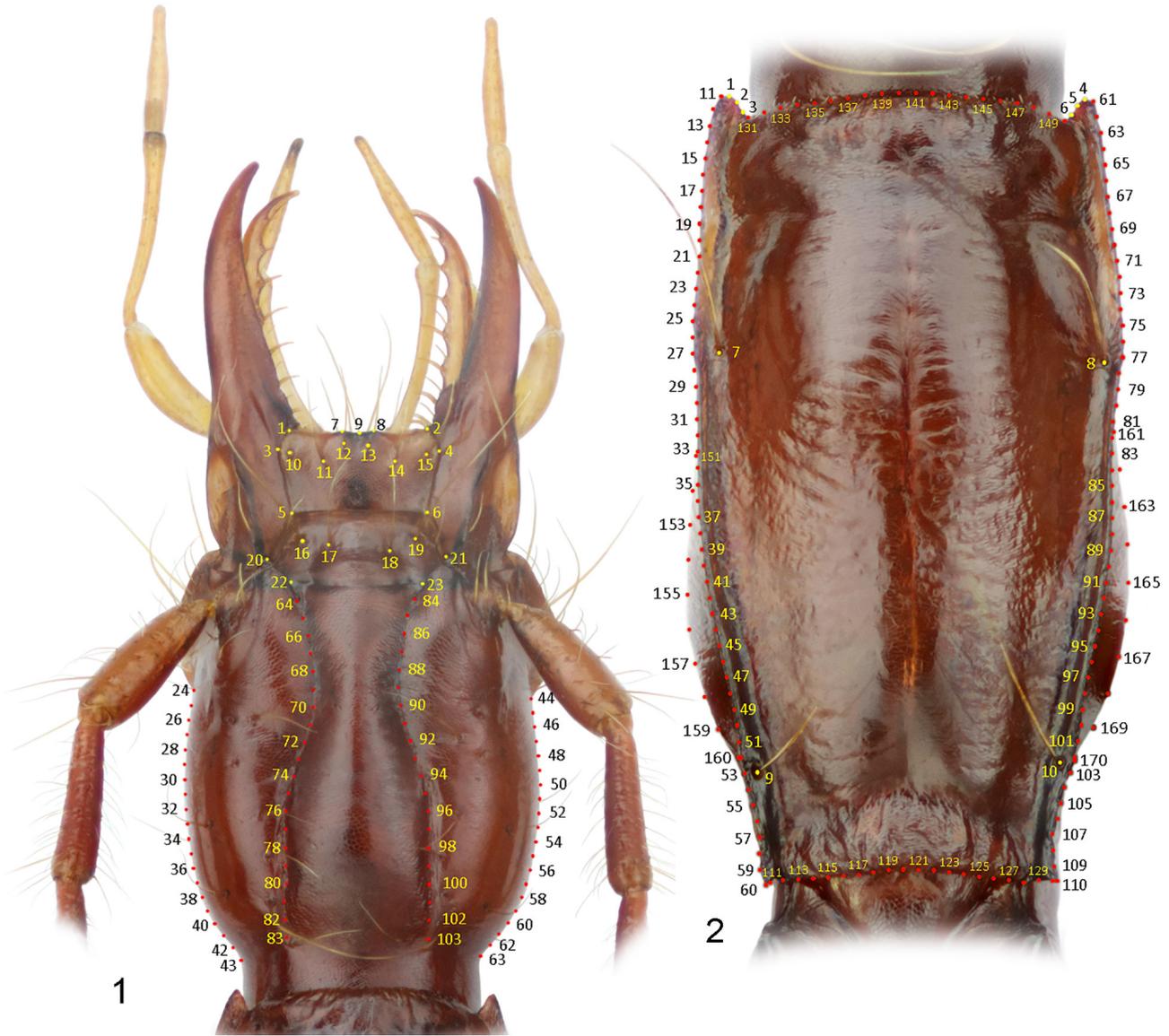
Specimens were studied and measured using an MBS-10 stereomicroscope with an ocular-micrometer. The female genitalia were extracted and prepared using a conventional technique and preserved in euparal on transparent glue boards pinned under the specimens. Genitalia preparations and microsculpture were studied using a metallographic microscope Biolam M-1 and photographed with an MC-6.3 camera under 20× magnification and LOMO-Microsystems MCView software. Photographs of beetles and parts of their bodies were taken with a Canon 5DS DSLR digital camera using the focus stacking technique

and subsequently processed with Zerene stacker software version 1.04 (<http://zerenesystems.com/stacker>). The holotype of the new species is deposited in the collection of the Zoological Institute of the Russian Academy of Sciences (ZIN, St Petersburg). Specimens of *T. setosus* are in the working collections of the authors (cAK, cIB, St Petersburg, Russia), as indicated in the material examined section. The measurements taken in the present paper are the same as in our previous articles (e.g., Belousov & Koval 2009), except for one point: the positions of setiferous pores were measured on both sides of the body to assess their variation more accurately. The body length was measured from the anterior margin of the labrum to the elytral apex, and the width of the pronotal base at the narrowest point, which is located near the level of the hind angles. The positions of the anterior and posterior setiferous pores of the pronotum, the discal, preapical, and umbilicate pores on the elytra are given as percentages of the length of the pronotum and elytra, respectively. The latter were measured from the apex of the scutellum to the apex of the elytra along the elytral suture.

The scarce available material forced us to use rather sophisticated methods of geometric morphometrics to analyse shape differences in species of the genus. Since only one female specimen of *Taniatrechus xeniae* sp. nov. is currently known, the use of geometric morphometrics cannot provide statistically consistent results and is employed rather for more exact description and interpretation of differences (although confidence ellipses were drawn for a 90% probability of principal components for *T. setosus*). To obtain comparable data for different specimens and to avoid projection distortions, each part of the body (i.e., head, pronotum, and elytra) was photographed separately in one focus plane. Specimens were successively positioned in a way that, at least, four control points for each body part were in focus: clypeal setae and hind supraorbital setae for the head; anterior and posterior ends of the mid-line and lateral margins at the same level for the pronotum; umbilicate pores 1 and 7 on the elytra.

Landmarks were collected using TPS programs: tpsdig264 and tpsUtil64 (Rohlf, 2015). The numbers of landmarks were as follows: 23 for the head, 10 for the pronotum, and 15 for each ely-

tron; their location is shown in Figs 1–3, yellow dots. Landmarks were placed at the sites of the setiferous pores or extreme points of shapes. The use of geometric morphometrics suggests that all compared specimens should have the same number of landmarks. For this reason, supraorbital setiferous pores, which are highly variable in number and location, were not analysed in this way. The same applies to the additional external (third) clypeal setiferous pores, which are occasionally either redoubled (e.g., Fig. 19) or, on the contrary, missing from one side and nearly always set asymmetrically on the left and right sides. Other fixed setiferous pores, including two internal clypeal, pronotal, and all elytral pores (with those of the umbilicate series and apical group), were used for setting landmarks. However, in the holotype of *T. xeniae* sp. nov., there are only five setae on the labrum, with only one median seta (Fig. 23). It is likely an aberrant state, and to make this specimen comparable to others, we set two landmarks in the location of the single median pore. To quantify curves and contours, we used semilandmarks, which were arranged as follows: four curves, each comprising 20 semilandmarks for the head (two curves for the head contour and two for the frontal furrows (Fig. 1); six curves for the pronotum (two curves, each comprising 50 semilandmarks for the lateral margins of the pronotum; two curves, each comprising 20 semilandmarks for the anterior and posterior margins of the pronotum (see Fig. 2); two curves, each comprising 10 semilandmarks for the lateral margins of the propleura visible from above); and one curve comprising 100 semilandmarks for each elytron (Fig. 3). Such a mixed use of the landmarks (applied largely for homologous structures, such as setae and body part extremes, as well as for short curves, e.g., for the anterior angles of the pronotum, Fig. 2) and semilandmarks (applied mostly for long segments of outlines) allows us, on the one hand, to keep the number of semilandmarks manageable and, on the other, to accurately digitise differences in small shapes. The tps-files were created using tpsUtil64. Landmarks and semilandmarks were collected in tpsdig264 with the tools “digitize landmark” and “draw curves”, respectively. After completion, the curves were resampled to the necessary numbers of semilandmarks, as mentioned above.



Figs 1–2. Location of landmarks (yellow dots) and semilandmarks (red dots) on the head (1) and pronotum (2) of *Taniatrechus setosus* Belousov et Dolzhansky, 1994.

The tpsUtil64 program was used for converting curves of semilandmarks to landmarks. The outlines files were created in tpsdig264 and edited as txt files with all landmarks (including those obtained from semilandmarks) as belonging to line number “0” (for instance, a total of 103 landmarks for the head) and all other curve-originated landmarks as belonging to different lines numbered in a sequential manner (as described in the MorphoJ User’s Guide). Generalized Procrustes analysis (GPA), Principal component analysis (PCA), and Canonical variate analysis (CVA) were conducted

in MorphoJ (Klingenberg, 2011) and partially in tpsRelW64. The “object” symmetry was chosen as a type of symmetry for the datasets of the pronotum and head, while “matching” symmetry, for the elytra. The right elytra were mirrored to form a total scope of data based on elytra.

The following abbreviations are used below: ZIN – collection of Zoological Institute, Russian Academy of Sciences, Saint Petersburg; cAK – working collection of A.G. Koval (St Petersburg, Russia); cIB – working collection of I.A. Belousov (St Petersburg, Russia).

Taxonomic part

Order **Coleoptera**

Family **Carabidae**

Subfamily **Trechinae**

Tribe **Trechini**

Genus ***Taniatrechus*** Belousov et Dolzhansky, 1994

The diagnosis and description of the genus *Taniatrechus* are modified to incorporate the new member and to include variation in major characters.

Diagnosis. Largest aphepoid trechine beetles of the Caucasus, which can be readily recognised by the following set of character states: two basal segments of male protarsi dentate and dilated, with appendages on the underside; body surface glabrous; microsculpture markedly transverse on pronotum and subisodiametric elsewhere, eyes completely reduced; frontal furrows very long, nearly entire; 9–12 supraorbital setiferous pores on each side of head (Figs 19–23); normally three setae on each side of clypeus; tooth on the right mandible unidentate, blade-like, or bidentate, with a small acute proximal denticle; labial tooth completely effaced; 8 true submental setae, occasionally with 1–2 additional median shorter setae (Fig. 4); both maxillary and labial palpi completely glabrous; submental suture distinct for its whole length; prothorax and pronotum clearly narrower than head (Fig. 18), with propleura visible from above; posterior lateral pore of pronotum distinctly shifted anteriad; elytra with two or three discal setiferous pores in stria 3 in addition to the preapical pore; umbilicate series complete, with humeral group rather aggregate, though umbilicate pore 1 slightly shifted inward and umbilicate pore 2 more approached lateral margin than other humeral pores; abdominal sternite IV–VI with 2, occasionally 3 paramedian setae on each side; male genitalia small, median lobe gently arched in distal portion, more markedly near base in lateral view, its apex poorly sclerotised; in dorsal view, lamella acute apically; endophallus armature hyaline, spatulate, located near right wall of median lobe, with a mesh-like structure; parameres stout, of subequal length, without ventral apophyses, each bearing 3–4 apical setae.

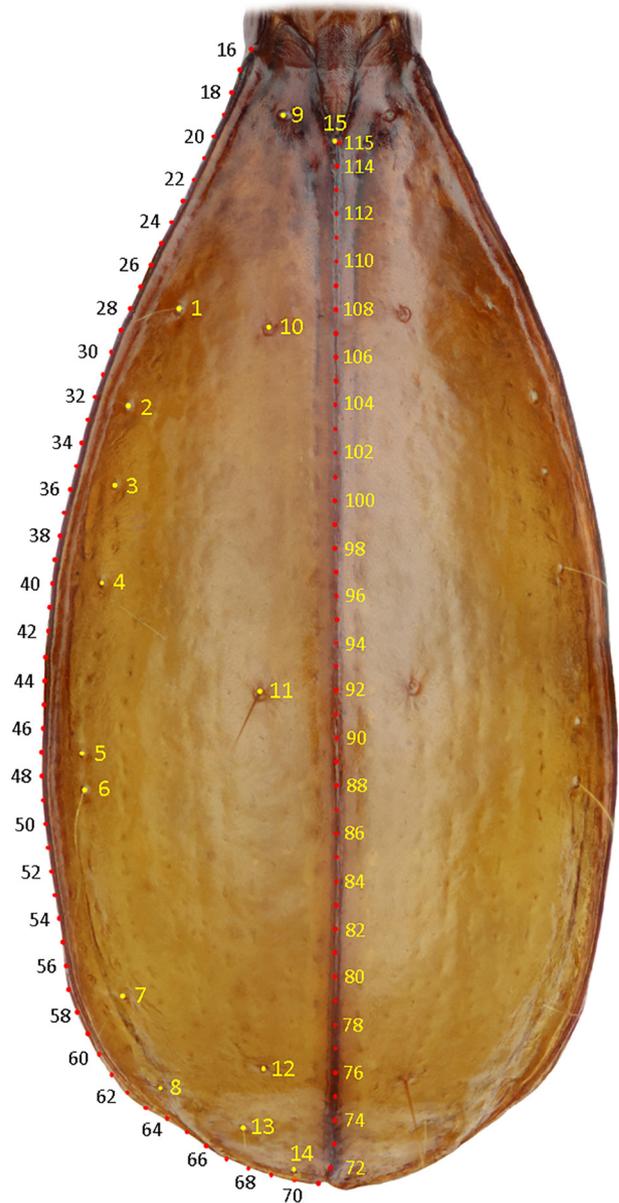
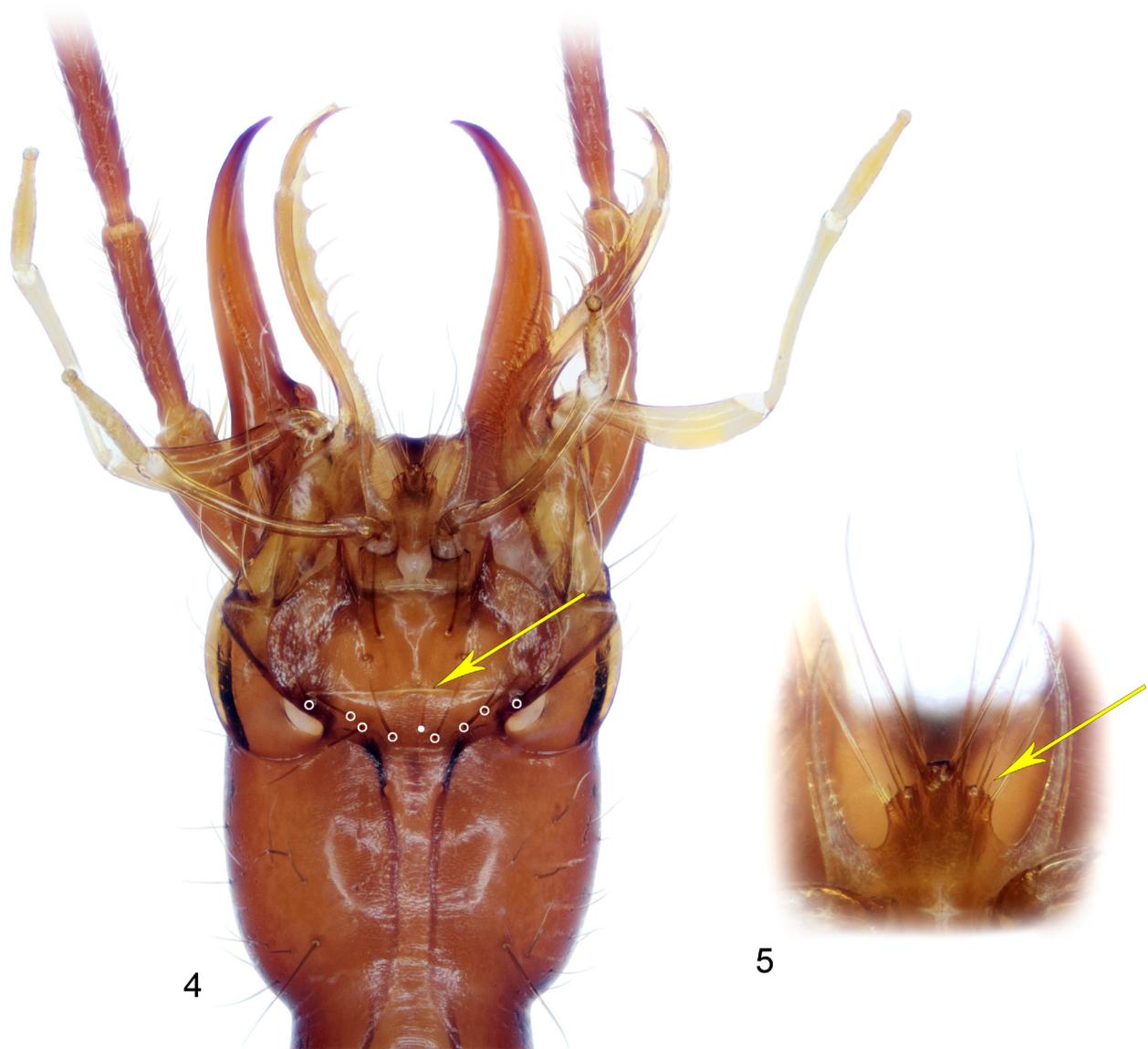


Fig. 3. Location of landmarks (yellow dots) and semi-landmarks (red dots) on the elytron of *Taniatrechus setosus* Belousov et Dolzhansky, 1994.

Description. For a thorough description, see Belousov & Dolzhansky (1994) and Belousov & Koval (2009). The focus here is on corrections, additional information, and variations in some characters.

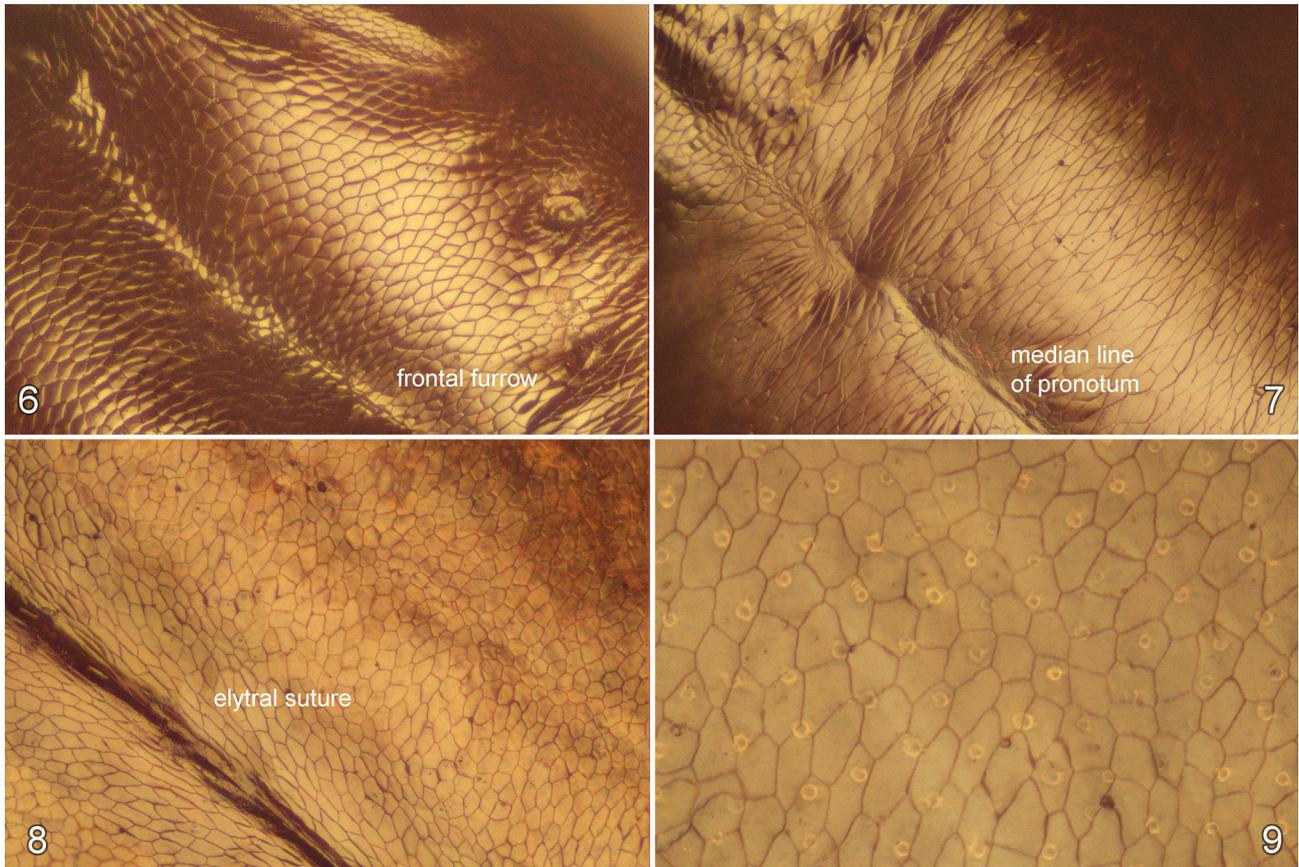
An increased number of supraorbital setiferous pores is one of the most striking morphological features of the genus *Taniatrechus*, which is fully shared only by members of the genus *Pheggomisetes* Knirsch, 1923. Although 3 or even 4 su-



Figs 4–5. *Taniatrechus setosus* Belousov et Dolzhansky, 1994. **4**, underside of head. Empty circles – true submental setae which are longer and more stable, filled circle – additional unstable seta. Labial tooth completely reduced. Submental suture (indicated by the yellow arrow) well distinguished for its whole length; **5**, glossa and paraglossae, under larger magnification. Additional small seta between setae 3 and 4 is indicated by the arrow on one side.

praorbital setae on each side of the head are known for some hypogean (e.g., Jeannel, 1928; Tian et al., 2023) and even epigean Trechini (some species of the *Kozlovites* Jeannel, 1935 lineage, unpublished data by the first author), the numbers exceeding 4 are extremely rare. In *Taniatrechus*, the number of supraorbital pores varies from 9 to 12, with the most common case of 10 setae, at least, on one side of the head (Figs 19–23). Such a chaetotaxy is found in all available specimens but two, which have 9 setae on each side. These numbers include

all setiferous pores of subequal size located on the upper and upper lateral surfaces of the head, although 1–3 anterior and 2–3 posterior setae are usually longer than others. One–three of the most exterior pores are likely homologous to the temporal setae of some other Trechini, but, for the moment, there is no way to reliably distinguish these from other supraorbital setae. Their grouping is rather variable among specimens and even between the left and right sides of one individual. Typically, all pores can be split into three major



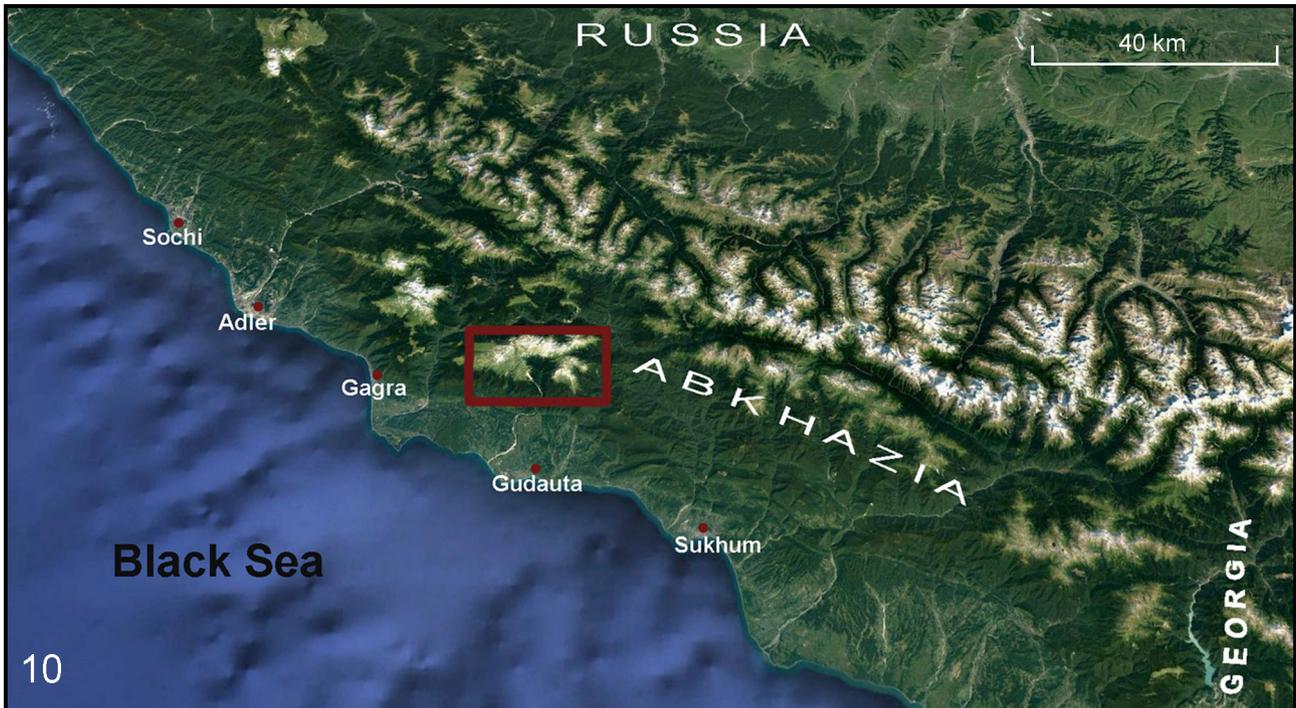
Figs 6–9. Microsculpture of *T. setosus* Belousov et Dolzhansky, 1994. **6**, frons and ophthalmic lobe of head; **7**, disc of pronotum near preapical impression; **8**, elytra behind anterior setiferous pore; **9**, the same under higher magnification, cuticular channels are clearly visible as pale circles.

groups: the posterior one consisting of 3–7 (usually 4–5) pores, the anterior one – 2–5 (usually 3–4) pores, and the exterior group composed of 1–3 (usually 2) pores. Approximately 9–11 setae (hairs) are located on and close to the underside of the head, including one much longer seta situated in the posterior portion of the genae outward from the gular suture (Fig. 4).

The second unusual trait of the head chaetotaxy is three setae on each side of the clypeus. The difference between one and two setae on each side of the clypeus is often considered to be an important taxonomic character, for instance, it is one of the diagnostic features between the Bembidiini and allied tribes, from one side, and Trechini with Bembidarenini, from the other (Maddison et al., 2019; Schmidt et al., 2021), although with a few exceptions found in true Trechini (e.g., see Belousov, 1998). By contrast, three clypeal setae are not so important from a taxonomical standpoint

and are found sporadically as a deviated state in some groups of Trechini. In *Taniatrechus*, the third clypeal pore (the most exterior one) is usually smaller and less stable (absent or, on the contrary, redoubled on one side in some specimens, Figs 19–23).

There is one more character of the head chaetotaxy that deserves to be mentioned, i.e., the presence of additional “scrobe” seta located along the outer upper edge of the mandible behind the usual fixed scrobe seta of Trechini (Figs 19–23). At first sight, this seta reminds setae of *Agonotrechus* Jeannel, 1923 (Belousov & Kabak, 2003), but it readily differs in being located at the upper outer edge of the mandible more basally while in scrobe or at the lower edge of the mandible in *Agonotrechus*. In *T. setosus*, all specimens have this seta, at least on one side (as it is shown in Figs 20 and 22), while it is absent in *Taniatrechus xeniae* sp. nov. Since the seta on its own and, particularly,



Figs 10–11. Distribution of *Taniatrechus* spp. **10**, position of map **11** within the Western Caucasus; **11**, locations of findings.

the pore are rather small and the seta might be broken, its absence in *T. xeniae* sp. nov. cannot be taken as fairly established.

The tooth on the right mandible is unidentate, blade-like, with a convex inner margin, or bidentate, with a more or less distinct proximal denticle

pointed apically and separated from the large distal portion by a more or less shallow notch (Figs 19–23). This structure is rather stable and is found in all studied specimens of *Taniatrechus*. To some extent, it resembles the triangular-shaped tooth of some *Cimmerites* Jeannel, 1928 (Belousov, 1998), but it is obvious that this similarity is rather superficial.

Earlier, the penultimate segment of the labial palpi was described as bearing four setae based on the number of pores, although the setae themselves seemed to be broken (Belousov & Koval, 2009). Several new specimens preserved in alcohol helped reexamine this character. The size and location of the pores on the penultimate segment turned out to be unstable, and none of these pores have well-developed seta, i.e., these pores are very similar to the numerous tiny pores of the last segment (Fig. 4). Therefore, both the maxillary and labial palpi are actually glabrous, without distinct setae.

The number of submental setae is to be adjusted to eight since one or two additional shorter median setae have pores of smaller size (the difference is more evident in liquid) and seem to be a part of the hairy coat of the head underside (Fig. 4).

The submental suture is distinct and nearly straight (Fig. 4, indicated by the yellow arrow). The paraglossae are crescent-shaped and glabrous, the glossa with a prominent apex deeply incised laterally, bearing four usual long setae on each side, the median pair being longest and set more ventrally. There is an additional very short seta between glossal setae 3 and 4 on each side (Fig. 5, indicated by the yellow arrow).

The presence of three elytral setiferous pores (apart from the preapical pore) in the new species of *Taniatrechus* deserves special attention since this feature bridges even more the gap between *Taniatrechus* and its putative relative, the genus *Pheggomisetes* Knirsch, 1923. For more discussion on this character, see the notes section under *T. xeniae* sp. nov.

The microsculpture of *Taniatrechus* also deserves to be specially considered. It is a rare case among Caucasian Trechini when the microsculpture consists of meshes much more transverse on the pronotum than on the elytra (Fig. 7 *vs.* Figs 8–9).

Newly available specimens demonstrate a high variation in the arrangement of pores of the apical triangle: in particular, the exterior pore may be located either much closer to the preapical pore, clearly before anterior end of the apical recurrent striole, or closer to the angulo-apical pore; the latter is barely distinguishable in some specimens, located just near the elytral apex and bearing a much shorter seta. The apical recurrent striole is very short, varying from shallow to distinct.

Taniatrechus setosus Belousov et Dolzhansky, 1994
(Figs 1–9, 19–22, 24)

Material examined. W Caucasus, **Abkhazia**, *Gudauta Distr.*, Bzyb Mt. Range, vic. of Mt. Khipsta: 1 male (genit. prep.), 1,857 m a.s.l., Souvenir Cave, -40 m [at a depth of 40 m], 19.VIII.2009, S.E. Mazina & Ja.V. Denisov leg. (cAK); 1 female, same cave, -60 m, traps, 22.VIII.2018 – 26.VIII.2019, R.S. Vargovitch leg. (cAK); 1 female, 2,386 m a.s.l., Illyuziya Cave, -400 m, X Pit, 7.I.2010, S.E. Mazina leg. (cAK); 1 female, 1,971 m a.s.l., Snezhnaya Cave, -520 m, 11.I.2010, V.V. Rystsov leg. (cAK); 1 female (genit. prep.), the same cave, -1,800 m, behind siphon of Lake Gurama, 21.I.2019, O.A. Kholodnyak leg. (cAK); 1 male, 2 females, the same cave, -1,710 m, Venskiy Hall, on clay floor, 5.I. 2022, Ju.A. Kozlovskaya & X.S. Dvoynova leg. (cIB, cAK).

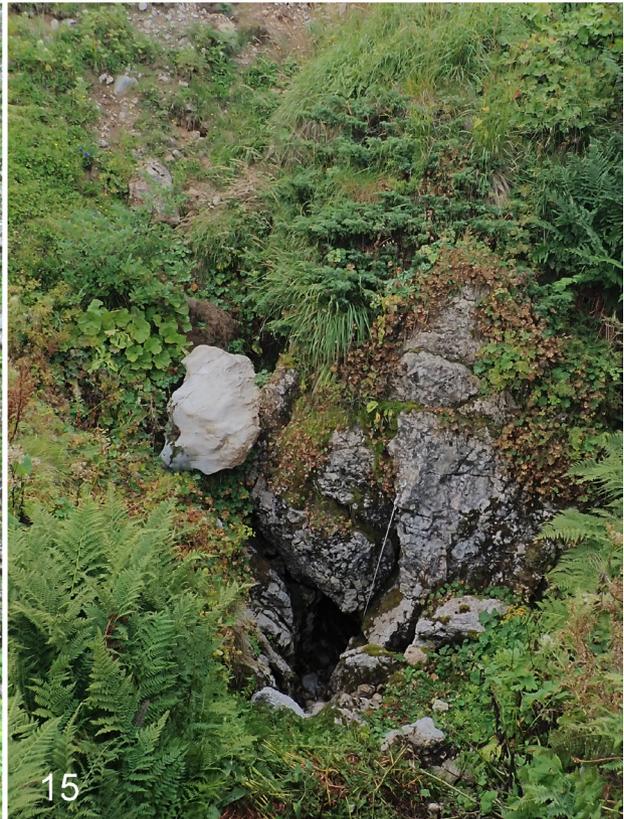
The newly available material complies with the earlier descriptions (Belousov & Dolzhansky, 1994; Belousov & Koval, 2009) in all essential morphological features. Therefore, we will focus herein on ecological data and variation in some characters with special reference to morphometric ratios, which are given in Table 1.

Notes. This genus and species have been described from one female specimen collected in Souvenir Cave (Fig. 15) at a depth of 150 m on 2 August 1979 (Belousov & Dolzhansky, 1994). This cave is located on the southern slopes of the Khipsta Karst Massif of the Razdelny Mountain Range (an isolated part of the Bzyb Mountain Range), south of Mount Khipsta, Western Caucasus, Abkhazia (Figs 10, 11). Souvenir Cave was first explored in 1977. Based on recent, more exact data, the total length of its passageways is 1,464 m, the depth is 408 m, and the absolute altitude of the entrance is 1,857 m (Shelepin, 2017). On 19 Au-

Table 1. Morphometric data, *Taniatrechus setosus*.

Index	Both sexes	Number, both sexes	Males	Number, males	Females	Number, females
Length, mm	6.68–7.63 (7.14)	6	7.09–7.09 (7.09)	1	6.68–7.63 (7.15)	5
Head						
Head width to pronotum width	1.05–1.10 (1.07)	6	1.08–1.08 (1.08)	1	1.05–1.10 (1.07)	5
Length to width	1.46–1.53 (1.50)	5	1.50–1.50 (1.50)	1	1.46–1.53 (1.50)	4
Head to neck	1.46–1.60 (1.52)	5	1.60–1.60 (1.60)	1	1.46–1.52 (1.50)	4
Antennae						
Antennae to elytra	1.76–1.97 (1.82)	6	1.87–1.87 (1.87)	1	1.76–1.97 (1.82)	5
Ant 3, length to width	6.63–7.18 (6.98)	5	6.98–6.98 (6.98)	1	6.63–7.18 (6.98)	4
Ant 3 to Ant 2	1.69–1.94 (1.83)	5	1.79–1.79 (1.79)	1	1.69–1.94 (1.84)	4
Pronotum						
Right anterior seta, %	8.94–15.0 (11.1)	5	10.5–10.5 (10.5)	1	8.94–15.0 (11.2)	4
Left anterior seta, %	9.23–14.1 (10.9)	5	10.2–10.2 (10.2)	1	9.23–14.1 (11.0)	4
Right posterior seta, %	23.5–32.2 (27.5)	5	23.5–23.5 (23.5)	1	25.6–32.2 (28.5)	4
Left posterior seta, %	19.5–32.2 (26.4)	6	24.4–24.4 (24.4)	1	19.5–32.2 (26.8)	5
Length to width	1.72–1.79 (1.76)	6	1.79–1.79 (1.79)	1	1.72–1.79 (1.75)	5
Width to base	1.48–1.73 (1.63)	6	1.68–1.68 (1.68)	1	1.48–1.73 (1.61)	5
Anterior margin to base	1.24–1.39 (1.32)	6	1.39–1.39 (1.39)	1	1.24–1.39 (1.31)	5
Prosternum width to pronotum width	0.98–1.03 (1.01)	5	1.03–1.03 (1.03)	1	0.98–1.03 (1.00)	4
Legs						
Tibia to tarsus	1.51–1.58 (1.53)	6	1.52–1.52 (1.52)	1	1.51–1.58 (1.53)	5
Elytra						
Length to width	1.92–2.04 (1.99)	6	2.02–2.02 (2.02)	1	1.92–2.04 (1.98)	5
Elytra width to head width	1.90–1.95 (1.92)	6	1.91–1.91 (1.91)	1	1.90–1.95 (1.92)	5
Elytra width to pronotum width	2.01–2.15 (2.05)	6	2.05–2.05 (2.05)	1	2.01–2.15 (2.05)	5
Length to height	2.57–2.78 (2.67)	4	2.61–2.61 (2.61)	1	2.57–2.78 (2.69)	3
D1, right elytron, %	19.6–39.6 (24.8)	5	39.6–39.6 (39.6)	1	19.62–4.1 (21.0)	4
D1, left elytron, %	17.4–23.3 (21.1)	6	21.5–21.5 (21.5)	1	17.4–23.3 (21.1)	5
D2, right elytron, %	47.9–50.0 (49.0)	5	49.7–49.7 (49.7)	1	47.9–50.0 (48.8)	4
D2, left elytron, %	45.9–54.4 (49.7)	6	49.2–49.2 (49.2)	1	45.95–4.4 (49.8)	5
Pre, right elytron, %	86.7–91.4 (89.4)	5	89.1–89.1 (89.1)	1	86.7–91.4 (89.5)	4
Pre, left elytron, %	87.3–90.7 (88.9)	6	87.38–7.3 (87.3)	1	88.0–90.7 (89.3)	5
Umb 1, right elytron, %	20.4–24.1 (21.7)	5	21.5–21.5 (21.5)	1	20.4–24.1 (21.7)	4
Umb 1, left elytron, %	19.4–22.8 (21.7)	6	22.8–22.8 (22.8)	1	19.4–22.8 (21.5)	5
Umb 2, right elytron, %	27.2–32.1 (29.3)	5	28.7–28.7 (28.7)	1	27.2–32.1 (29.5)	4
Umb 2, left elytron, %	28.5–30.9 (29.5)	6	30.03–0.0 (30.0)	1	28.5–30.9 (29.4)	5
Umb 3, right elytron, %	33.0–37.0 (35.2)	5	35.03–5.0 (35.0)	1	33.0–37.0 (35.2)	4
Umb 3, left elytron, %	34.03–6.4 (34.9)	6	34.5–34.5 (34.5)	1	34.0–36.4 (35.0)	5
Umb 4, right elytron, %	40.8–47.5 (43.6)	5	42.2–42.2 (42.2)	1	40.8–47.5 (43.9)	4
Umb 4, left elytron, %	35.6–45.1 (42.2)	6	35.6–35.6 (35.6)	1	41.0–45.1 (43.5)	5
Umb 5, right elytron, %	54.55–9.9 (56.3)	5	54.5–54.5 (54.5)	1	55.0–59.9 (56.8)	4
Umb 5, left elytron, %	54.4–58.0 (56.5)	6	55.1–55.1 (55.1)	1	54.4–58.0 (56.7)	5
Umb 6, right elytron, %	60.8–64.8 (62.4)	5	61.1–61.1 (61.1)	1	60.8–64.8 (62.8)	4
Umb 6, left elytron, %	62.0–63.6 (62.6)	6	62.0–62.0 (62.0)	1	62.0–63.6 (62.7)	5
Umb 7, right elytron, %	79.2–83.3 (80.8)	5	79.2–79.2 (79.2)	1	79.6–83.3 (81.2)	4
Umb 7, left elytron, %	79.9–83.8 (81.4)	6	80.2–80.2 (80.2)	1	79.9–83.8 (81.6)	5
Umb 8, right elytron, %	86.7–90.7 (89.0)	5	88.4–88.4 (88.4)	1	86.7–90.7 (89.1)	4
Umb 8, left elytron, %	87.4–90.5 (89.2)	6	88.48–8.4 (88.4)	1	87.4–90.5 (89.4)	5

Note. Ant # – number of antennomere, Umb # – number of umbilicate pore, D# – number of discal setiferous pore, Pre – preapical setiferous pore of elytra.



Figs 12–15. Entrances to caves. **12**, Illyuziya Cave (photo by A.L. Shelepin); **13**, Mezhenogo Cave (photo by A.L. Shelepin); **14**, Snezhnaya Cave (photo by I.N. Pelkin); **15**, Souvenir Cave, the type locality of *Taniatrechus setosus* Belousov et Dolzhansky, 1994 (photo by A.G. Koval).



Fig. 16. Bottom portion of Snezhnaya Cave. The Metrostroy Boulder Choke (photo by A.V. Shuvalov).

gust 2009, the second specimen (male) of this species was found walking on fine limestone gravel in a water-free tunnel at a depth of 40 m in the same cave. The air temperature at the collecting site was 2.8 °C (Belousov & Koval, 2009). The third specimen (female) of this species was collected by R.S. Vargovitsh using pitfall traps with fixing liquid (as described in Makarov & Koval, 1995), exposed from 22 August 2018 to 24 August 2019 in Souvenir Cave at a depth of 60 m. The air temperature at different depths of this cave at the end of August 2018 ranged from 2.8 °C at the top of the cave to 3.8 °C at its bottom (Vargovitsh, pers. comm.).

One year later, this species was collected for the first time outside the type locality in the Snezhnaya Cave System. This cave system is located within the same mountain range as Souvenir Cave, the Razdelny Mountain Range, a southeastern part of the Bzyb Mountain Range.

However, until now, their connection has not been found, although Souvenir Cave is situated within a convex polygon outlined by entrances to the Snezhnaya Cave System. It consists of six connected caves: Fantaziya Cave (entrance is located at an elevation of 1,318 m a.s.l.), Khrenova Yama Cave (entrance – 1,329 m a.s.l.), Banka Cave (entrance – 1,505 m a.s.l.), Snezhnaya Cave (entrance – 1,971 m a.s.l.), Mezhenogo Cave (entrance – 2,016 m a.s.l.), and Illyuziya Cave (entrance – 2,386 m a.s.l.) (Mavlyudov & Shelepin, 2019) (Figs 12–14). The Snezhnaya Cave System is the fourth deepest cave system in the world and, in addition, technically the most challenging. Its depth is 1,760 m and its total passage length is 40,840 m (Mavlyudov & Shelepin, 2019). Although a part of this system, Snezhnaya Cave, was discovered as early as 1971 (Tintilozov, 1976), *T. setosus* was found in this cave sys-

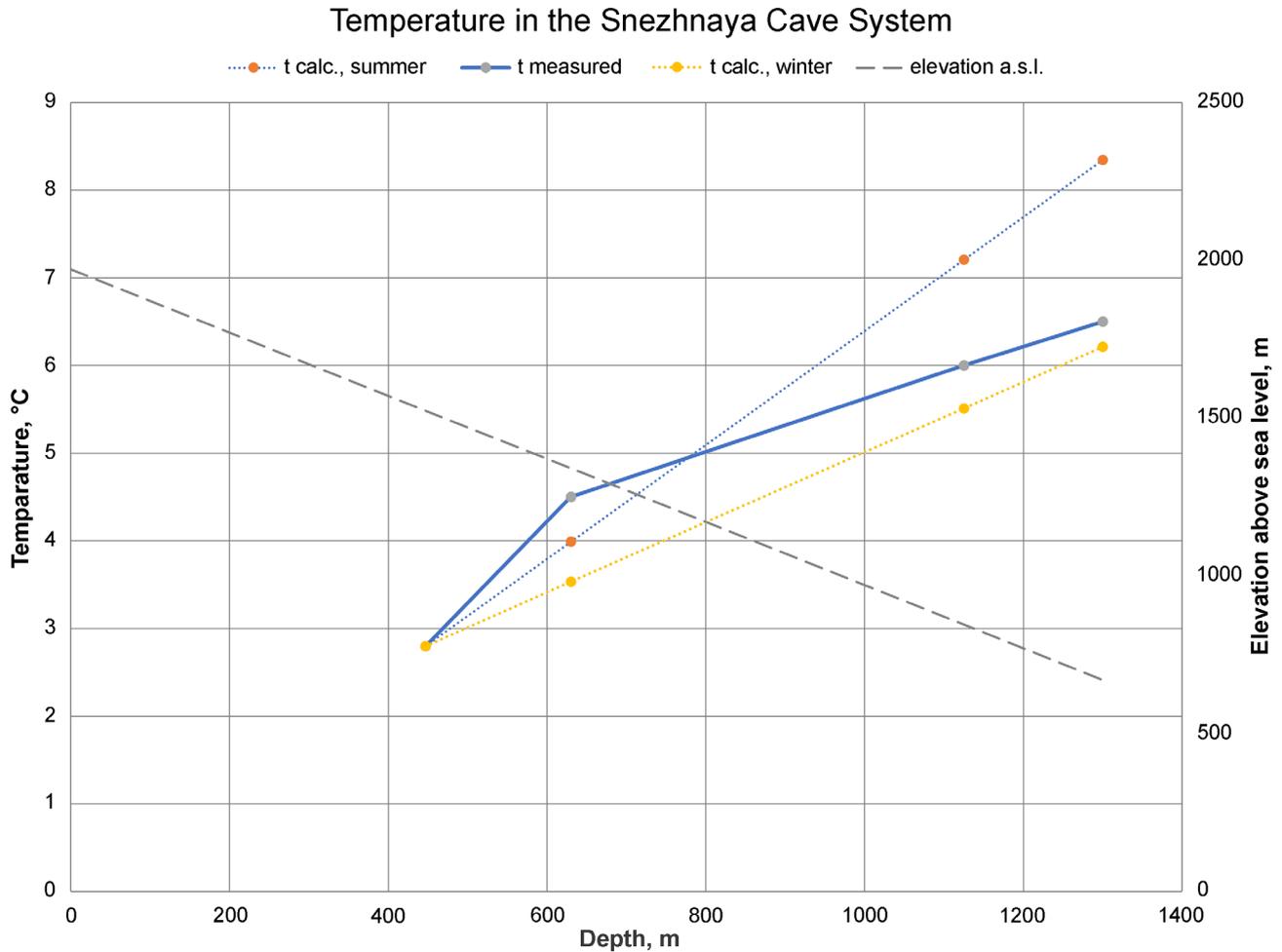


Fig. 17. Observed and calculated air temperatures at different depths in the Snezhnaya Cave System. Solid blue line – measured air temperatures, according to Mazina et al., 2011. Dotted lines – calculated temperatures based on the standard lapse rate (STLR, $-0.65\text{ }^{\circ}\text{C}$ per a 100 m rise in altitude, blue dotted line) and a slightly lower rate for wintertime and/or more humid areas based on the near-surface STLR (a $0.4\text{ }^{\circ}\text{C}$ drop for every 100 m elevation gain, yellow dotted line).

tem only in 2010. Totally, four female specimens have been collected here so far. One female was collected in Illyuziya Cave at a depth of 400 m in “X” Pit on 7 January 2010 by S.E. Mazina, the second female in Snezhnaya Cave at a depth of 520 m on 11 January 2010 by V.V. Rystsov. Supposedly, one more specimen of *T. setosus* was encountered in early January 2012, walking on a huge stone in the Metrostroy Boulder Choke, located in the bottom part of the Snezhnaya Cave System at a depth of 1,650 m from the entrance to Illyuziya Cave (Shuvalov, pers. comm.). The Metrostroy Boulder Choke is a pile of giant rocks with a total height of 127 m (Fig. 16) (Mavlyudov & Shelepin, 2019). The third female was

found in Snezhnaya Cave at a depth of approximately 1,800 m (from the upper entrance to Illyuziya Cave, the highest point of the whole cave system) by O.A. Kholodnyak (a member of A.V. Shuvalov’s expedition) in a new, still undescribed part of the cave behind the siphon of Lake Gurama on 21 January 2019 (Shuvalov, pers. comm.). To date, this finding is the deepest in the world for all cave Coleoptera.

The last expedition (December 2021 – January 2022) into Snezhnaya Cave resulted in finding three more specimens of *T. setosus* (one male and two females) collected by Ju.A. Kozlovskaya and X.S. Dvoynova. All specimens were found in Venskiy Hall at a depth of 1,710 m on 5 January.

Apparently, *T. setosus* inhabits the whole Snezhnaya Cave System. It is worth noting that all specimens of this species were collected in the cave portions which are never submerged, even during floods. Nonetheless, the relative air humidity is very high (98–100%) and drops to 94–96% only in a few locations. The air temperature in different parts of the Snezhnaya Cave System, except for near-entrance areas, is constant throughout the entire year regardless of the season and water regime, and it increases with depth. Thus, the temperature is 2.8 °C at a depth of 447 m (from the entrance of Snezhnaya Cave), 4.5 °C at 630 m, 6.0 °C at 1,125 m, and 6.5 °C at 1,300 m (Mazina et al., 2011). This increase in temperature largely correlates with the standard temperature lapse rate (STLR, a 0.65 °C temperature drop for every 100 m of elevation), as shown in Fig. 17 by the blue dotted line. On the other hand, near-surface temperature lapse rates (near-surface STLR) may significantly differ from the STLR depending on local relief and local climatic factors, such as clouds, winds, precipitation, and others. The yellow dotted line (Fig. 17), in turn, shows less steep dependence, which is often observed in areas with a more humid climate and/or in seasons with more humid and colder conditions (an approximately 0.4 °C drop in temperature for every 100 m of elevation; for details see, e.g., Kattel et al., 2015). Even in this case, the temperature in the Snezhnaya Cave System decreases with depth more slowly, and, except for the first observation, all other temperatures show a perfect linear trend with a rather slight inclination. In any case, both these lines give a rather narrow range of temperatures between 6.6 and 6.8 °C for the deepest finding of *T. setosus* mentioned above (its depth corresponds to 586 m a.s.l.). Therefore, from the standpoint of both temperature and elevation, there is still some room for further, still deeper findings of cave Coleoptera in this area. This assumption complies well with the recent finding of the new species *Plutomurus ortobalaganensis* Jordana et Baquero, 2012 (Collembola: Tomoceridae) at a depth of 1,980 m (269 m a.s.l.) meters below the surface in Krubera Cave (= Voronya Cave, = Krubera-Voronya Cave) (Jordana et al., 2012). This cave (2,249 m a.s.l.) is located in the karst massif of Mt. Arabika (Abkhazia, Gagra Mountain Range) and is in-

cluded, according to the latest data, in the Arabikskaya Cave System, which consist of six caves (Samokhin, 2019). These data give an impressive 2-km belt of subterranean habitats suitable for hypogean species. In southern China, this belt appears to be approximately twice as thick, reaching 3.5 km if based on the lowest (a lot of hypogean trechines at elevations barely exceeding 400 m, e.g., Tian et al., 2016) and highest (slightly above 3,800 m, Belousov & Kabak, 2021) findings of hypogean species. This enormous layer obviously includes complex networks of fissures with a total surface area hundreds of times greater than that of terrestrial habitats. In this context, true hypogean organisms can hardly be considered marginal exotic creatures and make up a significant share of life on Earth.

To summarise, *T. setosus* is currently known from two formally independent caves: Souvenir Cave (the type locality) and caves of the Snezhnaya System. The adjacent portions of these caves are spaced less than 150 m apart (Shelepin, pers. comm.). The small invertebrates, including *T. setosus*, are almost certainly able to pass from one cave to another through a web of fissures and microcavities.

Taniatrechus xeniae Belousov et Koval, sp. nov.
(Figs 18, 23, 25, 26)

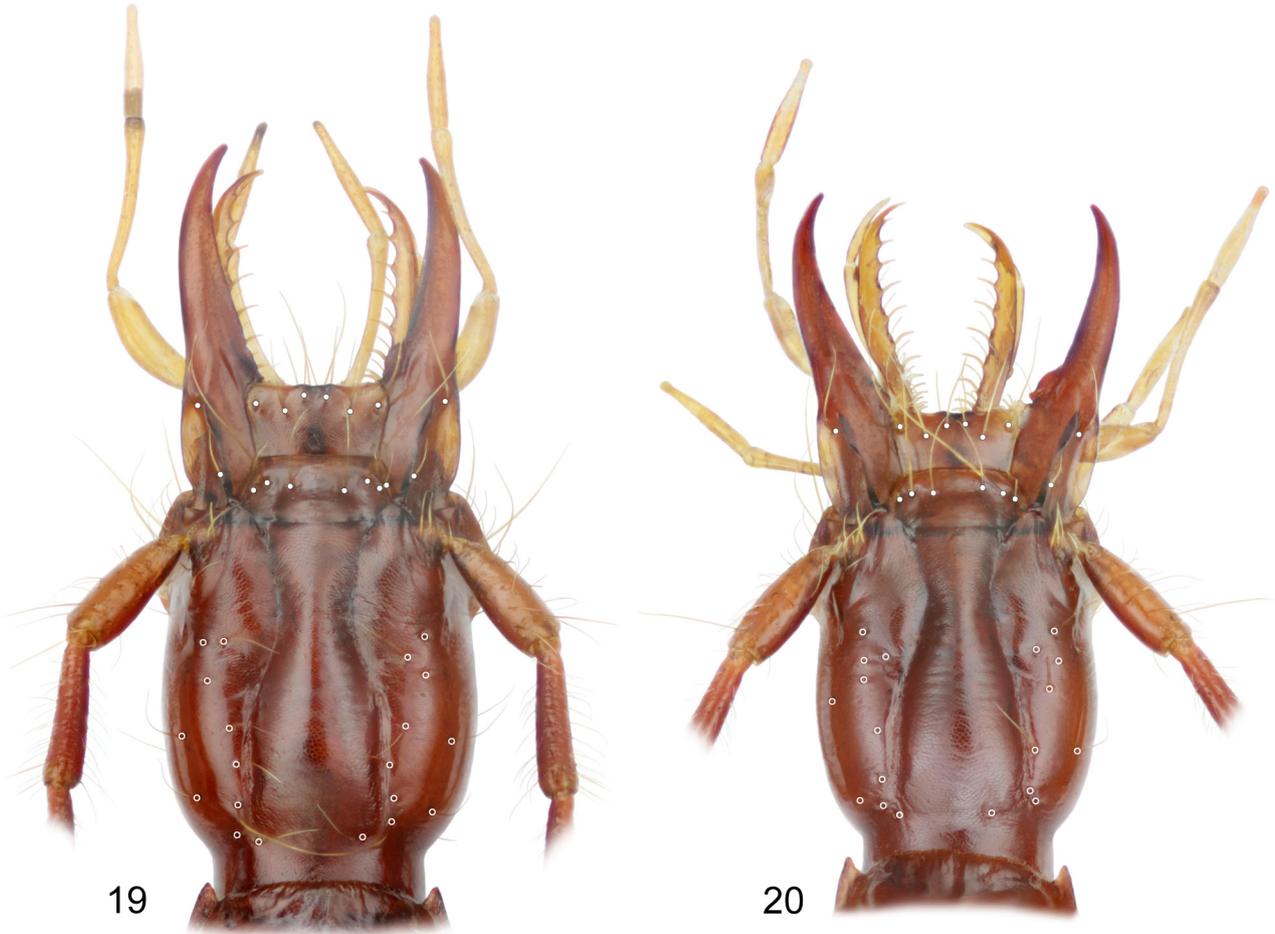
Holotype. Female (genit. prep.), **Abkhazia**, *Gudauta Distr.*, “W Caucasus, Abkhazia, Bzyb Mt. Range, 3.4 km NEE of Mt. Tshiptshira, 2,220 m, Prostor-naya Cave (= L-07 Cave), at a depth of 50 m, traps, 31.VIII.2010 – 11.VIII.2011. X.N. Gorbunova, T.V. Petrova leg.” (ZIN).

Description. Large trechine species, body length 7.9 mm. Fore-body narrow and parallel-sided, elytra slender anteriorly, clearly widened posteriorly, with maximum width clearly behind their mid-length; legs and antennae very long and slender, but not reaching elytral apex, at least, so in female holotype, antennomere 3 less than six times as long as wide and 1.73 times as long as antennomere 2, the latter barely longer than scapus. Colour amber reddish, with slightly paler, amber-yellowish elytra. Upper surface glabrous. Microsculpture of dorsum as given in description of genus: markedly transverse on pronotum and subsodiametric on head and elytra.



Fig. 18. *Taniatrechus xeniae* sp. nov. Habitus of the female holotype.

Head large, elongate, 1.53 times as long as wide, 1.03 times as wide as pronotum, slightly trapezoid in shape, gradually narrowed posteriad, with maximum width slightly behind level of clypeal suture. Neck well defined, approximately 1.5 times narrower than head. Eyes completely reduced. Tempora long, their contour subrectilinear, convex only in their most posterior portion. Genae with a few irregularly located hairs of which one genal and one temporal seta are more stable and located on each side of head. Still two hairs usually situated on lateroventral surface of gena. Frontal furrows very long, deeply impressed for most of their length, sinuate in anterior half and nearly straight, faintly divergent in posterior one, becoming very shallow but traceable near neck. From seven to ten supraorbital setae on each side of head. Labrum transverse, widest slightly before its mid-length, anterior margin nearly straight, only lateral portions rounded and faintly produced anteriorly, five (aberrant number?) rather short setae located slightly behind anterior margin. Clypeal suture well developed, three clypeal setae on each side. Mandibles very slender, slightly curved inwards in apical portion, their outer margin shallowly sinuate in basal half. Teeth on both right and left mandibles small, triangularly shaped, blade-like, with more prominent basal portion, their inner edge nearly straight, tooth of right mandible without acute proximal vertex. Maxillae slender, cardo with one ventral seta, stipes with three setiferous pores forming an obtuse triangle and one more seta shifted anteriorly. Maxillary palpi slender, glabrous, with penultimate segment s-shaped, rather thick in

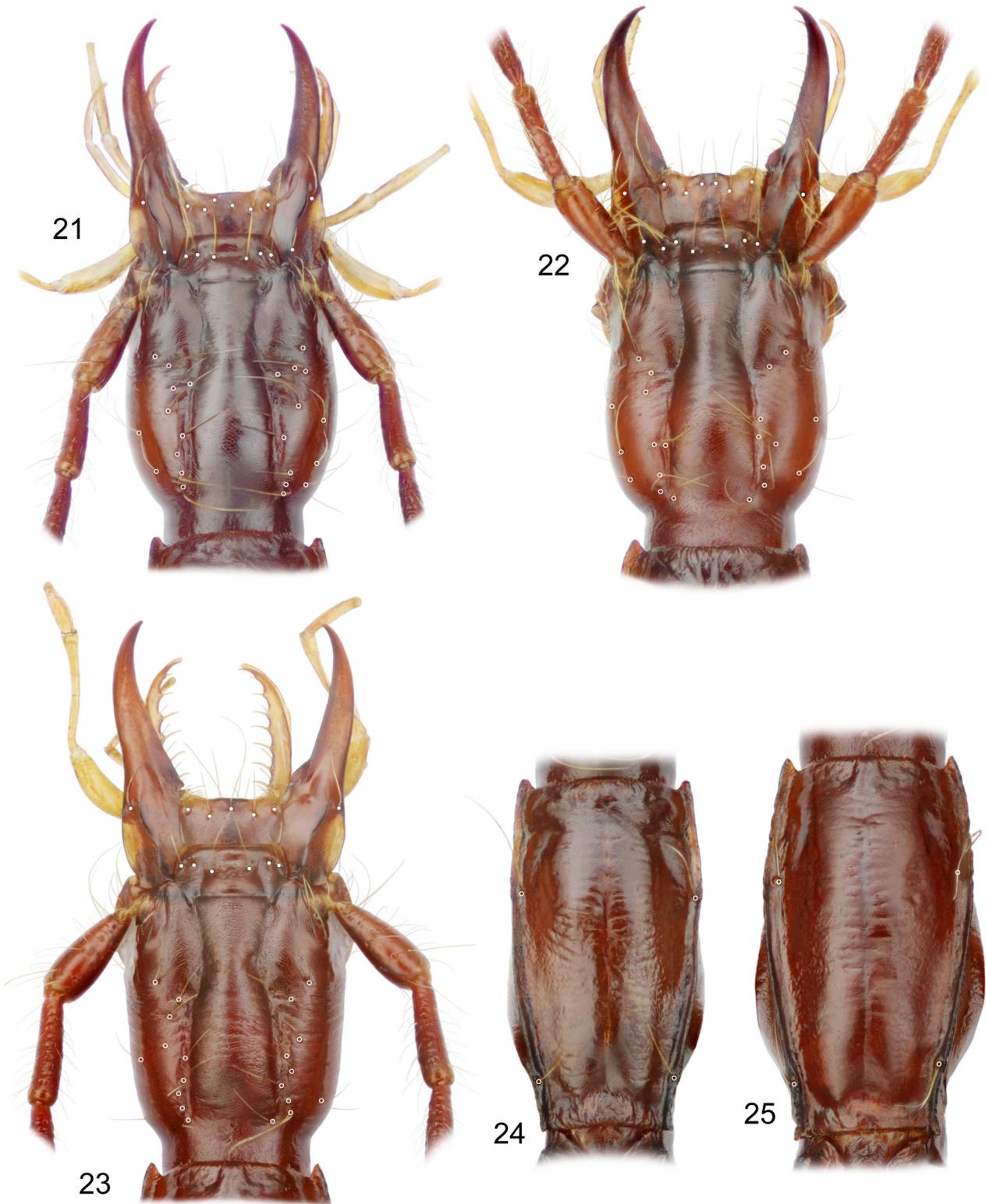


Figs 19–20. Head of *Taniatrechus setosus* Belousov et Dolzhansky, 1994. **19**, specimen from Souvenir Cave, collected by R. Vargovitsh; **20**, specimen from the same cave, collected by S. Mazina and Ja. Denisov. Supraorbital setae are shown as empty circles; clypeal setae, scrobe setae and labrum setae – filled circles.

apical portion, approximately 1.3 times as long as and markedly narrower than apical segment, the latter with slightly attenuate apical portion. Labial palpi slender, their penultimate segment s-shaped, becoming thicker in apical half, markedly longer and stouter than last segment. Labial tooth reduced. Submental suture distinct. Lateral lobes of mentum markedly produced, acute. Ligula slender, with two apical setae and three lateral setae on each side. Nine submental setae, of which the 3rd outer setae are longest and median seta shortest. Three inner setae short and asymmetrically located. Lateral setae clearly shifted anteriorly. Gular area transversally rugose (four transverse wrinkles distinct and one blurred).

Pronotum elongate, 1.77 times as long as wide, lateral margins largely straight, barely sinuate pos-

teriorly, undulate, or even notched in anterior and posterior thirds. Prosternum swollen, 1.07 times as wide as pronotum, its lateral portions clearly visible from above on both sides. Front angles rather acute and markedly produced anteriorly, hind angles small, acute, directed back and outwards. Anterior margin convex, posterior margin slightly concave. Sides distinctly sinuate before hind angles. Lateral groove rather wide, broadest near anterior lateral seta located in anterior third of pronotum (30–32%); posterior pronotal seta markedly shifted forwards (by 14–18% of pronotal length); lateral margins strongly reflexed upward. Prebasal transverse impression distinct but not sharp, basal surface rather smooth, with a few longitudinal wrinkles in lateral portions. Basal foveae small and shallow. Median line distinct, deepest



Figs 21–25. Head (21–23) and pronotum (24, 25) of *Taniatrechus setosus* Belousov et Dolzhansky, 1994 (21, 22, 24) and *T. xeniae* sp. nov. (23, 25). Supraorbital setae are shown as empty circles; clypeal setae, scrobe setae and labrum setae – filled circles. **21**, specimen from Illyuziya Cave, collected by S. Mazina; **22**, specimen from Snezhnaya Cave, collected by V. Rystsov; **24**, the same specimen as in Fig. 21.

Fig. 26. Hemisternites of *Taniatrechus xeniae* sp. nov.



near prebasal transverse impression. Discal foveae distinct. Apical transverse impression vague and shallow.

Elytra rather small compared to other parts of body, their maximum width clearly behind mid-length, with humeri completely effaced, 1.93 times as long as wide, 2.08 times as wide as head, and 2.15 times as wide as pronotum. Elytral striation very shallow, only striae 1–2 distinct, though stria 2 markedly shortened, stria 3 fragmentary, others largely disappearing, all visible striae irregular, undulate, without distinct punctures. Parascutellar striole distinct, parascutellar seta present. Apical recurrent striole rather short and shallow. Three discal setiferous pores and preapical pore in stria 3, their location in percentages to length of elytra: 22–43–53–87 on left elytron and 24–35–55–90 on right one. Preapical setiferous pore located in anastomosis of striae 2 and 3. Humeral group of umbilicate series in aggregate condition, although umbilicate pore 2 significantly larger and located much closer to elytral margin than other pores. Umbilicate series slightly less aggregate than in *T. setosus*: in humeral group, level of pore 2 closer to level of pore 1 (partially due to clearer inward shift of the latter), pore 5 nearly in middle between pore 4 and pore 6 (only on left elytron, quite likely an aberrant condition), pore 7 less spaced from pore 6; pores 3 and 4 as well as pores 7 and 8 most distant. Umbilicate pores 2, 6, and 8 bearing much longer setae. All pores

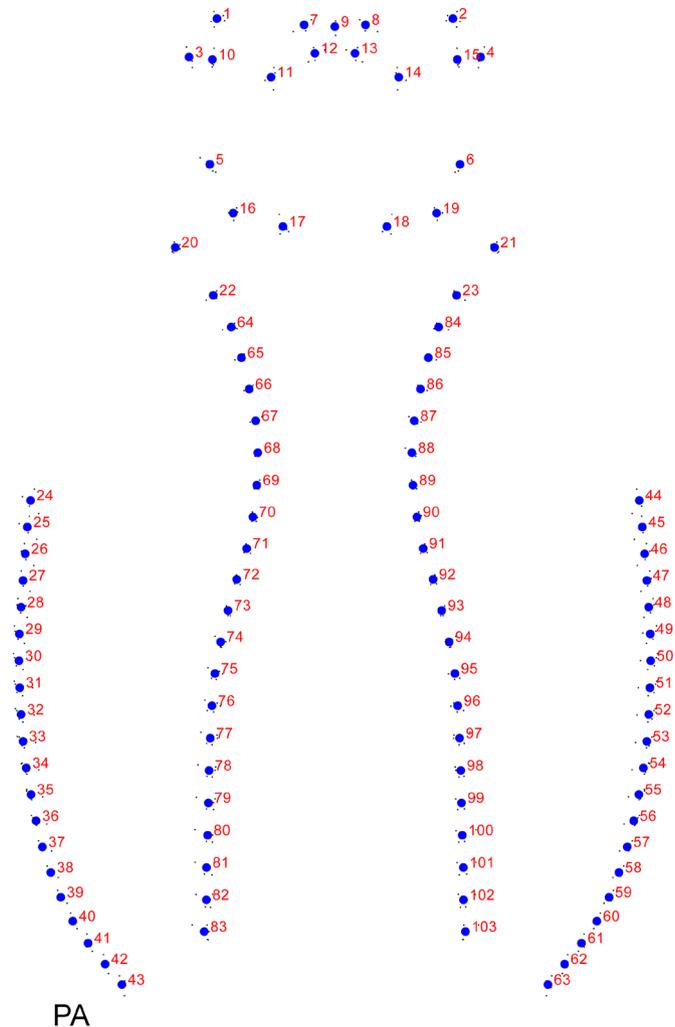


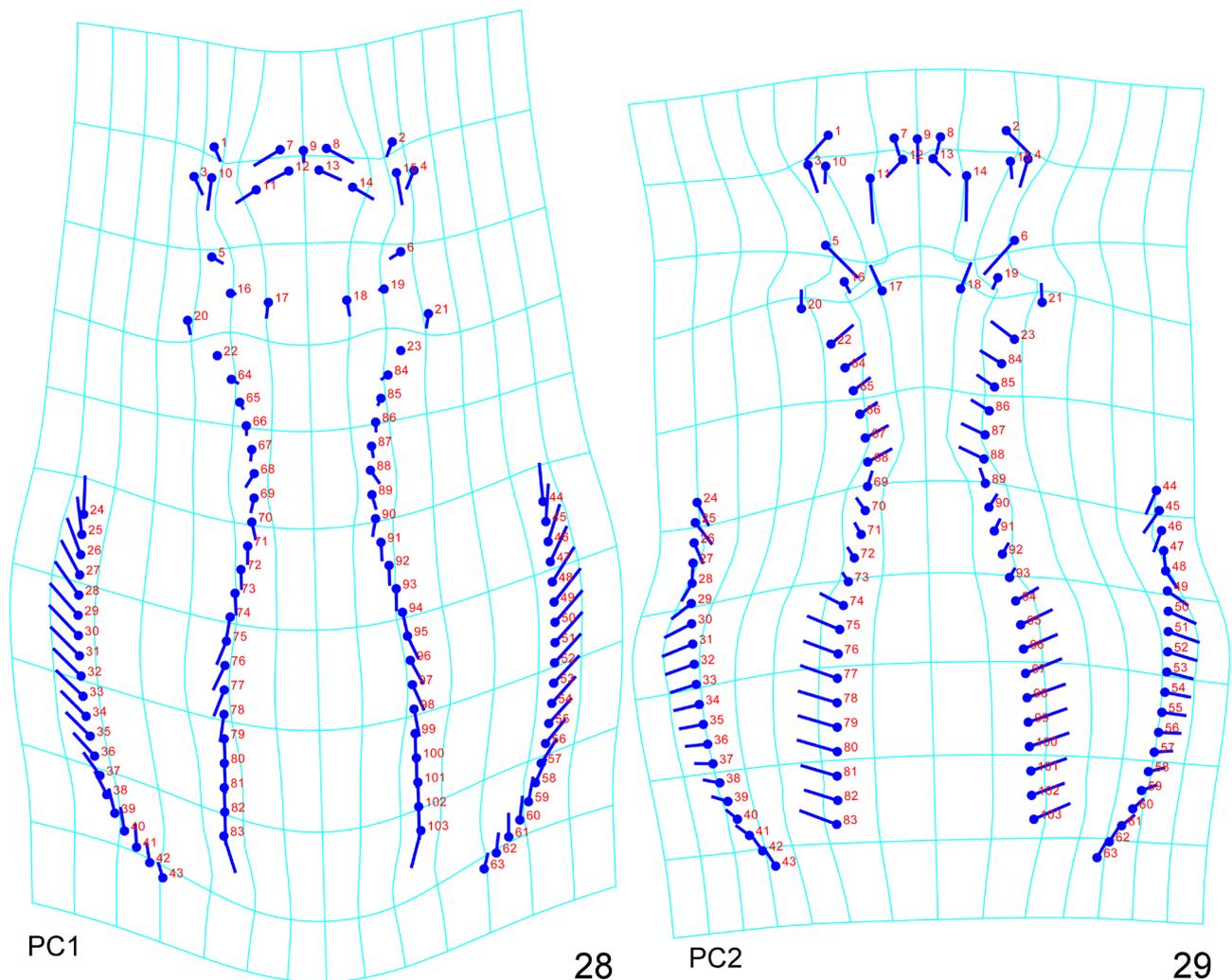
Fig. 27. GPA for the head shape in *Taniatrechus* spp. Procrustes superimposition (PA) for head landmarks.

of apical triangle present, although exterior pore and especially angulo-apical pore much smaller and bearing much shorter seta than preapical pore. Exterior pore located in a large but shallow impression, clearly spaced from apical striole and located markedly before its anterior end, much closer to preapical pore.

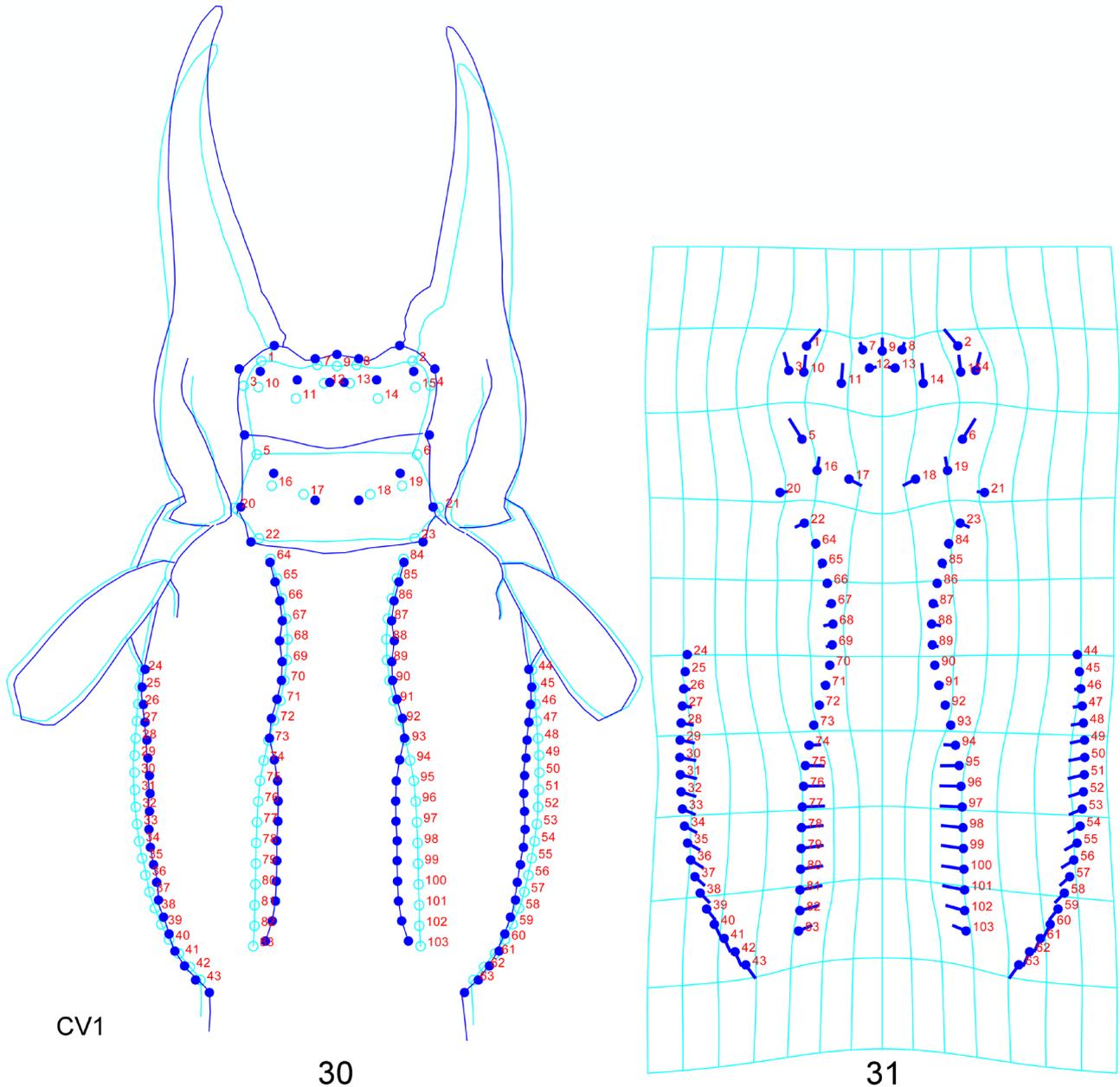
Metepisternites approximately as long as wide. Last visible abdominal sternite (sternite VII) with two pairs of setae, median ones being slightly shifted anteriorad, abdominal sternites IV–VI usually with a pair of paramedian setae on each side, only sternite VI with 3 setae on left side. Suture between abdominal sternites II and III distinct throughout.

Female genitalia as in Fig. 26. Both the right and left hemisternites are shown to give an idea of their different looks depending on the projection and effect of osmotic pressure in the euparal. Gonocoxite 2 rather thick, with broadly ovate apical portion, only slightly arcuate in its normal state (in contrast to the photograph). Laterotergites IX with blade-like stout processus.

Notes. The new taxon is easily distinguished by having three discal setiferous pores *vs.* only two in *T. setosus*. The number of discal setiferous pores and the placement of the preapical pore are important taxonomical characters in the tribe Trechini, which are used at both the specific



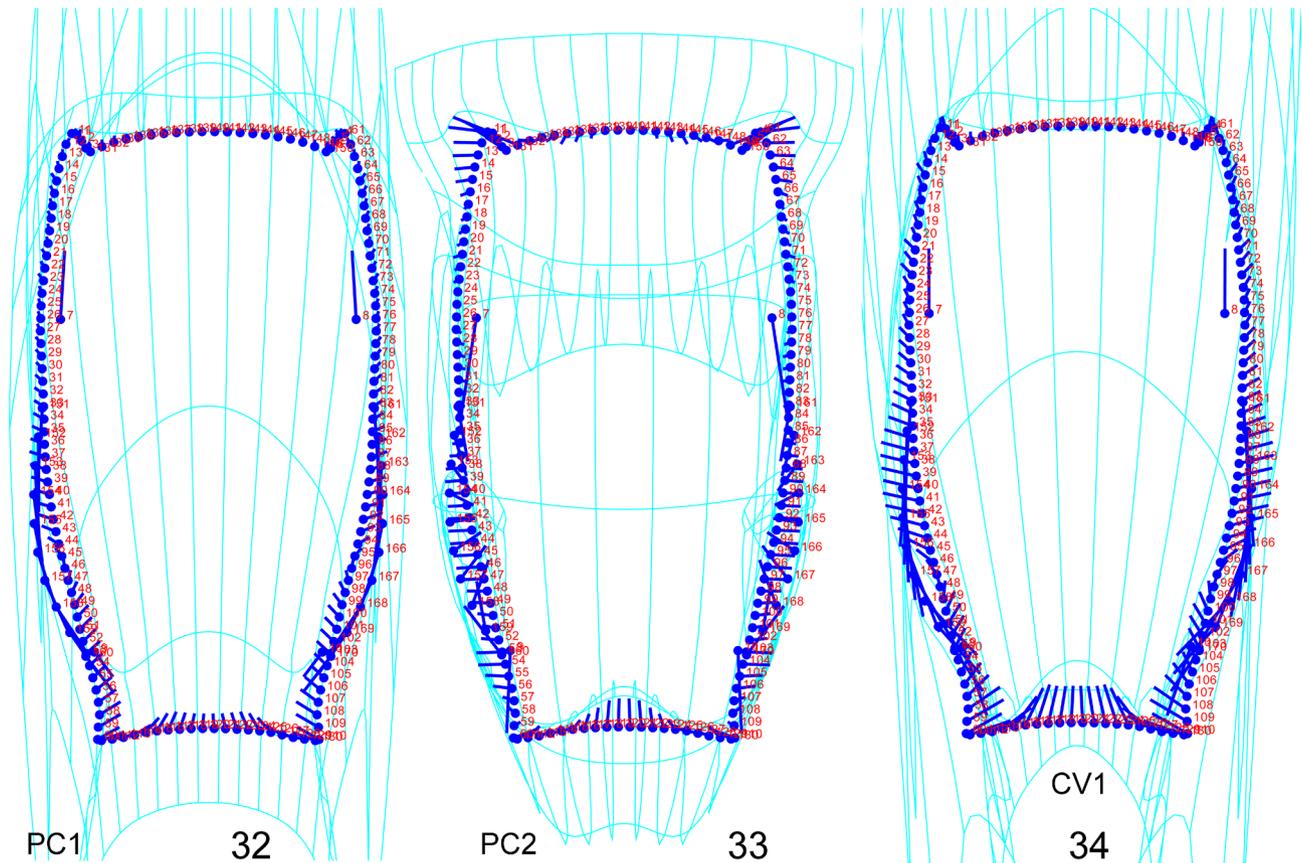
Figs 28, 29. PCA for the head shape in *Taniatrechus* spp. **28**, PC1 – first principal component; **29**, PC2 – second principal component. The two first components account for 71.4% of the cumulative variance without a significant drop between PC1 and PC2 (39.1% *vs.* 32.3%).



Figs 30–31. Canonical variate analysis (CVA) of differences between *Taniatrechus xeniae* sp. nov. and *T. setosus* Belousov et Dolzhansky, 1994 in the head shape. **30**, outline graph, dark blue dots – *T. xeniae* sp. nov.; **31**, lollipop graph, transformation from *T. setosus* (dark blue dots) to *T. xeniae* sp. nov.

and generic levels. Furthermore, the boundary between two and an increased number of discal setiferous pores is of high taxonomic importance since the first state is typical for the overwhelming majority of Trechini. For instance, among over 500 species of the genus *Trechus* Clairville, 1806 from the Caucasus and Asia, there are only a few species with three discal setiferous pores (e.g., *Trechus*

academiae Deuve, 1992, and unpublished data for Caucasian *Trechus*). On the other hand, taxa with increased numbers of discal setiferous pores often show significant variation in their number within and among taxa (e.g., the phyletic series of *Kozlovites* Jeannel, 1935). Bearing in mind the fact that all known specimens of *T. setosus* have only two discal setiferous pores on each elytron and the

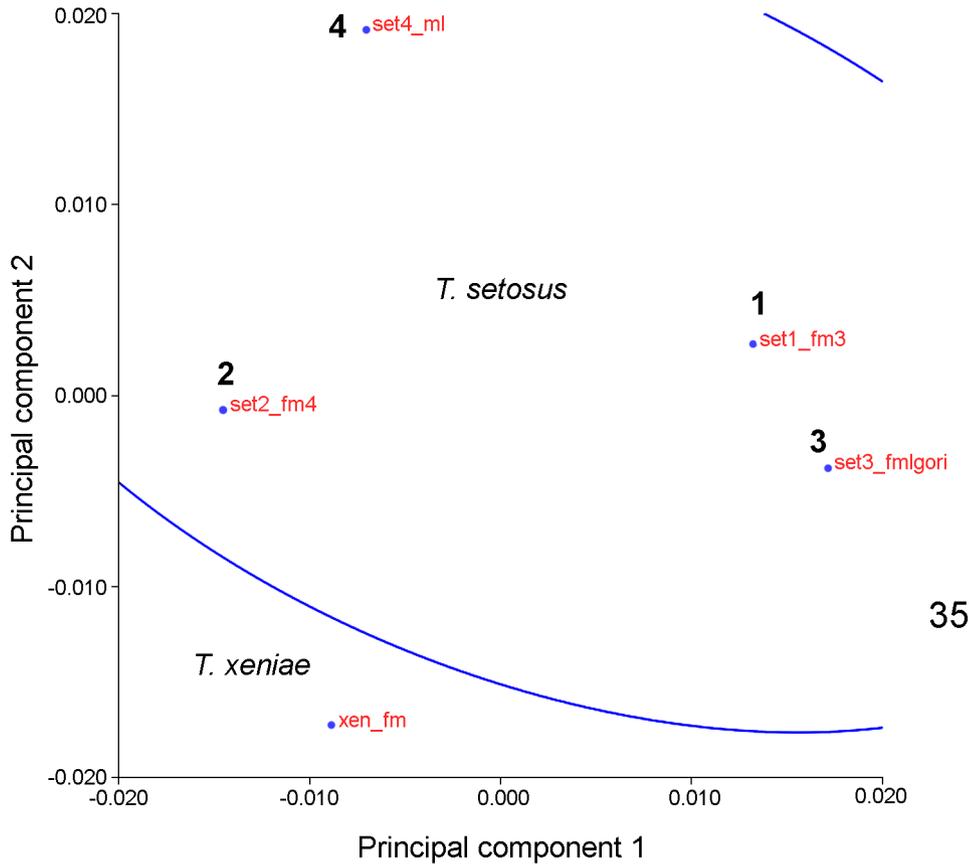


Figs 32–34. PCA and CVA for pronotum landmarks. **32**, PCA1 – first principal component; **33**, PCA2 – second principal component; **34**, CVA, differences in pronotum shape between two species, dark blue dots for *Taniatrechus xeniae* sp. nov.

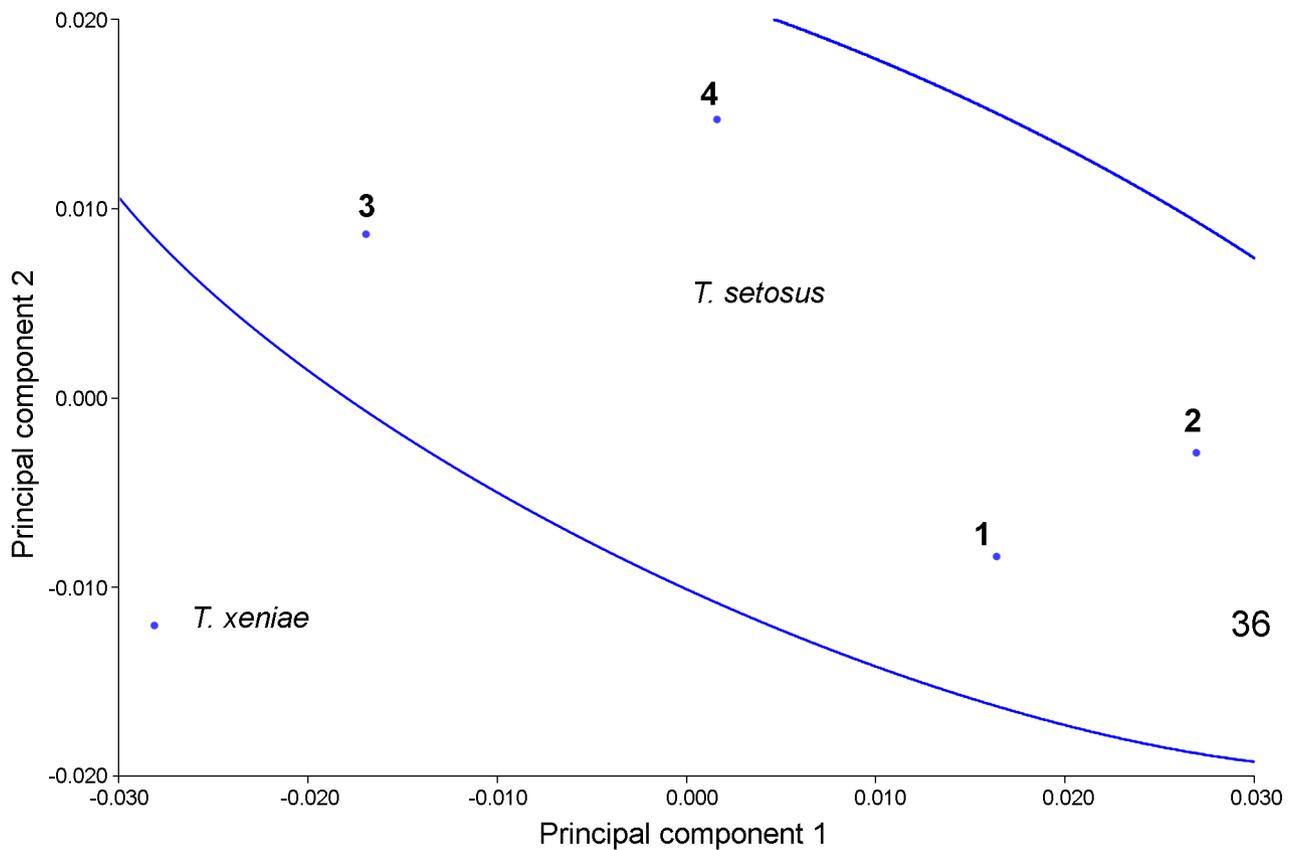
above-mentioned taxonomic importance of the difference between two and more setiferous pores in Trechini, an aberrant condition of this character in *Taniatrechus xeniae* sp. nov. seems unlikely, though not impossible. On the other side, in view of possible close relationships between *Taniatrechus* and *Pheggomisetes* Knirsch, 1923 (Belousov & Dolzhansky, 1994; Belousov & Koval, 2009), three discal setiferous pores of *Taniatrechus xeniae* sp. nov. bring the two genera even closer. GPA with the following PCA as well as morphometric indices show that the third elytral pore of *Taniatrechus xeniae* sp. nov. is located slightly behind the second pore in *T. setosus* but within or close to the upper limit of its range (53–55 vs. 46–55, on average 50 in *T. setosus*).

Apart from the number of the discal setiferous pores on the elytra, the two species differ in a few more characters, first of all in the shape of the head and pronotum.

Head. The generalised Procrustes fit (GPA) was conducted with all measured specimens of *Taniatrechus* based on 103 landmarks with preliminary pairing of symmetrical landmarks in MorphoJ software. Procrustes residuals are shown in Fig. 27. These data were treated using PCA. In Fig. 28, PC1 is shown, while PC2 is plotted in Fig. 29. The two first principal components are shown as wireframe graphs. These two components account for 71.4% of the cumulative variance without a sharp drop between PC1 and PC2 (39.1% vs. 32.3%). Examination of PC1 clearly shows that it is caused by different projections of the compared specimens. Despite all our efforts to photograph specimens in one focal plane (for details, see the material and methods section), the deformation on the wireframe graph and lollipop graph demonstrate significant longitudinal dispersion of frontal furrows landmarks and those of the head contour in opposite directions due



Figs 35, 36. Two first PC for head (35) and pronotum (36) landmarks, all GM-studied specimens. A 90% confidence ellipse is shown for specimens of *T. setosus* Belousov et Dolzhansky, 1994.



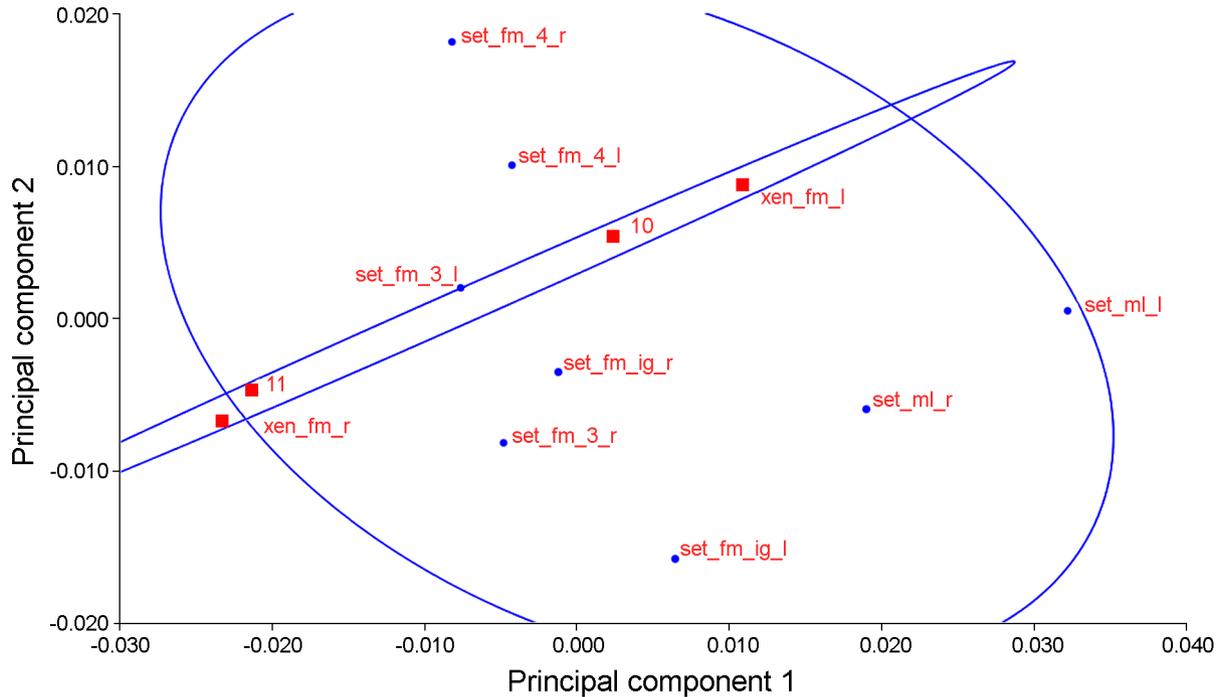


Fig. 37. Two first PC for landmarks of elytra (right elytra were mirrored), red squares – *Taniatrechus xeniae* sp. nov. (internal markers are based on the new stack of photographs made in correct projection), blue circles – *T. setosus* Belousov et Dolzhansky, 1994, all GM-studied specimens. A 90% confidence ellipses is shown for specimens of both species.

to the different head tilt in a few analysed specimens. PC2 seems much more promising from a taxonomic standpoint and shows the differences in real shape due to the shift of landmarks in the transverse direction, which is much more stable to projection distortions, especially bearing in mind the “object symmetry” option taken for all analyses. The two first PC for all specimens are shown in Fig. 35.

Canonical variate analysis (CVA) was used to reveal major differences in the head shape between *Taniatrechus xeniae* sp. nov. and *T. setosus*. Its graphic output for the scale factor 5 is shown in Figs 30–31. It is obvious that the differences between species largely match the shape variation of PCA2, with a slight correction by PC1. In other words, despite some upward tilt of the anterior portion of the head in *Taniatrechus xeniae* sp. nov., the latter species really differs from *T. setosus* in that its tempora are less convex and more markedly divergent anteriorly, and its frontal furrows are less divergent posteriorly. Additional-

ly, the anterior portion of the head appears to be slightly more massive, which, on the one hand, complies with the above-mentioned differences in other parts of the head, but, on the other hand, may be accentuated by the shooting angle.

Pronotum. The differences in the shape of pronotum were analysed in the same way. Therefore, we can skip to the obtained results without detailed explanations. Graphs for the two first PCA and CVA are given in Figs 32–34. These data are less straightforward for interpretation compared to those for the head. The impact of the pronotum tilt is also clear (see PC1 and CV1). PCA1 in this case accounts for 68.75% of the total variance (PCA1 and PCA2 together account for 85.82%). The inward shift of the landmarks located along the lateral margins behind the mid-length of pronotum ensures the major difference in pronotum shape between *Taniatrechus xeniae* sp. nov. and *T. setosus* (see Fig. 34, CV1). Therefore, we can describe the pronotum of *T. xeniae* sp. nov. as less quadrangular in the anterior two-thirds due

to more rectilinearly convergent lateral margins, which are less sinuate before the hind angles and leave the propleura more open from above. On the other hand, a high variability of the anterior portion of pronotum near its front angles is found in *T. setosus* and turned out to be species independent. This character reflects a degree of upward fold of the lateral margins near the front angles. The two first PC for all specimens are shown in Fig. 36.

Elytra. A similar analysis was conducted for elytra. As it was mentioned above, landmarks were used to assess the elytral chaetotaxy (only for homologous setae, additional discal setae of *Taniatrechus xeniae* sp. nov. were ignored), while semilandmarks were used to analyse the contours of elytra. No differences were found between the two species. Despite a significant shift in the position of umbilicate pore 5 on the left elytron in the holotype of *T. xeniae* sp. nov., its position on the right elytron is just within the typical range of *T. setosus*. As it became clear in postprocessing, the first photograph of the elytra was made in a wrong projection, making the right and left elytra clearly asymmetrical (grids for both elytra were affine transformed in reverse directions). For this reason, we have completely redone all photographs of the stack and remade the GPA and PCA analyses. However, we kept the original data to illustrate how the wrong shooting projection might affect results (the outer markers in Fig. 37). With all that in mind, the confidence ellipse for *T. xeniae* sp. nov. herein refers more to an error of measurement than a characteristic of the species.

A parametric comparison of traditional indices within the framework of linear morphometrics showed that there are some significant differences between two taxa. Even though *Taniatrechus xeniae* sp. nov. is known for a single specimen, *T. setosus* is represented by a series of individuals collected in different years and different places. Therefore, the statistically significant differences between these two species can be kept as likely, at least until new material becomes available. *Taniatrechus xeniae* sp. n. differs in having a smaller head compared to the elytra (elytra width to head width is 2.08 vs. 1.90–1.95 in *T. setosus*, *t*-test, $p \leq 0.001$ for both sexes, and $p \leq 0.01$ for females),

a slightly thicker antennomere 3, which is less than six times as long as thick vs. more than six times in *T. setosus* (*t*-test, $p \leq 0.01$), pronotum with an apex less wide as compared to the base (anterior margin to basal margin 1.13 vs. 1.24–1.39, *t*-test, $p \leq 0.05$), and prosternum more markedly wider than pronotum (1.07 vs. 0.98–1.03, *t*-test, $p \leq 0.05$).

Distribution and living conditions. The only known specimen of *Taniatrechus xeniae* sp. nov. was collected in a pitfall trap (Fig. 41) with fixing liquid (Makarov & Koval, 1995), which was left open for nearly one year in Prostornaya Cave at a depth of 50 m. The entrance to this cave (Fig. 38) is located at an elevation of 2,220 m a.s.l. in the central portion of the Bzyb Mountain Range, 3.4 km NEE of Mount Tshiptshira (Figs 10, 11). This cave was first explored by speleologists from Leningrad (now St Petersburg) in 1989 and was temporarily designated as L-07 Cave (L. Spiridonov, unpubl.). To date, this cave has not been described. Therefore, we give here its brief description.

The cave begins with a crack-like vertical pit sized 1.2–1.5 × 0.4–0.7 m and nearly 10 m deep. This pit ends up with a slight ledge (Fig. 39) in the upper dome-like portion of Obvalny Hall. The height of this hall is about 40 m. The bottom portion of the hall (Fig. 40) is 25–30 × 35–50 (m) and has an area of 1,200 square meters. The cave volume is approximately 40,000 m³. The large size of Obvalny Hall has given rise to the current name of the cave, Prostornaya Cave (“prostornaya” in Russian means spacious). In the hall, there are numerous lime and clay boulders and some water puddles. In Obvalny Hall, the air temperature was 4–5 °C in summertime (Gorbunova, pers. comm.). The total depth of the cave is 50 m. Prostornaya Cave is developed in dolomitic limestones with layers of lime sandstones and clays. Such karstic formation is common in this part of the Bzyb Mountain Range (Vakhrushev et al., 2001).

Etymology. The new species is named in honor of Xenia N. Gorbunova (St Petersburg) who participated in collecting entomological material in Prostornaya Cave and, for many years, collected insects and other invertebrates in other caves of the Western Caucasus and Crimea.



Figs 38–41. Prostornaya Cave, type locality of *Taniatrechus xeniae* sp. nov. **38**, cave entrance; **39**, upper part of the cave; **40**, Obvalny Hall; **41**, pitfall trap at the bottom of the cave. (Photos by T.V. Kovalyova).

Acknowledgements

The authors heartily thank Xenia N. Gorbunova and Tatiana V. Petrova (both from St Petersburg), who collected the new species during their exploration of Prostornaya Cave. We are also very grateful to Valentin A. Spodobin (St Petersburg) and other speleologists of St Petersburg, without whose assistance collecting insects and other invertebrates in this cave would not have been possible. We thank Leonid V. Spiridonov and Sergey L. Spiridonov (St Petersburg) for their advice and information on the history of exploration of Prostornaya Cave and their help in compiling its short description. We are very grateful to Tatiana V. Kovalyova (St Petersburg) for providing photographs of Prostornaya Cave, to Andrey V. Shuvalov (Moscow) for a very rare photograph of the bottom portion of Snezhnaya Cave and important information about this cave, and to Alexey L. Shelepin (Moscow) for two rare photographs. Our appreciation also goes to Svetlana E. Mazina, Jakov V. Denisov (both from Moscow), and Valentin V. Rystsov (St Pe-

tersburg), who collected *Taniatrechus* and gave some information about different caves. We thank heartfully Oleg A. Kholodnyak (Perm) for providing us with a female specimen of *T. setosus* collected by him. Our special thanks go to Robert S. Vargovitch (Kiev) for one female specimen of *T. setosus* collected by him, his help during common speleological expeditions, and for preparing the maps of the distribution of *Taniatrechus*. We are very thankful to Nikolay L. Ivanov (Moscow), who collected cave invertebrates in the Snezhnaya Cave System and has arranged with speleologists from different cities in Russia to do the same in other caves. We are also grateful to Oleg V. Merkuriev, Igor N. Pelkin, and Sergey V. Yashin (Sochi) for their assistance during our common expeditions in the caves of the Razdelny Mountain Range. The authors also thank speleologists Julia A. Kozlovskaya (Tomsk), Xenia S. Dvoynova (Moscow), and Yuri A. Popov (St Petersburg), participants of the expedition expedition to the Snezhnaya Cave System in December 2021 – January 2022 (head: Petr S. Koveshnikov, Moscow), for collecting new specimens of *T. setosus* and many other in-

vertebrates in this cave system. We thank the reviewers, Arnaud Faille (Stuttgart), and Kirill V. Makarov (Moscow) as well as editor, Dmitry A. Gapon (St Petersburg) for their valuable comments on our manuscript, which helped us improve its quality.

References

- Belousov I.A.** 1998. *Le complexe générique de Nannotrechus Winkler du Caucase et de la Crimée (Coleoptera, Carabidae, Trechini)*. Sofia – Moscow – St Petersburg: Pensoft Publishers. 256 p.
- Belousov I.A. & Dolzhansky V.Y.** 1994. A new aphaenopsoid genus of the tribe Trechini from the Caucasus (Coleoptera, Carabidae). *Mitteilungen der Münchner entomologischen Gesellschaft*, **84**: 59–63.
- Belousov I.A. & Kabak I.I.** 2003. New Trechini from China (Coleoptera, Carabidae). *Tethys entomological Research*, **7**: 15–86.
- Belousov I.A. & Kabak I.I.** 2021. Yalongaphaenops erwini gen. et sp. nov., the world's most high-altitude hypogean trechine beetle from China (Coleoptera, Carabidae, Trechinae). *ZooKeys*, **1044**: 197–220. <https://doi.org/10.3897/zookeys.1044.62572>
- Belousov I.A. & Koval A.G.** 2009. To the knowledge of the aphaenopsoid Trechine beetles (Coleoptera: Carabidae: Trechini) of the Caucasus. *Kavkazskiy entomologicheskii byuleten'*, **5**(2): 163–173. (In Russian). <https://doi.org/10.23885/1814-3326-2009-5-2-163-173>
- Jeannel R.** 1928. Monographie des Trechinae. Morphologie comparée et distribution géographique d'un groupe de Coléoptères. (Troisième livraison). Les Trechini cavernicoles. *L'Abeille, journal d'entomologie*, **35**: 1–808.
- Jordana R., Baquero E., Reboleira S. & Sendra A.** 2012. Reviews of the genera *Schaefferia* Absolon, 1900, *Deuteraphorura* Absolon, 1901, *Plutomurus* Yosii, 1956 and the *Anurida* Laboulbène, 1865 species group without eyes, with the description of four new species of cave springtails (Collembola) from Krubera-Voronya Cave, Arabika Massif, Abkhazia. *Terrestrial Arthropod Reviews*, **5**: 35–85. <https://doi.org/10.1163/187498312X622430>
- Kattel D.B., Yao T., Yang W., Gao Y. & Tian L.** 2015. Comparison of temperature lapse rates from the northern to the southern slopes of the Himalayas. *International Journal of Climatology*, **35**(15): 4431–4443. <https://doi.org/10.1002/joc.4297>
- Klingenberg C.P.** 2011. MorphoJ: an integrated software package for geometric morphometrics. *Molecular Ecology Resources*, **11**: 353–357. <https://doi.org/10.1111/j.1755-0998.2010.02924.x>
- Maddison D.R., Kanda K., Boyd O.F., Faille A., Porch N., Erwin T.L. & Roig-Juñent S.** 2019. Phylogeny of the beetle supertribe Trechitae (Coleoptera: Carabidae): Unexpected clades, isolated lineages, and morphological convergence. *Molecular Phylogenetics and Evolution*, **132**: 151–176. <https://doi.org/10.1016/j.ympev.2018.11.006>
- Makarov K.V. & Koval A.G.** 1995. Contribution to the biology of the ground beetle *Laemostenus tauricus* (Dejean, 1828) (Coleoptera, Carabidae) from Kizil-Koba Cave in the Crimea. *Entomologicheskoe obozrenie*, **74**(2): 307–313. (In Russian; English translation: *Entomological Review*, 1996, **75**(7): 30–37. <https://doi.org/10.1111/j.1754-8845.1996.tb00827.x>).
- Mavlyudov B.R. & Shelepin A.L.** 2019. Sistema Snezhnaya [The Snezhnaya Cave System]. In: **Shelepin A.L.** (Ed.). *Atlas peshcher Rossii* [Atlas of caves of Russia]: 751–762. Moscow: Russian Geographical Society & Russian Union of Speleologists. (In Russian).
- Mazina S.E., Bazarova E.P., Bashirov A.M., Gabbasova E.R., Gusev A.S., Kopachevskiy Yu.Yu., Kochetkov S.N., Savinov V.P. & Shadrin V.O.** 2011. Abioticheskie komponenty ekosistemy peshchery Snezhnoy (Illyuziya – Mezhenogo – Snezhnaya), sostoyanie i problemy issledovaniya [Abiotic components of an ecosystem of the Snezhnaya Cave System (Illyuziya – Mezhenogo – Snezhnaya Cave): a condition and research questions]. In: **Potapov S.S.** (Ed.). *Mineralogiya tekhnogeneza – 2011, sbornik trudov XII nauchnogo seminara* [Mineralogy of technogenesis – 2011, proceedings of XII Scientific Seminar]: 219–238. Miass: Institute of Mineralogy, Ural Branch of the Russian Academy of Sciences. (In Russian).
- Rohlf F.J.** 2015. The tps series of software. *Hystrix, the Italian Journal of Mammalogy*, **26**(1): 9–12. <http://dx.doi.org/10.4404/hystrix-26.1-11264>
- Samokhin G.V.** 2019. Sistema Arabikskaya [The Arabikskaya Cave System]. In: **Shelepin A.L.** (Ed.). *Atlas peshcher Rossii* [Atlas of caves of Russia]: 737–747. Moscow: Russian Geographical Society & Russian Union of Speleologists. (In Russian).
- Schmidt J., Scholz S. & Maddison D.** 2021. Balticer kernegeri gen. nov., sp. nov., an enigmatic Baltic amber fossil of the ground beetle subfamily Trechinae (Coleoptera, Carabidae). *Deutsche entomologische Zeitschrift*, **68**(1): 207–224. <https://doi.org/10.3897/dez.68.66181>
- Shelepin A.** 2017. Suvenir [Souvenir Cave]. *Peshchery: Informatsionno-poiskovaya sistema* [Caves: Information search system] [online]. Moscow: Russian Geographical Society. <https://speleoatlas.ru/>

- caves/suvenir-6439/ [updated 1 February 2017; viewed 25 March 2023]. (In Russian).
- Tian M.Y., Huang S. & Jia X.** 2023. A contribution to cavernicolous beetle diversity of South China Karst: eight new genera and fourteen new species (Coleoptera: Carabidae: Trechini). *Zootaxa*, **5243**(1): 001–066. <https://doi.org/10.11646/zootaxa.5243.1.1>
- Tian M.Y., Huang S., Wang X. & Tang M.** 2016. Contributions to the knowledge of subterranean trechine beetles in southern China's karsts: five new genera (Insecta, Coleoptera, Carabidae, Trechinae). *ZooKeys*, **564**: 121–156. <https://doi.org/10.3897/zookeys.564.6819>
- Tintilozov Z.K.** 1976. *Karstovye peshchery Gruzii (Morfologicheskii analiz)* [The karst caves of Georgia (Morphological analysis)]. Tbilisi: Metsniereba. 276 p. (In Russian).
- Vakhrushev B.A., Dublyansky V.N. & Amelichev G.N.** 2001. *Karst Bzybskogo khrehta. Zapadnyy Kavkaz* [The karst of the Bzyb Mountain Range. The Western Caucasus]. Moscow: Publishing house of the Peoples' Friendship University of Russia. 167 p. (In Russian).

Received 14 June 2023 / Accepted 18 September 2023. Editorial responsibility: D.A. Gapon