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Two new hyporhean species of the genus *Synurella* Wrześniowski, 1877 (Amphipoda: Crangonyctidae) from the Russian southern Caucasus

Два новых гипорейных вида рода *Synurella* Wrześniowski, 1877 (Amphipoda: Crangonyctidae) с российского Южного Кавказа

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KEY WORDS: Crustacea, Amphipoda, Crangonyctidae, *Synurella*, diversity, phylogeny, hypogean, Caucasus.

КЛЮЧЕВЫЕ СЛОВА: Crustacea, Amphipoda, Crangonyctidae, *Synurella*, разнообразие, филогения, подземный, Кавказ.

ABSTRACT. The article describes two new hyporhean species of the genus *Synurella* Wrześniowski, 1877 (Amphipoda: Crangonyctidae), *Synurella teshebi* sp.n. and *Synurella psezuapsi* sp.n., from Russian southern Caucasus. Both species phylogenetically belong to the "*behningi*" group, whose species are characterized by stygomorphic morphology, including lack of coloration and partial or complete reduction of eyes, rectangular (about 2.0X longer than wide) palmar margin of palm gnathopod II and some other morphological features. The new species differ from the related species of the "*behningi*" group in the structure and shape of epimeral plates, gnathopods II, pereopods VI and VII, telson and uropods. The distribution of the representatives of the genus *Synurella* in the southwestern Caucasus and the phylogenetic relationships between known species are discussed in the article.

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РЕЗЮМЕ. В статье описаны два новых гипорейных вида рода *Synurella* Wrześniowski, 1877 (Amphipoda: Crangonyctidae), *Synurella teshebi* sp.n. и *Synurella psezuapsi* sp.n., с территории российского Южного Кавказа. Оба вида филогенетически принадлежат к группе «*behningi*», для которых характерна стигоморфная морфология, включающая отсутствие окраски и частичную или полную редукцию глаз, прямоугольный (примерно в 2,0 раза длиннее, чем в ширину) проподус (ладонь) гнатопод II и некоторые другие морфологические особенности. Новый вид отличается от родственных видов группы «*behningi*» строением и формой эпимеральных пластинок, гнатопод II, переопод VI и VII, формой тельсона и уропод. В статье обсуждается распространение представителей рода *Synurella* на юго-западном Кавказе и филогенетические связи между известными видами.

Introduction

The crangonyctid genus *Synurella* Wrześniowski, 1877 (Amphipoda: Crangonyctidae) presently includes 16 described species, namely *Synurella ambulans* (F. Müller, 1846) (northern Germany) (the type species of the genus), *S. tenebrarum* (Wrzesniowski, 1888) (Zakopane, Poland), *S. longidactylus* S. Karaman, 1929 (Ohrid Lake), *S. taurica* Martynov, 1931 (southeastern Crimea and western foothills of Caucasus), *S. philareti* Birštein, 1948 (mouth of Dnieper River, Kherson), *S. behningi* (Birštein, 1948) (Bacha Cave, Abkhazia, southwestern Caucasus), *S. coeca* (Dobreanu et Manolache, 1951) (northwestern Germany), *S. intermedia* Dobreanu, Manolache et Puscariu, 1952 (Slovakia), *S. lepida* Mateus et Mateus, 1990 (endemic for Turkey), *S. ispani* Palatov et Marin, 2021 (endemic for Georgia), *S. spiridonovi* Marin et Palatov, 2021 (endemic for Georgia), *S. praemontana* Marin et Palatov, 2022 (western foothills of Caucasus, Shids River), *S. adegoyi* Marin et Palatov, 2022 (western foothills of Caucasus, Adegoy River), *S. montemflumina* Palatov et Marin, 2022 (western foothills of Caucasus, Olkhovka River), *S. inkiti* Palatov et Marin, 2022 (Inkit Lake, Abkhazia), *S. gizmavi* Palatov et Marin, 2022 (Gizmava Cave, Abkhazia) [Horton *et al*., 2024; Palatov, Marin, 2021; Marin, Palatov, 2022], and one fossil species from Baltic amber, *S. aliciae* Jażdżewski, Grabowski et Kupryjanowicz, 2014 [Jazdzewski *et al*., 2014]. Numerous synonyms are also known for abovementioned species, mainly for *S. ambulans* (see Horton *et al*. [2024]). The genus is widely distributed in the northwestern Palaearctic, in the north the genus is distributed to Pskov and eastern and southern parts of Lithuania, in the west — to Central

Germany and Italy, in the east – southern regions of the Eastern European Plain, in the south — to Balkan Peninsula, northern Turkey, the Crimean Peninsula and the southwestern Caucasus (e.g., Karaman [1929]; Martynov [1931]; Birštein [1948]; Sidorov, Palatov [2012]; Özbek [2018]; Palatov, Marin [2021]), from the northwestern Europe to southwestern Caucasus and northern Turkey (e.g., S. Karaman [1929]; Birštein [1948]; Dobreanu, Manolache [1951]; G.S. Karaman [1974, 1991]; Özbek [2018]). The species of the genus have been discovered in a wide range of surface ecosystems (lakes, springs, rivers, swamps, ponds) and subterranean realms (hyporheic zone (HZ), hypotelminorheic zone, phreatic interstitial zone, and caves), from coastal lowlands to mountainous regions (up to 1600 m a.s.l.) [Borutzky, 1927; Pljakić, 1957; Karaman, 1974; Holsinger, 1986; Heckes *et al.*, 1996; Culver *et al.*, 2006; Arbačiauskas, 2008; Sidorov, Palatov, 2012].

Currently, the taxonomy of the genus is still confusing, as well as the diversity of the genus is still far from being completely described. Taxonomic problems are mainly related to the lack of molecular genetic data for all described species, and clear species hypotheses cannot be presented without these data. Phylogenetically, the genus is divided into several groups, "*ambulans*" including mostly epigean/hypogean northwestern European species, "*behningi*" — mainly hypogean Caucasian species, "*intermedia*" group with species from Slovenia and Slovakia and some ancestral taxa, like *S. longidactyla* from the Balkan Peninsula [Marin, Palatov, 2022].

At the same time, the diversity of this genus is still far from being fully described, and modern studies show its high diversity in the southwestern Caucasus, where representatives of the "*ambulans*" and "*behningi*" groups probably survived in Colchis refugium during cold climatic periods during the Pliocene-Pleistocene [Marin, Palatov, 2022]. Currently, eight different species of this genus have already been described in the southwestern Caucasus [Marin, Palatov, 2022], but all available habitats and areas have not been fully studied, whereas the hypogeal lifestyle of these animals (especially from the "*behningi*" group) still makes their records unique and accidental. The article describes two new additional hypogean species of the genus *Synurella* from Russian southern Caucasus, pointing out that the diversity of the genus in this area has not been fully studied and many more species leading a hidden hypogeal lifestyle will have to be described in the future.

Material and methods

SAMPLE COLLECTION AND PROCESSING. Amphipods were collected using a hand net in various epigean and subterranean water resources in the southwestern part Caucasus (southern Russia) in 2024 year. After sampling, crustaceans were fixed in 90% solution of ethanol. The type material is deposited in the collection of Zoological Museum of Moscow State University, Moscow, Russia (ZMMU).

MORPHOLOGICAL STUDY. Morphological photographs were made with a digital camera attached to light microscope Olympus ZX10 and Olympus CX21. The article presents photographs of only the important distinguishing morphological features of the described species, whereas photographs of all morphological features of closely related species can be found in Marin and Palatov [2022]. The body length (bl., mm), the dorsal length from the distal margin of head to the posterior margin of telson, without uropod III and both antennas, is used as a standard measurement.

AMPLIFICATION AND DNA SEQUENCING. Total genomic DNA was extracted from muscle tissue using the innuPREP DNA Micro Kit (AnalitikJena, Germany). The COI mtDNA gene marker was amplified with the using of the universal primers LCO1490 (5'–GGTCAACAAATCATAAAGATATTGG–3') and HC02198 (5'–TAAACTTCAGGGTGACCAAAAAATCA–3') [Folmer *et al.*, 1994]. Polymerase chain reaction (PCR) was performed under standard conditions. Dataset of aligned sequences of COI mtDNA gene markers, about 586 base pairs in length used in the study were taken from GenBank (NCBI) (Table 1) and author data (see Marin & Palatov [2022]).

PHYLOGENETIC ANALYSIS. Consensus of complementary sequences was obtained with MEGA 7.0. The best evolutionary substitution model was determined using MEGA 7.0 and jModeltest2.1.141. A phylogenetic analysis was conducted using PhyML 3.0 (http://www.atgc-montpellier.fr/phyml/) [Guindon *et al.*, 2010] with several models based on BIC (Bayesian Information Criterion) and AIC (Akaike Information Criterion). The trees with the higher bootstrap probability were used for graphic display of relationships within the family. Bootstrap support is presented for ML analysis. The final visualization is presented on Fig. 1. Pairwise genetic divergences (*p*-distances) were calculated based on COI sequences using MEGA 7.0 with the Kimura 2-Parameter (K2P) model of evolution [Kimura, 1980].

SPECIES DELIMITATION. The species delimitation was explored under three different approaches using single-locus discovery tools: distance clustering ABGD (Automatic Barcode Gap Discovery) [Puillandre *et al.*, 2011] (https://spartexplorer.mnhn.fr/delimitation), phylogeny-aware PTP (Poisson Tree Process) [Zhang *et al.*, 2013] (https://species.h-its.org/) and Bayesian GMYC (Generalized Mixed Yule Coalescent) [Pons *et al.*, 2006; Reid, Carstens, 2012] (https://species.h-its.org/), as well as morphological evidence. The ABGD analysis was performed using online version of the program (https://bioinfo.mnhn.fr/abi/public/abgd/abgdweb.html) with the default program settings (Pmin: 0.001; Pmax: 0.1; steps: 10; Nb bins: 20); relative gap width (X) was evaluated as 0.1 and 1.0); distances were calculated using the Jukes-Cantor (JC69) substitution model as the model of nucleotide evolution. Poisson Tree Process (PTP) and the Bayesian variant of the method (bPTP) was run on the RAxML gene trees (see above) for $1x10^6$ MCMC (Markov chain Monte Carlo) generations thinning every 1000 and removing the distant outgroup that can improve the delimitation results. In GMYC analysis, the phylogenetic analyses were run in the BEAST2 package [Drummond *et al.*, 2012; Drummond, Bouckaert, 2015; Bouckaert *et al.*, 2014, 2019] using GTR, TN93 and HKY models, Yule process and Coalescent (constant size) tree priors and strict clock model. The MCMC chains were run for $10x10^6$ generations sampling every 10^4 generations were used. The best-scoring Bayesian Inference trees were estimated using GTR, HKY and TN93 models, used for further analysis and showed congruent results. Following gene tree inference, GMYC was implemented in the "splits" package (SPecies LImits by Threshold Statistics) [Ezard *et al.*, 2009] of the R software environment R v.3.5.1 (http://www.r-project.org/) with a single threshold used for COI mtDNA gene marker.

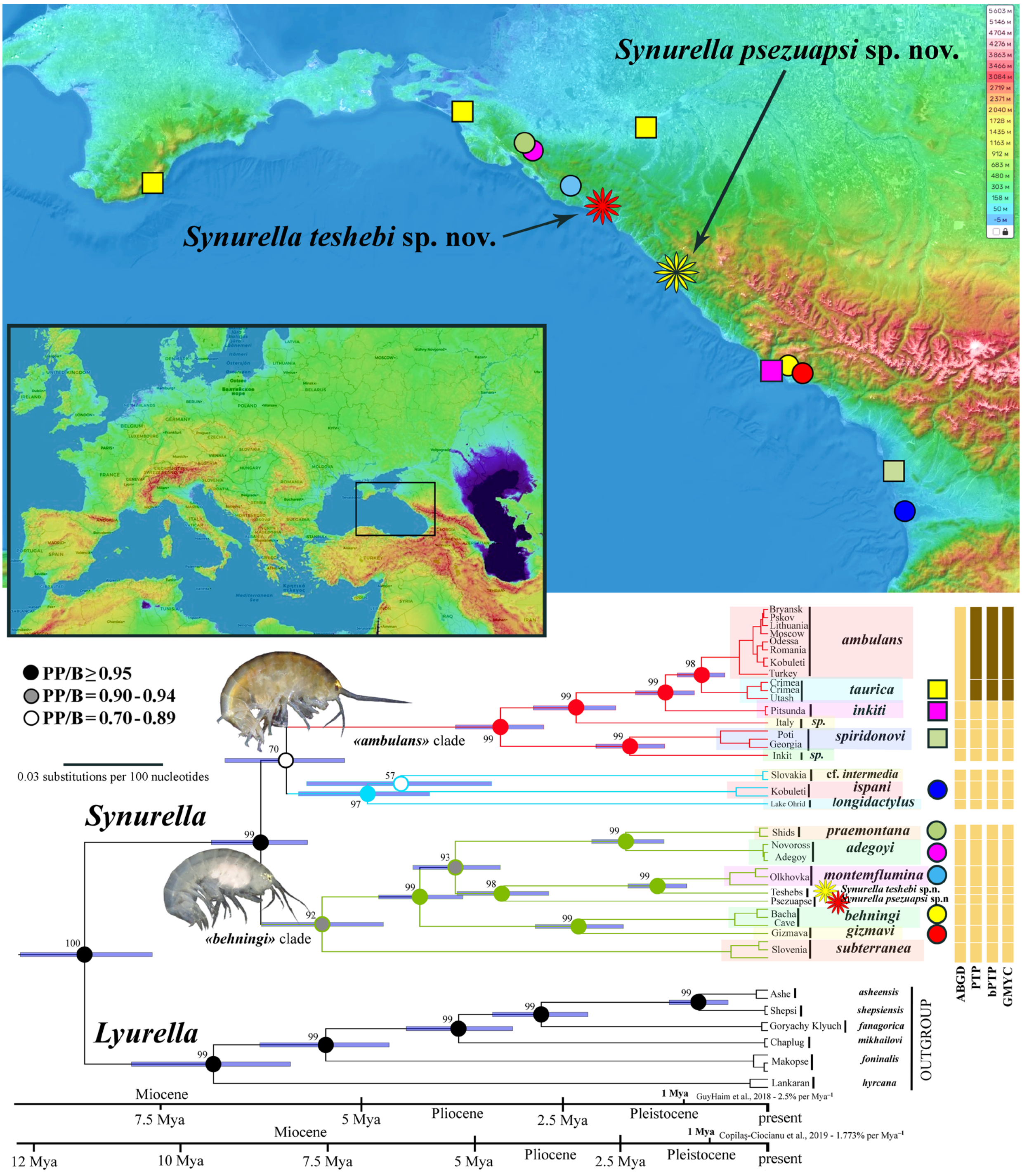

Fig. 1 The map of distribution and the time-calibrated phylogenetic tree (reconstruction) and the species delimitation analyses on COI mtDNA gene marker of the studied species of the genus *Synurella*. Posterior probabilities of the nodes are reported. Blue horizontal bars show the 95% HPD (highest posterior density) of node ages on an arbitrary time scale.

Рис. 1. Карта распространения и откалиброванное по времени филогенетическое дерево (реконструкция) и анализ видовой принадлежности по генному маркеру COI мтДНК исследуемых видов рода *Synurella*. Представлены апостериорный вероятности основных узлов. Синие горизонтальные полосы показывают 95% HPD возраста узлов в произвольном масштабе времени.

MOLECULAR CLOCK ANALYSIS was performed based on Bayesian Inference trees generated by GMYC analysis with the BEAST2 package (see above). A Maximum Clad Credibility Tree was obtained using TreeAnnotator v2.5.1, with 10% burn-in and selected mean node height [Bouckaert *et al.*, 2014]. The resulting trees were visualized with FigTree v1.4.3. The divergence time for the time scale (see Fig. 1) was calculated as 2.5% per Mya^{-1} [GuyHaim *et al.*, 2018] and 1.773% per Mya^{-1} [Copilaş-Ciocianu *et al.*, 2019].

Table 1. Comparison of pairwise genetic (COI mtDNA) distances (*p*-distances±SE) (substitutions per 100 nucleotides) between the studied species of the genus *Synurella* from the "*behningi*" group (clade).
Таблица 1. Сравнение попарных генетических (COI mtDNA) дистанций (*p*-distances±SE) (замен на 100 нуклеотидов) между изучаемыми видами рода *Synurella* из группы (клады) "*behningi*".

Synurella teshebi **sp.n.**		*S. monte-flumina*	***S. psezuapsi*** **sp.n.**	*S. behningi*	*S. adegoyi*	*S. gizmavi*	*S. subter-ranea*
S. monteflumina	0.076±0.014						
S. psezuapsi **sp.n.**	0.164±0.023	0.191±0.024					
S. behningi	0.179±0.024	0.203±0.025	0.164±0.023				
S. adegoyi	0.206±0.027	0.227±0.027	0.191±0.025	0.194±0.024			
S. gizmavi	0.207±0.026	0.216±0.027	0.230±0.028	0.128±0.020	0.206±0.027		
S. subterranea	0.234±0.029	0.257±0.031	0.256±0.031	0.245±0.028	0.252±0.031	0.233±0.028	
S. premontana	0.234±0.025	0.247±0.027	0.215±0.025	0.202±0.022	0.171±0.019	0.234±0.026	0.263±0.028

Results

PHYLOGENETIC PART. The molecular genetic analysis (Fig. 1) clearly confirmed the monophyly (PP=100) of the genus *Synurella* (see Fig. 1). The genus *Synurella* is a sister to the genus *Lyurella* Derzhavin, 1939 (PP=100) (see Fig. 1), whereas both of these genera form a clade, which is sister to the genus *Eosynurella* Martynov, 1931 [Marin, Palatov, 2021, 2022].

Three main clades within the genus *Synurella* (Fig. 1) are: the "*ambulans*" clade including mostly north-western European species, the "*behningi*" clade, which is represented by Caucasian species and the species from Slovakia, and the "*intermedia*", or Balkan, clade with ancestral *S. longidactyus,* the species from Slovakia and *S. ispani* from Georgia. The Time-calibrated evolutionary analysis (Fig. 1) revealed that the separation of the main clades occurred in the Late Miocene, about 8–6 Mya (95%HPD).

The newly described species were found to belong to the "*behningi*" clade, with the most related species – *S. monteflumina.* The genetic divergence between congeners from the clade vary from 7.6 to 26% (see Table 1) and could be considered as intraspecific for all studied species, supporting the hypothesis that the newly described *Synurella* represent new species. According to Time-calibrated evolutionary analysis (Fig. 1), *Synurella teshebi* sp.n. separated from *S. monteflumina* during the Pleistocene, while *S. psezuapsi* sp.n. separated from the congeners during the Pliocene time.

All species delimitation methods (ABGD, as well as implementing the coalescent tree-based approach PTP/bPTP and GMYC) represented congruent results, revealing 8 OTUs (i.e., operational taxonomic units, or putative species) within the "*behningi*" group (clade/lineage) (see Fig. 1). The ABGD analysis performed 8 OTUs with the prior maximal distance P=0.053318 and lower. The trees resulting from PTP and bPTP present similar results with 8 OTU. The ML (GMYC) model is 208.9362, compared to the likelihood of the null model 197.2257. As a result of the likelihood ratio test, the null model expecting uniform coalescent branching rates across entire tree was rejected (likelihood ratio=19.320026, p=6.036232e-05). The number of ML clusters in the analysis is 8 (confidence interval: 7–8 (95% CI); threshold time: – 0.02210916. The morphological analysis (see below) also strongly supports the presence of 8 separate species within the studied "*behningi*" group of the genus *Synurella*.

Taxonomic part

Order Amphipoda Latreille, 1816
Infraorder Gammarida Latreille, 1802
Family Crangonyctidae Bousfield, 1973
Genus *Synurella* Wrześniowski, 1877

Synurella psezuapsi **Palatov et Marin sp.n.**

Figs 2–3.

MATERIAL EXAMINED. HOLOTYPE, ♀ (bl. 3.8 mm) (ZMMU Mb-1307), Russian Federation, Krasnodar Kray, Sochi Urban Okrug, Lazarevsky city district, hyporheic waters of the Psezuapse River, 450 m upstream from its mouth, within the boundaries of the Lazarevskoye, 43°54′01.83″N, 39°20′10.75″E, about 2 m asl, hand net sampling, coll. D. Palatov, 31 December 2024.

ETYMOLOGY. The species is named after the place where it was discovered, in honor of the mountainous Psezuapse River, which flows into the Black Sea.

DIAGNOSIS. The species is known by single ♀. Body unpigmented, whitish. Distal segment of accessory flagellum of AI about 3.0X shorter than basal segment; primary flagellum of AI with 12 segments. Inner plate of MxI with 6 plumose marginal setae. GnI with propodus about 1.4X as long as wide, GnII with propodus about 2.5X as long as wide. Coxal plate longer than propodus of GnI–II. PVII basis with distinct posterior lobe. Coxal gill VII relatively small, about 0.25X of basis of PVII. Basal segment of UIII with 1 large and 1 small spiniform setae. Telson with distal notch reaching about 1/5 of its length. EpI with well-marked sharp posteroventral angle. EpII with 4 ventral spiniform setae. EpIII with 3 ventral spiniform setae and bluntly produced posterior angle.

DESCRIPTION. Body: moderately stout; the largest collected ♀ has bl. 3.8 mm.

Head: smooth, with bluntly produced anteroventral lobe (Fig. 3*d*); with reduced black-pigmented eyes even seen in fixed specimen (Fig. 2), and yellow dorsolateral spots seen alive.

Antenna I (Fig. 3*e*): about 50% of body length, about 1.7X longer than antenna II; primary flagellum with 12 segments, with aesthetascs on distal segments; accessory flagellum 2-segmented, distal segment about 3.0X shorter than basal one.

Antenna II (Fig. 3*f*): gland clone distinct, distally pointed; peduncle about 2.1X longer than flagellum, peduncle of segment IV about 1.2X longer than segment V; flagellum 5-segmented, without calceoli.

Fig. 2. *Synurella psezuapsi* Palatov et Marin sp.n., holotype ♀: general body view and head (enlarged).
Рис. 2. *Synurella psezuapsi* Palatov et Marin sp.n., голотип ♀: общий вид тела и голова (увеличено).

Mandible: left mandible with 4-dentate incisor, *lacinia mobilis* 5-dentate, with 4 robust plumose accessory setae; molar process with 1 long seta. Right mandible with 4-dentate incisor, *lacinia mobilis* toothed, triturative, lobes with numerous protuberances; underlying with a row of 3 robust plumose setae; molar process similar to left mandible. Palp 3-segmented, segment II with 5 setae; segment III about 3.5X longer than wide, with convex margins, with 7 separate D-setae, 1 C-setae, 1 B-seta and 4 separate E-setae.

Lateralia: with 8 teeth (Fig. 3*g*).

Labrum (upper lip): oval, apical margin with numerous small fine setae.

Labium (lower lip): inner lobes feebly developed.

Maxilla I (Fig. 3*h*): inner plate with 6 plumose marginal setae, outer plate with 7 apical comb-spines; palp 2-segmented, distal segment pubescent, about 2.5X of basal segment, apical margin of distal segment with 7–8 simple setae.

Maxilla II: inner, outer plates covered in pubescent setae; inner and outer plates subequal in length; outer plate weakly narrowing distally, with 11 apical setae; inner plate narrowing slightly distally, with group of dense short setae on apex, with oblique row of 7 short plumose setae.

Maxilliped: inner plate much shorter than outer plate, with 2 robust spiniform setae, 2 plumose and 1 simple setae apically, and 2 robust plumose setae laterally; outer plate narrow, with a double row of 16 medial stiff simple setae of different length; palp quadriarticulate, article I without setae on outer margin, article II with a row of 15 simple setae on inner margin, article III sub-trapezoidal; dactylus with a single seta on outer margin and with 2 thin setae at inner margin, nail long, slender.

Gnathopod I (Fig. 3*j*) smaller than gnathopod II; coxal plate sub-rectangular, distally rounded, with 4 apical and numerous facial setae, width/depth ratios about 0.46/1; basis width/length ratio about 0.33/1, without setae on anterior margin, with 7 long setae on posterior margin; merus as long as wide, with 10 distal setae; carpus about 0.57X of basis and 0.9X of propodus, widening distally, with 5 anterior simple setae and 10 posterior serrated setae; propodus 1.6X longer than broad, sub-rectangular, with 5 anterior simple setae, 3 inferior medial and 8 posterior serrated setae; distal margin of palm almost straight, slightly oblique, with double row of 3 inner and 3 outer robust setae, palmar groove (depression) feebly developed, with 2 inner and 2 outer robust setae; dactylus with a single outer seta.

Gnathopod II (Fig. 3*k*): coxal plate sub-rectangular, lightly narrowing distally, with 3 small apical setae, width/depth ratios about 0.45/1; basis width/length ratio about 0.27/1, with 5 setae inserted along posterior margin and with 1 long simple seta in anterior margin; ischium with 1 short simple seta; merus about as long as wide, with 4 distal setae; carpus about 0.62X of length of basis and 0.9X of propodus, widening distally, with 2 anterior simple setae and 4 groups of serrated posterior setae; propodus elongated, 2.5X longer than broad, with a single anterior seta, 6 superior medial, 3 inferior medial and 6 groups of posterior setae, palm oblique with a double row of 3 inner and 3 outer bifurcate robust setae, palm groove (depression) feebly developed, with 2 inner and 2 outer robust setae; dactylus without inner and with a single outer seta.

Pereopod III: coxal plate sub-rectangular, with 5 apical setae, width/depth ratio about 0.62/1; basis about 4.2X as long as wide, with long anterior and posterior simple setae; ischium about as long as wide; merus about 4.0X as long as wide, about 0.6X of basis, 1.4X of carpus and 1.2X of propodus in length; carpus about 3.7X as long as wide, about 0.88X of propodus in length; propodus about 5.7X as long as wide; dactylus elongated, about 0.4X of propodus, with 1 plumose seta on outer margin and 1 additional spiniform seta accompanying seta along ventral margin.

Pereopod IV: subequal to PIII in length; coxal plate expanded and broadly convex distally, posterior margin with shallow excavation, distal margin with 12 apical short setae and numerous facial setae, width/depth ratio about 1.5/1; basis about 4.4X as long as wide, with long anterior and posterior simple setae; ischium about as long as wide; merus about 4.2X as long as wide, about 0.6X of basis, 1.3X of carpus and equal to propodus in length; carpus about 4.2X as long as wide, about 0.9X of propodus in length; propodus about 5.9X as long as wide; dactylus about 0.3X of propodus, with 1 plumose seta on outer margin and 1 additional spiniform seta accompanying seta along ventral margin.

Pereopods V/VI/VII with length ratio about 1/1.25/0.90.

Pereopod V: coxal plate large, bilobate with distinct anterior and posterior lobes; posterior and anterior lobes with 1 margin

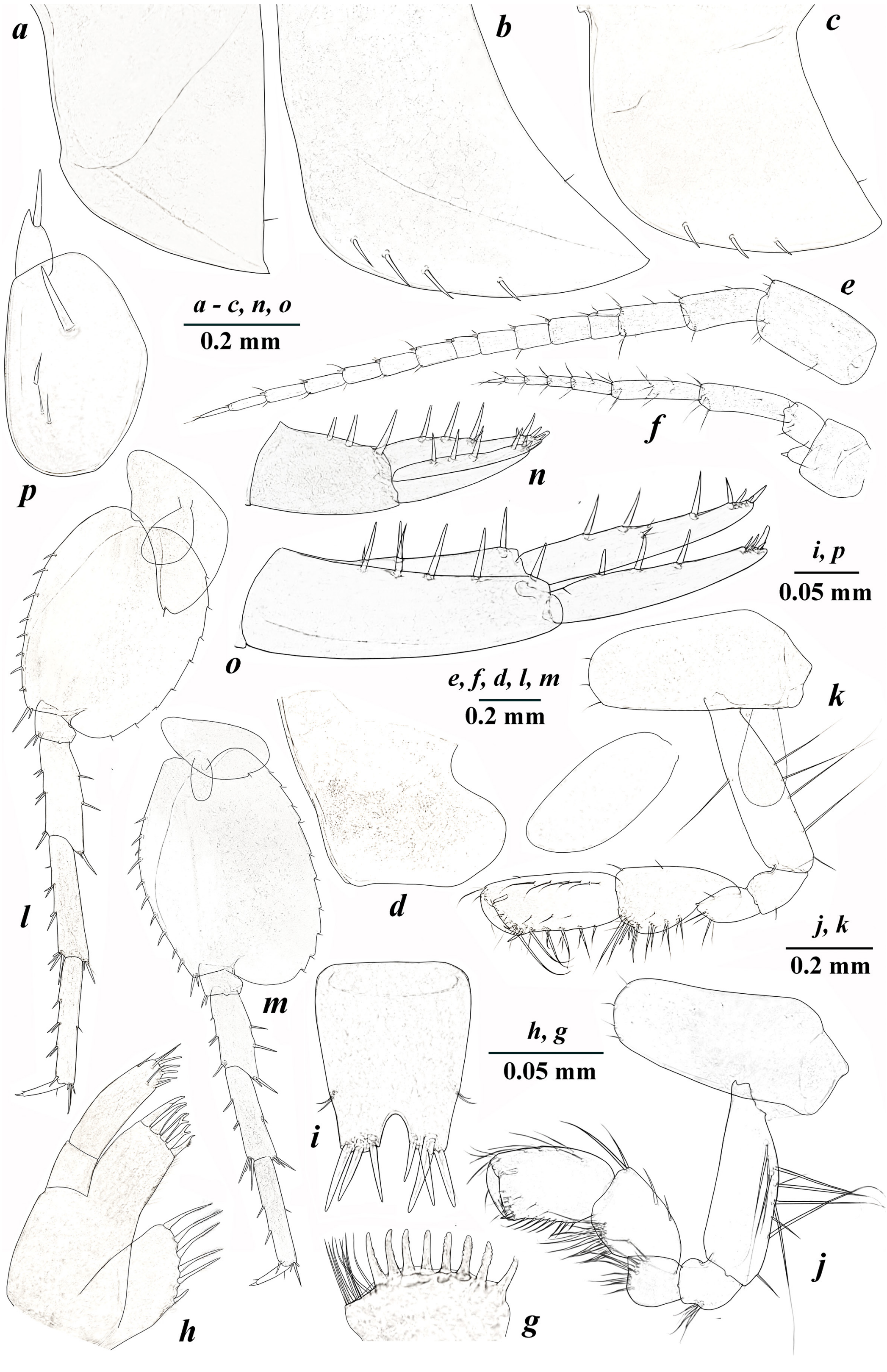

Fig. 3. *Synurella psezuapsi* Palatov et Marin sp.n., holotype ♀: *a–c* — epimeral plates I–III; *d* — head; *e* — antenna I; *f* — antenna II; *g* — lateralia; *h* — maxilla I; *i* — telson; *j* — gnathopod II; *k* — gnathopod II; *l* — pereopod VI; *m* — pereopod VII; *n* — uropod II; *o* — uropod I; *p* — uropod III.

Рис. 3. *Synurella psezuapsi* Palatov et Marin sp.n., голотип ♀: *a–c* — эпимеральные пластины I–III; *d* — голова; *e* — антенна I; *f* — антенна II; *g* — латералия; *h* — максилла I; *i* — тельсон; *j* — гнатопода I; *k* — гнатопода II; *l* — переопода VI; *m* — переопода VII; *n* — уропода II; *o* — уропода I; *p* — уропода III.

simple seta each; basis about 1.35X as long as wide, with numerous facial setae, posterior margin slightly convex, armed with 9 shallow serrations, with distal corner, anterior margin with 10 split-tipped robust and 2 distal setae; ischium about as long as wide; merus about 2.8X as long as wide, about 0.50X of basis, 0.84X of carpus and propodus in length; propodus about 5.8X as long as wide; dactylus elongated, approximately 0.43X of propodus, with 1 plumose seta on outer margin and 1 additional spiniform setae accompanying with seta along ventral margin.

Pereopod VI (Fig. 3*l*): coxal plate bilobate, with distinct posterior and vestigial anterior lobes; anterior lobe without setae, posterior lobe with a single margin seta; basis about 1.3X as long as wide, with numerous facial setae, posterior margin convex, armed with 8 shallow serrations, anterior margin with 8 split-tipped robust and 2 distal setae; ischium about as long as wide; merus about 3.0X as long as wide, about 0.5X of basis, 0.9X of carpus and propodus in length; propodus about 5.6X as long as wide; dactylus elongated, approximately 0.4X of propodus, with 1 plumose seta on outer margin and 1 additional spiniform seta accompanying seta along ventral margin.

Pereopod VII (Fig. 3*m*): coxal plate small, semi-lunar, with 1 posterior seta; basis about 1.36X as long as wide, with numerous facial setae, posterior margin convex, armed with 10 plumose setae and widely produced posterior lobe, anterior margin with 11 split–tipped robust and 2 distal setae; ischium about as long as wide; merus about 2.5X as long as wide, about 0.37X of basis, 0.9X of carpus and propodus in length; propodus about 5.4X as long as wide; dactylus elongated, approximately 0.4X of propodus, with 1 plumose seta on outer margin and 1 additional spiniform seta accompanying seta along ventral margin.

Gills, brood plates: coxal gills on somites II–VII, somites II–VII with lanceolate sternal gill on each. Coxal gills II–VII ovoid, gills/bases pereopod ratios about 0.79/1, 0.72/1, 0.75/1, 0.44/1, 0.32/1 and 0.19/1, respectively. Brood plates on somites II–V slender, setaceous, decreasing in size posteriorly.

Pleopods I–III peduncles with 2 coupling hooks in retinacula, without lateral setae; outer and inner rami with 6 and 7 segments, respectively.

Epimeral plate I (Fig. 3*a*) distally produced and sharped, ventral margin without spiniform setae, posterior margin with a single seta. Epimeral plate II (Fig. 3*b*) distally strongly produced and sharped, ventral margin armed with 4 spiniform setae, posterior margin with a single small seta. Epimeral plate III (Fig. 3*c*) distally bluntly produced, ventral margin armed with 3 spiniform setae, posterior margin with a single small seta.

Urosomites completely fused, smooth (Fig. 2).

Uropod I (Fig. 3*o*): peduncle about 3.1X as long as wide, with dorsoexternal row of 4 robust spiniform setae, 1 subdistal and 3 dorsointernal robust spiniform setae; exopodite equal to endopodite; endopodite with 3 dorsolateral and 4 short apical spiniform setae; exopodite with 3 dorsolateral and 4 short apical spiniform setae.

Uropod II (Fig. 3*n*): peduncle about 1.8X as long as wide, about 0.9X of endopodite in length, with 3 dorsal robust spiniform setae; exopodite almost equal to endopodite in length, with 3 dorsal and 5 apical robust spiniform setae; endopodite with 3 dorsal and 4 apical robust spiniform setae.

Uropod III (Fig. 3*p*): uniramous, peduncle oval, about 1.5X as long as wide, with 1 strong long spiniform seta and 3 simple setae; apical margin of ramus armed with 1 strong spiniform seta.

Telson (Fig. 3*i*): close to triangular, about 1.2X as long as broad; distal margin with V-shaped distal notch, reaching about 1/5 of its length, each lobe armed with 3–4 robust spiniform setae, with 2 additional submarginal plumose setae.

COLORATION. The body and appendages whitish transparent; pigmented black reduced, but eyes well seen (Fig. 2).

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TAXONOMIC REMARKS. The new species distinctly belongs to the "*behningi*" species complex (after Marin & Palatov [2022]), with the phylogenetically closest species — *Synurella monteflumina* Palatov et Marin, 2022 known from the Olkhovka River, located at the western foothills of Caucasus (see Fig 1).

The new species can be clearly separated from *Synurella behningi* (after Marin & Palatov [2022]) by the following features: 1) shorter distal article of accessory flagellum of AI; 2) palm (propodus) of GnII longer, about 2.5X as long as wide (vs. about 1.8X as long as wide); 3) posteriorly produced EpII; 4) EpIII with bluntly produced distoventral angle (vs. mostly triangular); 5) basal segment of UIII with well-marked distolateral lobe, distal segment with 1 strong spiniform seta (vs. distolateral lobe of basal segment of UIII feebly developed, distal segment with 1 strong spiniform seta) and 6) shape of telson close to triangular (vs. close to rectangular).

The new species can be clearly separated from *Synurella monteflumina* (after Marin & Palatov [2022]) by the following features: 1) inner lobes of maxilla I with 6 setae (vs. 5 setae); 2) ventrally produced EpII with 4 ventral spiniform setae (vs. 4 ventral spiniform setae); 3) propodus of GnII longer, about 2.5X as long as wide (vs. about 2.3X as long as wide); 4) EpII with 3 ventral spiniform setae (vs. 4 species); and 5) shape of telson close to triangular (vs. close to rectangular).

From other species of the "*behningi*" group (see Marin & Palatov [2022]), the new species can be clearly separated by elongated palm of GnII and mostly triangular telson, as well as some features of epimeral plates and uropod III (see Marin & Palatov [2022]).

DISTRIBUTION AND ECOLOGY. Hyporhean (stygobiotic) species, which is presently known only from a single locality (43°54′01.83″N, 39°20′10.75″E) in the lower part of the Psezuapse River.

***Synurella teshebi* Marin et Palatov sp.n.**

Fig. 4.

MATERIAL EXAMINED. HOLOTYPE, ♀ (bl. 3.5 mm) (ZMMU Mb-1308), Russian Federation, Krasnodar Kray, Gelendzhik Urban Okrug, basin of the Teshebs River, hyporhea of the Vtoraya Shchel River (a tributary of the Teshebs River), 44°22′08.18″N, 38°33′40.18″E, about 30 m asl, hand net sampling, coll. I. Marin & D. Palatov, 14 June 2024.

ETYMOLOGY. The species is named after the place where it was discovered, in honor of the small mountainious Teshebs River, which flows into the Black Sea.

DIAGNOSIS. The species is known by a single ♀. Body unpigmented, whitish. Distal segment of accessory flagellum of AI about 3.0X shorter than basal segment. Inner plate of MxI with 5 plumose marginal setae. GnI with propodus about 1.5X as long as wide, GnII with propodus about 2.1X as long as wide. Coxal plate longer than propodus of GnI–II. PVII basis with distinct posterior lobe. Coxal gill VII relatively small, about 0.25X of basis of PVII. Basal segment of UIII with 1 large spiniform seta. Telson with distal notch reaching about 1/5 of its length. EpI with well-marked sharp posteroventral angle. EpII with 4 ventral spiniform setae and sharply produced posteroventral angle. EpIII with 2 ventral spiniform setae and bluntly produced posterior angle.

DESCRIPTION. Body: moderately stout; the collected ♀ has bl. 3.5 mm.

Head: smooth, with bluntly produced anteroventral lobe.

Antenna I (Fig. 4*d*): about 50% of body length, about 1.7X longer than antenna II; primary flagellum with 11 segments, with aesthetascs on distal segments; accessory flagellum 2-segmented, distal segment about 3.0X shorter than basal one.

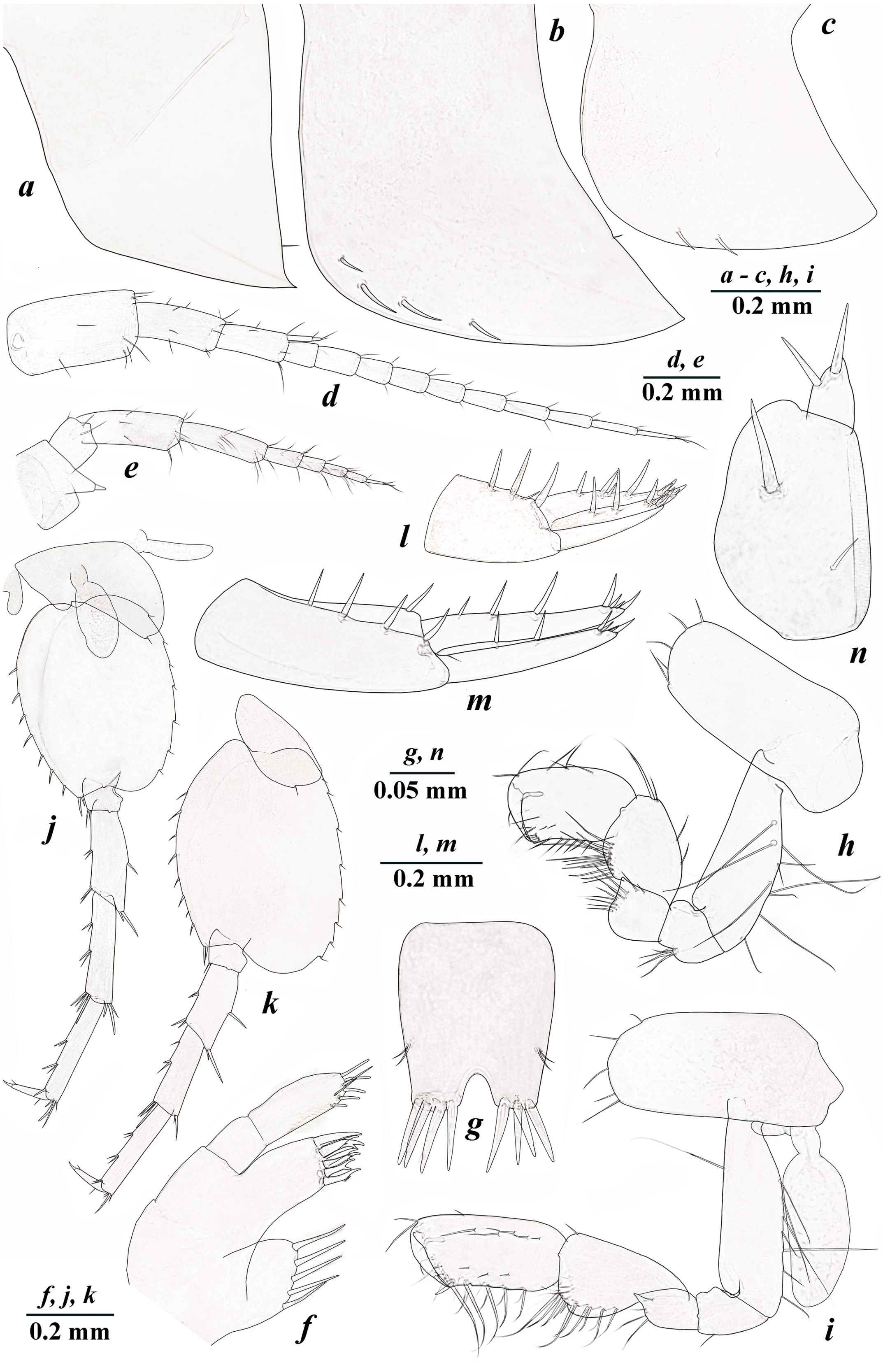

Fig. 4. *Synurella teshebi* Marin et Palatov sp.n., holotype ♀: *a–c* — epimeral plates I–III; *d* — antenna I; *e* — antenna II; *f* — maxilla I; *g* — telson; *h* — gnathopod I; *I* — gnathopod II; *j* — pereopod VI; *k* — pereopod VII; *l* — uropod II; *m* — uropod I; *n* — uropod III.

Рис. 4. *Synurella teshebi* Marin et Palatov sp.n., голотип ♀: *a–c* — эпимеральные пластины I–III; *d* — антенна I; *e* — антенна II; *f* — максилла I; *g* — тельсон; *h* — гнатопода I; *i* — гнатопода II; *j* — переопода VI; *k* — переопода VII; *l* — уропода II; *m* — уропода I; *n* — уропода III.

Antenna II (Fig. 4*e*): gland clone distinct, distally pointed; peduncle about 1.9X longer than flagellum, peduncle of segment IV subequal to segment V; flagellum 5-segmented, without calceoli.

Mandible: left mandible with 4-dentate incisor, *lacinia mobilis* 5-dentate, with 4 robust plumose accessory setae; molar process with a single seta. Right mandible with 4-dentate incisor, *lacinia mobilis* toothed, triturative, lobes with numerous protuberances; underlying with a row of 3 robust plumose setae; molar process similar to left mandible. Palp 3-segmented, segment II with 6–7 setae; segment III about 3.5X longer than wide, with convex margins, with 7 separate D-setae, 1 C-seta, 1 B-seta and 4 separate E-setae.

Lateralia: with 8 teeth.

Labrum (upper lip): oval, apical margin with numerous small fine setae.

Labium (lower lip): inner lobes feebly developed.

Maxilla I (Fig. 4*f*): inner plate with 5 plumose marginal setae, outer plate with 7 apical comb-spines; palp 2-segmented, distal segment pubescent, about 2.0X of basal segment, apical margin of distal segment with 6–7 simple setae.

Maxilla II: inner, outer plates covered in pubescent setae; inner and outer plates subequal in length; outer plate weakly narrowing distally, with 11 apical setae; inner plate narrowing slightly distally, with group of dense short setae on apex, with oblique row of 6 short plumose setae.

Maxilliped: inner plate much shorter than outer plate, with 2 robust spiniform setae, 1 robust plumose and 1 simple setae apically, and 2–3 robust plumose setae laterally; outer plate narrow, with a double row of 12 medial stiff simple setae of different length; palp quadriarticulate, article I without setae, article II with a row of 14 simple setae on inner margin, article III sub-trapezoidal; dactylus with a single seta on outer margin and with 2 thin setae at inner margin, nail long, slender.

Gnathopod I (Fig. 4*h*) smaller than gnathopod II; coxal plate sub-rectangular, distally rounded, with 5 long apical setae, width/depth ratios about 0.47/1; basis width/length ratio about 0.35/1, without setae on anterior margin, with 6–7 long setae on posterior margin; merus as long as wide, with 8 distal setae; carpus about 0.51X of basis and 0.88X of propodus, widening distally, with 3–4 anterior simple setae and numerous posterior serrated setae; propodus 1.8X longer than broad, sub-rectangular, with 4 anterior simple setae, 3 inferior medial and 6 posterior serrated setae; distal margin of palm almost straight, slightly oblique, with double row of 3 inner and 3 outer robust setae, palmar groove (depression) feebly developed, with 2 inner and 2 outer robust setae; dactylus with 1 outer seta.

Gnathopod II (Fig. 4*i*): coxal plate sub-rectangular, with rounded distal margin, with 5 small apical setae, width/depth ratios about 0.45/1; basis width/length ratio about 0.29/1, with 7 long spiniform setae inserted along posterior margin and with 1 long simple spiniform seta in anterior margin; ischium with 1 short simple seta; merus about as long as wide, with 4 distal setae; carpus about 0.6X of length of basis and 0.88X of propodus, widening distally, with 1 anterior simple seta and 5 groups of plumose posterior setae; propodus elongated, 2.2X longer than broad, with 1 anterior seta, 5 superior medial, 3 inferior medial and 5 groups of posterior setae, palm oblique with a double row of 3 inner and 3 outer robust setae, palm groove (depression) feebly developed, with 2 inner and 2 outer robust setae; dactylus without inner and with 1 outer seta.

Pereopod III: coxal plate sub-rectangular, with 5 apical setae, width/depth ratio about 0.44/1; basis about 4.0X as long as wide, with long anterior and posterior simple setae; ischium about as long as wide; merus about 3.5X as long as wide, about 0.6X of basis, 1.2X of carpus and equal to propodus in length; carpus about 4.0X as long as wide, about 0.8X of propodus in length; propodus about 6.2X as long as wide; dactylus elongated, about 0.3X of propodus, with 1 plumose seta on outer margin and 1 additional spiniform seta accompanying seta along ventral margin.

Pereopod IV: subequal to PIII in length; coxal plate expanded and broadly convex distally, posterior margin with shallow excavation, distal margin with 12 apical short setae and numerous facial setae, width/depth ratio about 1.38/1; basis about 3.8X as long as wide, with long anterior and posterior simple setae; ischium about as long as wide; merus about 3.9X as long as wide, about 0.65X of basis, 1.3X of carpus and equal to propodus in length; carpus about 3.9X as long as wide, about 0.89X of propodus in length; propodus about 4.7X as long as wide; dactylus about 0.4X of propodus, with 1 plumose seta on outer margin and 1 additional spiniform seta accompanying seta along ventral margin.

Pereopods V/VI/VII with length ratio about 1/1.08/0.94.

Pereopod V: coxal plate large, bilobate with distinct anterior and posterior lobes; posterior and anterior lobes with 1 margin simple seta each; basis about 1.28X as long as wide, with numerous facial setae, posterior margin slightly convex, armed with 7 shallow serrations, with distal corner, anterior margin with 9 split-tipped robust and 2 distal setae; ischium about as long as wide; merus about 2.8X as long as wide, about 0.55X of basis, 0.95X of carpus and propodus in length; propodus about 5.1X as long as wide; dactylus elongated, approximately 0.50X of propodus, with 1 plumose seta on outer margin and 1 additional spiniform seta accompanying seta on ventral margin.

Pereopod VI (Fig. 4*j*): coxal plate bilobate, with distinct posterior and vestigial anterior lobes; anterior lobe without setae, posterior lobe with 1 margin seta; basis about 1.2X as long as wide, with numerous facial setae, posterior margin convex, armed with 7 shallow serrations, anterior margin with 7 split-tipped robust and 2 distal setae; ischium about as long as wide; merus about 3.1X as long as wide, about 0.57X of basis, subequal of carpus and propodus in length; propodus about 5.5X as long as wide; dactylus elongated, approximately 0.4X of propodus, with 1 plumose seta on outer margin and 1 additional spiniform seta accompanying seta on ventral margin.

Pereopod VII (Fig. 4*k*): coxal plate small, semi-lunar, with 1 posterior seta; basis about 1.4X as long as wide, with numerous facial setae, posterior margin convex, armed with 8 spiniform setae and widely produced posterior lobe, anterior margin with 8 split-tipped robust and 2 distal setae; ischium about as long as wide; merus about 2.0X as long as wide, about 0.3X of basis, 0.9X of carpus and propodus in length; propodus about 4.7X as long as wide; dactylus elongated, approximately 0.42X of propodus, with 1 plumose seta on outer margin and 1 additional spiniform seta accompanying seta on ventral margin.

Gills, brood plates: coxal gills on somites II–VII, somites II–VII with lanceolate sternal gill on each. Coxal gills II–VII ovoid, gills/bases pereopod ratios about 0.81/1, 0.69/1, 0.62/1, 0.45/1, 0.47/1 and 0.12/1, respectively. Brood plates on somites II–V slender, setaceous, decreasing in size posteriorly.

Pleopods I–III peduncles with 2 coupling hooks in retinacula, without lateral setae; outer and inner rami with 5 and 5–6 segments, respectively.

Epimeral plate I (Fig. 4*a*) distally produced and sharped, ventral margin without setae or spines, posterior margin with a single seta. Epimeral plate II (Fig. 4*b*) distally strongly produced and sharped, ventral margin armed with 4 spiniform setae, posterior margin with a small single seta. Epimeral plate III (Fig. 4*c*) distally bluntly produced, ventral margin armed with 2 spiniform setae, posterior margin with a small single seta.

Urosomites completely fused, smooth.

Uropod I (Fig. 4*m*): peduncle about 2.9X as long as wide, with dorsoexternal row of 3 robust spiniform setae, 1 subdistal spiniform seta and 1 dorsointernal robust spiniform seta; exopodite equal to endopodite; endopodite with 3 dorsolateral and 4 short apical spiniform setae; exopodite with 2 dorsolateral and 4 short apical spiniform setae.

Uropod II (Fig. 4*l*): peduncle about 1.6X as long as wide, about 0.8X of endopodite in length, with 3 dorsal robust spiniform setae; exopodite almost equal to endopodite in length, with 2 dorsal and 5 apical robust spiniform setae; endopodite with 3–4 dorsal and 4 apical robust spiniform setae.

Uropod III (Fig. 4*n*): uniramous, peduncle oval, about 1.5X as long as wide, with a single strong long spine; apical margin of ramus armed with 2 strong spiniform setae.

Telson (Fig. 4*g*): close to rectangular, about 1.2X as long as broad; distal margin with U-shaped distal notch, reaching about 1/5 of its length, each lobe armed with 4 robust spiniform setae, with 2 additional submarginal plumose setae.

COLORATION. The body and appendages whitish transparent; pigmented black eyes well seen.

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TAXONOMIC REMARKS. The new species distinctly belong to the "*behningi*" species complex [after Marin, Palatov, 2022], with the phylogenetically closest species — *Synurella monteflumina* and newly described species from the Psezuapse River (see above) (Fig 1).

The new species can be clearly separated from *Synurella behningi* (after Marin & Palatov [2022]) by the following features: 1) shorter distal article of accessory flagellum of AI; 2) propodus of GnII longer, about 2.3X as long as wide (vs. about 1.8X as long as wide; 3) posteriorly produced EpII; 4) EpIII with bluntly produced distoventral angle (vs. mostly triangular) with 2 ventral spiniform setae (vs. 3 spiniform setae); and 5) basal segment of UIII with well-marked distolateral lobe (vs. feebly developed).

The new species can be clearly separated from *S. monteflumina* [after Marin, Palatov, 2022] by the following features: 1) EpII with 4 ventral spiniform setae (vs. 3 ventral spiniform setae); 2) EpIII with 2 ventral spiniform setae (vs. 3 ventral spiniform setae); 3) basis of PVI with 8 spiniform setae along anterior margin (vs. 10 spiniform setae); and 4) distal segment of UIII with 2 strong spiniform setae (vs. 1 spiniform setae).

The new species can be clearly separated from *Synurella psezuapsi* sp.n. by the following features: 1) EpIII with 2 ventral spiniform setae (vs. 3 ventral spiniform setae); 2) slightly shorter palm of GnII (2.3X vs. 2.5X (see above)); 3) sub-rectangular telson (vs. triangular in shape).

From other species of the "*behningi*" group (see Marin & Palatov [2022]), the new species can be clearly separated by features of epimeral plates, uropod III and telson (see Marin & Palatov [2022]).

DISTRIBUTION AND ECOLOGY. Hyporhean (stygobiotic) species, which is presently known only from a single locality (44°22′08.18″N, 38°33′40.18″E) in the Teshebs River.

Discussion

The discovery of new species of the genus *Synurella* in the southwestern part of the Caucasus, in the Colchis Lowland, is changing our understanding of the origins and phylogenetic relationships within the genus. We believe that there may still be many more undiscovered species in this region, and we should therefore view the conclusions presented below as tentative.

Firstly, it is important to note that all known species of the genus *Synurella* reported east of the Balkans have been be found in the Colchis lowland area (see Fig. 1), which is where the possible center of origin for at least the "*behningi*" group (clade) seems to be located. At the same time, most of the described species from the "*ambulans*" group also inhabit this region, and it is possible that the center of diversity and origin for this clade is also located here [Marin, Palatov, 2022]. According to the molecular and genetic data obtained, representatives of the genus inhabited the Caucasus region a long time ago, in the Late Miocene period, approximately 7.5–6Mya, possibly even before the formation of the Caucasus Mountains, when this region was part of the bottom of the Paratethys [Popov *et al.*, 2004, 2006; Neubauer *et al.*, 2015]. Later, the growth of the Great Caucasian Range obviously shaped the diversity and distribution of the genus *Synurella* in the region.

If we take in account the species described above in the article, then *Synurella teshebi* sp.n. from the Teshebs River is rather young, and split from *S. monteflumina* from the Olkhovka River, a tributary of the Doguab River, during the middle of the Pleistocene, about 2–1.5Mya, when the modern river and mountains in the region were already presented. Probably, the separation of these species is related to the secondary division of the previously unified water basin of the modern neighboring Doguab–Vulan–Teshebs river system. According to our expectations, the undescribed hyporhean *Synurella* species should also inhabit the basins of the modern Tekos–Vulan, Bzhid, Pshada and other small mountain rivers flowing into the Black Sea along the southwestern part of the Caucasian Ridge. At the same time, *Synurella psezuapsi* sp.n. from the lower Psezuapse River separated from this group of species back in the Pliocene, about 4–3Mya, which fully confirms the hypothesis of the connection between the diversity of *Synurella* in the region and local mountain formation, since the central part of the Caucasus began to grow significantly earlier than the western foothills [Adamia *et al.*, 2011; Avdeev, 2011; Avdeev, Niemi, 2011; Tarkhnishvili *et al.,* 2012; Tarkhnishvili, 2014; Sosson *et al.*, 2017; Mosar *et al.,* 2022; Trikhunkov *et al.*, 2024].

An interesting fact is that, with the increasing number of known species and addition of new molecular genetic data based on mitochondrial COI mtDNA gene marker (Fig. 1), we have discovered that the "*behningi*" group split off from the Balkan ("*intermedia*") clade, and, these two clades obviously existed in parallel, even though we previously believed the Balkan "*intermedia*" clade was ancestral to both the "*behningi*" and "*ambulans*" groups, considered as sister [Marin, Palatov, 2022]. The ancestral forms of the Caucasian "*behningi*" group are probably the same for the entire genus *Synurella* and appeared as early as the Miocene, and do not originate from the "*ambulans*" or "*intermedia*" groups, as we previously assumed [Marin, Palatov, 2022]. All known species of the "*behningi*" group are hypogean/hyporhean, which apparently contributed to their survival in the region [McInerney *et al.*, 2014] during global climate change in the Pleistocene [Kolakovsky, 1991; Krever *et al.*, 2001; Cane *et al.*, 2006; Schmitt, 2007; Nieto, 2011; Naidina, Richards, 2016; Paillard, 2017; Niedziałkowska *et al.*, 2024], and especially during the last glacial maximum (LGM) (23–18Kya) [Clark *et al.*, 2009; Hughes, Gibbard, 2015].

Thus, the discovery of new species has slightly altered our understanding of the origin of the “*behningi*” group, pushing back the time of its formation to the Miocene period. It also revealed that the presence of species from this clade in the Caucasus, on the territory that later became the Colchis Lowland, likely occurred in parallel with representatives of the same genus on the Balkan Peninsula, for example *S. longidactylus* S. Karaman, 1929 from the Ohrid Lake, previously considered to be basal within the genus [Marin, Palatov, 2022]. However, due to the fact that we are fully confident that the studied diversity is still far from the real diversity of the genus Synurella in the area, these conclusions should also not be considered final. Currently, it makes sense to focus on studying diversity, searching for and describing new species in order to accumulate data for further molecular genetic analysis using a larger number of gene markers.

Author Contributions. Both authors have made absolutely equal contributions to all parts of the study.

Conflicts of Interest. The authors declare no conflict of interest.

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