

# Lifestyle switching and refugee availability are the main factors in the evolution and distribution of the genus *Synurella* Wrześniowski, 1877 (Amphipoda: Crangonyctidae)

## Смена образа жизни и наличие рефугиумов как основные факторы эволюции и распространения рода *Synurella* Wrześniowski, 1877 (Amphipoda: Crangonyctidae)

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

**ABSTRACT.** The article represents an integrative revision of the Caucasian representatives of the genus *Synurella* Wrześniowski, 1877 (Amphipoda: Crangonyctidae) with a description of five new species, namely *Synurella premontana* Marin et Palatov sp.n. (Shids river basin), *S. adegoyi* Marin et Palatov sp.n. (Adegoy river basin), *S. monteflumina* Palatov et Marin sp.n. (Olkhovka river basin), *S. gizmavi* Palatov et Marin sp.n. (Gizmava Cave) and *S. inkiti* Palatov et Marin sp.n. (Inkit Lake). *S. taurica* Martynov, 1931 (Yalta area and southwestern Krasnodar Krai) and *S. behningi* (Birštein, 1948) (Bacha Cave) are re-described based on topotypic material and their taxonomy and distribution are discussed in the article. *Synurella donensis* (Martynov, 1919) should be transferred to the genus *Pontonyx* Palatov et Marin, 2021. The molecular phylogeny confirmed the monophyly of the “*Synurella*” clade of the family Crangonyctidae, and of the genus *Synurella* itself. Three main clades are presented within the genus *Synurella*: “*ambulans*”, comprising mainly northwestern European epigean species; “*behningi*”, consisting of the Caucasian subterranean species; and “*intermedia*” with epigean species from Slovenia and Slovakia, which are closely related to probably basal (=ancestral) species of the genus, *Synurella longidactylus* S. Karaman, 1929 from Ohrid Lake. Phylogenetic analysis revealed that lifestyle switching (hypogean vs. epigean) should be considered as a driving factor in the evolution/distribution of the genus *Synurella*, while existing of refugee in the northern Black Sea region (for example, Colchis) allowed the genus to survive during the Pliocene. The Balkan Peninsula is considered as the “center of origin” of the genus in the late

Miocene, while the southwestern Caucasus is the modern diversity “hotspot” of the genus. The expansion of the genus to the north and northwest, as well as to Central and Eastern Europe, probably occurred during the late Pleistocene by the epigean species originated in the Caucasus.

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**РЕЗЮМЕ.** В статье представлена интегративная ревизия кавказских представителей рода *Synurella* Wrześniowski, 1877 (Amphipoda: Crangonyctidae) с описанием пяти новых видов, а именно *Synurella premontana* Marin et Palatov sp.n. (бассейн реки Шидс), *S. adegoyi* Marin et Palatov sp.n. (бассейн реки Адегой), *S. monteflumina* Palatov et Marin sp.n. (бассейн реки Ольховка), *S. gizmavi* Palatov et Marin sp.n. (пещера Гизмава) и *S. inkiti* Palatov et Marin sp.n. (озеро Инкит). *S. taurica* Martynov, 1931 (район Ялты и юго-западная часть Краснодарского края) и *S. behningi* (Birštein, 1948) (пещера Бача) переописаны на основе топотипического материала, их таксономия и распространение обсуждаются в статье. Также установлено, что *Synurella donensis* (Martynov, 1919) следует отнести к роду *Pontonyx* Palatov et Marin, 2021. Молекулярная филогения подтвердила монофилию клады “*Synurella*” (“*Synurella*” Clade) семейства Crangonyctidae и самого рода

*Synurella*. В пределах рода *Synurella* представлены три основные клады: “*ambulans*”, включающая в основном северо-западноевропейские эпигейные виды; “*behningi*”, состоящая из кавказских гипогейных видов; и “*intermedia*” с эпигейными видами из Словении и Словакии, которые тесно связаны с вероятно базальным (= предковым) видом рода, *Synurella longidactylus* S. Karaman, 1929 из Охридского озера. Филогенетический анализ показал, что смену образа жизни (гипогейный vs. эпигейный) следует рассматривать как движущий фактор эволюции/распространения рода *Synurella*, в то время как рефугиумы в северном Причерноморье (например, Колхидская низменность) позволили роду выжить здесь в Плиоцене. Балканский полуостров считается “центром происхождения” рода в позднем Миоцене, при этом юго-западный Кавказ является современной “горячей точкой” разнообразия рода. Экспансия рода на север и северо-запад, а также в Центральную и Восточную Европу, началась в позднем плейстоцене за счет эпигейных видов, произошедших на современной территории Кавказа.

## Introduction

The family Crangonyctidae Bousfield, 1973 consists of predominantly freshwater amphipods, living in groundwater or epigeal water reservoirs with hypogean connection or origination [Holsinger, 1974, 1978; Lowry, Myers, 2017; Zhang, Holsinger, 2003; Copilaş-Ciocianu *et al.*, 2019; Palatov, Marin, 2020; Marin, Palatov, 2021b; Cannizzaro *et al.*, 2021]. At the same time, some of crangonyctid genera, for example *Pontonyx* Palatov et Marin, 2021, *Eosynurella* Martynov, 1931 and *Synurella* Wrześniowski, 1877, include epigeal species. In this regard, the question of the ancestral lifestyle and the role of lifestyle in the evolution of these amphipods remains open.

The genus *Synurella* Wrześniowski, 1877 (Amphipoda: Crangonyctidae) is included in the so-called “*Synurella*” Clade, widespread in the northwestern Palaearctic (Turkey) [Martynov, 1919; Birštein, 1948; Dobreanu, Manolache, 1951; S. Karaman, 1929; G.S. Karaman, 1974, 1991; Özbek, 2018]. The currently known distribution of the genus *Synurella* is limited in the east by the Volga River, in the west it is distributed in England, Germany and Italy, in the south — on the Balkan Peninsula, northern part of the Republic of Türkiye (Turkey), the Crimean Peninsula and the southwestern Caucasus (e.g., Karaman [1929]; Martynov [1931b]; Birštein [1948]; Özbek [2018]; Palatov, Marin [2021]). The genus was recently partly revised; some species were synonymized or transferred to other crangonyctid genera [Marin, Palatov, 2020, 2021a], some new genera were also erected [Marin, Palatov, 2021a; Cannizzaro *et al.*, 2021]. Several new species were also recently described [Palatov, Marin, 2021b]. The genus presently includes 10 valid species: *Synurella ambulans* (F. Müller, 1846) (from England and north-

ern Germany to western and southwestern Russia) (the type species of the genus), *S. tenebrarum* (Wrześniowski, 1888) (Zakopane, Poland), *S. donensis* (Martynov, 1919) (Rostov-on-Don, Russia), *S. longidactylus* S. Karaman, 1929 (Ohrid Lake), *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 (northern Republic of Türkiye (Turkey)), *S. ispani* Palatov et Marin, 2021 (Ispani peat bog, Georgia), *S. spiridonovi* Marin et Palatov, 2021 (Kobuleti area, Georgia) [Horton *et al.*, 2021; Palatov, Marin, 2021a], as well as one fossil species from Baltic amber, *S. aliciae* Jazdzewski, Grabowski et Kupryjanowicz, 2014 [Jazdzewski *et al.*, 2014]. Numerous synonyms are also known for the abovementioned species, mainly for *S. ambulans* (see Horton *et al.* [2021]).

However, the recent taxonomy of the genus is still confusing, and its diversity is still far from being completely described. The taxonomy of the Western European “*Synurella ambulans*” species complex is clearly known, since different scientists consider subspecies/synonyms in different taxonomic status [Sidorov, Palatov, 2012]. In addition, the morphological variability of known species can be interpreted in different ways, and clear species hypotheses cannot be presented without molecular genetic data, which are absent for most species. Due to this incomplete taxonomic knowledge, erroneous conclusions about the origin and distribution of species have been formulated.

The recent studies showed the presence and rather high diversity of *Synurella* spp. in surface (epigeal) reservoirs, such as ponds, swamps and peat bogs, of a number of different regions (e.g., Sidorov, Palatov [2012]; Palatov, Marin [2021b]). Such epigeal lifestyle very likely allows spreading over long distances similar to widely distributed *Gammarus* spp. (Amphipoda: Gammaridae). Whether the genus is hypogean or epigeal in its origin is also important for understanding its evolution, as well as the entire “*Synurella*” Clade and the family Crangonyctidae.

The goal of this article is the description and partial revision of the Caucasian/Ciscaucasian representatives of the genus *Synurella* based on an integrated approach, as well as resolving of some questions of its origin, phylogeny, lifestyle and ways of distributions. Based on freshly collected material and literature data, we analyse and discuss the diversity of the genus, its morphological boundaries and the species distribution. The article also presents the first insight to the role of lifestyle in the genus *Synurella*, its “hypogean vs. epigeal” transitions and the historical role of climatic Pleistocene-Pliocene refugee in its evolution and distribution.

## Material and methods

**SAMPLE COLLECTION AND PROCESSING.** Amphipods were collected using a hand net in various epigeal

and subterranean water resources in the southern Caucasus (southwestern Russia and Abkhazia) in 2013–2022 years. All samples were fixed in 90% solution of ethanol. Photographs of alive coloration *in situ* were made using digital camera CanonG16. Photographs of morphological features were made with a digital camera attached to light microscope Olympus ZX10 and Olympus CX21. The scanning electron microscopy (SEM) images were made using the Vega3 Tescan microscope in the Yu.A. Orlov Paleontological Museum of the Paleontological Institute of the Russian Academy of Sciences, Moscow. 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 antennae, is used as a standard measurement. The type material is deposited at the collection of Zoological Museum of Moscow State University, Moscow, Russia (ZMMU). Additional material is deposited in the author's personal collection at the A.N. Severtsov Institute of Ecology and Evolution of the Russian Academy of Sciences, Moscow, Russia (LEMMI).

**AMPLIFICATION AND DNA SEQUENCING.** The mitochondrial cytochrome oxidase c subunit I (COI mtDNA) gene has been proving as extremely informative in previous studies at both population and species level [Avisé, 1993; Palatov, Marin, 2020; Marin, Palatov, 2021a, b]. 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'-GGTCAACAAAT-CATAAAGATATTGG-3') and HC02198 (5'-TAAACT-TCAGGGTGACCAAAAAATCA-3') [Folmer *et al.*, 1994]. Polymerase chain reaction (PCR) were performed on an amplifier T100 (Bio-Rad, USA) under the following standard protocol and conditions. The volume of 10  $\mu$ L of reaction mixture contained 1  $\mu$ L of total DNA, 2  $\mu$ L of 5xPCR mix (Dialat, Russia), 1  $\mu$ L of each primer and 5  $\mu$ L of H<sub>2</sub>O. The amplification products were separated by using gel electrophoresis of nucleic acids on a 1.5% agarose gel in 1xTBE, and then stained and visualized with 0.003% EtBr using imaging UV software. PCR products were then sequenced using Genetic Analyzer ABI 3500 (Applied Biosystems, USA) and BigDye 3.1 (Applied Biosystems, USA) with forward and reverse primers. Dataset of aligned sequences of COI mtDNA gene markers, about 617 base pairs in length used in the study were taken from GenBank (NCBI) (Table 1, Supplementary Table1) and author's personal data.

**PHYLOGENETIC ANALYSIS.** Dataset of consensus sequence 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 in Fig. 1. Pairwise genetic divergences (*p*-distances) was calculated based on available COI sequences using MEGA 7.0 with the Kimura 2-Parameter (K2P) model of evolution [Kimura, 1980].

**MEDIAN JOINT NETWORK** [Bandelt *et al.*, 1999] was reconstructed with PopArt (Population Analysis with Reticulate Trees) software [Leigh, Bryant, 2015].

**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] (<http://www.wabi.snv.jussieu.fr/public/abgd/>), phylogeny-aware PTP (Poisson Tree Process) [Zhang *et al.*, 2013] and Bayesian GMYC (Generalized Mixed Yule Coalescent) [Pons *et al.*, 2006; Reid, Carstens, 2012] 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) (<https://species.lh-its.org/>) was run on the RAxML gene trees (see above) for 1x10<sup>6</sup> MCMC (Markov chain Monte Carlo) generations thinning every 1000 and removing the distant outgroup that can improve the delimitation results.

In GMYC (Generalized Mixed Yule Coalescent), 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<sup>6</sup> generations sampling every 10<sup>4</sup> generations were used. The best-scoring Bayesian Inference trees were estimated using GTR model, used for further analysis. Following gene tree inference, GMYC was implemented in the "splits" package (SPecies LIimits by Threshold Statistics) [Ezard *et al.*, 2009] of the software environment R v.3.5.1 (<http://www.r-project.org/>) with a single threshold used for COI mtDNA gene marker.

**MOLECULAR CLOCK ANALYSIS** was performed based on Bayesian Inference (BI) trees generated by GMYC analysis with the BEAST2 package (see above). Maximum

Table 1. Comparison of pairwise genetic (COI mtDNA) distances (*p*-distances) (substitutions per 100 nucleotides $\pm$ SE) between the genus *Synurella* and related genera from the "*Synurella*" clade of the family Crangonyctidae. Таблица 1. Сравнение попарных генетических (COI mtDNA) дистанций (*p*-distances) (замен на 100 нуклеотидов $\pm$ SE) между родом *Synurella* и родственными родами из клады "*Synurella*" семейства Crangonyctidae.

	<i>Synurella</i>	<i>Lyurella</i>	<i>Palaearcticarellus</i>	<i>Pontonyx</i>	<i>Volgonyx</i>	<i>Eosynurella</i>
<i>Lyurella</i>	0.259 $\pm$ 0.024					
<i>Palaearcticarellus</i>	0.275 $\pm$ 0.025	0.238 $\pm$ 0.022				
<i>Pontonyx</i>	0.281 $\pm$ 0.026	0.264 $\pm$ 0.025	0.252 $\pm$ 0.023			
<i>Volgonyx</i>	0.283 $\pm$ 0.028	0.295 $\pm$ 0.034	0.287 $\pm$ 0.030	0.275 $\pm$ 0.030		
<i>Eosynurella</i>	0.291 $\pm$ 0.026	0.251 $\pm$ 0.022	0.244 $\pm$ 0.023	0.227 $\pm$ 0.024	0.276 $\pm$ 0.028	
<i>Diasynurella</i>	0.318 $\pm$ 0.030	0.296 $\pm$ 0.028	0.293 $\pm$ 0.027	0.265 $\pm$ 0.028	0.284 $\pm$ 0.030	0.262 $\pm$ 0.025

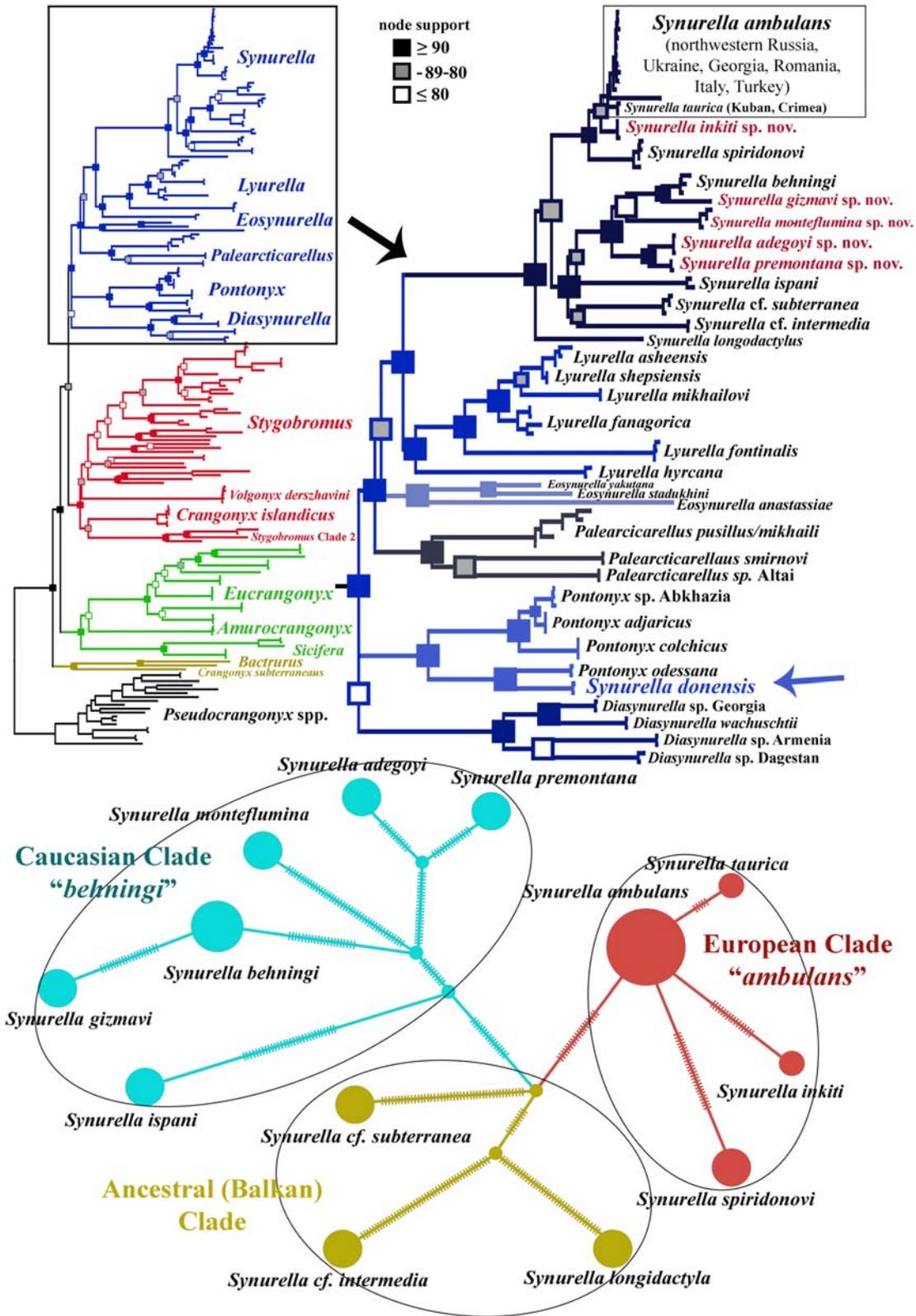


Fig. 1. The phylogenetic reconstruction (tree) of molecular genetic (COI mtDNA gene marker) scenario (ML, GTR+G+I model) of the family Crangonyctidae. The genus *Pseudocrangonyx* Akatsuka et Komai, 1922 (Amphipoda: Pseudocrangonyctidae) is used as outgroup.

Рис. 1. Филогенетическая реконструкция (дерево) молекулярно-генетического сценария (генный маркер COI мтДНК) (ML, модель GTR+G+I) семейства Crangonyctidae. Представители рода *Pseudocrangonyx* Akatsuka et Komai, 1922 (Amphipoda: Pseudocrangonyctidae) использованы в качестве аутгруппы.

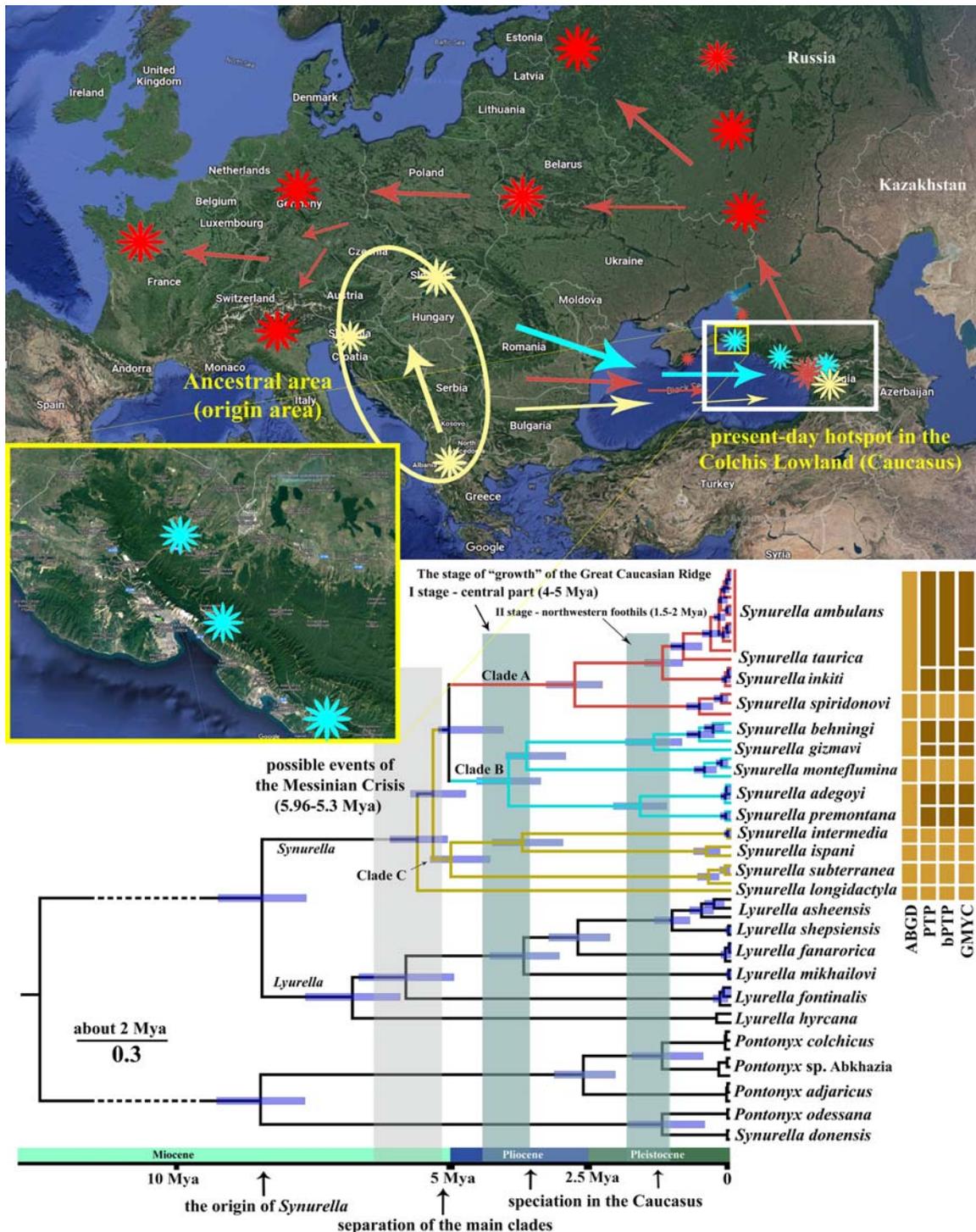


Fig. 2. The map of distribution (A), the time-calibrated phylogenetic tree (reconstruction) and the species delimitation analyses on COI mtDNA gene marker of the studied species of the genus *Synurella*. Posterior probabilities of the nodes are reported. Vertical scales represent the results of species delimitation analyses using species delimitation methods (ABGD, PTP and bPTP, GMYC), morphological evidences (Morphology) and the summary coincident results (Consensus) of different species delimitation approaches. Blue horizontal bars show the 95% HPD (the highest posterior density) of node ages on an arbitrary time scale.

Рис. 2. Карта распространения (A), откалиброванное по времени филогенетическое дерево (реконструкция) и анализ видовой принадлежности по генному маркеру COI мтДНК исследуемых видов рода *Synurella*. Представлены апостериорные вероятности основных узлов. Вертикальные шкалы представляют результаты анализа делимитации видов с использованием способы разделения видов (ABGD, PTP и bPTP, GMYC), морфологических признаков (Morphology) и сводных результатов (Consensus) различных подходов к делимитации видов. Синие горизонтальные полосы показывают 95% HPD возраста узлов в произвольном масштабе времени.

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. Calibration points were chosen based on the adapted time-scale [McInerney *et al.*, 2014] and the analysis of historical events. The final visualization is presented on Fig. 2, showing the maximum clade credibility BA tree with the supported species-delimitation schemes under each method, and then summarizing consensus between methods and stating how disagreements were resolved and considered for species-tree analyses. There were considerable differences among species delimitation methods with respect to the number of distinct species.

ABBREVIATIONS: Mx — maxilla; Gn — gnathopod; P — pereopod; Pp — pereopods; Pl — pleopod; Ep — epimeral plate; U — uropod.

## Results

**PHYLOGENETIC PART.** The molecular genetic analysis (Fig. 1) clearly confirmed the monophyly (Bayesian-PP=1.00; ML-BS=95%) of the “*Synurella*” Clade, and the genus *Synurella* itself (see Fig. 1). The “*Synurella*” clade also includes Palaearctic genera *Eosynurella* Martynov, 1931, *Lyurella* Derzhavin, 1939 and *Palaearcticarellus* Palatov et Marin, 2020 (see Fig. 1). The genetic divergence between genera within the Clade vary from 23 to 32% (from 0.227±0.024 to 0.318±0.030 substitutions per 100 nucleotides) (see Table 1) that makes it possible to separate all main lineages well at the genetic level. According to the obtained data (see Fig. 1), the genus *Lyurella* Derzhavin, 1939 also known from the southwestern Caucasus is considered as a sister clade to the genus *Synurella*. The estimated time of divergent time between *Synurella* and *Lyurella* is 0.259±0.018 substitutions per 100 nucleotides, which can be estimated as about 10.36 Mya (min. and max. after Guy-Haim *et al.* [2018]; average — 2.5% Mya<sup>-1</sup> for COI mtDNA gene marker after Lefébure *et al.* [2006], Copilaş-Ciocianu & Petrussek [2015] for the genus *Niphargus* Schiödt, 1849 (Crustacea: Amphipoda: Niphargidae)). The estimated divergence time of the split between *Synurella* and *Lyurella* is about 14.6 Mya, according to Copilaş-Ciocianu *et al.* [2019] (1.773% Mya<sup>-1</sup> for COI mtDNA gene marker). Such data and estimation are supported by the time-calibrated phylogenetic analysis (Fig. 2), which showed the separation of the genera in the late Miocene.

Within the genus *Synurella*, *Synurella longidactylus* S. Karaman, 1929 from the Lake Ohrid, the oldest and the deepest lake in the Balkans, seems to be an earlier derived taxon having some possible ancestral morphological features, such as long epimeral ventral spines and long dactyli of ambulatory pereopods [S. Karaman, 1929].

Three main clades were revealed within the genus (Fig. 1): the “*ambulans*” clade including mostly northwestern European species, the “*behningi*” clade — mainly Caucasian species, and the “*intermedia*” clade with the species from Slovenia and Slovakia, which are close to the ancestral *S. longidactylus*. The divergence time between the main clades is estimated as about 8.2 Mya for the “*ambulans*” and “*behningi*” clades ( $p$ -distance = 0.206±0.019 substitutions per 100 nucleotides), and about 9.2 Mya for differentiation of the “*ambulans/behningi*” and the ancestral Balkan “*intermedia*” clades ( $p$ -distance = 0.230±0.021 substitutions per 100 nucleotides) (see Fig. 1). The Time-calibrated evolutionary analysis (Fig. 2) showed that the separation of the

main clades occurred in the Late Miocene/early Pliocene, about 6.5–4.5 Mya (95%HPD). It was probably associated with the events of the Messinian Crisis, when the main basins of the Paratethys were completely drained, which led to the separation of the previously unified taxa of the animals inhabiting them. Further specialization probably was shaped by “the growth” of the Great Caucasian Ridge, which occurred in two stages: 5–6 Mya — an active growth of its central part, and 1.5–2 Mya — the beginning of “the growth” of its marginal parts, for example, on the territory of the modern Novorossiysk, where the sampling of the studied species was accomplished (see Fig. 2). Molecular genetic analysis also revealed that *Synurella donensis* Martynov, 1931 (see Martynov [1931a]) actually belongs to the genus *Pontonyx* Palatov et Marin, 2021, being a sister lineage to *Pontonyx odessana* (Sidorov et Kovtun, 2015) (see Figs 1–3), and should be transferred into the genus *Pontonyx* [Marin, Palatov, in press].

The ABGD analysis revealed 9 OTUs (i.e., operational taxonomic units, or putative species) with the prior maximal distance  $P=0.059948$ , or 11 OTUs with the prior maximal distance  $P=0.035938$  within the genus *Synurella*, respectively (see Fig. 2). Species delimitation analyses performed by implementing the coalescent tree-based approach (i.e., PTP/bPTP and GMYC) led to almost identical results but some differences were apparent relative to ABGD (Fig. 2). The trees resulting from PTP and bPTP present similar results with 12 OTU in the studied taxa (Fig. 2). The ML (GMYC) model is 208.8949, compared to the likelihood of the null model 199.1945. As a result of the likelihood ratio test, the null model expecting uniform coalescent branching rates across entire tree was rejected (likelihood ratio = 19.40084,  $p=6.125786e-05$ ). The number of ML clusters in the analysis is 10 (confidence interval: 8–11), while the analyzed group includes 13 ML entities (interval: 11–14) (95% CI); threshold time: -0.02220715. The morphological analysis (see below) strongly supports the presence of 13 separate species within the studied taxa of the genus *Synurella*. Thus, an integrative approach to species delimitation resulting in the phylogenetic tree (see Figs 1, 2) supported 3 well-resolved major clades and at least 13 subclades, representing separate species (see Figs 1, 2).

The interspecific genetic divergence between the studied species of the genus *Synurella* are presented in Table 2, showing distinct species-specific genetic divergence. The  $p$ -distances between the studied species of the genus *Synurella* usually exceed 20%, varying from 8.4% to 27% (Table 1). The lower  $p$ -distances (±SE) were found between *S. ambulans* (northwestern Europe) and *S. inkitii* sp.n. (Inkit Lake) (0.0960.012 substitutions per 100 nucleotides) as well as *S. premontana* sp.n. (Shids River) and *S. adegoyi* sp.n. (Adegoy River) (0.084±0.014 substitutions per 100 nucleotides) (Table 2).

The intraspecific genetic divergence ( $p$ -distance) within the widely distributed *S. ambulans* is about 0.5–1% (the average — 0.005±0.002 substitutions per 100 nucleotides), while the population from the delta of Kuban River (Utash, see below) and slope of Ai-Petri massif (Crimean Peninsula) is differing from other studied populations (Pskov, Moscow, Bryansk, Odessa, south Georgia and northern Turkey) for about 2.3% (0.023±0.0106 substitutions per 100 nucleotides). This population was already described as a separate species, *Synurella taurica* Martynov, 1931 [Martynov, 1931b], but lately synonymized with *S. ambulans* by Karaman [1974]. Due to the distinctive morphological features (see below) and its geographical/genetic isolation, we would like to res-

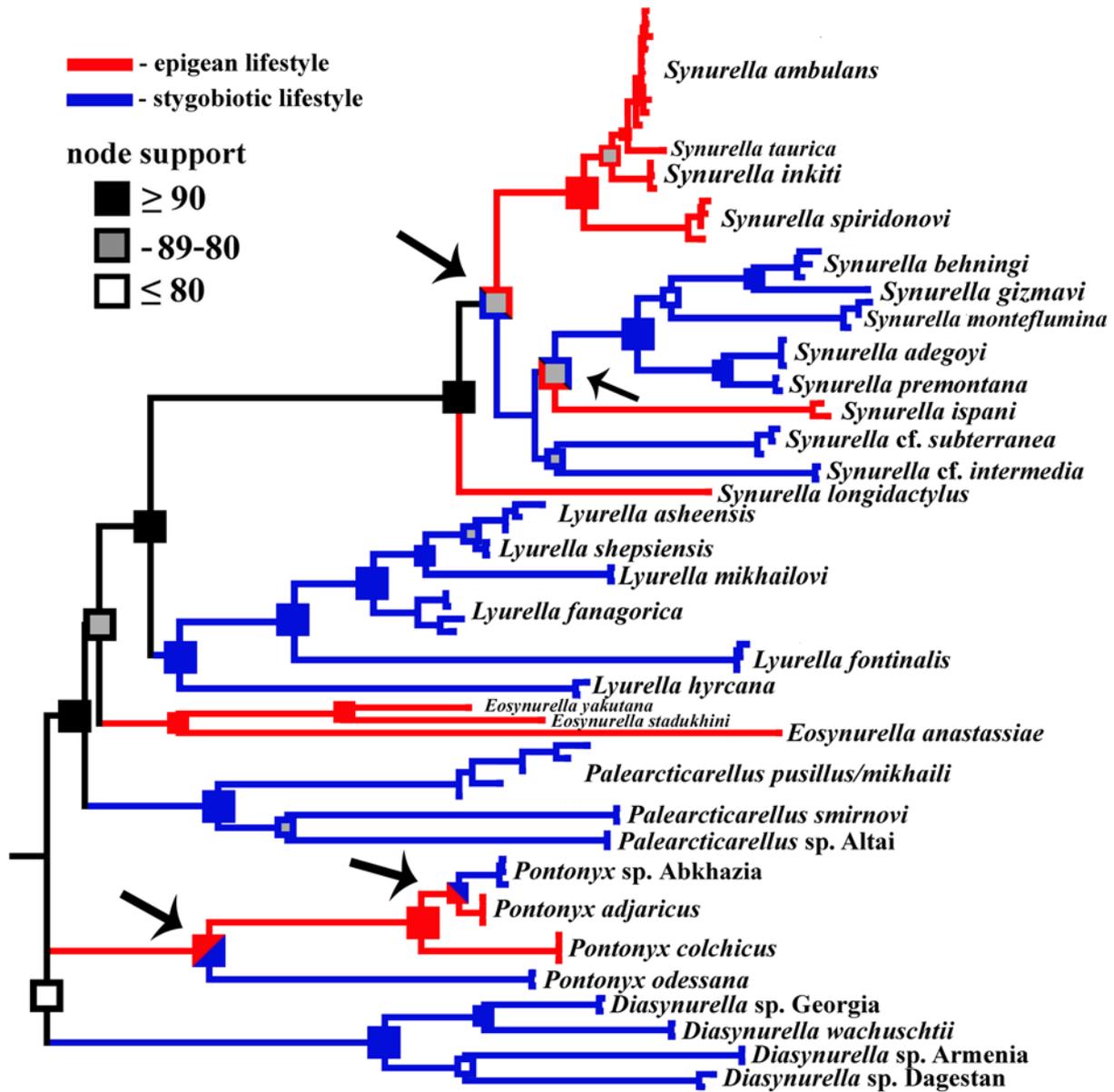


Fig. 3. The phylogenetic reconstruction (tree) of molecular phylogenetic (COI mtDNA gene marker) scenario (GTR+G+I model (Bayesian Information Criterion (BIC)) of the “*Synurella*” Clade of the family Crangonyctidae, indicating lifestyle of the species (hypogean (stygobiotic) (blue) vs. epigean (red)). Arrows indicate lifestyle switching.

Рис. 3. Филогенетическая реконструкция (дерево) молекулярно-филогенетического сценария (генный маркер COI мтДНК) (модель GTR+G+I (Бэйсовский информационный критерий (BIC)) клады “*Synurella*” семейства Crangonyctidae, показывающая образ жизни видов (подземный (синий) vs. надземный (красный)). Стрелками указаны моменты смены образа жизни.

urrect the taxonomic status of this population as a valid species, despite a small genetic divergence from other populations of *S. ambulans*. Some of species delimitation methods also supports such taxonomic decision (see Fig. 2).

We assume that the ancestral form and modern lineages of the “*ambulans*” and “*intermedia*” clades appeared in the Caucasus during the Pliocene (Fig. 2), where they were able to survive cold periods of Pliocene-Pleistocene, apparently in warm refuge of its southern part (for example, Colhis). The appearance and the spread of the epigean forms of the “*ambulans*” clade (*S. ambulans*) to the territory of Western Europe and Russia occurred during the Late Pleistocene,

apparently after the warming and retreat of glaciers. At the same time, the presence of basal and modern species in the Caucasus (*S. taurica* and *S. inkiti* sp.n.) additionally indicates the origin of the clade from the Caucasian ancestors.

The phylogenetic lineages (species) within the “*Synurella*” Clade are represented by both epigean and subterranean forms (Fig. 3). The species of the genus *Eosynurella* are mainly epigean [Derzhavin, 1930; Martynov, 1931a; G.S. Karaman, 1974, 1991]. Two of four known lineages (species) with the genus *Pontonyx* are also known as epigean [Marin, Palatov, 2021a]. The earlier derived (possibly, ancient) taxa of the genus *Synurella*, *S. longidactylus*, is known

Table 2. Comparison of pairwise genetic (COI mtDNA) distances ( $p$ -distances) (substitutions per 100 nucleotides $\pm$ SE) between the studied species of the genus *Synurella*. New species are indicated with bold. Таблица 2. Сравнение попарных генетических (COI mtDNA) дистанций ( $p$ -distances) (замен на 100 нуклеотидов $\pm$ SE) между изучаемыми видами рода *Synurella*. Новые виды выделены жирным шрифтом.

	<i>longidactylus</i>	<i>intermedia</i>	<i>subterranea</i>	<i>spiridonovi</i>	<i>ispani</i>	<i>ambulans</i>
<i>intermedia</i>	0.272 $\pm$ 0.035					
<i>subterranea</i>	0.217 $\pm$ 0.025	0.239 $\pm$ 0.028				
<i>spiridonovi</i>	0.231 $\pm$ 0.027	0.256 $\pm$ 0.027	0.244 $\pm$ 0.025			
<i>ispani</i>	0.221 $\pm$ 0.024	0.247 $\pm$ 0.028	0.253 $\pm$ 0.027	0.213 $\pm$ 0.025		
<i>ambulans</i>	0.195 $\pm$ 0.03	0.231 $\pm$ 0.024	0.198 $\pm$ 0.021	0.143 $\pm$ 0.018	0.211 $\pm$ 0.025	
<b><i>gizmavi</i></b>	0.251 $\pm$ 0.030	0.247 $\pm$ 0.030	0.220 $\pm$ 0.026	0.240 $\pm$ 0.027	0.248 $\pm$ 0.030	0.238 $\pm$ 0.026
<i>behningi</i>	0.222 $\pm$ 0.024	0.237 $\pm$ 0.024	0.229 $\pm$ 0.023	0.161 $\pm$ 0.019	0.200 $\pm$ 0.023	0.172 $\pm$ 0.020
<b><i>inkiti</i></b>	0.211 $\pm$ 0.020	0.232 $\pm$ 0.026	0.243 $\pm$ 0.031	0.127 $\pm$ 0.020	0.219 $\pm$ 0.026	<b>0.096<math>\pm</math>0.012</b>
<i>monteflumina</i>	0.241 $\pm$ 0.027	0.248 $\pm$ 0.028	0.243 $\pm$ 0.024	0.232 $\pm$ 0.026	0.243 $\pm$ 0.026	0.227 $\pm$ 0.024
<b><i>premontana</i></b>	0.195 $\pm$ 0.024	0.263 $\pm$ 0.030	0.217 $\pm$ 0.030	0.217 $\pm$ 0.024	0.228 $\pm$ 0.025	0.199 $\pm$ 0.022
<b><i>adegoyi</i></b>	0.234 $\pm$ 0.025	0.246 $\pm$ 0.025	0.231 $\pm$ 0.026	0.227 $\pm$ 0.025	0.243 $\pm$ 0.028	0.232 $\pm$ 0.023
	<b><i>gizmava</i></b>	<i>behningi</i>	<b><i>inkiti</i></b>	<b><i>monteflumina</i></b>	<b><i>premontana</i></b>	
<i>intermedia</i>						
<i>subterranea</i>						
<i>spiridonovi</i>						
<i>ispani</i>						
<i>ambulans</i>						
<b><i>gizmavi</i></b>						
<i>behningi</i>	0.147 $\pm$ 0.017					
<b><i>inkiti</i></b>	0.150 $\pm$ 0.029	0.150 $\pm$ 0.020				
<i>monteflumina</i>	0.204 $\pm$ 0.027	0.196 $\pm$ 0.021	0.230 $\pm$ 0.027			
<b><i>premontana</i></b>	0.201 $\pm$ 0.029	0.196 $\pm$ 0.023	0.220 $\pm$ 0.026	0.233 $\pm$ 0.028		
<b><i>adegoyi</i></b>	0.188 $\pm$ 0.028	0.194 $\pm$ 0.023	0.227 $\pm$ 0.028	0.220 $\pm$ 0.028	<b>0.084<math>\pm</math>0.014</b>	

from the Lake Ohrid, mostly as the lake-dwellers [Karaman, 1974], similar to *Palaearcticarellus pusillus* (Martynov, 1930) from the Teletskoe Lake, located at Altai Mountains [Martynov, 1930]. All species of the “*ambulans*” clade with the genus, namely *S. ambulans*, *S. spiridonovi* and *S. inkiti* sp.n., are known from epigeal water resources, as well as *S. ispani* is also known from the Ispani peat bog habitats (Colchis lowland, southwestern Georgia, Caucasus) [Palatov, Marin, 2021a]. All other studied species of the genus, including the newly discovered species, are known from the subterranean water resources such as wells and springs (see below).

## Taxonomic part

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

INCLUDED SPECIES. *Synurella ambulans* (F. Müller, 1846) (type species of the genus), *Synurella taurica* Martynov, 1931, *S. subterranea* (S. Karaman, 1931), *S. montenegrina* (G. Karaman, 1974), *S. behningi* (Birštein, 1948), *S. longidactylus* S. Karaman, 1929, *S. tenebrarum* (Wrześniowski, 1888), *S. coeca* (Dobreanu et Manolache, 1951), *S. intermedia* Dobreanu, Manolache et Puscaru, 1952; *S. lepida* Mateus et Mateus, 1990; *S. ispani* Palatov et Marin, 2021; *S. spiridonovi* Marin et Palatov, 2021; *S. premontana* Marin et Palatov sp.n.; *S. adegoyi* Marin et Palatov sp.n.; *S. monteflumina* Palatov et Marin sp.n.; *S. gizmavi* Palatov et Marin sp.n.; *S. inkiti* Palatov et Marin sp.n.

Meanwhile, *Synurella philareti* Birštein, 1948 and *S. donensis* Martynov, 1919 should be transferred in the genus *Pontonyx* Palatov et Marin, 2021, with the type species *Pontonyx odessana* (Sidorov et Kovtun, 2015) [Marin, Palatov, in press].

DIFFERENTIAL DIAGNOSIS. The genus *Synurella* can be distinguished from all other Palaearctic crangonyctid genera by the combination of the following features: 1) pigmented or unpigmented body with well-developed pigmented eyes (vs. depigmented in *Crangonyx*, *Amurocrangonyx*, *Diasynurella* and *Palaearcticarellus*); 2) completely fused urosomal segments (vs. free urosomal segments in *Amurocrangonyx*, *Crangonyx* and *Palaearcticarellus*; urosomal segments 2–3 are partially fused in *Diasynurella*; fused in *Lyurella*); 3) trapezoidal or subquadrate propodus (palm) of GnI (vs. oval propodus of GnI in *Amurocrangonyx*, *Crangonyx* and *Palaearcticarellus*); 4) the presence of a row of 3–5 bifurcated closing bristles along the inner surface of the distoventral palmar corner of propodus (palm) of GnII (vs. 1–2 simple single strong bristles, not organized in a row in *Pontonyx*); 5) vestigial 2-segmented UIII (vs. well-developed 2-segmented UIII in *Amurocrangonyx* and *Crangonyx*; mostly reduced 1-segmented in *Lyurella*); 6) the absence of an additional terminal knob on peduncle of UIII (vs. present in *Pontonyx* and *Volgonyx*); 7) simple endopodite of UI (vs. paddle-like in *Volgonyx*); 8) a single additional spine-like setae on dactyli of PpIII–VII (vs. *Amurocrangonyx*, *Eosynurella* and *Lyurella*); 9) two hooks in retinacula of pleopods (vs. more than 2 hooks in *Amurocrangonyx*, *Crangonyx*, *Lyurella*, *Eosynurella*, *Pontonyx*, *Palaearcticarellus* and *Volgonyx*); 10) reduced but still marked inner lobes of the lower lip (labium) (vs. completely reduced in *Eosynurella*).

**TAXONOMIC REMARKS.** According to the available species descriptions and molecular genetic data, we consider *Synurella subterranea* S. Karaman, 1931 (Slovenia) and *Synurella montenegrina* G. Karaman, 1974 (Montenegro) as valid species, clearly differing from *S. ambulans*. These species probably belong to “*intermedia*” clade and clearly differ from *S. ambulans* by the presence of several (more than two) spines on basal article of uropod III.

*Synurella ambulans* (F. Müller, 1846)

Fig. 4a–c.

**MATERIAL EXAMINED.** 9♀♀, 7♂♂ (LEMMI), Russian Federation, Moscow Oblast, Orekhovo-Zuyevo District, 55°33'33.2"N 38°50'56.7"E, in a stream flowing from a small spring on the outskirts of the forest, hand net sampling, 1.05.2022, coll. I. Marin; 2♀♀ (LEMMI), Georgia, Samegrelo-Zemo Svaneti, Khobi Municipality, small pond near road Chaladidi–Kulevi–Poti, 42°11'42.0"N 41°42'19.9"E, about 2 m above sea level, hand net sampling, coll. I. Marin & V. Maslova, 29.01.2019; 2♀♀, 5♂♂ (LEMMI), Ukraine, Odessa Oblast, Berezivka District, Tiligul river, 47°11'30.3"N 30°54'31.3"E, about 2 m above sea level, hand net sampling, coll. D. Palatov, 18.11.2010.

**DIAGNOSIS.** Body pigmented. Distal article of accessory flagellum of AI is about 2.0X shorter than basal one. Inner plate of MxI with 7 plumose marginal setae. GnI with palm about 1.3–1.5X as long as wide in males and females. GnII with palm about 1.6–1.7X as long as wide in males and females. Coxal plates subequal or longer than palm of GnI–II in length. PVII basis without distinct posterior lobe. Coxal gill VII very small. EpI with distinct protruding sharp posteroventral tooth. EpII with 3–4 ventral spines. EpIII with distinct protruding posteroventral tooth, and 1–2 ventral spines. Basal article (peduncle) of UIII with 1–2 spines. Telson with distal notch, reaching about 1/4 of its length in females and to 1/2 in males.

**GENBANK ACCESSION NUMBERS.** KF290224, HE794981–HE794981, HE794987–HE794989, LK028562, LK028563, OP292669, OP292670.

**TAXONOMIC REMARKS.** The complete description of the species was presented by Müller [1846], Schäferna [1922], Borutzky [1929], Sidorov & Palatov [2012]. Some authors report a significant morphological variability (see review in Sidorov & Palatov [2012]), but the review and the taxonomic analysis of morphological features of this species are out of the present study. The taxonomic revision of *S. ambulans*, its current distribution and possible diversity of included cryptic species should be accomplished within the special study later.

**DISTRIBUTION AND ECOLOGY.** Widely distributed epigeal species, inhabiting different surface water resources, such as small streams and lake, without predators (mostly fishes), swamps, and peat bogs. Presently known from the northwestern Europe (the Great European Plain) and Black Sea region. It is known from Belgium, Germany (type locality), Poland, Lithuania, Belarus, southern Ukraine (Odessa) (present study), northwestern Russia (Pskov, Bryansk, Kaluga, Vladimir, Ryazan, Moscow regions), Georgia (Kobuleti area) (present study) and northwestern Black Sea coastal area of the Republic of Türkiye (Turkey) [Sidorov, Palatov, 2012; Özbek, 2018; present study]. It is possible to assume that such a wide distribution of the species is due to its habitation in surface (epigeal) water reservoirs, such as ponds, swamps and peat bog, and the possible spread by birds, as is known for the genus *Gammarus*.

*Synurella taurica* Martynov, 1931

Figs 4d–g; 5–7.

**MATERIAL EXAMINED.** Neotype, ♀ (bl. 7.0 mm), ZMMU Mb-1228, Russian Federation, Crimean Peninsula, Yalta area, Ai-Petri massif, eastern slope of the Mogabi Mountain, Turtle Lake, 44°28'30.5"N 34°05'06.8"E, hand net sampling, coll. I. Marin & D. Palatov, 5.04.2022; Additional material. 1♀, (bl. 6.8 mm), Mb-1239, 1♂ (bl. 7.0 mm), ZMMU Mb-1240, 5♀♀, 3♂♂ (LEMMI), same locality and data as for neotype; 7♀♀, 4♂♂ (LEMMI), eastern slope of the Mogabi Mountain (Ai-Petri massif), small forest pond, 44°28'58.03"N 34°05'49.56"E, hand net sampling, coll. I. Marin & D. Palatov, 5.04.2022. 7♀♀, 3♂♂ (LEMMI), Russian Federation, Krasnodar Krai, Anapa Urban Okrug, a small pond in the Utash village, 45°6'3.6"N 37°17'33.6"E, about 3 m above sea level, hand net sampling, coll. I. Marin & D. Palatov, 18.05.2019; 5♀♀ (LEMMI), Russian Federation, Republic of Adygea, Adygeysk Urban Okrug, fire pond of the gas station near the Psekups settlement, 44°50'19"N 39°12'47"E, about 30 meters above sea level, hand net sampling, coll. I. Marin & D. Palatov, 11.05.2019.

**DIAGNOSIS.** Body pigmented. Distal article of accessory flagellum of AI is about 1.8–2.2X shorter than basal one. Inner plate of MxI with 8 plumose marginal setae. GnI with palm about 1.5X as long as wide in females and about 1.6–1.7X as long as wide in males. GnII with palm about 1.8X as long as wide in males and females. Coxal plates slightly shorter than palm of GnI–II in males and longer in females. PVII basis without distinct posterior lobe. Coxal gill VII small in males and very large in females. EpI with distinct protruding sharp posteroventral tooth. EpII with 3–4 ventral spines. EpIII with distinct protruding posteroventral tooth, and 1–2 ventral spines. Basal article (peduncle) of UIII with 1–3 spines. Telson with distal notch, reaching about 1/4 of its length.

**GENBANK ACCESSION NUMBERS.** OP306065–OP306067.

**TAXONOMIC REMARKS.** The species is morphologically close to *S. ambulans*, but can be separated by less developed inner lobes of labium (Fig. 6a), narrower basis of PV–VI (Fig. 6j), more expanded posteroventral angle of basis of PV–VII (Fig. 6f, j, l), less produced posteroventral margins of EpI–III (Fig. 7a–c) and shallower distal notch of telson (Fig. 7d, e). Due to the distinctive morphological features and geographical isolation of the species, we would like to preserve its taxonomic status as a valid species, despite a small genetic divergence (about 2% by COI mtDNA) from other populations of *S. ambulans*. Some of species delimitation methods also supports such taxonomic decision (see Fig. 2).

**DISTRIBUTION AND ECOLOGY.** Epigeal species, which is presently known only from two localities: surface waters resources of the eastern slope of the Mogabi Mountain (Ai-Petri massif) of the Crimean Peninsula and small ponds in the delta of Kuban river (see above).

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

Figs 8–13.

**MATERIAL EXAMINED.** Holotype, ♂ (bl. 6.0 mm), ZMMU Mb-1229, South-western Caucasus, Abkhazia, Gagra District, drainage canals around the Inkit Lake, 43°10'24.4"N 40°19'04.5"E, hand net sampling, 11.02.2018, coll. D. Palatov. Paratype. 1♀ (bl. 7.2 mm), ZMMU Mb-1230, same locality and data as holotype. Additional material. 5♂♂, 2♀♀ (LEMMI), same locality and data as for holotype.

**ETYMOLOGY.** The species is named after the Inkit Lake (Pitsunda, Abkhazia), where the species was discovered.

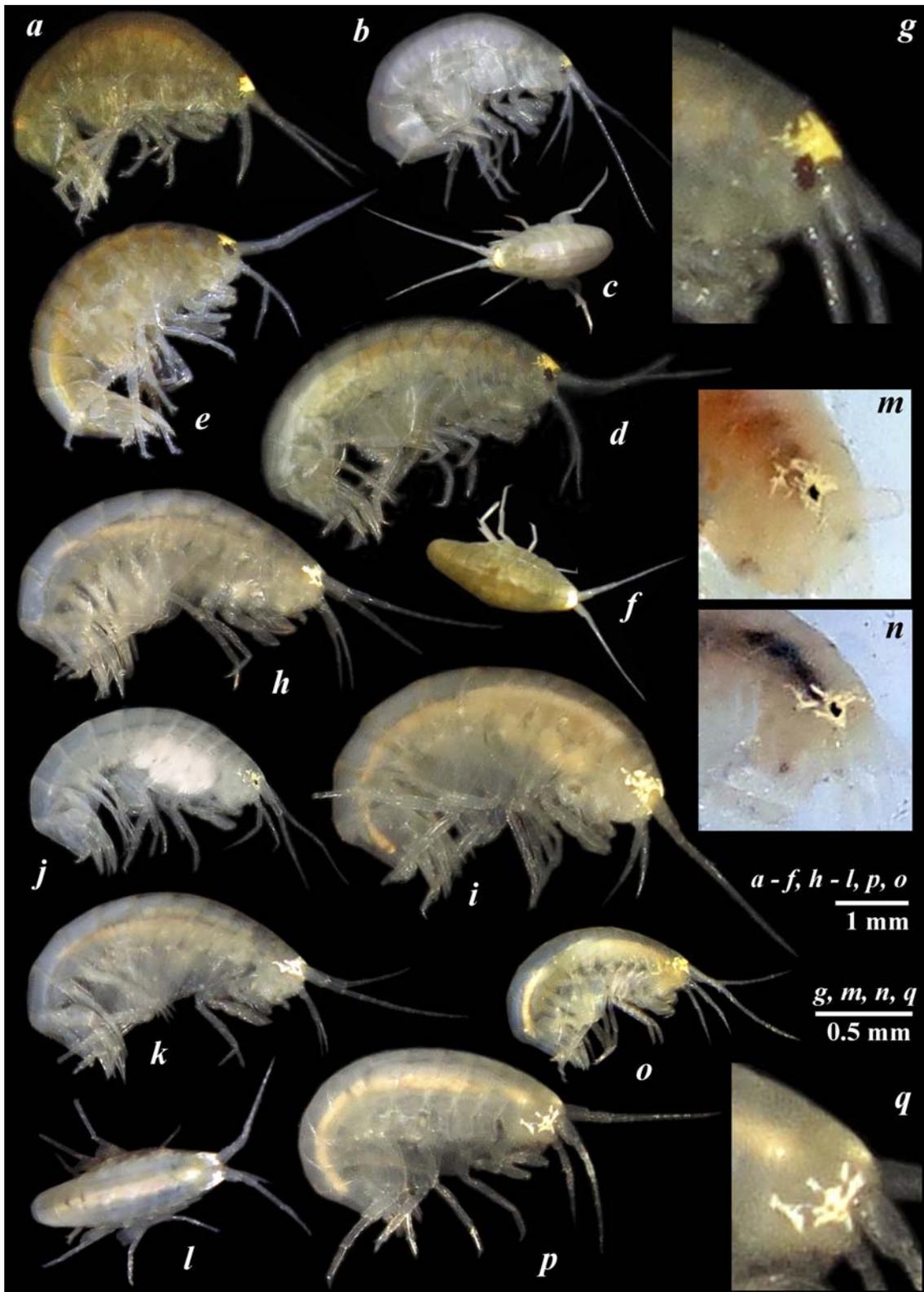


Fig. 4. Live coloration of *Synurella ambulans* (F. Müller, 1846) (a–c), *S. taurica* Martynov, 1931 (d–g), *S. adegoyi* Marin et Palatov sp.n. (h–n), *S. premontana* Marin et Palatov sp.n. (o–q) with well-marked dorsal yellow pots on the head: a, b, e, d, h–k, p, o — general lateral view; c, f, l — dorsal view; g, m, n, q — head, lateral view.

Рис. 4. Прижизненная окраска *Synurella ambulans* (F. Müller, 1846) (a–c), *S. taurica* Martynov, 1931 (d–g), *S. adegoyi* Marin et Palatov sp.n. (h–n), *S. premontana* Marin et Palatov sp.n. (o–q) с хорошо заметными дорсальными желтыми пятнами на голове: a, b, e, d, h–k, p, o — общий вид сбоку; c, f, l — вид сзади; g, m, n, q — голова, вид сбоку.

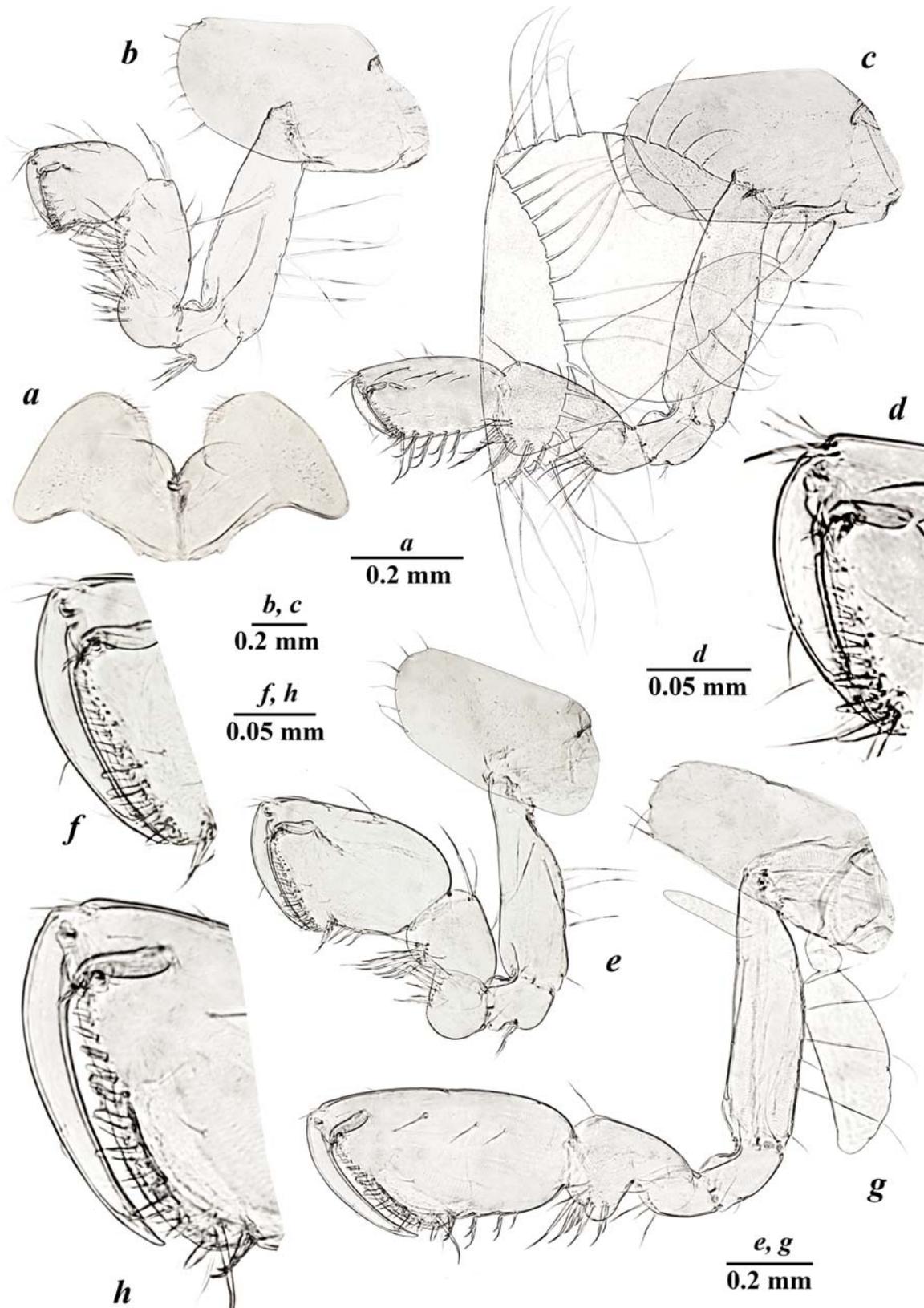


Fig. 5. *Synurella taurica* Martynov, 1931, ♀ (a-d), ♂ (e-g): a — labium (lower lip); b, e — gnathopod I; f — distoventral palmar margin of chela of GnI; c, g — gnathopod II; d, h — distoventral palmar margin of chela of GnII.

Рис. 5. *Synurella taurica* Martynov, 1931, ♀ (a-d), ♂ (e-g): a — лабиум (нижняя губа); b, e — гнатопода I; f — дистовентральный пальмарный край ладони (клешни) GnI; c, g — гнатопода II; d, h — дистовентральный пальмарный край ладони (клешни) GnII.

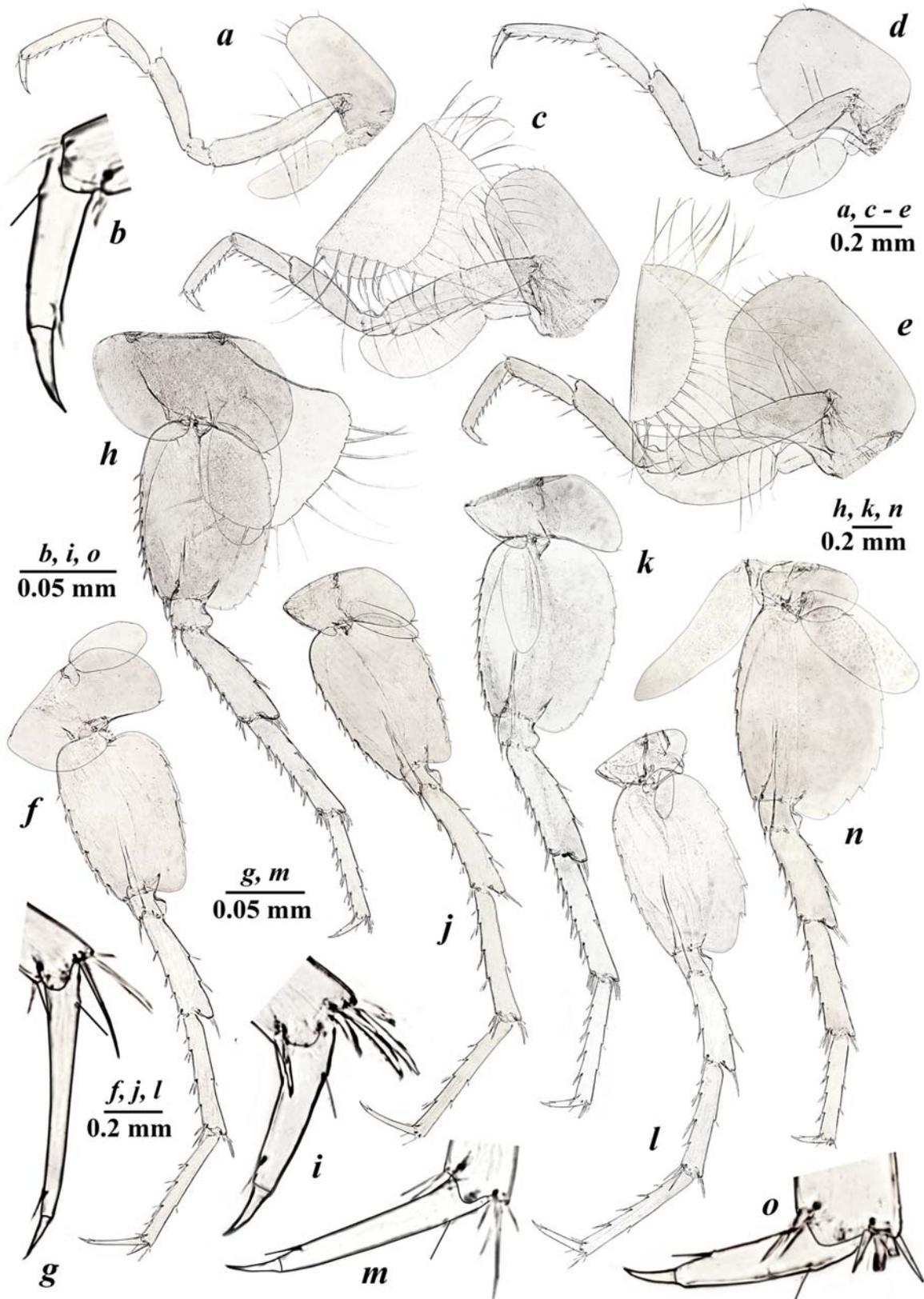


Fig. 6. *Symurella taurica* Martynov, 1931, ♀ (*a, b, d, f, g, j, l, m*), ♂ (*c, e, h, i, k, n, o*): *a, c* — pereopod III; *b* — dactylus of PIII; *c, e* — pereopod IV; *f, h* — pereopod V; *g, i* — dactylus of PV; *j, k* — pereopod VI; *l, n* — pereopod VII; *m, o* — dactylus of PVII.

Рис. 6. *Symurella taurica* Martynov, 1931, ♀ (*a, b, d, f, g, j, l, m*), ♂ (*c, e, h, i, k, n, o*): *a, c* — переопода III; *b* — дактилус PIII; *c, e* — переопода IV; *f, h* — переопода V; *g, i* — дактилус PV; *j, k* — переопода VI; *l, n* — переопода VII; *m, o* — дактилус PVII.

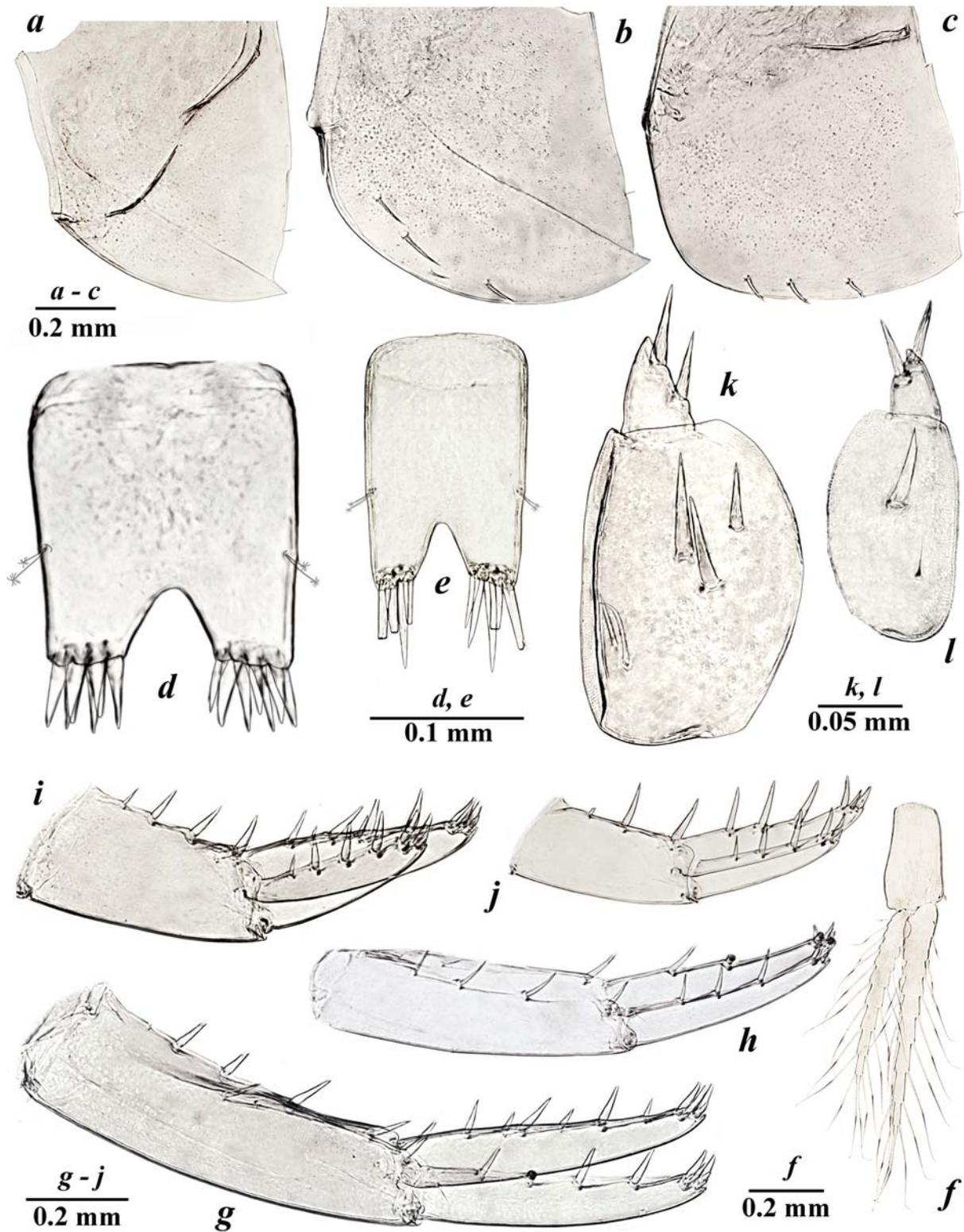


Fig. 7. *Synurella taurica* Martynov, 1931, ♀ (a-d, f, g, i, k), ♂ (e, g, h, j, l): a — epimeral plate I; b — epimeral plate II; c — epimeral plate III; d, e — telson; f — pleopod II; g, i — uropod I; h, j — uropod II; k, l — uropod III.

Рис. 7. *Synurella taurica* Мартынов, 1931, ♀ (a-d, f, g, i, k), ♂ (e, g, h, j, l): a — эпимеральная пластинка I; b — эпимеральная пластинка II; c — эпимеральная пластинка III; d, e — тельсон; f — плеопода II; g, i — уропода I; h, j — уропода II; k, l — уропода III.

**DIAGNOSIS.** Body pigmented. Distal article of accessory flagellum of AI is about 2.7X shorter than basal one. Inner plate of MxI with 4–6 plumose marginal setae. GnI with palm about as 1.4X long as wide in males and females. GnII with palm about 1.8X as long as wide in males and females. Coxal plates slightly shorter or subequal than palm of GnI–II in males. PVII basis with distinct distal corner in females. Coxal gill VII small in males and large in females. EpI with distinct protruding posteroventral tooth. EpII with 1–4 ventral spines. EpIII with distinct protruding posteroventral tooth, and 1–2 ventral spines. Basal article (peduncle) of UIII with 1–2 spines. Telson with distal notch, reaching about 1/3–1/4 of its length.

**DESCRIPTION.** Body: moderately stout; the largest collected ♂ has bl. 6.0 mm; the largest collected ♀ has bl. 7.5 mm.

Head (Fig. 13a): smooth, with bluntly produced anteroventral lobe; with well-developed pigmented eyes.

Antenna I (Fig. 8a, b): about 50% of body length, about 1.5X longer than antenna II; primary flagellum with 11–13 articles, with aesthetascs on distal articles; accessory flagellum 2-articulated, distal article about 2.7X shorter than basal one (Fig. 8c).

Antenna II (Fig. 8d, e): gland clone distinct, distally pointed; peduncle about 1.9–2.1X longer than flagellum, with robust setae tightly covering articles 3 and 4, peduncle of article 4 about 1.1X longer than article 5; flagellum 6 or 7-articulated, without calceoli in females, and with calceoli in males (Fig. 13b).

Mandible: left mandible (Fig. 9d) incisor 4-dentate, *lacinia mobilis* 4-dentate, with 3 robust plumose accessory setae; molar process with 1 seta (Fig. 9e). Right mandible (Fig. 9f) incisor 4-dentate, *lacinia mobilis* toothed, triturative, lobes with numerous protuberances; underlying with a row of 3 robust plumose setae; molar process similar to left mandible (Fig. 9g). Palp 3-articulated, article 2 with 5–6 setae; article 3 about 2.8X longer than wide, with convex margins, with 6–7 separate D-setae, 1 C-seta, 1 B-seta and 3 separate E-setae.

Lateralial with 8 teeth.

Labrum (upper lip) (Fig. 9a): oval, apical margin with numerous small fine setae.

Labium (lower lip) (Fig. 9b, c): inner lobes feebly developed.

Maxilla I (Fig. 9h): inner plate with 4–6 plumose marginal setae, outer plate with 6–7 apical comb-spines; palp 2-articulated, distal article pubescent, about 2.5X of basal article, apical margin of distal article with 6 setae.

Maxilla II (Fig. 9i): inner, outer plates covered in pubescent setae; inner and outer plates subequal in length; outer plate weakly narrowing distally, with 8 apical setae; inner plate narrowing slightly distally, with group of dense short setae on apex, with oblique row of 4 short plumose setae.

Maxilliped (Fig. 9j): inner plate much shorter than outer plate, with 2 spines and 1 robust plumose seta apically, and 3 robust plumose setae laterally; outer plate narrow, with a row of 8 medial stiff simple setae of different length; palp 4-articulated, article I with 1 seta on outer margin; article II with a row of 12 simple setae on inner margin, without setae on outer margin; article III trapezoidal; dactylus with 1 seta on outer margin, nail long, slender, with 2 thin setae at hinge.

Gnathopod I (Figs 8f, h, 13c, d) different in males and females. Male (Figs 8h, 13c): gnathopod I smaller than gnathopod II; coxal plate sub-rectangular, distally rounded,

with 7–8 apical and numerous facial setae, width/depth ratio is 0.52–0.55/1; basis width/length ratio is 0.36/1, without setae on anterior margin, with 1 long seta on inner face and 3–4 long setae on posterior margin; merus with 6 distal setae; carpus is 0.37X of basis and 0.39X of propodus, with 6 serrated in inner margin and 2 simple setae in outer margin; propodus suboval, 1.4X longer than broad, with 1–2 simple setae in anterior margin and 5 serrated setae in posterior margin; distal margin of palm almost straight, slightly oblique, with double row of 9 inner and 8 outer robust setae; palmar groove (depression) (Fig. 13d) feebly developed, with 4 inner and 4 outer robust setae; dactylus with 1 outer seta.

Female (Fig. 8f, g): gnathopod I smaller than gnathopod II; coxal plate sub-rectangular, distally rounded, with 7–8 apical and numerous facial setae, width/depth ratio is 0.52–0.55/1; basis width/length ratio is 0.36/1, with 1–2 short setae on anterior margin, 8 long setae on inner face and 1 long seta on posterior margin; merus with 9–10 distal setae; carpus is 0.50X of basis and 0.89X of propodus, with 10–13 serrated setae in inner margin and 3 simple setae in outer margin; propodus trapezoidal, 1.4X longer than broad, with 4 simple anterior setae, 2 small simple inferior medial and 6 posterior serrated setae; distal margin of palm almost straight, with double row of 5 inner and 5 outer robust setae; palmar groove (depression) (Fig. 8g) feebly developed, with 4 inner and 3 outer robust setae; dactylus with 1 outer seta.

Gnathopod II (Figs 8i–l, 13e, f) different in males and females. Male (Figs 8k, l, 15e, f): coxal plate sub-rectangular, with 5 apical and numerous facial setae, width/depth ratio is 0.48/1; basis width/length ratio is 0.3/1, with several (5–6) long setae inserted along posterior margin and with 1 long simple seta in anterior margin; ischium with 1 short simple seta; merus with 1 distal seta; carpus is 0.30X of length of basis and 0.34X of propodus, with 1 anterior simple seta and 8–9 serrated posterior setae; propodus sub-oval, 1.8X longer than broad, with 1 simple anterior seta, 2–3 superior medial setae and 3–5 groups of posterior setae; palm oblique with a double row of 10–12 inner and 8–10 outer robust setae; palm groove (depression) (Figs 8l, 13f) feebly developed, with 2–3 inner and 3 outer robust setae; dactylus without inner and with 1 outer seta.

Female (Fig. 8i, j): coxal plate sub-rectangular, with 9 apical and numerous facial setae, width/depth ratio is 0.55/1; basis width/length ratio is 0.3/1, with several (4–5) long setae inserted along posterior margin and with 4 long simple setae in anterior margin; ischium without setae; merus with 5 distal setae; carpus is 0.37X of length of basis and 0.34X of propodus, with 2 anterior simple setae and 5 groups of serrated posterior setae; propodus rectangular, 1.8X longer than broad, with 1 simple anterior seta, 4 superior medial, 1–2 inferior medial and 5 groups of posterior setae; palm slightly oblique with a double row of 6 inner and 6 outer robust setae; palm groove (depression) (Fig. 8j) feebly developed, with 4 inner and 3 outer robust setae; dactylus without inner and with 1 outer seta.

Pereopod III (Figs 10a, 11a): coxal plate sub-rectangular, with 6–8 apical and numerous facial setae, width/depth ratio is 0.48–0.53/1; basis about 4.0–4.2X as long as wide, with long anterior and posterior simple setae; merus about 0.55–0.62X of basis, about 1.3X of carpus and 1.1X of propodus in length; carpus about 0.77–0.85X of propodus in length; dactylus (Figs 10b, 11b) about 0.37–0.45X of propodus, with 1 plumose seta on outer margin and 1 additional spine accompanying with 1 seta on ventral margin.

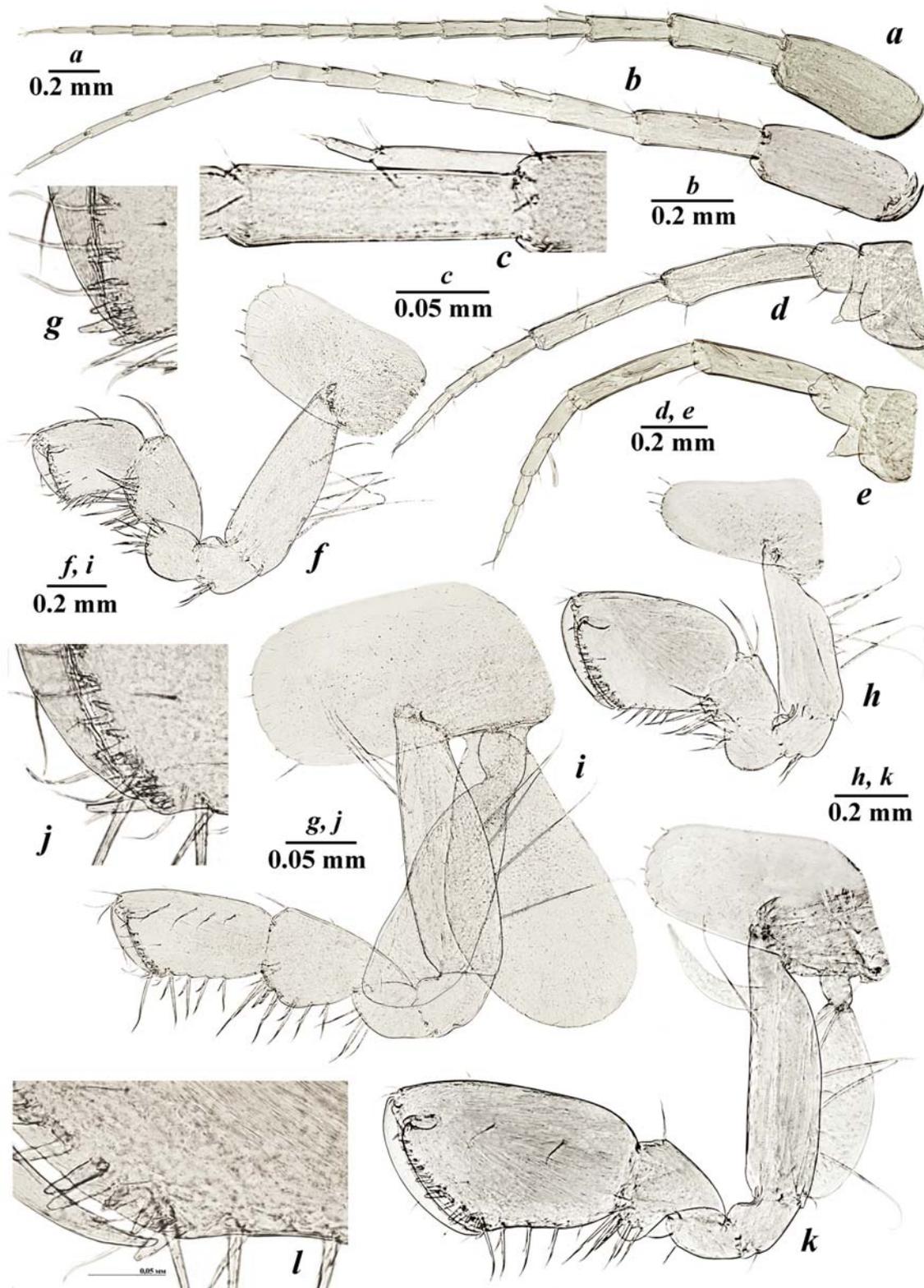


Fig. 8. *Synurella inkiti* Palatov et Marin sp.n., ♂ (b, e, h, l, k), ♀ (a, c, d, g, f, g, i, j): a, b — antenna I; c — accessory flagellum of antenna I; d, e — antenna II; f, h — gnathopod I; g — distoventral palmar margin of chela of GnI; i, k — gnathopod II; j, l — distoventral palmar margin of chela of GnII.

Рис. 8. *Synurella inkiti* Palatov et Marin sp.n., ♂ (b, e, h, l, k), ♀ (a, c, d, g, f, g, i, j): a, b — антенна I; c — добавочный жгутик антенны I; d, e — антенна II; f, h — гнатопода I; g — дистовентральный край ладони (клешни) GnI; i, k — гнатопода II; j, l — дистовентральный край ладони (клешни) GnII.

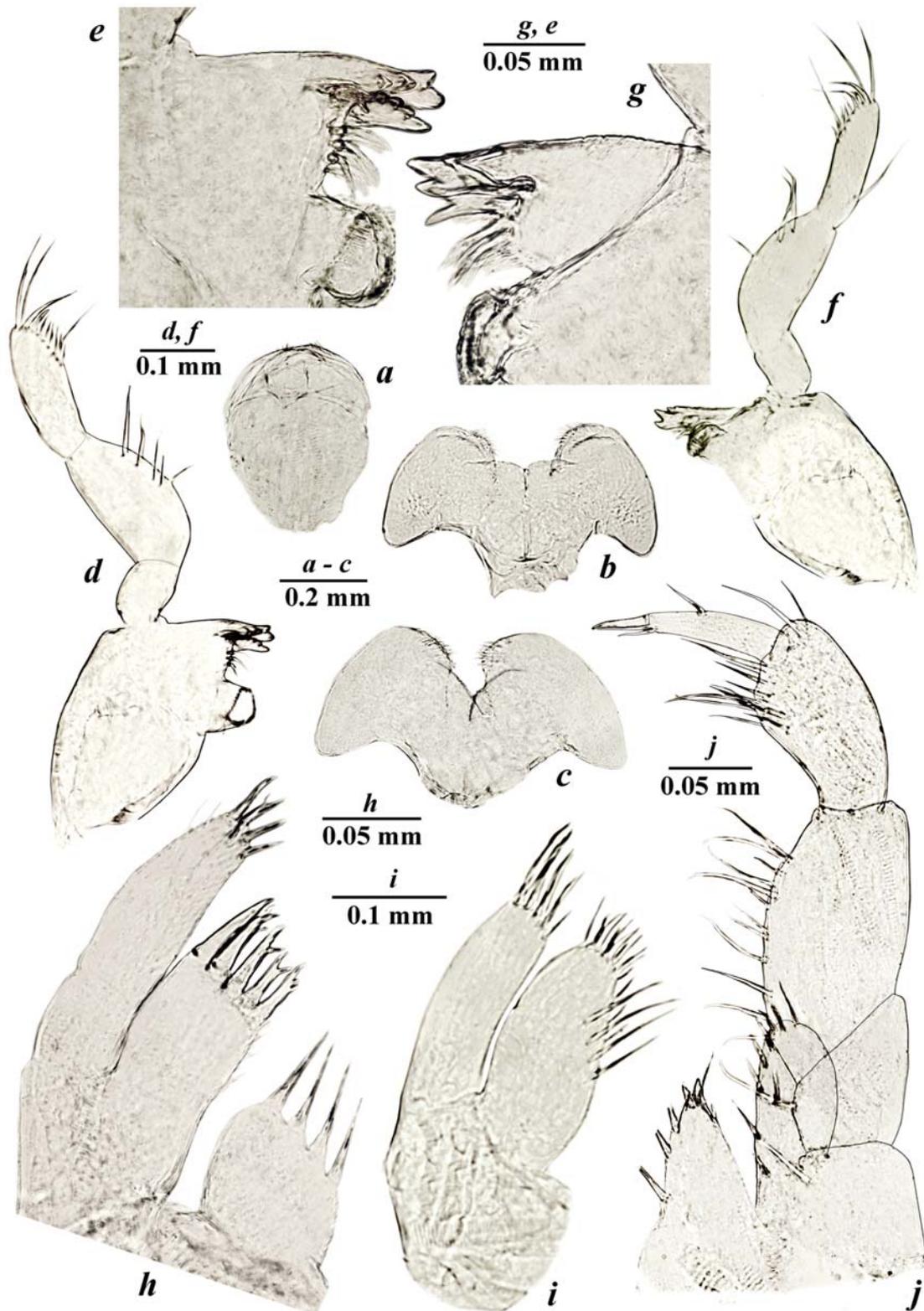


Fig. 9. *Synurella inkiti* Palatov et Marin sp.n., ♂ (*a, c-j*), ♀ (*b*): *a* — labrum (upper lip); *b, c* — labium (lower lip); *d* — left mandible; *e* — same, incisor process and *pars incisiva*; *f* — right mandible; *g* — same, incisor process and *pars incisiva*; *h* — maxilla I; *i* — maxilla II; *j* — maxilliped.

Рис. 9. *Synurella inkiti* Palatov et Marin sp.n., ♂ (*a, c-j*), ♀ (*b*): *a* — лабрум (верхняя губа); *b, c* — лабиум (нижняя губа); *d* — левая мандибула; *e* — то же, режущий отросток и резцовая часть; *f* — правая мандибула; *g* — то же, режущий отросток и резцовая часть; *h* — максилла I; *i* — максилла II; *j* — максиллипод.

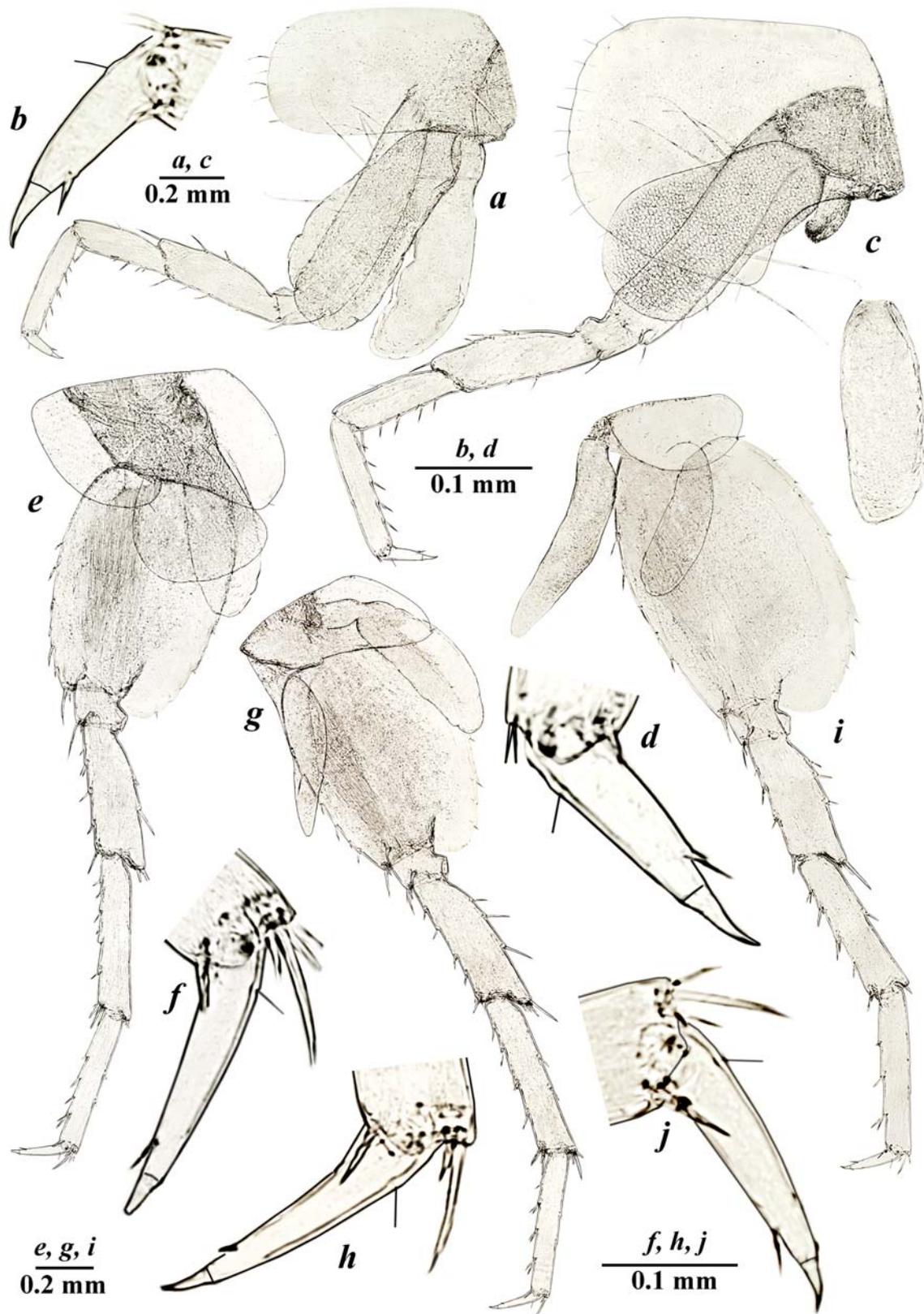


Fig. 10. *Synurella inkiti* Palatov et Marin sp.n., ♀: *a* — pereopod III; *b* — dactylus of PIII; *c* — pereopod IV; *d* — dactylus of PIV; *e* — pereopod V; *f* — dactylus of PV; *g* — pereopod VI; *h* — dactylus of PVI; *i* — pereopod VII; *j* — dactylus of PVII.  
 Рис. 10. *Synurella inkiti* Palatov et Marin sp.n., ♀: *a* — переопода III; *b* — дактилус PIII; *c* — переопода IV; *d* — дактилус PIV; *e* — переопода V; *f* — дактилус PV; *g* — переопода VI; *h* — дактилус PVI; *i* — переопода VII; *j* — дактилус PVII.

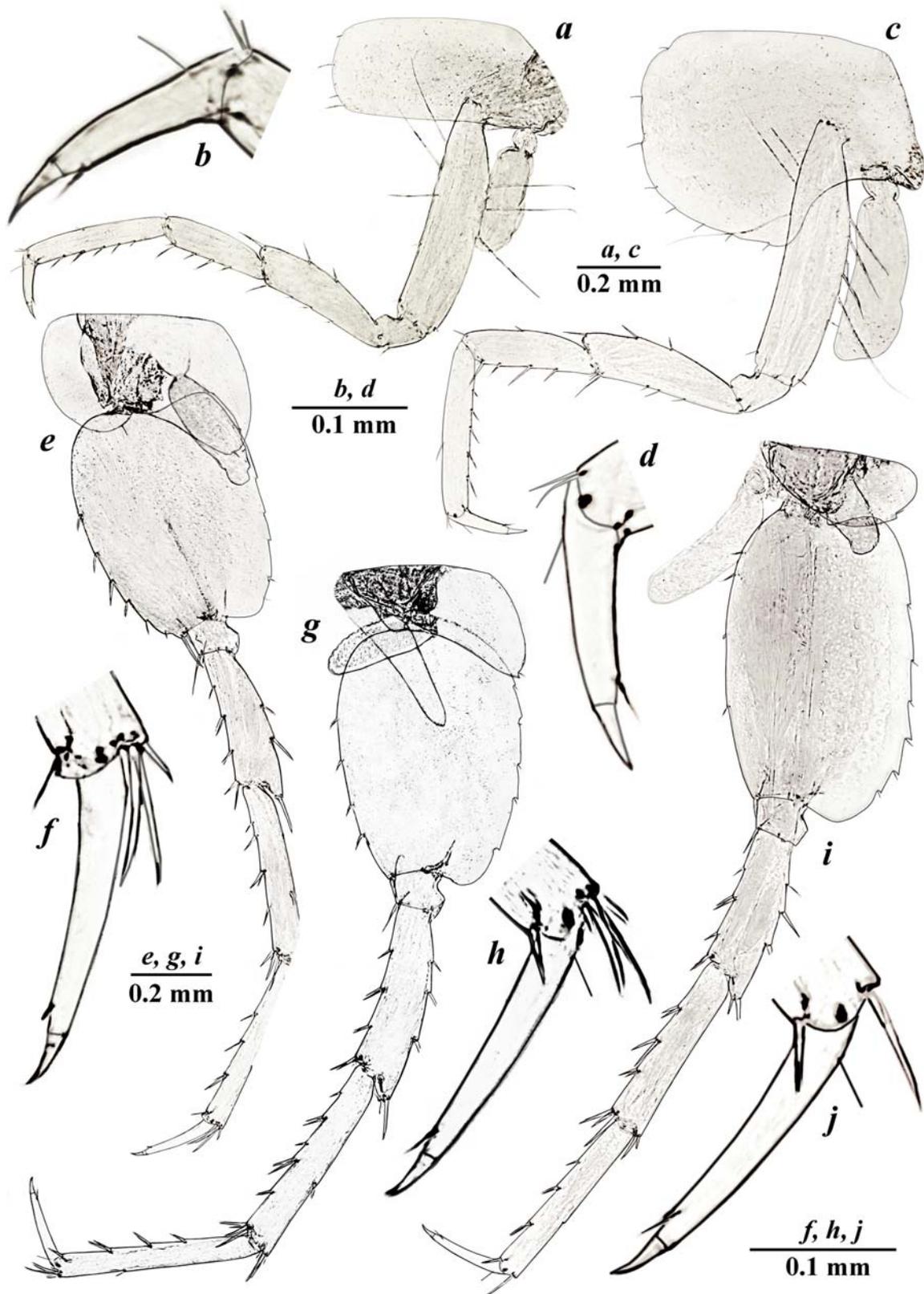


Fig. 11. *Synurella inkiti* Palatov et Marin sp.n., ♂: *a* — pereopod III; *b* — dactylus of PIII; *c* — pereopod IV; *d* — dactylus of PIV; *e* — pereopod V; *f* — dactylus of PV; *g* — pereopod VI; *h* — dactylus of PVI; *i* — pereopod VII; *j* — dactylus of PVII.

Рис. 11. *Synurella inkiti* Palatov et Marin sp.n., ♂: *a* — переопода III; *b* — дактилус PIII; *c* — переопода IV; *d* — дактилус PIV; *e* — переопода V; *f* — дактилус PV; *g* — переопода VI; *h* — дактилус PVI; *i* — переопода VII; *j* — дактилус PVII.

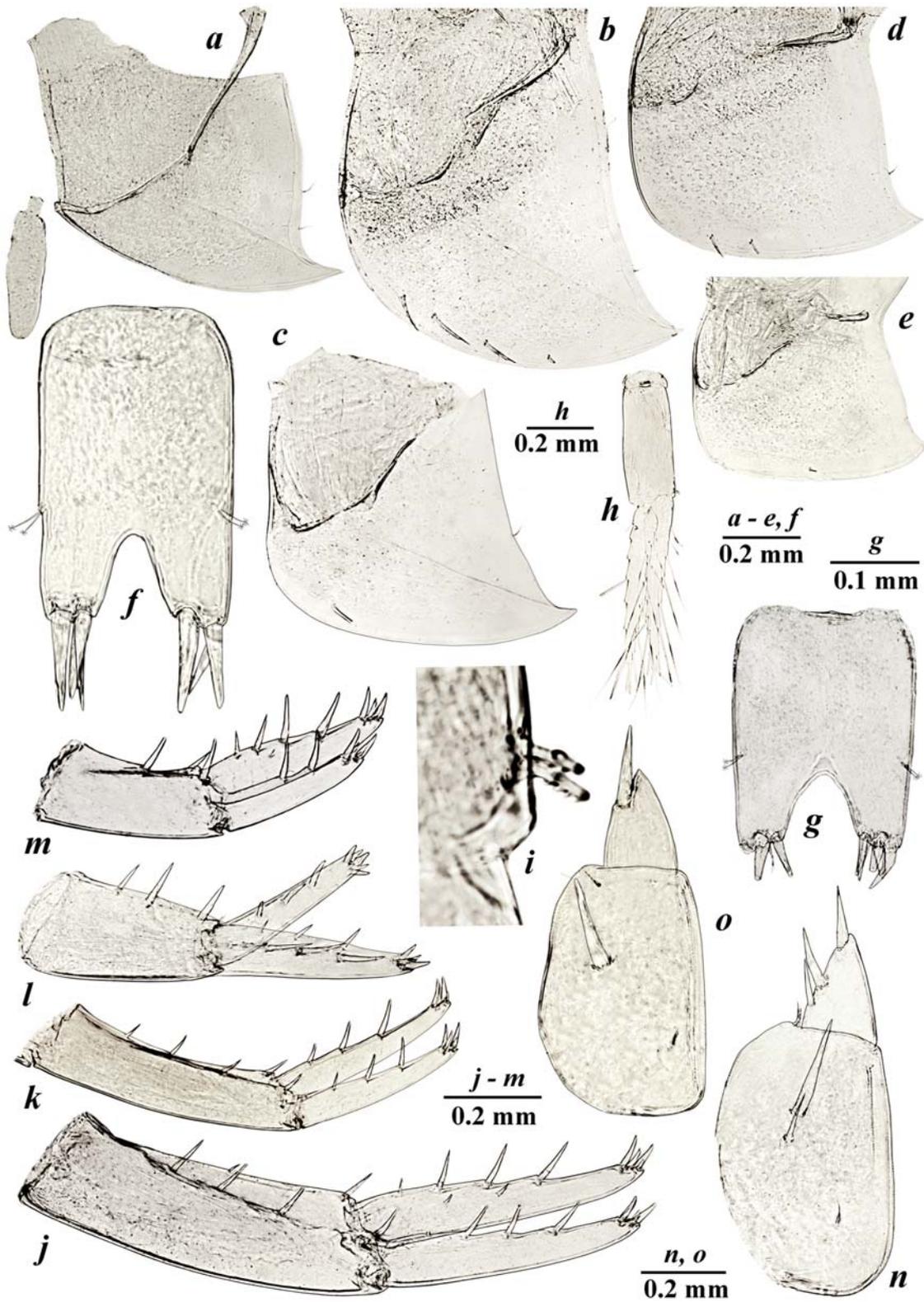


Fig. 12. *Synurella inkiti* Palatov et Marin sp.n., ♂ (c, e, f, h, i, k, m, n), ♀ (a, b, d, g, j, l, o): a — epimeral plate I; b, c — epimeral plate II; d, e — epimeral plate III; f, g — telson; h — pleopod III; i — hooks of retinacula of pleopod II; j, k — uropod I; l, m — uropod II; n, o — uropod III.

Рис. 12. *Synurella inkiti* Palatov et Marin sp.n., ♂ (c, e, f, h, i, k, m, n), ♀ (a, b, d, g, j, l, o): a — эпимеральная пластинка I; b, c — эпимеральная пластинка II; d, e — эпимеральная пластинка III; f, g — тельсон; h — плеопода III; i — крючки ретинакулы плеоподы II; j, k — уропода I; l, m — уропода II; n, o — уропода III.

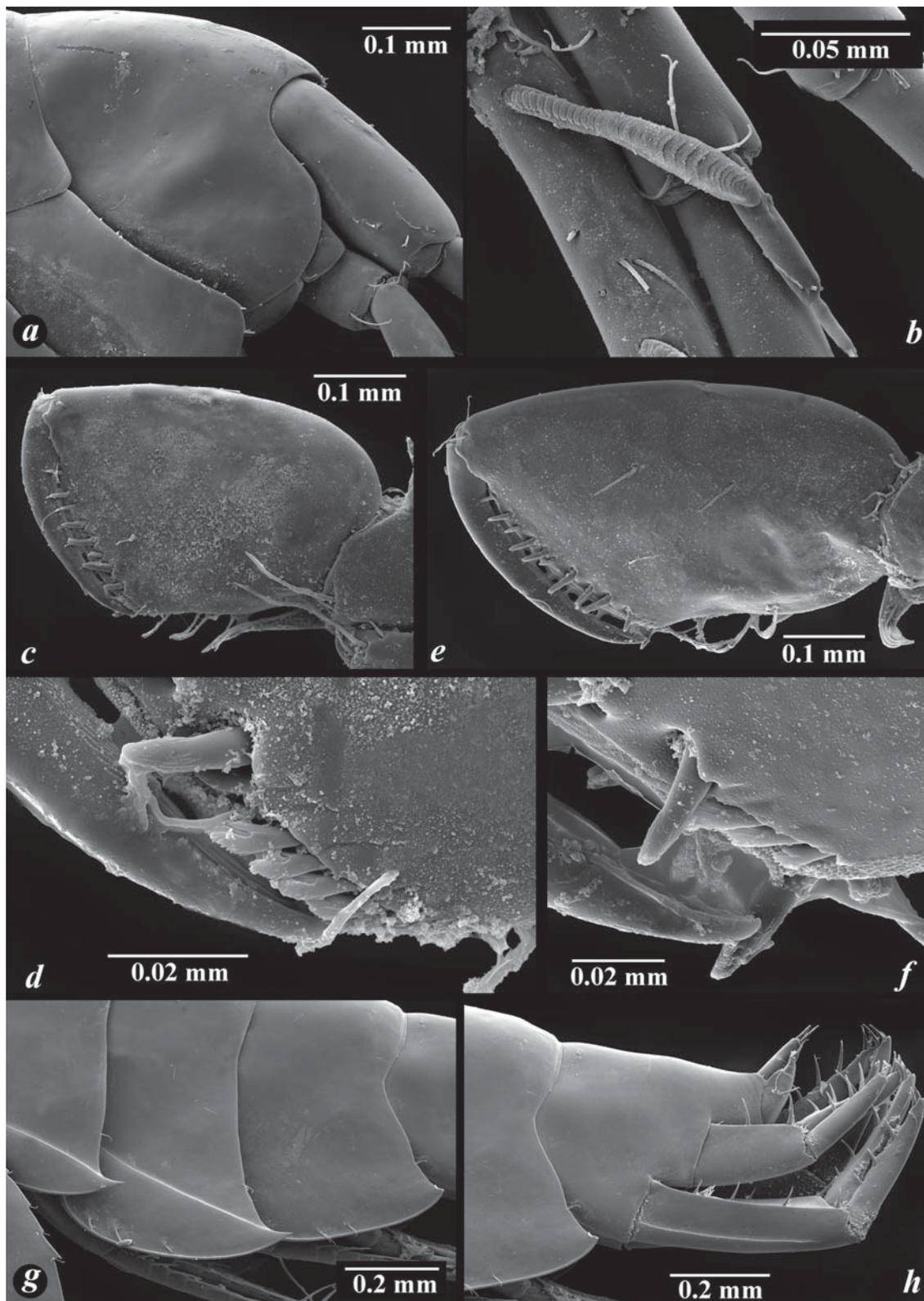


Fig. 13. *Synurella inkiti* Palatov et Marin sp.n., ♂: *a* — head; *b* — calceola on article V of peduncle of antenna II; flagellum; *c* — palm (chela) of GnI; *d* — distoventral margin of palm (chela) of GnI; *e* — palm (chela) of GnII; *f* — distoventral margin of palm (chela) of GnII; *g* — epimeral plates I–III; *h* — urosomal segments.

Рис. 13. *Synurella inkiti* Palatov et Marin sp.n., ♂: *a* — голова; *b* — кальцеола на сегменте V антенны II; *c* — ладонь (клешня) GnI; *d* — дистовентральный край ладони (клешни) GnI; *e* — ладонь (клешня) GnII; *f* — дистовентральный край ладони (клешни) GnII; *g* — эпимеральные пластинки I–III; *h* — уросомальные сегменты.

Pereopod IV (Figs 10c; 11c): subequal to PIII in length; coxal plate expanded and broadly convex distally, posterior margin with shallow excavation, distal margin with 8–14 short apical setae and numerous facial setae, width/depth ratio is 1.20–1.25/1; basis about 4.1–4.3X as long as wide, with long anterior and posterior simple setae; merus about 0.45–0.60X of basis, about 1.25X of carpus and subequal to propodus in length; carpus subequal to propodus in length; dactylus about 0.38–0.42X of propodus, with 1 plumose seta on outer margin and 1 additional spine accompanying with 1 seta on ventral margin.

Pereopods V, VI, VII with the length ratio is 1.00/1.01/0.98 in male and 1.00/1.12/1.01 in female.

Pereopod V (Figs 10e, 11e): coxal plate large, bilobate with distinct anterior and posterior lobes; posterior and anterior lobes with 1 margin simple seta each, with numerous facial setae; basis about 1.34–1.40X as long as wide, with numerous facial setae, posterior margin slightly convex, armed with 8–12 shallow serrations, with distal corner, anterior margin with 6 split-tipped robust and 3–4 distal setae; merus about 0.64–0.66X of basis, 0.85–0.92X of carpus and 1.02–0.85X of propodus in length; dactylus (Figs 10f, 11f) approximately 0.40–0.48X of propodus, with 1 plumose seta on outer margin and 1 additional spine accompanying with 1 seta on ventral margin.

Pereopod VI (Figs 10g, 11g): coxal plate bilobate, with distinct posterior and vestigial anterior lobes; anterior lobe without setae, posterior lobe with 1 margin seta, each with numerous facial setae; basis about 1.4X as long as wide, with numerous facial setae, posterior margin convex, armed with 6–8 shallow serrations, anterior margin with 4–6 split-tipped robust and 4 distal setae; merus about 0.7–0.8X of basis, 0.96–0.98X of carpus and subequal to propodus in length; dactylus (Figs 10h, 11h) approximately 0.35–0.45X of propodus, with 1 plumose seta on outer margin and 1 additional spine accompanying with 1 seta on ventral margin.

Pereopod VII (Figs 10i, 11i): coxal plate small, semi-lunar, with 1 posterior seta; basis about 1.38–1.60X as long as wide, with numerous facial setae, posterior margin convex, armed with 6–10 serrated setae and with distinct distal corner, anterior margin with 4–6 split-tipped robust and 3 distal setae; merus about 0.56–0.58X of basis, 0.87–0.93X of carpus and 0.87–0.93X of propodus in length; dactylus (Figs 10j, 11j) approximately 0.37–0.48X of propodus in length, with 1 plumose seta on outer margin and 1 additional spine accompanying with 1 seta on ventral margin.

Gills, brood plates (Figs 10, 11): coxal gills on somites II–VII, somites II–VII with lanceolate sternal gill on each. Male: coxal gills II–VII ovoid, gills/bases pereopod ratios are 0.80/1, 0.53/1, 0.63/1, 0.53/1, 0.44/1 and 0.23/1, respectively. Female: coxal gills II–VII ovoid, gills/bases pereopod ratios are 0.93/1, 0.99/1, 0.71/1, 0.71/1, 0.70/1 and 0.51/1, respectively. Brood plates on somites II–V slender, setaceous, decreasing in size posteriorly.

Pleopods (Fig. 12h). Pleopod I peduncle with 2 coupling hooks in retinacula, without lateral setae; outer and inner rami with 7 and 10 articles, respectively. Pleopods II and III peduncles with 2 coupling hooks in retinacula, without setae (Fig. 12i); outer and inner rami with 7 and 8 articles, respectively.

Epimera (Fig. 13g). Epimeral plate I (Fig. 12a) distally produced and sharpened, ventral margin without spines, posterior margin without setae in male and with 2 setae in female. Epimeral plate II (Fig. 12b, c) distally produced and sharpened,

ventral margin armed with 1–4 spines, posterior margin with 1–3 setae. Epimeral plate III (Fig. 12d, e) distally produced, ventral margin armed with 1–2 spines, posterior margin with 1 seta.

Urosomites completely fused, smooth (Fig. 13h).

Uropod I (Fig. 12j, k): peduncle about 3.2–4.4X as long as wide, with dorsoexternal row of 3 robust spines, 1 subdistal spine and 1 dorsointernal robust spine; exopodite slightly shorter than endopodite; endopodite not paddle-like, with 3–4 dorsolateral, 4 apical spines and 1 ventral seta; exopodite with 3–4 dorsolateral and 4 apical spines.

Uropod II (Fig. 12l, m): peduncle about 2.0–4.4X as long as wide, about 0.82–0.94X of endopodite in length, with 1 outer and 2–3 inner robust spines; exopodite about 0.80–0.88X of endopodite in length, with 2–3 dorsal, 0–3 lateral and 5 apical robust spines; endopodite with 3–4 dorsal and 5 apical robust spines.

Uropod III (Fig. 12n, o): uniramous, peduncle oval or trapezoidal, about 1.51–1.57X as long as wide, with 1–2 weak spines and 1 simple seta; lateral and apical margin of ramus armed with 1–3 spines.

Telson (Fig. 12g): close to square or trapezoidal, about 1.33–1.63X as long as broad; distal margin with V-shaped distal notch, reaching about 1/3–1/4 of its length, each lobe armed with 4–5 robust spines, with 2 additional submarginal plumose setae.

COLORATION. The body and appendages yellowish or grayish transparent; well-pigmented black eyes well seen.

GENBANK ACCESSION NUMBERS. OP306069, OP306070.

TAXONOMIC REMARKS. The new species can be clearly separated from *Synurella ambulans*: 1) basis of PVII with posteroventral projection (lobe) (Figs 10i, 11i) (vs. basis of PVII oval, without posteroventral projection (lobe) in *S. ambulans* [Sidorov, Palatov, 2012: figs 5E, 9B]); 2) inner plate of MxI with 4–6 plumose marginal setae (Fig. 9h) (vs. inner plate of MxII with oblique row of 7 short plumose setae in *S. ambulans* [Sidorov, Palatov, 2012: fig. 4C]); 3) palm of GnII wider in distal part, with distoventral spines stronger (see Fig. 4k).

DISTRIBUTION AND ECOLOGY. Epigeal species, which is presently known only from a single locality in Abkhazia, southwestern Caucasus.

### *Synurella behningi* (Birštein, 1948)

Figs 14–17.

MATERIAL EXAMINED. Neotype, ♀ (bl. 6.5 mm), ZMMU Mb-1231, South-western Caucasus, Abkhazia, Gudauta region, Bacha Cave, 43°13'50"N 40°30'57.5"E, inside a small subterranean spring, coll. D. Palatov, 6.02.2020. Additional material. 4♀♀ (LEMMI), same locality and data as for holotype.

DIAGNOSIS. Only females are presently known. Body unpigmented, yellowish. Distal article of accessory flagellum of AI is about 2.3X shorter than basal article. Inner plate of MxI with 6 plumose marginal setae. GnI with palm about 1.7X as long as wide, GnII with palm about 2.2X as long as wide in females. Coxal plate longer than palm of GnI–II in females. PVII with basis bearing distinct posterior lobe. Coxal gill VII small about 0.3X of basis of PVII. Epl with short posteroventral tooth. EplI with 3–4 ventral spines. EplII with slightly producing posteroventral tooth, and 3 ventral spines. Basal article (peduncle) of UIII with 1–2 spines. Telson with distal notch, reaching about 1/4 of its length.

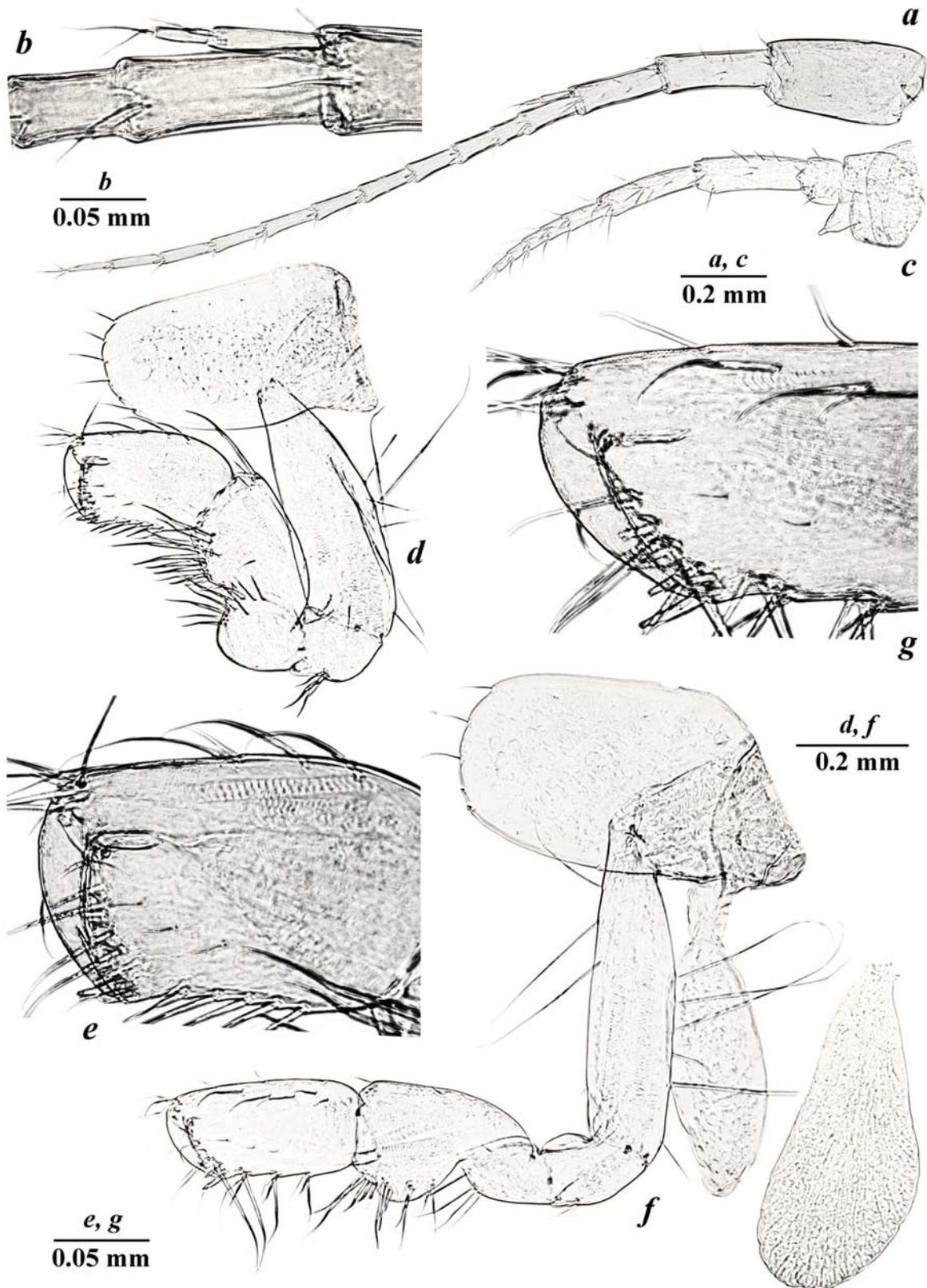


Fig. 14. *Synurella behningi* (Birštein, 1948), ♀: *a* — antenna I; *b* — accessory flagellum of antenna I; *c* — antenna II; *d* — gnathopod I; *e* — distoventral palmar margin of chela of GnI; *f* — gnathopod II; *g* — distoventral palmar margin of chela of GnII.

Рис. 14. *Synurella behningi* (Birštein, 1948), ♀: *a* — антенна I; *b* — добавочный жгутик антенны I; *c* — антенна II; *d* — гнатопода I; *e* — дистовентральный край ладони (клешни) GnI; *f* — гнатопода II; *g* — дистовентральный край ладони (клешни) GnII.

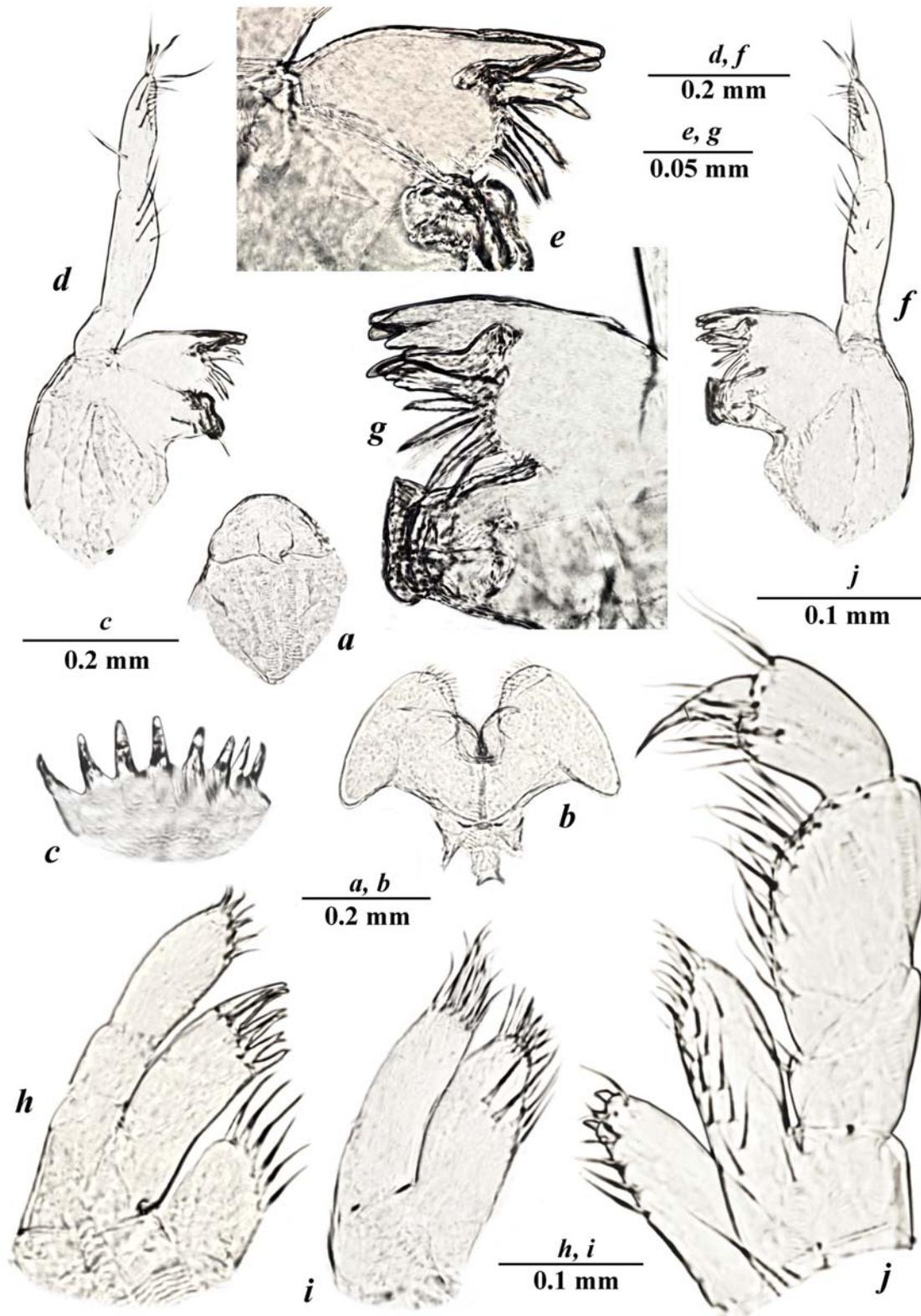


Fig. 15. *Synurella behningi* (Birštein, 1948), ♀: *a* — labrum (upper lip); *b* — labium (lower lip); *c* — lateralial; *d* — left mandible; *e* — same, incisor process and *pars incisiva*; *f* — right mandible; *g* — same, incisor process and *pars incisiva*; *h* — maxilla I; *i* — maxilla II; *j* — maxilliped.

Рис. 15. *Synurella behningi* (Birštein, 1948), ♀: *a* — лабрум (верхняя губа); *b* — лабиум (нижняя губа); *c* — латералия; *d* — левая мандибула; *e* — то же, режущий отросток и резцовая часть; *f* — правая мандибула; *g* — то же, режущий отросток и резцовая часть; *h* — максилла I; *i* — максилла II; *j* — максиллипод.

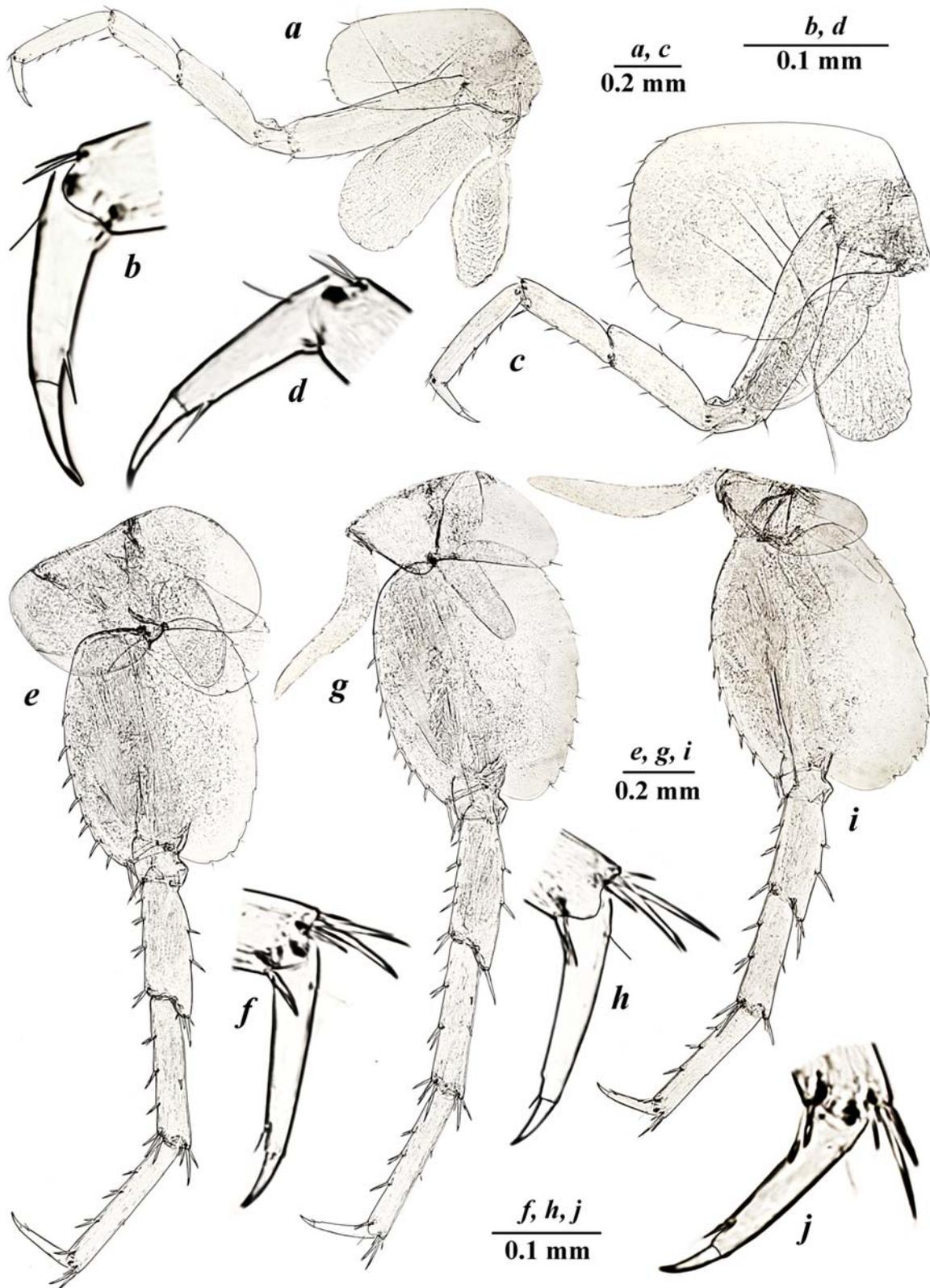


Fig. 16. *Synurella behningi* (Birštein, 1948), ♀: *a* — pereopod III; *b* — dactylus of PIII; *c* — pereopod IV; *d* — dactylus of PIV; *e* — pereopod V; *f* — dactylus of PV; *g* — pereopod VI; *h* — dactylus of PVI; *i* — pereopod VII; *j* — dactylus of PVII.

Рис. 16. *Synurella behningi* (Birštein, 1948), ♀: *a* — переопода III; *b* — дактилус PIII; *c* — переопода IV; *d* — дактилус PIV; *e* — переопода V; *f* — дактилус PV; *g* — переопода VI; *h* — дактилус PVI; *i* — переопода VII; *j* — дактилус PVII.

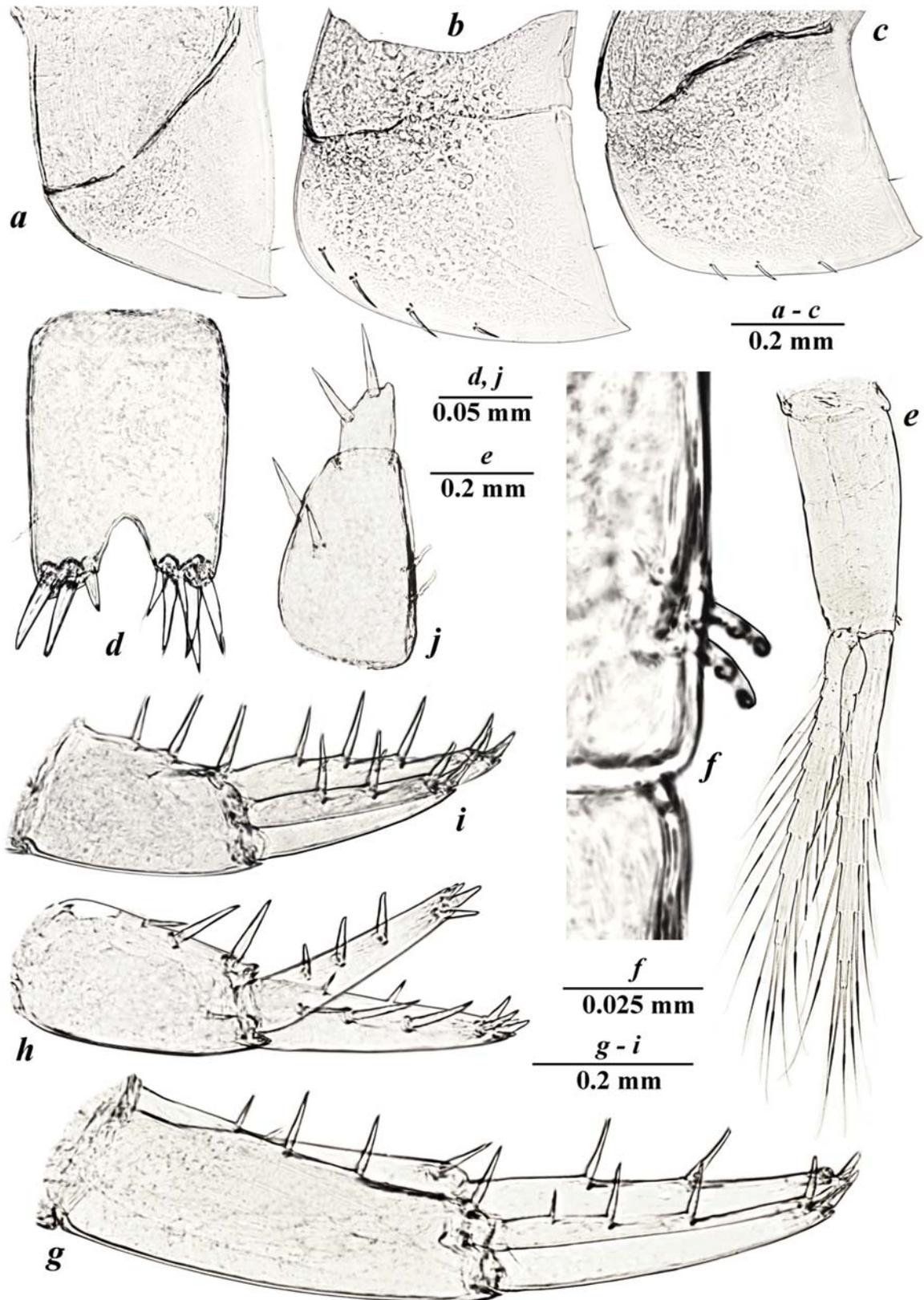


Fig. 17. *Synurella behningi* (Birštein, 1948), ♀: *a* — epimeral plate I; *b* — epimeral plate II; *c* — epimeral plate III; *d* — telson; *e* — pleopod I; *f* — hooks of retinacula of pleopod II; *g* — uropod I; *h*, *i* — uropod II; *j* — uropod III.

Рис. 17. *Synurella behningi* (Birštein, 1948), ♀: *a* — эпимеральная пластинка I; *b* — эпимеральная пластинка II; *c* — эпимеральная пластинка III; *d* — тельсон; *e* — плеопода I; *f* — крючки ретинакулы плеоподы II; *g* — уропода I; *h*, *i* — уропода II; *j* — уропода III.

DESCRIPTION. Body: moderately stout; the largest collected ♀ has bl. 6.5 mm.

Head: smooth, with bluntly produced anteroventral lobe; with reduced black-pigmented eyes and yellow dorsolateral spots.

Antenna I (Fig. 14a): about 50% of body length, about 1.9X longer than antenna II; primary flagellum with 12 articles, with aesthetascs on distal articles; accessory flagellum 2-articulated, distal article about 2.3X shorter than basal one (Fig. 14b).

Antenna II (Fig. 14c): gland clone distinct, distally pointed; peduncle about 2.0X longer than flagellum, with robust setae tightly covering articles 3 and 4, peduncle of article 4 about 1.2X longer than article 5; flagellum 6-articulated, without calceoli in females.

Mandible: left mandible (Fig. 15d) incisor 4-dentate, *lacinia mobilis* 5-dentate, with 3 robust plumose accessory setae; molar process with 1 seta (Fig. 15e). Right mandible (Fig. 15f) incisor 4-dentate, *lacinia mobilis* toothed, triturative, lobes with numerous protuberances; underlying with a row of 3 robust plumose setae; molar process similar to left mandible (Fig. 15g). Palp 3-articulated, article 2 with 5–6 setae; article 3 about 3.1X longer than wide, with convex margins, with 8–9 separate D-setae, 2 C-setae, 1 B-seta and 4 separate E-setae.

Lateralial with 8 teeth.

Labrum (upper lip) (Fig. 15a): oval, apical margin with numerous small fine setae.

Labium (lower lip) (Fig. 15b): inner lobes feebly developed.

Maxilla I (Fig. 15h): inner plate with 6 plumose marginal setae, outer plate with 7 apical comb-spines; palp 2-articulated, distal article pubescent, about 2.5X of basal article, apical margin of distal article with 8 setae.

Maxilla II (Fig. 15i): inner, outer plates covered in pubescent setae; inner and outer plates subequal in length; outer plate weakly narrowing distally, with 10 apical setae; inner plate narrowing slightly distally, with group of dense short setae on apex, with oblique row of 5 short plumose setae.

Maxilliped (Fig. 15j): inner plate much shorter than outer plate, with 2 spines, 1 robust plumose and 1 simple setae apically, and 5 robust plumose setae laterally; outer plate narrow, with a double row of 24 medial stiff simple setae of different length; palp 4-articulated, article I with 2 setae on outer margin, article II with a row of 20 simple setae on inner margin, without setae on outer margin; article III sub-trapezoidal; dactylus with 1 seta on outer margin and with 2 thin setae at inner margin, nail long, slender, with 1 thin seta at hinge.

Gnathopod I (Fig. 14d) smaller than gnathopod II; coxal plate sub-rectangular, distally rounded, with 6 apical and numerous facial setae, width/depth ratio is 0.58/1; basis width/length ratio is 0.35/1, with 1 short seta on anterior margin, 3 long setae on inner face and 6 long setae on posterior margin; merus with 10 distal setae; carpus is 0.45X of basis and 0.75X of propodus, with 12 serrated setae in inner margin and 4 simple setae in outer margin; propodus 1.7X longer than broad, with 4 simple anterior setae, 3 inferior medial and 5 posterior serrated setae; distal margin of palm almost straight, slightly oblique, with double row of 3 inner and 4 outer robust setae; palmar groove (depression) (Fig. 14g) feebly developed, with 3 inner and 2 outer robust setae; dactylus with 1 outer seta.

Gnathopod II (Fig. 14f): coxal plate sub-rectangular, with 5 apical and numerous facial setae, width/depth ratio is

0.54/1; basis width/length ratio is 0.30/1, with 5 long setae inserted along posterior margin and with 2 long simple setae in anterior margin; ischium with 2 short simple setae; merus with 4–5 distal setae; carpus is 0.56X of length of basis and 0.87X of propodus, with 2–3 anterior simple setae and 4 groups of plumose posterior setae; propodus 2.2X longer than broad, with 2 simple anterior setae, 5 superior medial, 3 inferior medial and 3 groups of posterior setae; palm oblique with a double row of 3 inner and 3 outer bifurcate robust setae; palm groove (depression) (Fig. 14e) feebly developed, with 3 inner and 3 outer robust setae; dactylus without inner and with 1 outer seta.

Pereopod III (Fig. 16a): coxal plate sub-rectangular, with 6 apical and numerous facial setae, width/depth ratio is 0.46/1; basis about 4.0X as long as wide, with long anterior and posterior simple setae; merus about 0.60X of basis, about 1.24X of carpus and 1.04X of propodus in length; carpus about 0.83X of propodus in length; dactylus (Fig. 16b) about 0.48X of propodus, with 1 plumose seta on outer margin and 1 additional spine accompanying with 1 seta on ventral margin.

Pereopod IV (Fig. 16c): subequal to PIII in length; coxal plate expanded and broadly convex distally, posterior margin with shallow excavation, distal margin with 14 apical short setae and numerous facial setae, width/depth ratio is 1.26/1; basis about 3.9X as long as wide, with long anterior and posterior simple setae; merus about 0.63X of basis, about 1.20X of carpus and about 1.03X of propodus in length; carpus about 0.86X of propodus in length; dactylus (Fig. 16d) about 0.50X of propodus, with 1 plumose seta on outer margin and 1 additional spine accompanying with 1 seta on ventral margin.

Pereopods V, VI, VII with the length ratio 1/1.08/0.93.

Pereopod V (Fig. 16e): coxal plate large, bilobate with distinct anterior and posterior lobes; posterior and anterior lobes with 1 margin simple seta each, with numerous facial setae; basis about 1.28X as long as wide, with numerous facial setae, posterior margin slightly convex, armed with 10 shallow serrations, with distal corner, anterior margin with 8 split-tipped robust and 4 distal setae; merus about 0.60X of basis, 0.95X of carpus and propodus in length; dactylus (Fig. 16f) approximately 0.50X of propodus, with 1 plumose seta on outer margin and 1 additional spine accompanying with 1 seta on ventral margin.

Pereopod VI (Fig. 16g): coxal plate bilobate, with distinct posterior and vestigial anterior lobes; anterior lobe without setae, posterior lobe with 1 margin seta, each with numerous facial setae; basis about 1.26X as long as wide, with numerous facial setae, posterior margin convex, armed with 10 shallow serrations, anterior margin with 8 split-tipped robust and 4 distal setae; merus about 0.62X of basis, subequal to carpus and 0.90X of propodus in length; dactylus (Fig. 16h) approximately 0.47X of propodus, with 1 plumose seta on outer margin and 1 additional spine accompanying with 1 seta on ventral margin.

Pereopod VII (Fig. 16i): coxal plate small, semi-lunar, with 1 posterior seta; basis about 1.32X as long as wide, with numerous facial setae, posterior margin convex, armed with 9 serrated setae and with wide distal lobe, anterior margin with 6 split-tipped robust and 3 distal setae; merus about 0.47X of basis, subequal to carpus and 0.85X of propodus in length; dactylus (Fig. 16j) approximately 0.45X of propodus in length, with 1 plumose seta on outer margin and 1 additional spine accompanying with 1 seta on ventral margin.

Gills, brood plates (Fig. 16): coxal gills on somites II–VII, somites II–VII with lanceolate sternal gill on each. Coxal gills II–VII ovoid, gills/bases pereopod ratios are 0.80/1, 0.73/1, 0.73/1, 0.47/1, 0.44/1 and 0.30/1, respectively. Brood plates on somites II–V slender, setaceous, decreasing in size posteriorly.

Pleopods (Fig. 17e). Pleopod I peduncle with 2 coupling hooks in retinacula, without lateral setae; outer and inner rami with 7 and 10 articles, respectively. Pleopod II peduncle with 2 coupling hooks in retinacula, without setae (Fig. 17f); outer and inner rami with 7 and 9 articles, respectively. Pleopod III peduncle with 2 coupling hooks in retinacula, without lateral setae; outer and inner rami with 6 and 8 articles, respectively.

Epimera. Epimeral plate I (Fig. 17a) distally produced and sharpened, ventral margin without spines, posterior margin with 1 seta. Epimeral plate II (Fig. 17b) distally produced and sharpened, ventral margin armed with 4 spines, posterior margin with 1 seta. Epimeral plate III (Fig. 17c) distally produced and sharpened, ventral margin armed with 3 spines, posterior margin with a single seta.

Urosomites completely fused, smooth.

Uropod I (Fig. 17g): peduncle about 2.8X as long as wide, with dorsoexternal row of 3 robust spines, 1 subdistal spine and 2 dorsointernal robust spines; exopodite slightly shorter than endopodite; endopodite not paddle-like, with 2 dorsolateral, 4 apical spines and 1 ventral seta; exopodite with 3 dorsolateral and 4 apical spines.

Uropod II (Fig. 17h): peduncle about 0.91X of endopodite in length, with 3 dorsal robust spines; exopodite about 0.77X of endopodite in length, with 2–3 dorsal, 2 lateral and 5 apical robust spines; endopodite with 3 dorsal and 4 apical robust spines.

Uropod III (Fig. 17i): uniramous, peduncle trapezoidal, about 1.6X as long as wide, with a 2 weak spines and 2 simple setae; lateral and apical margin of ramus armed with 2 spines.

Telson (Fig. 17d): close to rectangular, about 1.4X as long as broad; distal margin with U-shaped distal notch, reaching about 1/4 of its length, each lobe armed with 5 robust spines, with 2 additional submarginal plumose setae.

COLORATION. The body and appendages yellowish or grayish transparent; small pigmented eyes well seen.

GENBANK ACCESSION NUMBERS. OP293099–OP293102.

TAXONOMIC REMARKS. The new species can be clearly separated from *Synurella ambulans* and described above *Synurella behningi* (Birštein, 1948) by: 1) distal article of accessory flagellum of AI is about 2.3X shorter than basal article (vs. 3.0X in *S. ambulans*); 2) broadened basis of PVII with posteroventral projection (lobe) (Fig. 16i) (vs. basis of PVII oval, without posteroventral projection (lobe) [Sidorov, Palatov, 2012: figs 5E, 9B]); 3) palm of GnI is about 1.7X longer than wide in females (Fig. 14d) (vs. 1.3–1.4 about as long as wide [Sidorov, Palatov, 2012: fig. 7A]).

Birštein [1948] proposed that *S. behningi* belong to the subgenus *Boruta* Wrzeźniowski, 1888 based on morphological difference from *S. ambulans*, namely 1) rectangular (about 2.0X longer than wide) palmar margin of GnII in males and 2) reduction of inner lobes of lower lip, which is not confirmed by our data.

DISTRIBUTION AND ECOLOGY. Hypogean (stygobiotic) species, which is presently known only in the Bacha Cave, Abkhazia, southwestern Caucasus.

### *Synurella gizmavi* Palatov et Marin sp.n.

Figs 18–22.

MATERIAL EXAMINED. Holotype, ♀ (bl. 6.5 mm), ZMMU Mb-1232, South-western Caucasus, Abkhazia, Gudauta region, Gizmava Cave, 43°11'16.1"N 40°38'35.9"E, inside a small subterranean spring, coll. D. Palatov, 5.02.2020. Additional material. 2♀♀ (LEMMI), same locality and data as for holotype.

ETYMOLOGY. The species is named after the Gizmava Cave, where the species was discovered.

DIAGNOSIS. Only females are presently known. Body unpigmented, yellowish. Distal article of accessory flagellum of AI is about 2.0X shorter than basal one. Inner plate of MxI with 5 plumose marginal setae. GnI with palm about 1.7X as long as wide, GnII with palm about 2.5X as long as wide in females. Coxal plate longer than palm of GnI–II in females. PVII basis with distinct posterior lobe. Coxal gill VII well expressed, about 0.4X of basis of PVII. EpI with short posteroventral tooth. EpII with 3 ventral spines. EpIII with slightly producing posteroventral tooth, and 2 ventral spines. Basal article (peduncle) of UIII with 1 spine. Telson with distal notch, reaching about 1/5 of its length.

DESCRIPTION. Body: moderately stout; the largest collected ♀ has bl. 6.5 mm.

Head (Fig. 22a): smooth, with bluntly produced anteroventral lobe; with reduced black-pigmented eyes and yellow dorsolateral spots.

Antenna I (Fig. 18a): about 50% of body length, about 1.7X longer than antenna II; primary flagellum with 11 articles, with aesthetascs on distal articles; accessory flagellum 2-articulated, distal article about 2.0X shorter than basal one.

Antenna II (Fig. 18b): gland clone distinct, distally pointed; peduncle about 1.8–2.0X longer than flagellum, with robust setae tightly covering articles 3 and 4, peduncle of article 4 about 1.1X longer than article 5; flagellum 6-articulated, without calceoli in females.

Mandible: left mandible (Fig. 19d) incisor 4-dentate, *lacinia mobilis* 5-dentate, with 4 robust plumose accessory setae; molar process with 1 seta (Fig. 19e). Right mandible (Fig. 19f) incisor 4-dentate, *lacinia mobilis* toothed, tritaurative, lobes with numerous protuberances; underlying with a row of 3 robust plumose setae; molar process similar to left mandible (Fig. 19g). Palp 3-articulated, article 2 with 3–4 setae on inner margin and 1 seta on outer margin; article 3 about 2.0X longer than wide, with convex margins, with 6 separate D-setae, 1 C-seta, 1 B-seta and 4 separate E-setae.

Lateralialia with 8 teeth.

Labrum (upper lip) (Fig. 19a): oval, apical margin with numerous small fine setae.

Labium (lower lip) (Fig. 19b): inner lobes feebly developed.

Maxilla I (Fig. 19g): inner plate with 5 plumose marginal setae, outer plate with 7 apical comb-spines; palp 2-articulated, distal article pubescent, about 2.9X of basal article, apical margin of distal article with 11 setae (Fig. 19h).

Maxilla II (Fig. 19i): inner, outer plates covered in pubescent setae; inner and outer plates subequal in length; outer plate weakly narrowing distally, with 12 apical setae; inner plate narrowing slightly distally, with group of dense short setae on apex, with oblique row of 6 short plumose setae.

Maxilliped (Fig. 19j): inner plate much shorter than outer plate, with 2 spines, 1 robust plumose and 1 simple setae apically, and 2 robust plumose setae laterally; outer plate narrow, with a double row of 20 medial stiff simple

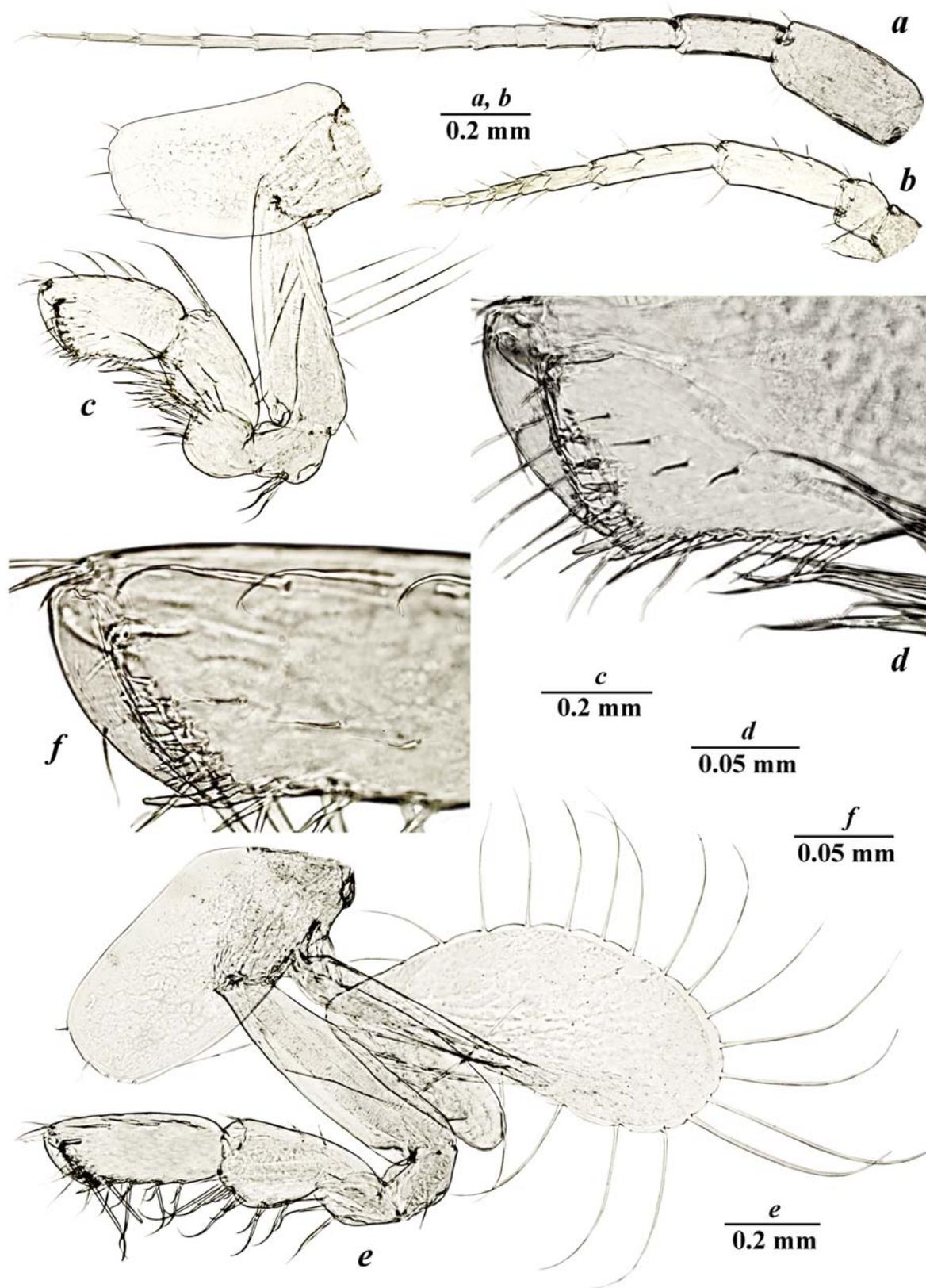


Fig. 18. *Synurella gizmavi* Palatov et Marin sp.n., ♀: *a* — antenna I; *b* — antenna II; *c* — gnathopod I; *d* — distoventral palmar margin of chela of GnI; *e* — gnathopod II; *f* — distoventral palmar margin of chela of GnII.

Рис. 18. *Synurella gizmavi* Palatov et Marin sp.n., ♀: *a* — антенна I; *b* — антенна II; *c* — гнатопода I; *d* — дистовентральный край ладони (клешни) GnI; *e* — гнатопода II; *f* — дистовентральный край ладони (клешни) GnII.

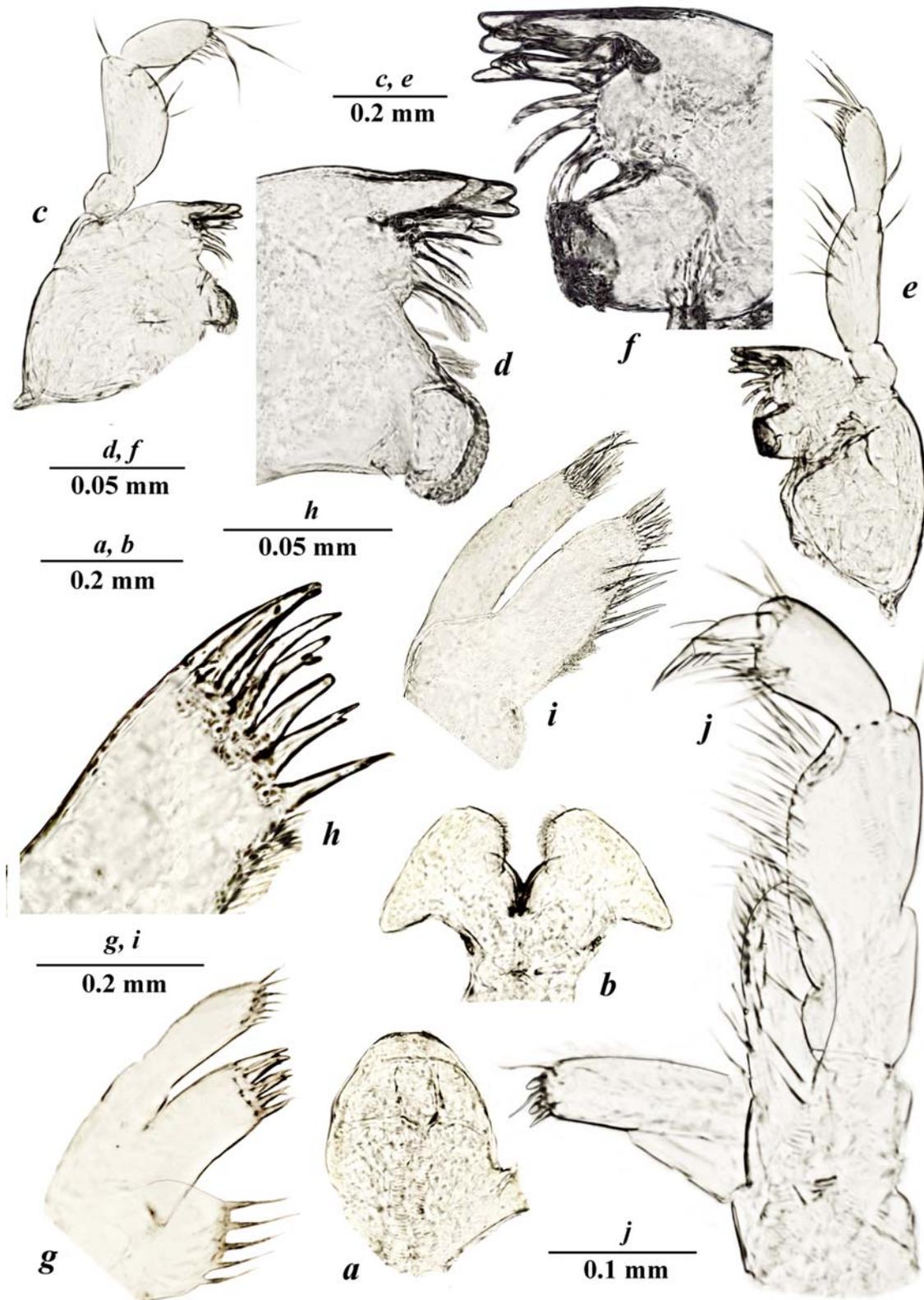


Fig. 19. *Synurella gizmavi* Palatov et Marin sp.n., ♀: a — labrum (upper lip); b — labium (lower lip); c — left mandible; d — same, incisor process and *pars incisiva*; e — right mandible; f — same, incisor process and *pars incisiva*; g — maxilla I; h — distal margin of inner plate of maxilla I; i — maxilla II; j — maxilliped.

Рис. 19. *Synurella gizmavi* Palatov et Marin sp.n., ♀: a — лабрум (верхняя губа); b — лабиум (нижняя губа); c — левая мандибула; d — то же, режущий отросток и резцовая часть; e — правая мандибула; f — то же, режущий отросток и резцовая часть; g — максилла I; h — дистальный край внутренней пластины максиллы I; i — максилла II; j — максиллипод.

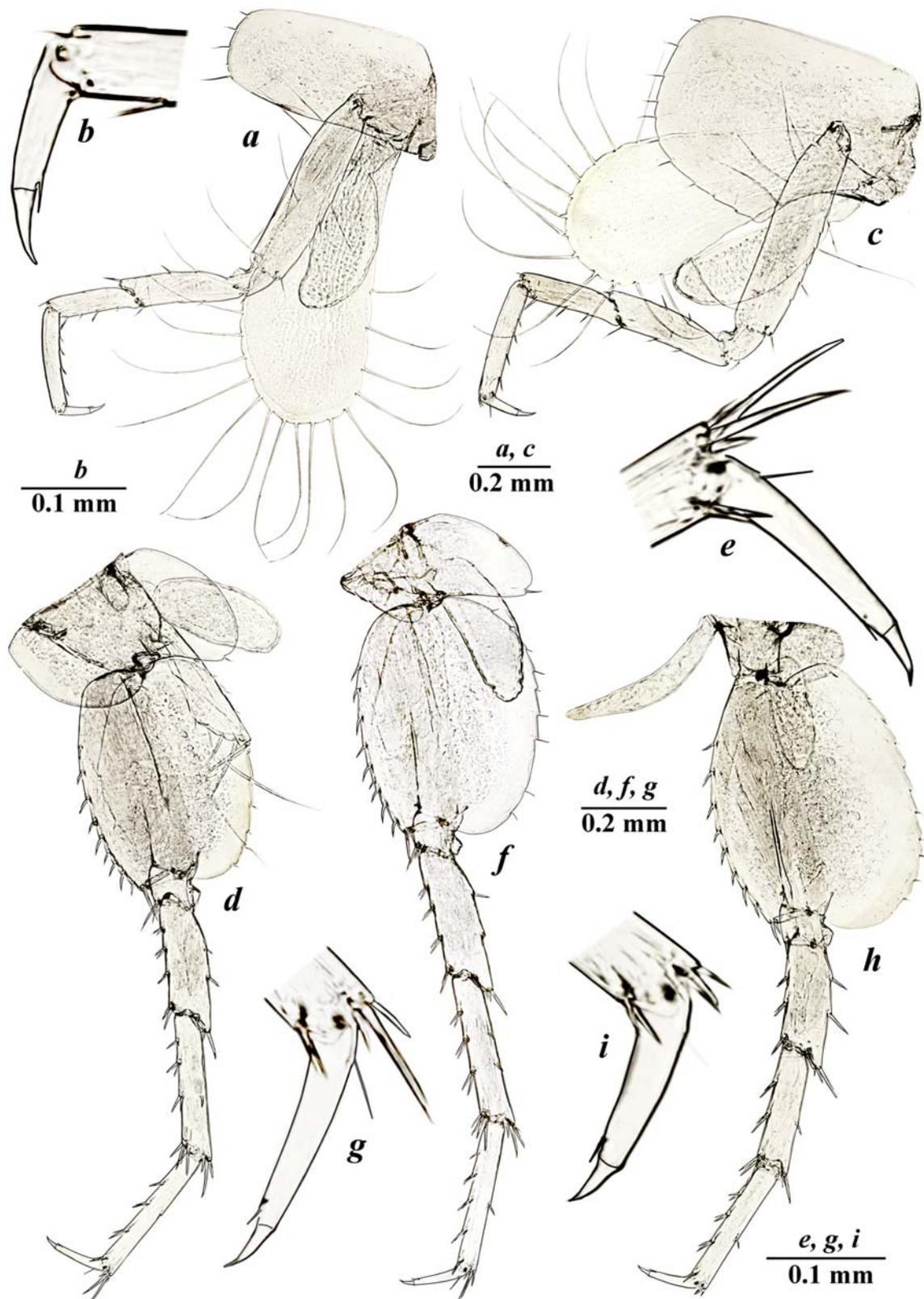


Fig. 20. *Synurella gizmavi* Palatov et Marin sp.n., ♀: *a* — pereopod III; *b* — dactylus of PIII; *c* — pereopod IV; *d* — pereopod V; *e* — dactylus of PV; *f* — pereopod VI; *g* — dactylus of PVI; *h* — pereopod VII; *i* — dactylus of PVII.

Рис. 20. *Synurella gizmavi* Palatov et Marin sp.n., ♀: *a* — переопода III; *b* — дактилус PIII; *c* — переопода IV; *d* — переопода V; *e* — дактилус PV; *f* — переопода VI; *g* — дактилус PVI; *h* — переопода VII; *i* — дактилус PVII.

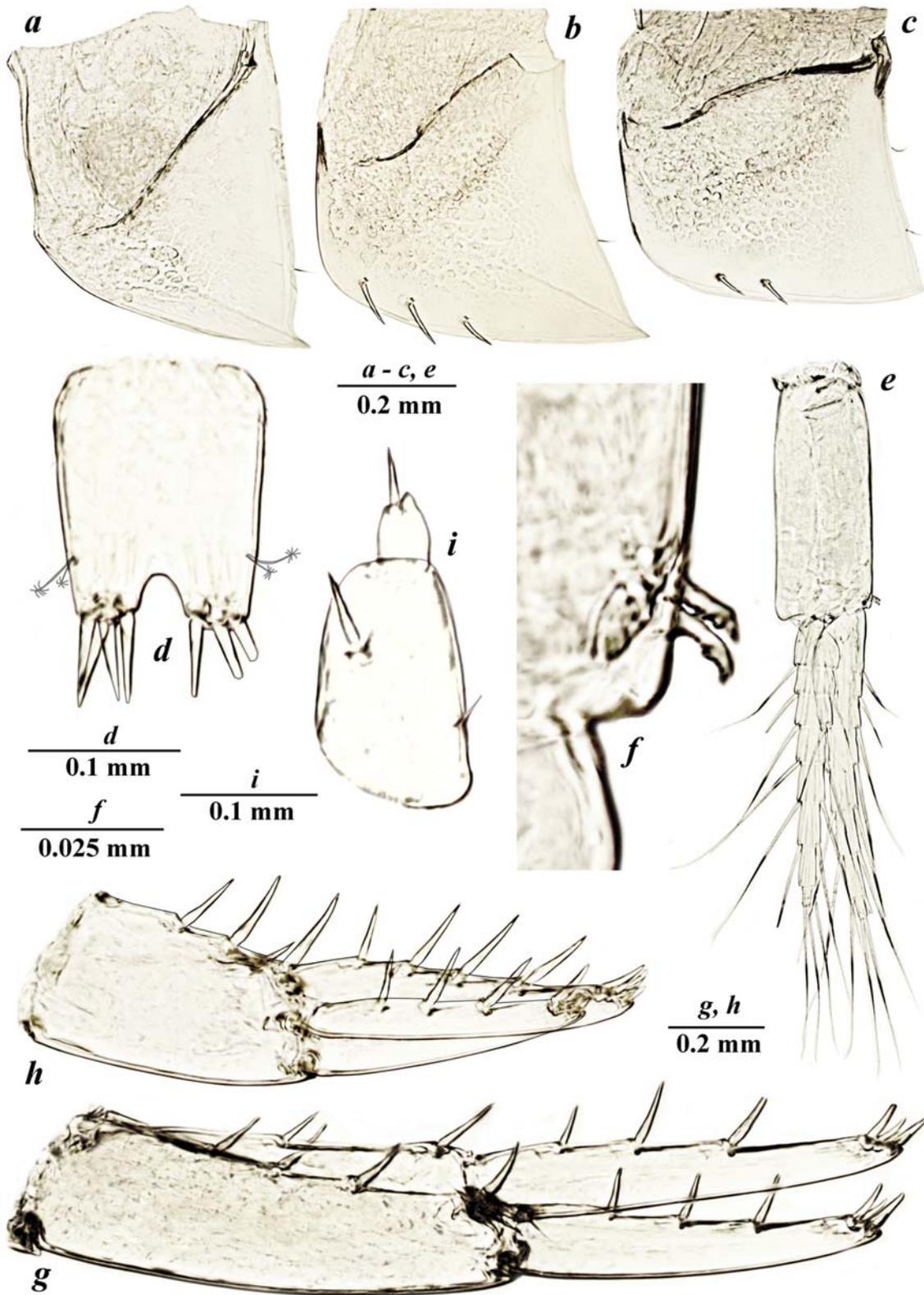


Fig. 21. *Synurella gizmavi* Palatov et Marin sp.n., ♀: *a* — epimeral plate I; *b* — epimeral plate II; *c* — epimeral plate III; *d* — telson; *e* — pleopod I; *f* — hooks of retinacula of pleopod II; *g* — uropod I; *h* — uropod II; *i* — uropod III.

Рис. 21. *Synurella gizmavi* Palatov et Marin sp.n., ♀: *a* — эпимеральная пластинка I; *b* — эпимеральная пластинка II; *c* — эпимеральная пластинка III; *d* — тельсон; *e* — плеопода I; *f* — крючки ретинакулы плеоподы II; *g* — уропода I; *h* — уропода II; *i* — уропода III.

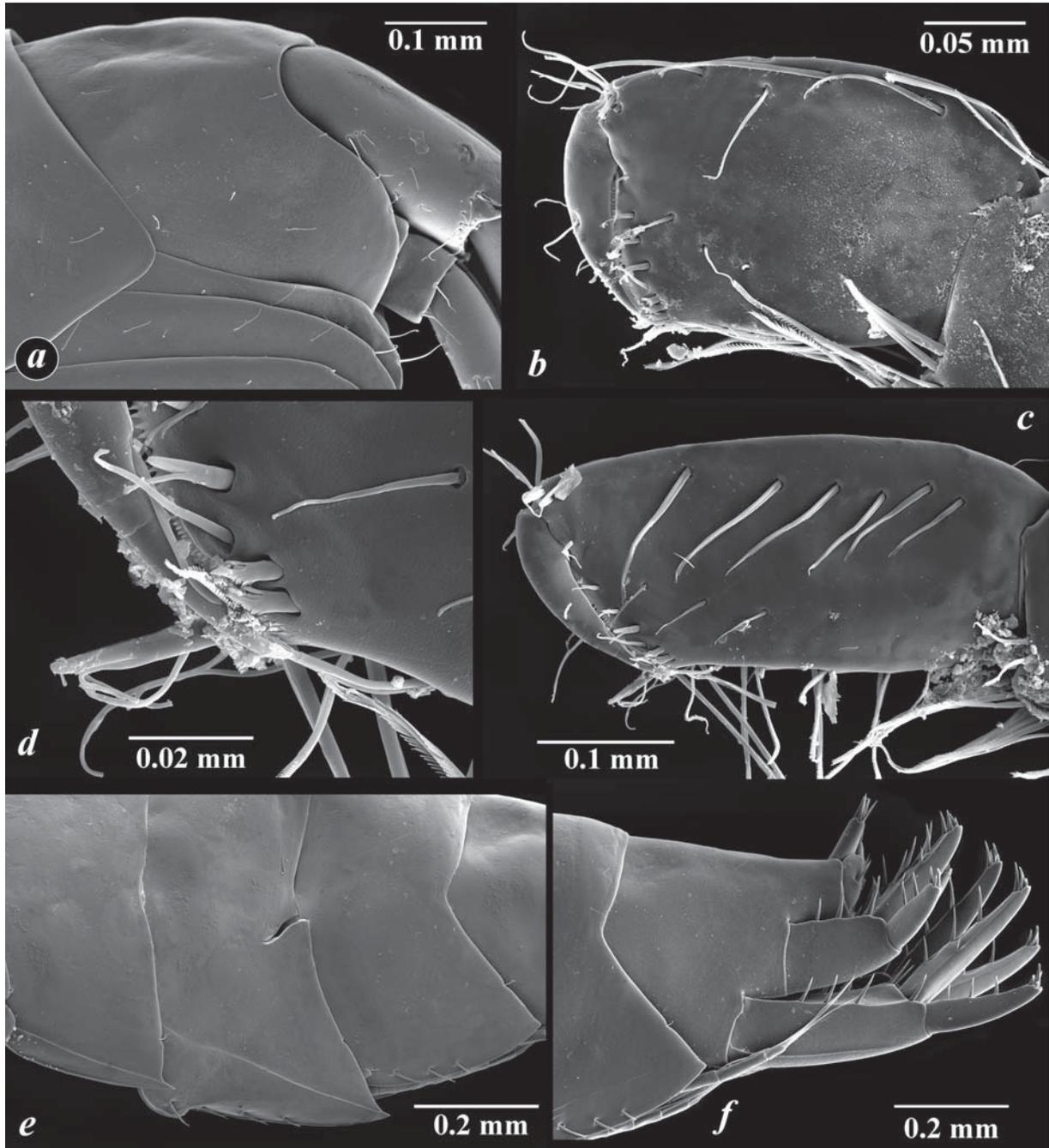


Fig. 22. *Synurella gizmavi* Palatov et Marin sp.n., ♀: *a* — head; *b* — palm (chela) of GnI; *c* — palm (chela) of GnII; *d* — distoventral palmar margin of chela GnI; *e* — epimeral plates I–III; *f* — urosomal segments.

Рис. 22. *Synurella gizmavi* Palatov et Marin sp.n., ♀: *a* — голова; *b* — дистовентральный край ладони (клешни) GnI; *c* — ладонь (клешня) GnII; *d* — дистовентральный пальмарный край ладони (клешни) GnI; *e* — эпимеральные пластинки I–III; *f* — уросомальные сегменты.

setae of different length; palp 4-articulated, article I with 1 seta on outer margin, article II with a row of 24 simple setae on inner margin and 2 setae on outer margin, article III sub-trapezoidal; dactylus with 1 seta on outer margin and with 2 thin setae at inner margin, nail long, slender, with 1 thin seta at hinge.

Gnathopod I (Figs 18c, 22b) smaller than gnathopod II; coxal plate sub-rectangular, distally rounded, with 6 apical

and numerous facial setae, width/depth ratio is 0.56/1; basis width/length ratio is 0.33/1, without setae on anterior margin, 3 long setae on inner face and 5 long setae on posterior margin; merus with 11 distal setae; carpus is 0.42X of basis and 0.75X of propodus, with 13–14 serrated setae in inner margin and 3 simple setae in outer margin; propodus 1.7X longer than broad, with 5 simple anterior setae, 4 inferior medial and 7 posterior serrated setae; distal margin of palm

almost straight, slightly oblique, with double row of 4 inner and 4 outer robust setae; palmar groove (depression) (Figs 18*d*, 22*d*) feebly developed, with 4 inner and 3 outer robust setae; dactylus with 1 outer seta.

Gnathopod II (Figs 18*e*, 22*c*): coxal plate sub-rectangular, with 5 apical and numerous facial setae, width/depth ratio is 0.50/1; basis width/length ratio is 0.28/1, with 6 long setae inserted along posterior margin and with 4 long simple setae in anterior margin; ischium with 1 short simple seta; merus with 5 distal setae; carpus is 0.52X of length of basis and 0.78X of propodus, with 3–4 anterior simple setae and 3 groups of plumose posterior setae; propodus 2.5X longer than broad, with 3 simple anterior, 6 superior medial, 3 inferior medial and 4 groups of posterior setae; palm oblique with a double row of 4 inner and 4 outer bifurcate robust setae; palm groove (depression) (Fig. 18*f*) feebly developed, with 3 inner and 3 outer robust setae; dactylus without inner and with 1 outer seta.

Pereopod III (Fig. 20*a*): coxal plate sub-rectangular, with 5 apical and numerous facial setae, width/depth ratio is 0.50/1; basis about 4.3X as long as wide, with long anterior and posterior simple setae; merus about 0.58X of basis, about 1.28X of carpus and 1.08X of propodus in length; carpus about 0.84X of propodus in length; dactylus (Fig. 20*b*) about 0.43X of propodus, with 1 plumose seta on outer margin and 1 additional spine accompanying with 1 seta on ventral margin.

Pereopod IV (Fig. 20*c*): subequal to PIII in length; coxal plate expanded and broadly convex distally, posterior margin with shallow excavation, distal margin with 11 apical short setae and numerous facial setae, width/depth ratio is 1.30/1; basis about 4.6X as long as wide, with long anterior and posterior simple setae; merus about 0.55X of basis, about 1.17X of carpus and about 0.98X of propodus in length; carpus about 0.84X of propodus in length; dactylus about 0.43X of propodus, with 1 plumose seta on outer margin and 1 additional spine accompanying with 1 seta on ventral margin.

Pereopods V, VI, VII with the length ratio 1/1.10/0.95.

Pereopod V (Fig. 20*d*): coxal plate large, bilobate with distinct anterior and posterior lobes; posterior and anterior lobes with 1 margin simple seta each, with numerous facial setae; basis about 1.33X as long as wide, with numerous facial setae, posterior margin slightly convex, armed with 11 shallow serrations, with distal corner, anterior margin with 8 split-tipped robust and 4 distal setae; merus about 0.64X of basis, 0.97X of carpus and 0.96X of propodus in length; dactylus (Fig. 20*g*) approximately 0.43X of propodus, with 1 plumose seta on outer margin and 1 additional spine accompanying with 1 seta on ventral margin.

Pereopod VI (Fig. 20*f*): coxal plate bilobate, with distinct posterior and vestigial anterior lobes; anterior lobe without setae, posterior lobe with 1 margin seta, each with numerous facial setae; basis about 1.31X as long as wide, with numerous facial setae, posterior margin convex, armed with 10 shallow serrations, anterior margin with 9 split-tipped robust and 4 distal setae; merus about 0.65X of basis, 0.97X of carpus and 0.95X of propodus in length; dactylus (Fig. 20*g*) approximately 0.41X of propodus, with 1 plumose seta on outer margin and 1 additional spine accompanying with 1 seta on ventral margin.

Pereopod VII (Fig. 20*h*): coxal plate small, semi-lunar, with 1 posterior seta; basis about 1.38X as long as wide, with numerous facial setae, posterior margin convex, armed with 10 serrated setae and with wide distal lobe, anterior margin with 8 split-tipped robust and 3 distal setae; merus about

0.48X of basis, about 1.03X of carpus and 0.89X of propodus in length; dactylus (Fig. 20*i*) approximately 0.43X of propodus in length, with 1 plumose seta on outer margin and 1 additional spine accompanying with 1 seta on ventral margin.

Gills, brood plates (Fig. 20): coxal gills on somites II–VII, somites II–VII with lanceolate sternal gill on each. Coxal gills II–VII ovoid, gills/bases pereopod ratios are 0.89/1, 0.74/1, 0.75/1, 0.60/1, 0.65/1 and 0.42/1, respectively. Brood plates on somites II–V slender, setaceous, decreasing in size posteriorly.

Pleopods (Fig. 21*e*). Pleopod I peduncle with 2 coupling hooks in retinacula, without lateral setae; outer and inner rami with 10 articles. Pleopod II peduncle with 2 coupling hooks in retinacula, without setae (Fig. 21*f*); outer and inner rami with 9 articles. Pleopod III peduncle with 2 coupling hooks in retinacula, without lateral setae; outer and inner rami with 8 articles.

Epimera (Fig. 22*e*). Epimeral plate I (Fig. 17*a*) distally produced and sharpened, ventral margin without spines, posterior margin with 1 seta. Epimeral plate II (Fig. 21*b*) distally produced and sharpened, ventral margin armed with 3 spines, posterior margin with 1 seta. Epimeral plate III (Fig. 21*c*) distally produced and sharpened, ventral margin armed with 2 spines, posterior margin with 2 setae.

Urosomites completely fused, smooth (Fig. 22*f*).

Uropod I (Fig. 21*g*): peduncle about 3.0X as long as wide, with dorsoexternal row of 3 robust spines, 1 subdistal spine and 2 dorsointernal robust spines; exopodite slightly shorter than endopodite; endopodite not paddle-like, with 3 dorsolateral, 4 apical spines and 1 ventral seta; exopodite with 3 dorsolateral and 4 apical spines.

Uropod II (Fig. 21*h*): peduncle about 0.80X of endopodite in length, with 1 outer and 3 inner robust spines; exopodite about 0.83X of endopodite in length, with 4 dorsal and 5 apical robust spines; endopodite with 3 outer and 5 apical robust spines.

Uropod III (Fig. 21*i*): uniramous, peduncle trapezoidal, about 1.54X as long as wide, with a weak spine and 1 seta; apical margin of ramus armed with a weak spine.

Telson (Fig. 21*d*): close to trapezoidal, about 1.26X as long as broad; distal margin with U-shaped distal notch, reaching about 1/4–1/5 of its length, each lobe armed with 4 robust spines, with 2 additional submarginal plumose setae.

COLORATION. The body and appendages yellowish or grayish transparent; well-pigmented black eyes well seen.

GENBANK ACCESSION NUMBERS. OP306064, OP306068.

TAXONOMIC REMARKS. The new species distinctly belong to the “*behningi*” species complex (Figs 1; 2). At the same time, it can be clearly separated from *Synurella behningi* by the following features: 1) inner plate of MxI with 5 plumose marginal setae (Fig. 19*g*) (vs. 7 plumose marginal setae (Fig. 11*h*)); 2) palm of GnII about 2.5X longer than wide (Fig. 18*e*) (vs. 2.3X (Fig. 14*f*)); and 3) telson with distal notch, reaching about 1/5 of its length (Fig. 21*d*) (vs. 1/4 of telson (Fig. 17*d*)).

DISTRIBUTION AND ECOLOGY. Hypogean (stygobiotic) species, which is presently known only from the Gizmava Cave, Abkhazia, southwestern Caucasus.

*Synurella praemontana* Marin et Palatov **sp.n.**  
Figs 4*o–q*; 23–27.

MATERIAL EXAMINED. Holotype, ♂ (bl. 6.5 mm), ZMMU Mb-1233, Russian Federation, south-western Caucasus, Krasnodar

Krai, Krymsky district, the upper stream of the Shids River, 44°48'09.03"N 37°59'26.54"E, inside a small well, coll. I. Marin & S. Marina, 24.07.2021. Paratypes. 1♀ (bl. 7.0 mm), ZMMU Mb-1234, 1♀ (bl. 6.5 mm), ZMMU Mb-1235, same locality and data as for holotype. Additional material: 5♀♀, 7♂♂ (LEMMI), same locality and data as for holotype.

**ETYMOLOGY.** The new species is named after the foothill part of the Caucasus Mountains, where it was discovered; *praemontana* (Latin) = foothills.

**DIAGNOSIS.** Body unpigmented, whitish. Distal article of accessory flagellum of AI is about 5.0X shorter than basal one. Inner plate of MxI with 7 plumose marginal setae. GnI with palm about 1.6X as long as wide in females and about 1.7X as long as wide in males. GnII with palm about 2.4X as long as wide in females and about 2.2X as long as wide in males. Coxal plate longer than palm of GnI–II in males and females. PVII basis with distinct posterior lobe in males and females. Coxal gill VII small, about 0.1X of basis of PVII. EpI with very short posteroventral tooth. EpII with 6 ventral spines. EpIII with blunt distoventral margin, and 4 ventral spines. Basal article (peduncle) of UIII with 2 spines. Telson without, or with distal notch, not reaching about 1/6–1/7 of its length.

**DESCRIPTION.** Body: moderately stout; largest collected ♀ has bl. 7.0 mm, largest collected ♂ has bl. 6.5 mm.

Head (Fig. 27a): smooth, with bluntly produced anteroventral lobe; with marked black-pigmented eyes and yellow dorsolateral spots.

Antenna I (Fig. 23a, b): about 50% of body length, about 1.6–1.9X longer than antenna II; primary flagellum with 9 articles in male and 15 articles in female, with aesthases on distal articles; accessory flagellum 2-articulated, distal article about 5.0X shorter than basal one (Fig. 23c).

Antenna II (Fig. 19d, f): gland clone distinct, distally pointed; peduncle about 2.0–2.2X longer than flagellum, with robust setae tightly covering articles 3 and 4, peduncle of article 4 about 1.0–1.2X longer than article 5; flagellum 5–6-articulated, without calceoli in females, and with calceoli in males (Fig. 23e).

Mandible: left mandible (Fig. 24c) incisor 4–5-dentate, *lacinia mobilis* 5-dentate, with 4 robust plumose accessory setae; molar process with 1 seta (Fig. 24d). Right mandible (Fig. 24e) incisor 4-dentate, *lacinia mobilis* toothed, triturative, lobes with numerous protuberances; underlying with a row of 3 robust plumose setae; molar process similar to left mandible (Fig. 24f). Palp 3-articulated, article 2 with 6–7 setae; article 3 about 2.6X longer than wide, with convex margins, with 8–10 separate D-setae, 1 C-seta, 1 B-seta and 4 separate E-setae.

Lateralialia with 8 teeth.

Labrum (upper lip) (Fig. 24a): oval, apical margin with numerous small fine setae.

Labium (lower lip) (Fig. 24b): inner lobes feebly developed.

Maxilla I (Fig. 24g): inner plate with 7 plumose marginal setae, outer plate with 7 apical comb-spines; palp 2-articulated, distal article pubescent, about 2.7X of basal article, apical margin of distal article with 11 simple setae (Fig. 24h).

Maxilla II (Fig. 24i): inner, outer plates covered in pubescent setae; inner and outer plates subequal in length; outer plate narrowing distally, with 13 apical setae; inner plate narrowing slightly distally, with group of dense short setae on apex, with oblique row of 8 short plumose setae.

Maxilliped (Fig. 24j): inner plate much shorter than outer plate, with 2 spines, 1 robust plumose and 1 simple

setae apically, and 4–6 robust plumose setae laterally; outer plate narrow, with a double row of 26 medial stiff simple setae of different length; palp 4-articulated, article I with 1 seta on outer margin, article II with a row of 22 simple setae on inner margin and 1 seta on outer margin, article III sub-trapezoidal; dactylus with 1 seta on outer margin and with 3 thin setae at inner margin, nail long, slender, with 1 thin seta at hinge.

Gnathopod I (Figs 23g, i, 27c) smaller than gnathopod II; coxal plate sub-rectangular, distally rounded, with 7–10 apical and numerous facial setae, width/depth ratio is 0.54–0.56/1; basis width/length ratio is 0.34–0.36/1, without setae on anterior margin, 3–4 long setae on inner face and 4–7 long setae on posterior margin; merus with 10–11 distal setae; carpus is 0.49X of basis and 0.75X of propodus in males and carpus is 0.55X of basis and 0.91X of propodus in females, with 12–14 serrated setae in inner margin and 6–8 simple setae in outer margin; propodus 1.6–1.7X longer than broad, with 4–5 simple anterior setae, 4 inferior medial and 7–9 posterior serrated setae. Male: distal margin of palm almost straight, slightly oblique, with double row of 6 inner and 5 outer bifurcate robust setae; palmar groove (depression) (Figs 23h, 27d) feebly developed, with 4 inner and 2 outer robust setae; dactylus with 1 outer seta. Female: distal margin of palm almost straight, slightly oblique, with double row of 3 inner and 3 outer bifurcate robust setae; palmar groove (depression) feebly developed, with 2 inner and 2 outer robust setae; dactylus with 1 outer seta.

Gnathopod II (Figs 23j, l, 27e) different in males and females. Male (Figs 23j, 27e, f): coxal plate sub-rectangular, with 7 apical and numerous facial setae, width/depth ratio is 0.47/1; basis width/length ratio is 0.26/1, with 5–6 long setae inserted along posterior margin and with 1 long simple seta in anterior margin; ischium with 2 short simple setae; merus with 4 distal setae; carpus is 0.50X of length of basis and 0.72X of propodus, with 2 anterior simple setae and 4–5 groups of plumose posterior setae; propodus 2.2X longer than broad, with 2 small simple anterior setae, 7 superior medial, 3 inferior medial and 5 groups of posterior setae; palm oblique with a double row of 8 inner and 7 outer robust setae; palm groove (depression) (Fig. 27f, g) feebly developed, with 4 inner and 2 outer robust setae; dactylus without inner and with 1 outer seta.

Female (Fig. 23k, l): coxal plate sub-rectangular, with 7 apical and numerous facial setae, width/depth ratio is 0.58/1; basis width/length ratio is 0.27/1, with 5–6 long setae inserted along posterior margin and with 4 long simple setae and 1 short seta in anterior margin; ischium with 2 short simple setae; merus with 6 distal setae; carpus is 0.58X of length of basis and 0.92X of propodus, with 3–4 anterior simple setae and 5 groups of plumose posterior setae; propodus 2.4X longer than broad, with 3 simple anterior setae, 6 superior medial, 4 inferior medial and 6 groups of posterior setae; palm oblique with a double row of 6 inner and 5 outer bifurcate robust setae; palm groove (depression) (Fig. 23k) feebly developed, with 3 inner and 2 outer robust setae; dactylus without inner and with 1 outer seta.

Pereopod III (Fig. 25a, c): coxal plate sub-rectangular, with 8–9 apical and numerous facial setae, width/depth ratio is 0.43–0.50/1; basis about 4.2–5.0X as long as wide, with long anterior and posterior simple setae; merus about 0.60X of basis, about 1.40–1.97X of carpus and 1.28–1.30X of propodus in length; carpus about 0.95–1.02X of propodus in length; dactylus (Figs 25b, d, 27b) about 0.30–0.35X of propodus, with 1 plumose seta on outer margin and 1 additional spine accompanying with 1 seta on ventral margin.

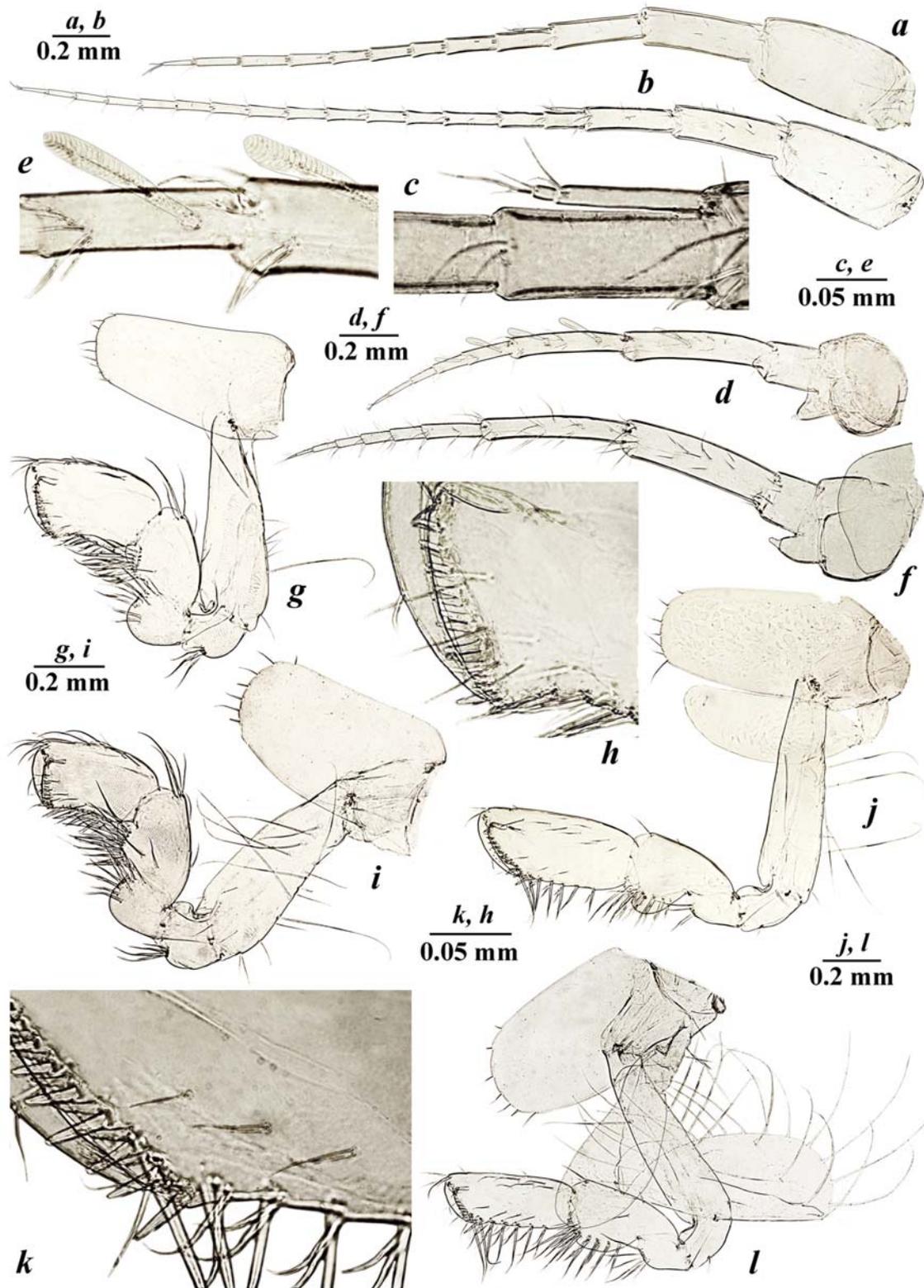


Fig. 23. *Synurella praemontana* Marin et Palatov sp.n., ♂ (a, d, e, g, h, j, k), ♀ (b, c, f, i, l): a, b — antenna I; c — accessory flagellum of antenna I; d, f — antenna II; e — calceoli; g, i — gnathopod I; h — distoventral palmar margin of chela of GnI; j, l — gnathopod II; k — distoventral palmar margin of chela of GnII.

Рис. 23. *Synurella praemontana* Marin et Palatov sp.n., ♂ (a, d, e, g, h, j, k), ♀ (b, c, f, i, l): a, b — антенна I; c — добавочный жгутик антенны I; d, f — антенна II; e — калцеоли; g, i — гнатопода I; h — дистовентральный край ладони (клешни) GnI; j, l — гнатопода II; k — дистовентральный край ладони (клешни) GnII.

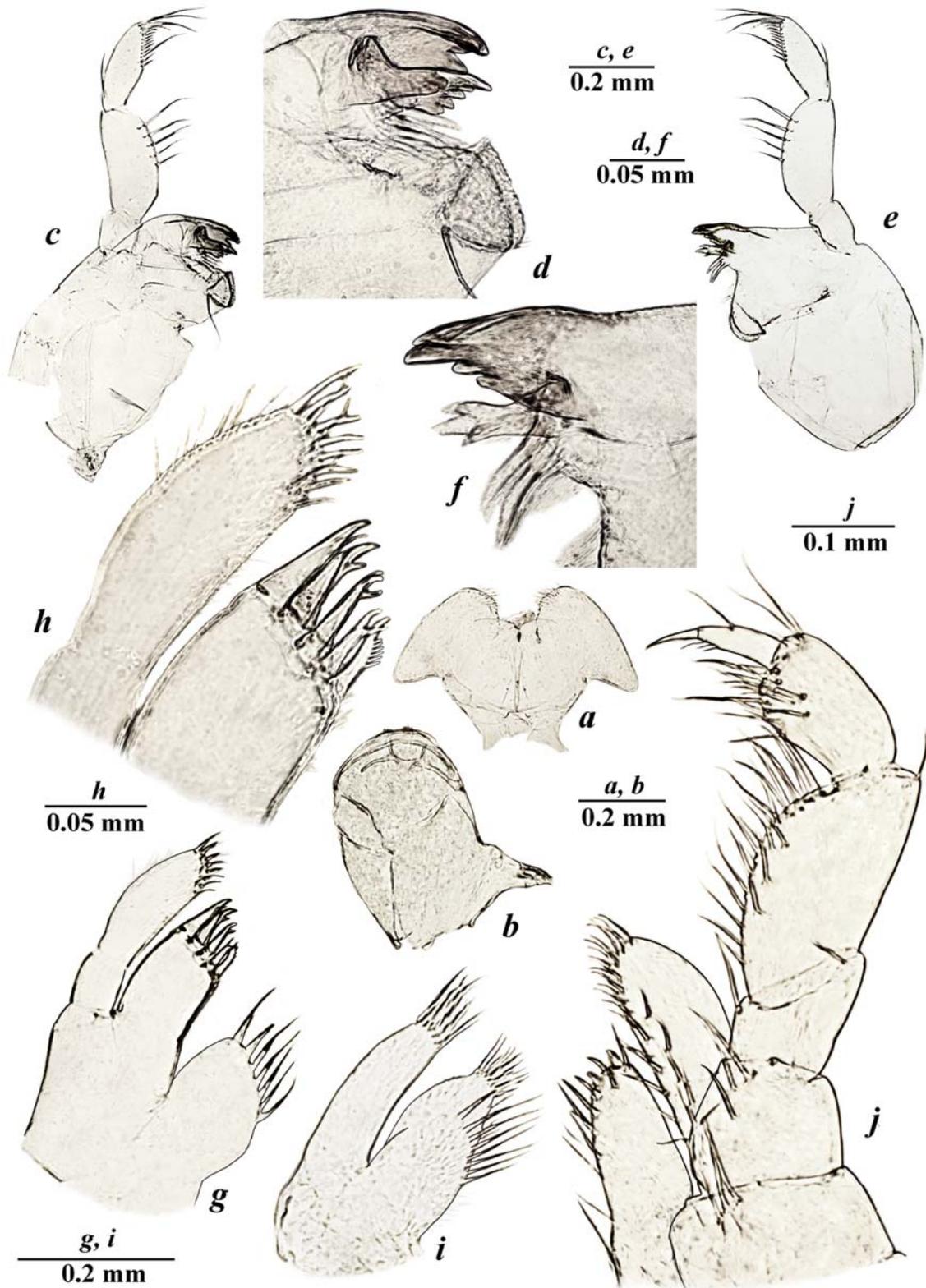


Fig. 24. *Synurella praemontana* Marin et Palatov sp.n., ♀: a — labrum (upper lip); b — labium (lower lip); c — left mandible; d — same, incisor process and *pars incisiva*; e — right mandible; f — same, incisor process and *pars incisiva*; g — maxilla I; h — distal margin of inner plate of maxilla I; i — maxilla II; j — maxilliped.

Рис. 24. *Synurella praemontana* Marin et Palatov sp.n., ♀: a — лабрум (верхняя губа); b — лабиум (нижняя губа); c — левая мандибула; d — то же, режущий отросток и резцовая часть; e — правая мандибула; f — то же, режущий отросток и резцовая часть; g — максилла I; h — дистальный край внутренней пластины максиллы I; i — максилла II; j — максиллипод.

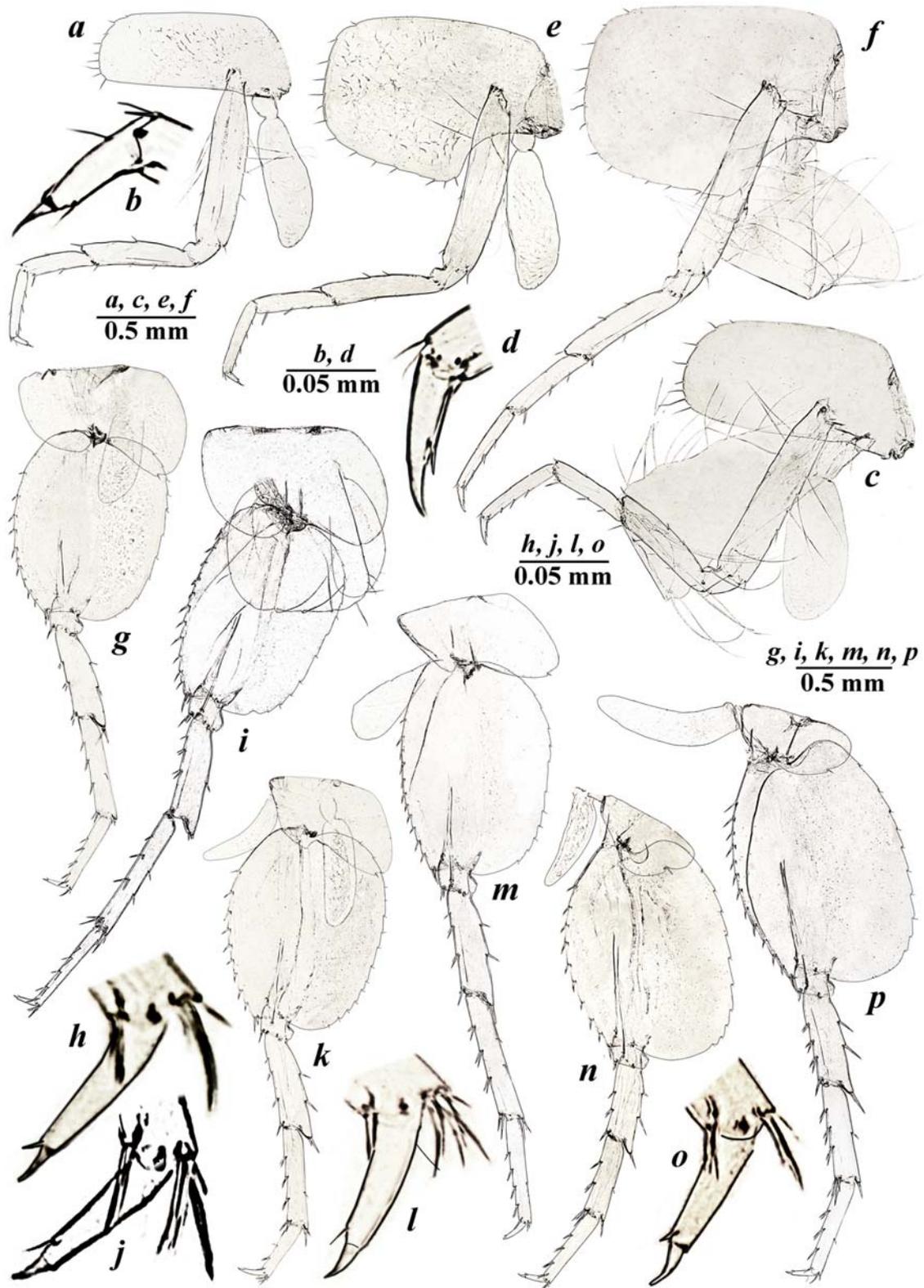


Fig. 25. *Synurella praemontana* Marin et Palatov sp.n., ♂ (*a, b, e, g, h, k, l, n, o*), ♀ (*e, f, i, j, m, p*): *a, c* — pereopod III; *b, d* — dactylus of PIII; *e, f* — pereopod IV; *g, i* — pereopod V; *h, j* — dactylus of PV; *k, m* — pereopod VI; *l* — dactylus of PVI; *n, p* — pereopod VII; *o* — dactylus of PVII.

Рис. 25. *Synurella praemontana* Marin et Palatov sp.n., ♂ (*a, b, e, g, h, k, l, n, o*), ♀ (*e, f, i, j, m, p*): *a, c* — переопода III; *b, d* — дактилус PIII; *e, f* — переопода IV; *g, i* — переопода V; *h, j* — дактилус PV; *k, m* — переопода VI; *l* — дактилус PVI; *n, p* — переопода VII; *o* — дактилус PVII.

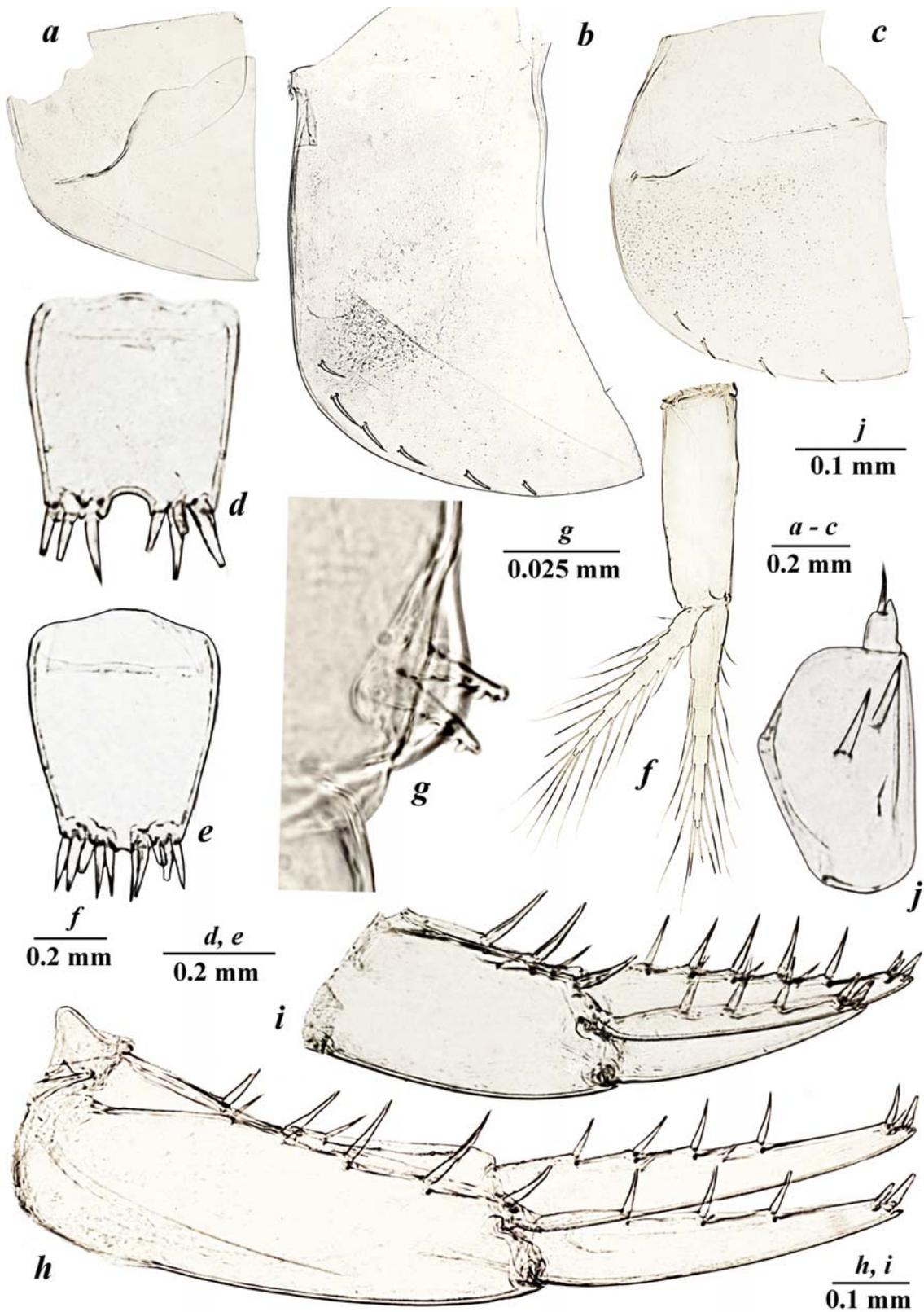


Fig. 26. *Synurella praemontana* Marin et Palatov sp.n., ♀ (a-c, e-j), ♂ (d): a — epimeral plate I; b — epimeral plate II; c — epimeral plate III; d, e — telson; f — pleopod III; g — hooks of retinacula of pleopod III; h — uropod I; i — uropod II; j — uropod III.

Рис. 26. *Synurella praemontana* Marin et Palatov sp.n., ♀ (a-c, e-j), ♂ (d): a — эпимеральная пластинка I; b — эпимеральная пластинка II; c — эпимеральная пластинка III; d, e — тельсон; f — плеопода III; g — крючки ретинакулы плеоподы III; h — уропода I; i — уропода II; j — уропода III.

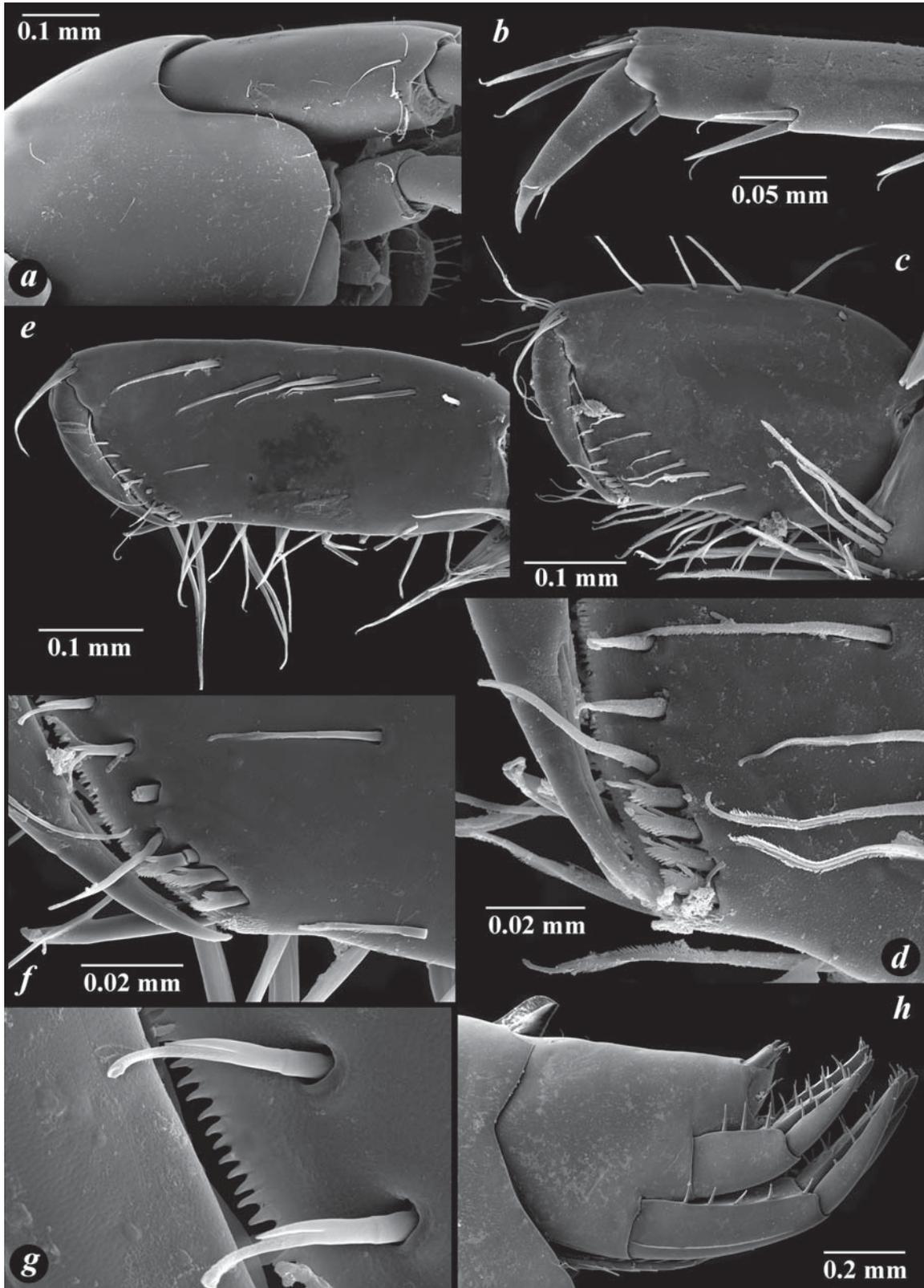


Fig. 27. *Synurella praemontana* Marin et Palatov sp.n., ♂: *a* — head; *b* — dactylus of PVI; *c* — palm (chela) of GnI; *d* — distoventral margin of palm (chela) of GnI; *e* — palm (chela) of GnII; *d*, *e* — distoventral margin of GnII; *g* — same, cutting edge; *h* — urosomal segments.

Рис. 27. *Synurella praemontana* Marin et Palatov sp.n., ♂: *a* — голова; *b* — дактилус PVI; *c* — ладонь (клешня) GnI; *d* — дистовентральный край ладони (клешни) GnI; *e* — ладонь (клешня) GnII; *g* — то же, режущая кромка; *h* — сегменты уросомы.

Pereopod IV (Fig. 25f, e): subequal to PIII in length; coxal plate expanded and broadly convex distally, posterior margin with shallow excavation, distal margin with 15 apical short setae and numerous facial setae, width/depth ratio is 1.30–1.36/1; basis about 5.2–5.4X as long as wide, with long anterior and posterior simple setae; merus about 0.60–0.62X of basis, about 1.32–1.49X of carpus and about 1.30–1.52X of propodus in length; carpus subequal of propodus in length; dactylus about 0.30X of propodus, with 1 plumose seta on outer margin and 1 additional spine accompanying with 1 seta on ventral margin.

Pereopods V, VI, VII with the length ratio 1/1.01/0.94 in males and 1/1.09/0.92 in females.

Pereopod V (Fig. 25g, i): coxal plate large, bilobate with distinct anterior and posterior lobes; posterior and anterior lobes with 1 margin simple seta each, with numerous facial setae; basis about 1.25–1.50X as long as wide, with numerous facial setae, posterior margin slightly convex, armed with 11–13 shallow serrations, with distal corner, anterior margin with 10–11 split-tipped robust and 4 distal setae; merus about 0.58X of basis, subequal of carpus and 1.22–1.29X of propodus in length; dactylus (Fig. 25h, j) approximately 0.25–0.30X of propodus, with 1 plumose seta on outer margin and 1 additional spine accompanying with 1 seta on ventral margin.

Pereopod VI (Fig. 25k, m): coxal plate bilobate, with distinct posterior and vestigial anterior lobes; anterior lobe without setae, posterior lobe with 1 margin seta, each with numerous facial setae; basis about 1.26–1.45X as long as wide, with numerous facial setae, posterior margin convex, armed with 12–15 shallow serrations, anterior margin with 9–11 split-tipped robust and 4 distal setae; merus about 0.57X of basis, 0.92–1.08X of carpus and 1.20–1.90X of propodus in length; dactylus (Fig. 25l) approximately 0.31–0.46X of propodus, with 1 plumose seta on outer margin and 1 additional spine accompanying with 1 seta on ventral margin.

Pereopod VII (Fig. 25n, p): coxal plate small, semi-lunar, with 1 posterior seta; basis about 1.40–1.43X as long as wide, with numerous facial setae, posterior margin convex, armed with 10–13 serrated setae and with wide distal lobe, anterior margin with 9–12 split-tipped robust and 3 distal setae; merus about 0.44–0.47X of basis, about 1.12–1.14X of carpus and 1.10–1.14X of propodus in length; dactylus (Fig. 25o) approximately 0.30–0.30X of propodus in length, with 1 plumose seta on outer margin and 1 additional spine accompanying with 1 seta on ventral margin.

Gills, brood plates (Fig. 25): coxal gills on somites II–VII, somites II–VII with lanceolate sternal gill on each. Male: coxal gills II–VII ovoid, gills/bases pereopod ratios are 0.83/1, 0.75/1, 0.75/1, 0.52/1, 0.55/1 and 0.11/1, respectively. Female: coxal gills II–VII ovoid, gills/bases pereopod ratios are 0.83/1, 0.74/1, 0.72/1, 0.54/1, 0.48/1 and 0.13/1, respectively. Brood plates on somites II–V slender, setaceous, decreasing in size posteriorly.

Pleopods (Fig. 26f). Pleopod I peduncle with 2 coupling hooks in retinacula, without lateral setae; outer and inner rami with 8 and 10 articles, respectively. Pleopod II peduncle with 2 coupling hooks in retinacula, without setae (Fig. 26g); outer and inner rami with 7 and 9 articles, respectively. Pleopod III peduncle with 2 coupling hooks in retinacula, without lateral setae; outer and inner rami with 7 and 8 articles, respectively.

Epimera (Fig. 26e). Epimeral plate I (Fig. 26a) distally produced and sharpened, ventral margin without spines in

females and with a spine in males, posterior margin with 1 small seta. Epimeral plate II (Fig. 26b) distally produced, ventral margin armed with 6 spines, posterior margin with 1 seta. Epimeral plate III (Fig. 26c) distally blunted, weakly produced, ventral margin armed with 3–4 spines, posterior margin with 1 seta.

Urosomites completely fused, smooth.

Uropod I (Fig. 26h): peduncle about 2.9–3.1X as long as wide, with dorsointernal row of 2–4 robust spines, 1 subdistal spine and dorsoexternal row of 3 spines; exopodite slightly shorter than endopodite; endopodite not paddle-like, with 3–4 dorsolateral, 5 apical spines and 1 ventral seta; exopodite with 3 dorsolateral and 5 apical spines.

Uropod II (Fig. 26i): peduncle subequal of endopodite in length, with 3 dorsal and 1 subdistal robust spines; exopodite about 0.82X of endopodite in length, with 4–5 dorsal, 1–3 lateral and 4 apical robust spines; endopodite with 3 dorsal and 4 apical robust spines.

Uropod III (Fig. 26j): uniramous, peduncle trapezoidal, about 1.45–1.60X as long as wide, with a 2 weak spines and 2 simple setae; apical margin of ramus armed with a weak spine.

Telson different in males and females. Male (Fig. 26e): close to trapezoidal, about 1.30X as long as broad; distal margin with almost invisible U-shaped distal notch, reaching about 1/45 of its length, each lobe armed with 5 robust spines, with 2 additional submarginal plumose setae. Female (Fig. 26d): close to square, about 1.06X as long as broad; distal margin with weakly expressed U-shaped distal notch, reaching about 1/9 of its length, each lobe armed with 4 robust spines, with 2 additional submarginal plumose setae.

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

GENBANK ACCESSION NUMBERS. OP306071, OP306072.

TAXONOMIC REMARKS. The new species distinctly belong to the “*behningi*” species complex (Fig 1, 2). The new species can be clearly separated from *Synurella behningi* by the following features: 1) ventrally produced EpII with 6 ventral spines (Fig. 26b) (vs. medium EpII with 4 ventral spines (Fig. 17b)); 2) EpIII with blunt distoventral margin (Fig. 26c) (vs. sharply produced posteroventral tooth (Fig. 17c)); 3) short distal article of UIII (see Fig. 26j); and 4) telson with distal notch, reaching about 1/6 of its length (Fig. 26d) (vs. 1/4 of telson (Fig. 17d)).

The new species can be clearly separated from *Synurella gizmavi* sp.n. by the following features: 1) inner plate of MxI with 7 plumose marginal setae (Fig. 24g) (vs. 5 plumose marginal setae (Fig. 19g)); 2) ventrally bluntly produced EpII with 6 ventral spines (Fig. 26b) (vs. sharply produced plate with 3 ventral spines (Fig. 21b)); 3) EpIII with blunt distoventral margin, with 4 ventral spines (Fig. 26c) (vs. 2 ventral spines (Fig. 21)); short distal article of UIII (see Fig. 26j); and 4) telson with distal notch, reaching about 1/6 of its length (Fig. 26d) (vs. 1/5 of telson (Fig. 21d)).

DISTRIBUTION AND ECOLOGY. Hypogean (stygo-biotic) species, which is presently known only from a single well, located in the upper stream of the Shids River.

#### *Synurella adegoyi* Marin et Palatov sp.n.

Figs 28–32.

MATERIAL EXAMINED. Holotype, ♀ (bl. 6.5 mm), ZMMU Mb-1236 – Russian Federation, south-western Caucasus, Krasnodar Krai, Gelendzyk area, the upper stream of the Adegoy River,

44°44'27.39"N 37°54'03.71"E, in the river hypogea, hand net sampling, 8.11.2021, coll. I. Marin & S. Sinelnikov. Paratypes, 1♀, 1♂ (bl. 6.2 and 4.5 mm), ZMMU Mb-1237, same locality and data as holotype. Additional material: 12♀♀ (LEMMI, same locality and data as holotype).

**ETYMOLOGY.** The species is named after the Adegey River, in the upper stream of which the species was discovered.

**DIAGNOSIS.** Body unpigmented, whitish. Distal article of accessory flagellum of AI is about 2.7X shorter than basal one. Inner plate of MxI with 5 plumose marginal setae. GnI with palm about 1.8X as long as wide in females and about 1.9X as long as wide in males. GnII with palm about 2.6X as long as wide in females and about 2.3X as long as wide in males. Coxal plate longer than palm of GnI–II in males and females. PVII basis with distinct posterior lobe. Coxal gill VII relatively small, about 0.3X of basis of PVII. EpI with very short posteroventral tooth. EpII with 4 ventral spines. EpIII with blunt distoventral margin, and 3 ventral spines. Basal article (peduncle) of UIII with 1 spine. Telson without, or with distal notch, not reaching about 1/8–1/10 of its length.

**DESCRIPTION.** Body: moderately stout; the largest collected ♀ has bl. 6.5 mm.

Head (Fig. 32a): smooth, with bluntly produced anteroventral lobe; with reduced black-pigmented eyes and yellow dorsolateral spots.

Antenna I (Fig. 28a): about 50% of body length, about 1.7X longer than antenna II; primary flagellum with 11 articles, with aesthetascs on distal articles; accessory flagellum 2-articulated, distal article about 2.7X shorter than basal one (Fig. 28b).

Antenna II (Fig. 28c): gland clone distinct, distally pointed; peduncle about 1.8X longer than flagellum, with robust setae tightly covering articles 3 and 4, peduncle of article 4 about 1.1X longer than article 5; flagellum 5-articulated, without calceoli in females.

Mandible: left mandible (Fig. 29d) incisor 4-dentate, *lacinia mobilis* 5-dentate, with 3 robust plumose accessory setae; molar process with 1 seta (Fig. 29e). Right mandible (Fig. 29f) incisor 4-dentate, *lacinia mobilis* toothed, trituberculate, lobes with numerous protuberances; underlying with a row of 2 robust plumose setae; molar process similar to left mandible (Fig. 29g). Palp 3-articulated, article 2 with 6–7 setae; article 3 about 2.9X longer than wide, with convex margins, with 7–8 separate D-setae, 2 C-setae, 1 B-seta and 3 separate E-setae.

Lateralialia with 8 teeth.

Labrum (upper lip) (Fig. 29a): oval, apical margin with numerous small fine setae.

Labium (lower lip) (Fig. 29b): inner lobes feebly developed.

Maxilla I (Fig. 29g): inner plate with 5 plumose marginal setae, outer plate with 7 apical comb-spines; palp 2-articulated, distal article pubescent, about 2.7X of basal article, apical margin of distal article with 7 simple setae (Fig. 29h).

Maxilla II (Fig. 29i): inner, outer plates covered in pubescent setae; inner and outer plates subequal in length; outer plate weakly narrowing distally, with 12 apical setae; inner plate narrowing slightly distally, with group of dense short setae on apex, with oblique row of 5 short plumose setae.

Maxilliped (Fig. 29j): inner plate much shorter than outer plate, with 2 spines, 1 robust plumose and 1 simple setae apically, and 5 robust plumose setae laterally; outer

plate narrow, with a double row of 18 medial stiff simple setae of different length; palp 4-articulated, article I with a long seta on outer margin, article II with a row of 16 simple setae on inner margin and without setae on outer margin, article III sub-trapezoidal; dactylus with 1 seta on outer margin and with 2 thin setae at inner margin, nail long, slender, with 1 thin seta at hinge.

Gnathopod I (Figs 28d, 32c) smaller than gnathopod II; coxal plate sub-rectangular, distally rounded, with 6 apical and numerous facial setae, width/depth ratio is 0.50/1; basis width/length ratio is 0.32/1, without setae on anterior margin, 3 long setae on inner face, 7–8 long setae on posterior margin; merus with 10 distal setae; carpus is 0.56X of basis and 0.91X of propodus, with 12–13 serrated setae in inner margin and 5 simple setae in outer margin; propodus 1.8–1.9X longer than broad, with 5 simple anterior, 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) (Figs 28e, 32d) feebly developed, with 2 inner and 2 outer robust setae; dactylus with 1 outer seta.

Gnathopod II (Figs 28f; 32e): coxal plate sub-rectangular, with 6 apical and numerous facial setae, width/depth ratio is 0.48/1; basis width/length ratio is 0.28/1, with several (5–6) long setae inserted along posterior margin and with 1 long simple seta and 1 short seta in anterior margin; ischium with 2 short simple setae; merus with 5 distal setae; carpus is 0.64X of length of basis and 0.95X of propodus, with 2 anterior simple and 4 groups of plumose posterior setae; propodus 2.3–2.6X longer than broad, with 2 simple anterior setae, 5 superior medial, 2 inferior medial and 5 groups of posterior setae; palm oblique with a double row of 4 inner and 4 outer bifurcate robust setae; palm groove (depression) (Figs 28g; 32f) feebly developed, with 3 inner and 3 outer robust setae; dactylus without inner and with 1 outer seta.

Pereopod III (Fig. 30a): coxal plate sub-rectangular, with 5 apical and numerous facial setae, width/depth ratio is 0.44/1; basis about 4.8X as long as wide, with long anterior and posterior simple setae; merus about 0.62X of basis, about 1.5X of carpus and about 1.3X of propodus in length; carpus about 0.86X of propodus in length; dactylus (Fig. 30b) about 0.42X of propodus, with 1 plumose seta on outer margin and 1 additional spine accompanying with 1 seta on ventral margin.

Pereopod IV (Fig. 30c): subequal to PIII in length; coxal plate expanded and broadly convex distally, posterior margin with shallow excavation, distal margin with 10 apical short setae and numerous facial setae, width/depth ratio is 1.45/1; basis about 4.8X as long as wide, with long anterior and posterior simple setae; merus about 0.65X of basis, about 1.36X of carpus and about 1.22X of propodus in length; carpus about 0.90X of propodus in length; dactylus about 0.38X of propodus, with 1 plumose seta on outer margin and 1 additional spine accompanying with 1 seta on ventral margin.

Pereopods V, VI, VII with the length ratio 1/1.05/0.93.

Pereopod V (Fig. 30d): coxal plate large, bilobate with distinct anterior and posterior lobes; posterior and anterior lobes with 1 margin simple seta each, with numerous facial setae; basis about 1.38X as long as wide, with numerous facial setae, posterior margin slightly convex, armed with 9 shallow serrations, with distal corner, anterior margin with 8 split-tipped robust and 4 distal setae; merus about 0.55X of basis, 0.90X of carpus and subequal of propodus in length;

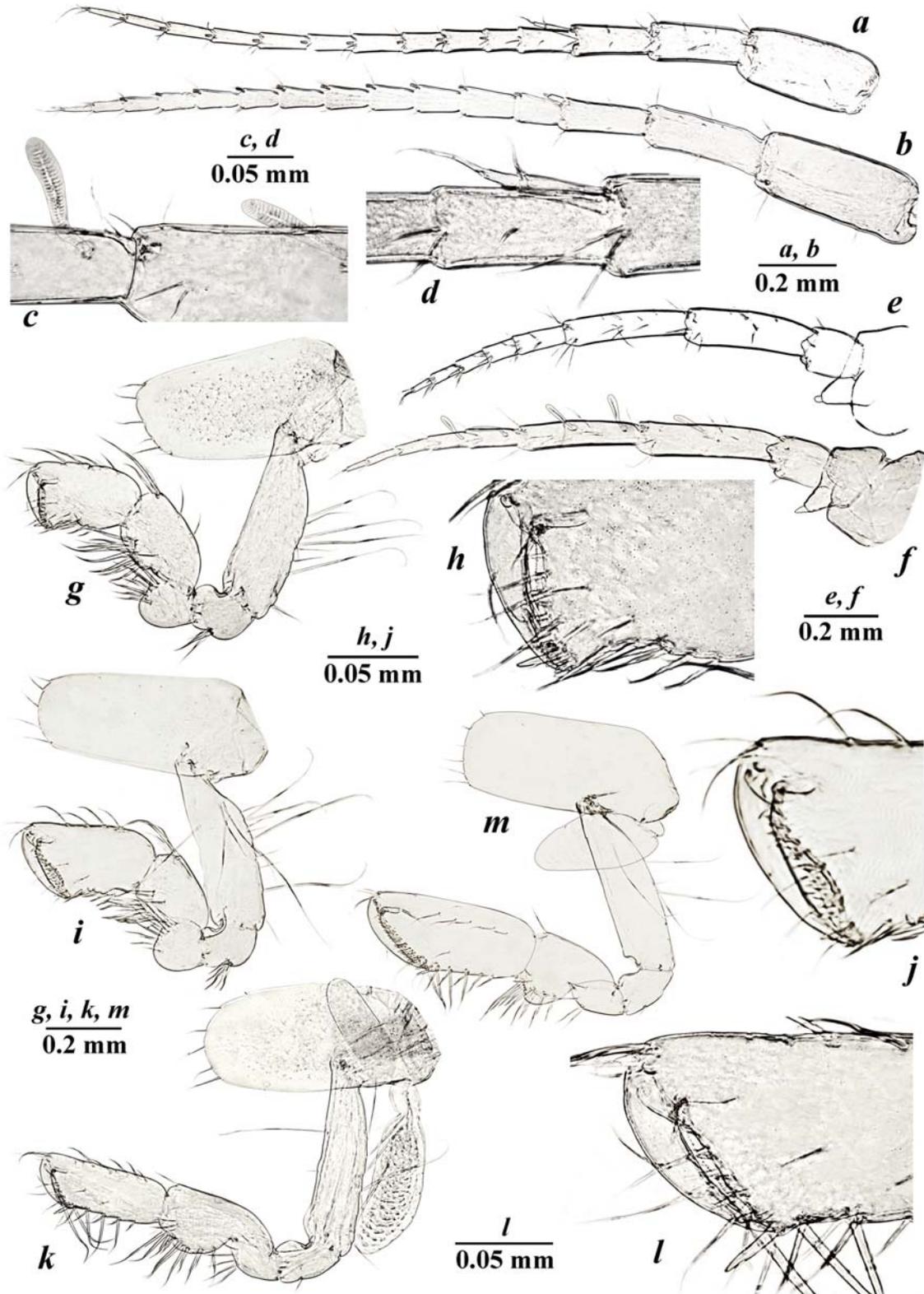


Fig. 28. *Synurella adegoyi* Marin et Palatov sp.n., ♀ (*a, d, e-h, k, l*), ♂ (*b, c, f, i, j, m*): *a, b* — antenna I; *c* — calceoli; *d* — accessory flagellum of antenna I; *e, f* — antenna II; *g, i* — gnathopod I; *h, j* — distoventral margin of palm (chela) of GnI; *k, m* — gnathopod II; *l* — distoventral margin of palm (chela) of GnII.

Рис. 28. *Synurella adegoyi* Marin et Palatov sp.n., ♀ (*a, d, e-h, k, l*), ♂ (*b, c, f, i, j, m*): *a, b* — антенна I; *c* — кальцели; *d* — добавочный жгутик антенны I; *e, f* — антенна II; *g, i* — гнатопода I; *h, j* — дистовентральный край ладони (клешни) GnI; *k, m* — гнатопода II; *l* — дистовентральный край ладони (клешни) GnII.

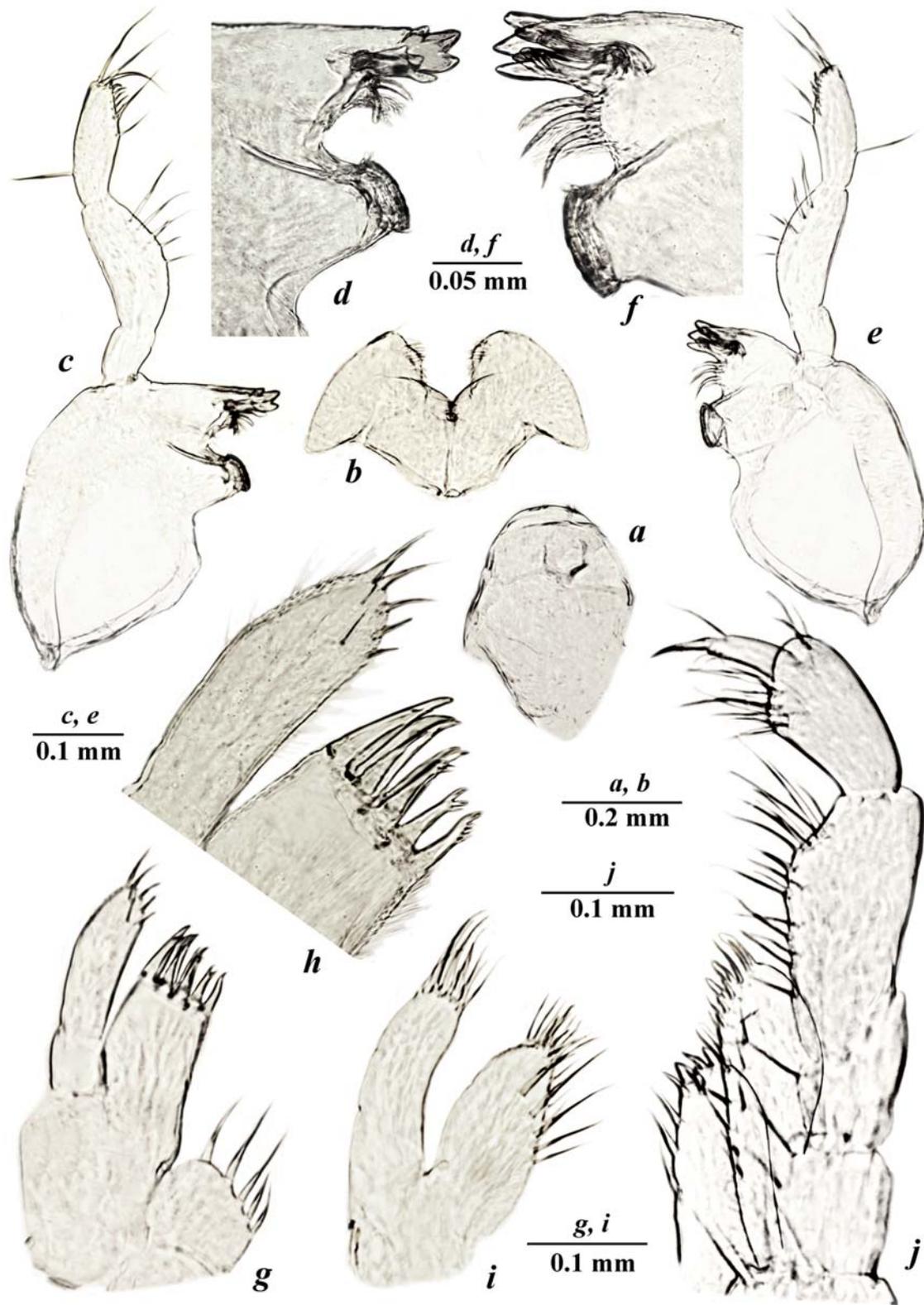


Fig. 29. *Synurella adegoyi* Marin et Palatov sp.n., ♀: *a* — labrum (upper lip); *b* — labium (lower lip); *c* — left mandible; *d* — same, incisor process and *pars incisiva*; *e* — right mandible; *f* — same, incisor process and *pars incisiva*; *g* — maxilla I; *h* — distal margin of inner plate of maxilla I; *i* — maxilla II; *j* — maxilliped.

Рис. 29. *Synurella adegoyi* Marin et Palatov sp.n., ♀: *a* — лабрум (верхняя губа); *b* — лабиум (нижняя губа); *c* — левая мандибула; *d* — то же, режущий отросток и резцовая часть; *e* — правая мандибула; *f* — то же, режущий отросток и резцовая часть; *g* — максилла I; *h* — дистальный край внутренней пластины максиллы I; *i* — максилла II; *j* — максиллипод.

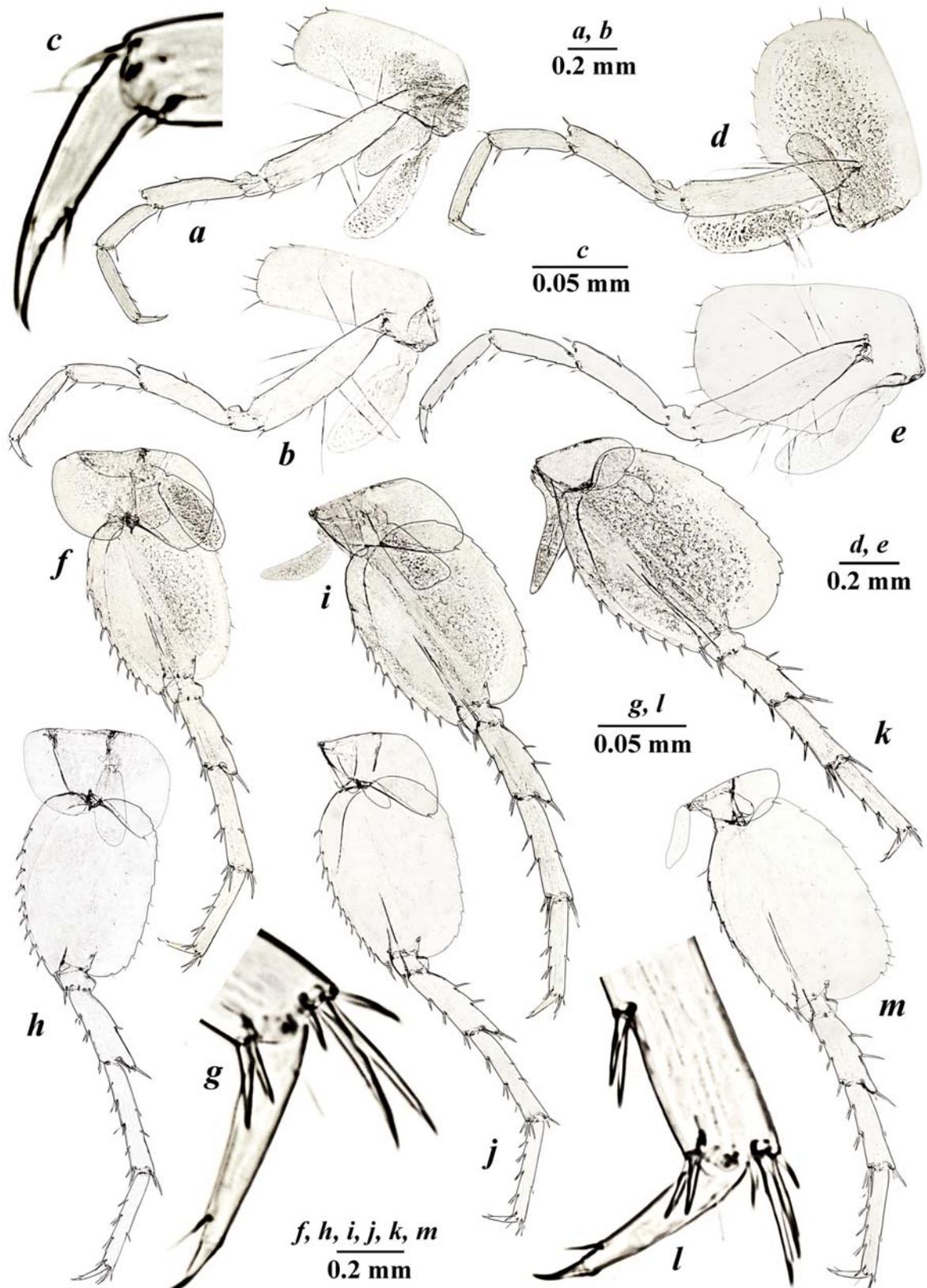


Fig. 30. *Synurella adegoyi* Marin et Palatov sp.n., ♀ (*a, c, d, f, g, i, k, l*) and ♂ (*b, e, h, j, m*): *a, b* — pereopod III; *c* — dactylus of PIII; *d, e* — pereopod IV; *f, h* — pereopod V; *g, l* — dactylus of PV; *i, j* — pereopod VI; *k, m* — pereopod VII; *l* — dactylus of PVII.

Рис. 30. *Synurella adegoyi* Marin et Palatov sp.n., ♀ (*a, c, d, f, g, i, k, l*) и ♂ (*b, e, h, j, m*): *a, b* — переопода III; *c* — дактилус PIII; *d, e* — переопода IV; *f, h* — переопода V; *g, l* — дактилус PV; *i, j* — переопода VI; *k, m* — переопода VII; *l* — дактилус PVII.

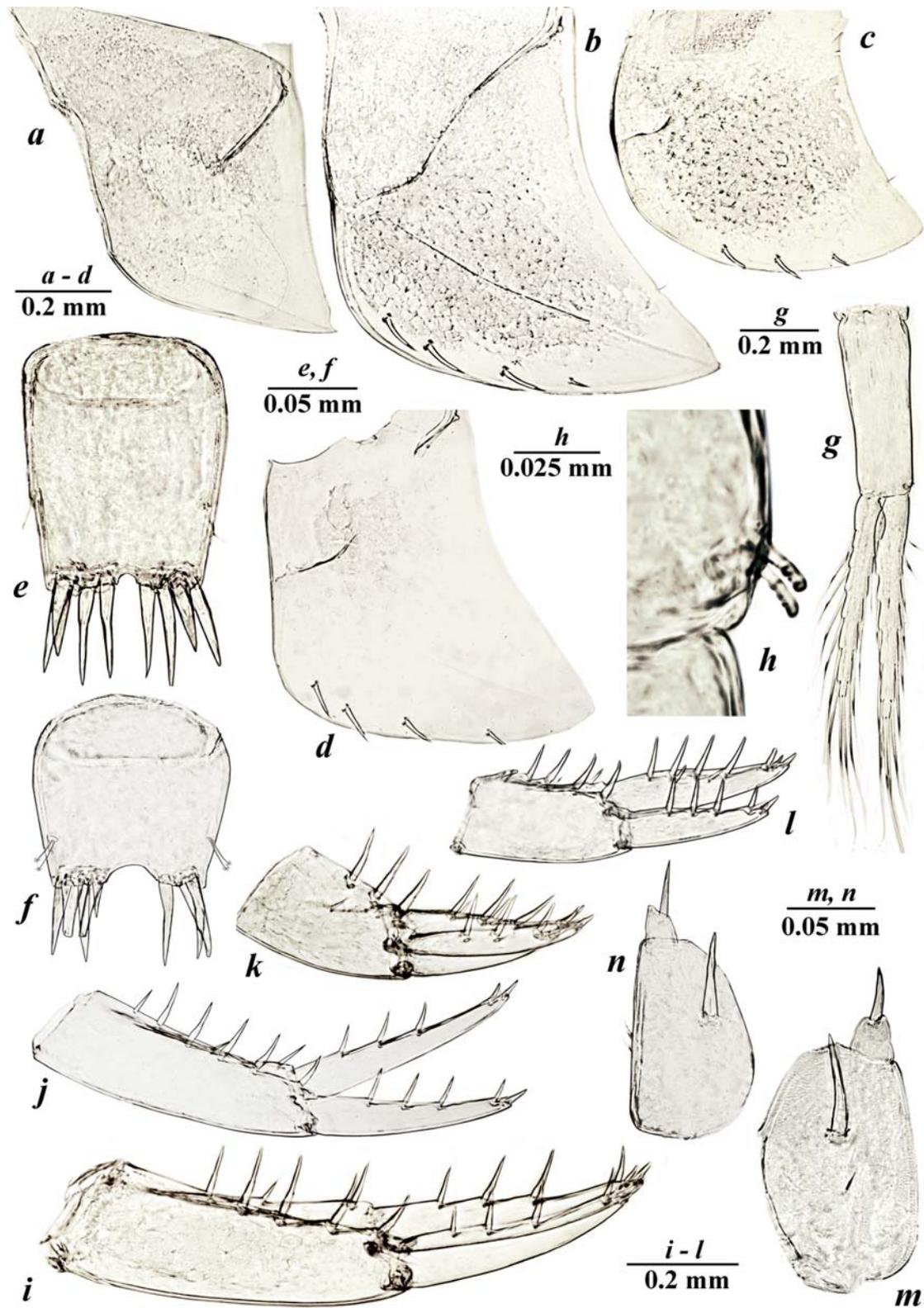


Fig. 31. *Synurella adegoyi* Marin et Palatov sp.n., ♀ (*a-c, e, g, h, i, k, m*) and ♂ (*d, f, j, l, n*): *a* — epimeral plate I; *b, d* — epimeral plate II; *c* — epimeral plate III; *e, f* — telson; *g* — pleopod III; *h* — hooks of retinacula of pleopod III; *i, j* — uropod I; *k, l* — uropod II; *m, n* — uropod III.

Рис.31. *Synurella adegoyi* Marin et Palatov sp.n., ♀ (*a-c, e, g, h, i, k, m*) и ♂ (*d, f, j, l, n*): *a* — эпимеральная пластинка I; *b, d* — эпимеральная пластинка II; *c* — эпимеральная пластинка III; *e, f* — тельсон; *g* — плеопода III; *h* — крючки ретинакулы плеопода III; *i, j* — уропода I; *k, l* — уропода II; *m, n* — уропода III.

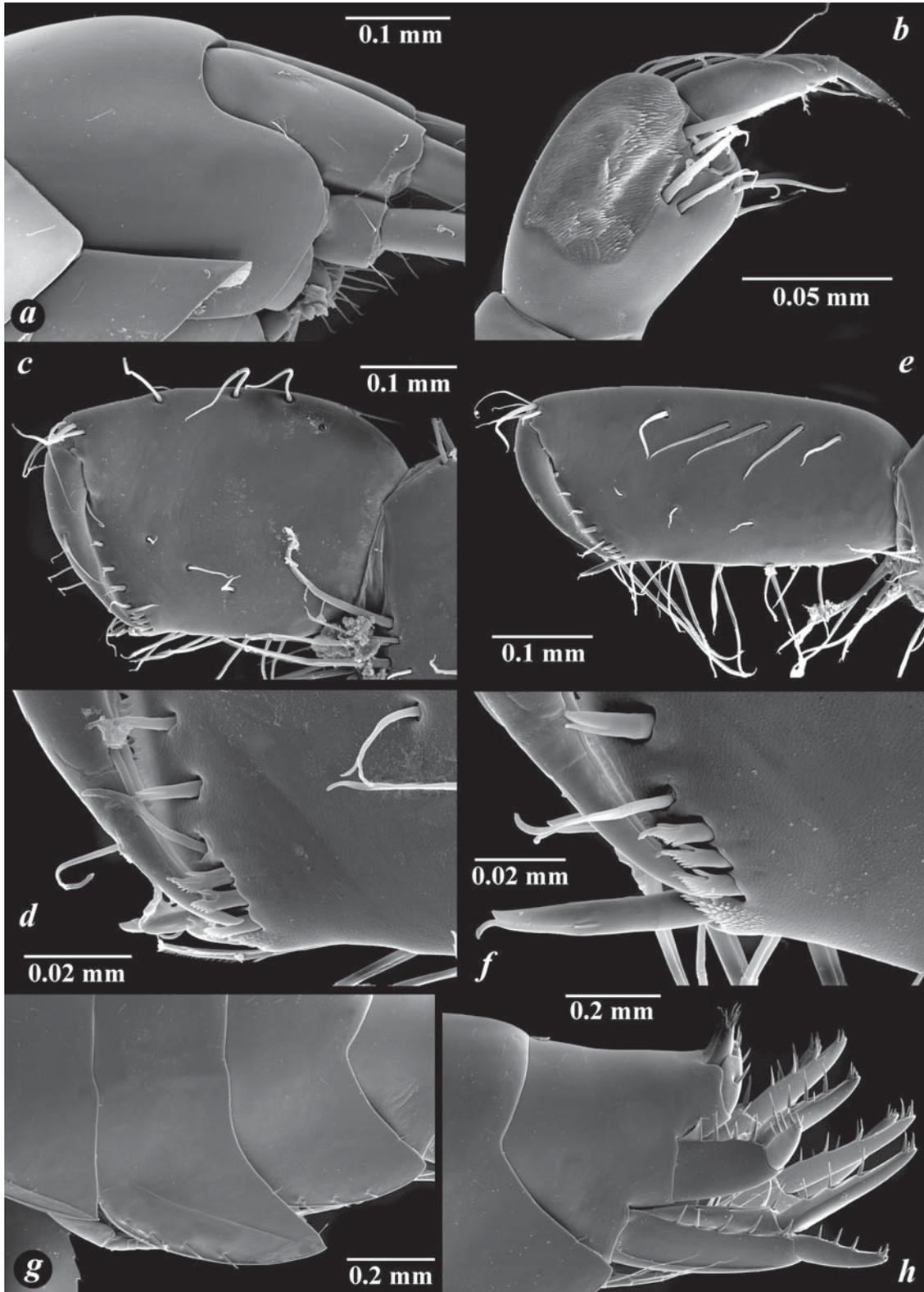


Fig. 32. *Synurella adegoyi* Marin et Palatov sp.n., ♀: *a* — head; *b* — article 3 and dactylus of palp of maxilliped; *c* — palm (chela) of GnI; *d* — distoventral margin of GnI; *e* — palm (chela) of GnII; *f* — distoventral margin of palm (chela) of GnII; *g* — epimeral plates I-III; *h* — urosomal segments.

Рис. 32. *Synurella adegoyi* Marin et Palatov sp.n., ♀: *a* — голова; *b* — сегмент 3 и дактилус щупика максиллипед; *c* — ладонь (клешня) GnI; *d* — дистовентральный край ладони (клешни) GnI; *e* — ладонь (клешня) GnII; *f* — дистовентральный край ладони (клешни) GnII; *g* — эпимеральные пластинки I-III; *h* — уросомальные сегменты.

dactylus (Fig. 30g) approximately 0.40X of propodus, with 1 plumose seta on outer margin and 1 additional spine accompanying with 1 seta on ventral margin.

Pereopod VI (Fig. 30f): coxal plate bilobate, with distinct posterior and vestigial anterior lobes; anterior lobe without setae, posterior lobe with 1 margin seta, each with numerous facial setae; basis about 1.36X as long as wide, with numerous facial setae, posterior margin convex, armed with 10 shallow serrations, anterior margin with 9 split-tipped robust and 4 distal setae; merus about 0.51X of basis, 0.96X of carpus and 1.05X of propodus in length; dactylus (Fig. 30g) approximately 0.36X of propodus, with 1 plumose seta on outer margin and 1 additional spine accompanying with 1 seta on ventral margin.

Pereopod VII (Fig. 30h): coxal plate small, semi-lunar, with 1 posterior seta; basis about 1.32X as long as wide, with numerous facial setae, posterior margin convex, armed with 10 serrated setae and with wide distal lobe, anterior margin with 9 split-tipped robust and 3 distal setae; merus about 0.38X of basis, subequal of carpus and 0.87X of propodus in length; dactylus (Fig. 30i) approximately 0.45X of propodus in length, with 1 plumose seta on outer margin and 1 additional spine accompanying with 1 seta on ventral margin.

Gills, brood plates (Fig. 30): coxal gills on somites II–VII, somites II–VII with lanceolate sternal gill on each. Coxal gills II–VII ovoid, gills/bases pereopod ratios are 0.81/1, 0.69/1, 0.71/1, 0.50/1, 0.42/1 and 0.18/1, respectively. Brood plates on somites II–V slender, setaceous, decreasing in size posteriorly.

Pleopods (Fig. 31e). Pleopod I peduncle with 2 coupling hooks in retinacula, without lateral setae; outer and inner rami with 6 and 8 articles, respectively. Peduncles of pleopods II and III with 2 coupling hooks in retinacula, without setae (Fig. 31f); outer and inner rami with 7 and 5 articles, respectively.

Epimera (Fig. 32g). Epimeral plate I (Fig. 31a) distally produced and sharpened, ventral margin without spines, posterior margin with 1 short seta. Epimeral plate II (Fig. 31b) distally produced and sharpened, ventral margin armed with 3 spines, posterior margin with 1 short seta. Epimeral plate III (Fig. 31c) distally produced and bluntly pointed, ventral margin armed with 3 spines, posterior margin with 1 short seta.

Urosomites completely fused, smooth (Fig. 32h).

Uropod I (Fig. 31g): peduncle about 3.0X as long as wide, with dorsoexternal row of 4 robust spines, 1 subdistal spine and 2 dorsointernal robust spines; exopodite slightly shorter than endopodite; endopodite not paddle-like, with 3 dorsolateral, 4 apical spines and 1 ventral seta; exopodite with 3 dorsolateral and 4 apical spines.

Uropod II (Fig. 31h): peduncle about 0.94X of endopodite in length, with 3 dorsal robust spines; exopodite about 0.93X of endopodite in length, with 3 dorsal and 4 apical robust spines; endopodite with 3 dorsal, 2 lateral and 5 apical robust spines.

Uropod III (Fig. 31i): uniramous, peduncle sub-ovale, about 1.6X as long as wide, with a weak spine and 1 simple seta; apical margin of ramus armed with a weak spine.

Telson (Fig. 31d): close to rectangular or trapezoidal, about 1.26X as long as broad; distal margin with weakly expressed U-shaped distal notch, reaching about 1/20 of its length, each lobe armed with 4 robust spines, with 2 additional submarginal plumose setae.

COLORATION. The body and appendages whitish or grayish transparent; with well-pigmented black eyes and dorsolateral yellow spots on the head.

GENBANK ACCESSION NUMBERS. OP324571, OP324572.

TAXONOMIC REMARKS. The new species distinctly belong to the “*behningi*” species complex (Figs 1; 2). The new species can be clearly separated from *Synurella behningi* by the following features: 1) coxal plate II distinctly longer (see Fig. 28f vs. 14f); 2) EpII strongly produced ventrally (Fig. 31b); 3) short distal article of UIII (see Fig. 31i); and 4) telson with distal notch, reaching about 1/8 of its length (Fig. 31d) (vs. 1/4 of telson (Fig. 17d)).

The new species can be clearly separated from *Synurella gizmavi* sp.n. by the following features: 1) EpII strongly and bluntly produced ventrally, with 4 ventral spines (Fig. 31b) (vs. sharply produced with 3 ventral spines (Fig. 21b)); 2) shorter distal article of UIII (see Fig. 31i); and 3) telson with distal notch, reaching about 1/8 of its length (Fig. 31d) (vs. 1/5 of telson (Fig. 21d)).

The new species can be clearly separated from *Synurella praemontana* sp.n. by the following features: 1) inner plate of MxI with 5 plumose marginal setae (Fig. 25g) (vs. 7 plumose marginal setae (Fig. 20g)); 2) longer distal article of accessory flagellum of AI, which is about 2.7X shorter than basal article (Fig. 24b) (vs. 0.5X (see Fig. 19c)); 3) EpII with 4 ventral spines (Fig. 27b) (vs. with 6 ventral spines (Fig. 22b)); and 4) telson with distal notch, reaching about 1/8 of its length (Fig. 27d) (vs. 1/6 of telson (Fig. 22d)).

DISTRIBUTION AND ECOLOGY. Hypogean (stygobiotic) species, which is presently known only from a group of wells and hyporhean biotopes in the upper stream of the Adegov River, Krasnodar Krai.

*Synurella monteflumina* Palatov et Marin **sp.n.**  
Figs 33–36.

MATERIAL EXAMINED. Holotype, ♀ (bl. 5.5 mm), ZMMU Mb-1238, Russian Federation, south-western Caucasus, Krasnodar Krai, Gelendzyk area, the middle reaches of the Olkhovka River, in the coastal well, 44°32'4.4"N 38°20'11.7"E, hand net sampling, coll. D. Palatov & I. Marin, 6.06.2021. Additional material: 3♀♀ (LEMMI), same locality and data as for holotype.

ETYMOLOGY. The species is named after the place of its discovery in a small spring on the bank of the mountain river: *monte* (Lat.) — mountain and *flumina* (Lat.) — river.

DIAGNOSIS. Only females are known. Body unpigmented, whitish. Distal article of accessory flagellum of AI is about 3.0X shorter than basal one. Inner plate of MxI with 5 plumose marginal setae. GnI with palm about 1.6X as long as wide, GnII with palm about 2.4X as long as wide in females. Coxal plate longer than palm of GnI–II in females. PVII basis with distinct posterior lobe. Coxal gill VII relatively small, about 0.3X of basis of PVII. EpI with short posteroventral tooth. EpII with 3 ventral spines. EpIII with blunt distoventral margin, and 3 ventral spines. Basal article (peduncle) of UIII with 1 spine. Telson with distal notch, not reaching about 1/5 of its length.

DESCRIPTION. Body: moderately stout; the largest collected ♀ has bl. 5.5 mm.

Head: smooth, with bluntly produced anteroventral lobe; with reduced black-pigmented eyes and yellow dorsolateral spots.

Antenna I (Fig. 33a): about 50% of body length, about 1.7X longer than antenna II; primary flagellum with 12 articles, with aesthetases on distal articles; accessory flagellum 2-articulated, distal article about 3.0X shorter than basal one (Fig. 33b).

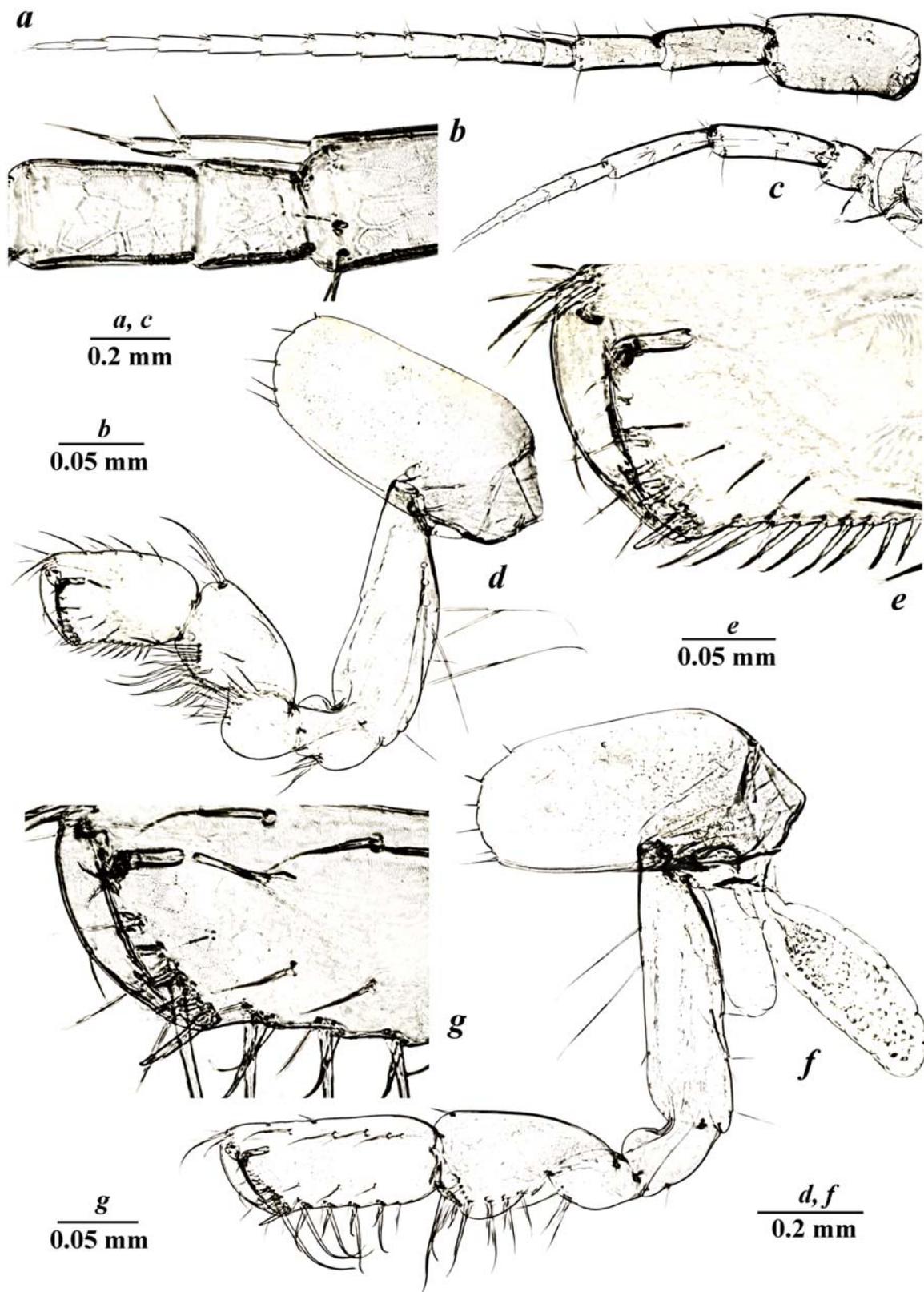


Fig. 33. *Synurella monteflumina* Palatov et Marin sp.n., ♀: *a* — antenna I; *b* — accessory flagellum of antenna I; *c* — antenna II; *d* — gnathopod I; *e* — distoventral palmar margin of chela of GnI; *f* — gnathopod II; *g* — distoventral palmar margin of chela of GnII.

Рис. 33. *Synurella monteflumina* Palatov et Marin sp.n., ♀: *a* — антенна I; *b* — добавочный жгутик антенны I; *c* — антенна II; *d* — гнатопода I; *e* — дистовентральный край ладони (клешни) GnI; *f* — гнатопода II; *g* — дистовентральный край ладони (клешни) GnII.

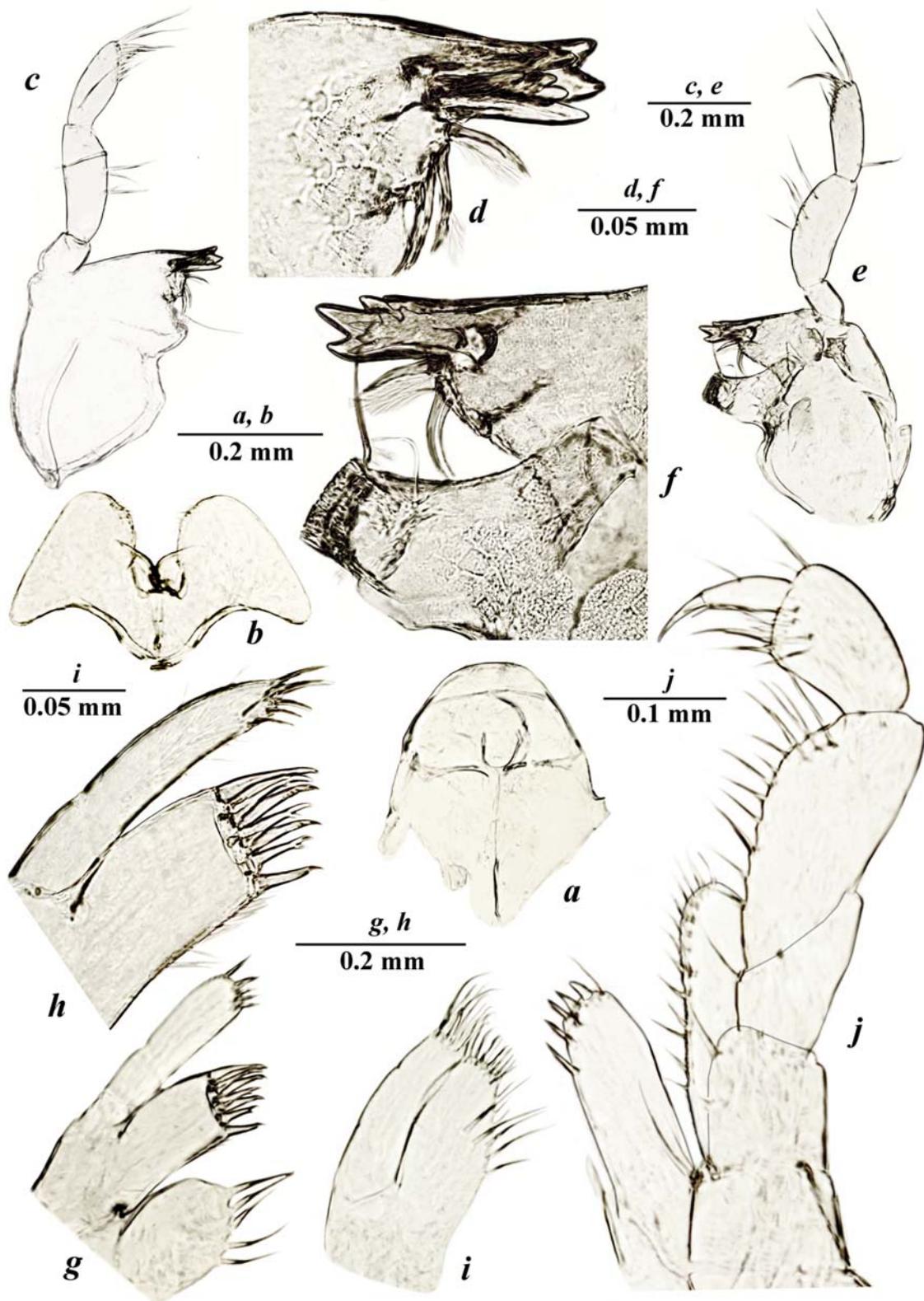


Fig. 34. *Synurella monteflumina* Palatov et Marin sp.n., ♀: a — labrum (upper lip); b — labium (lower lip); c — left mandible; d — same, incisor process and *pars incisiva*; e — right mandible; f — same, incisor process and *pars incisiva*; g — maxilla I; h — distal margin of inner plate of maxilla I; i — maxilla II; j — maxilliped.

Рис. 34. *Synurella monteflumina* Palatov et Marin sp.n., ♀: a — лабрум (верхняя губа); b — лабиум (нижняя губа); c — левая мандибула; d — то же, режущий отросток и резцовая часть; e — правая мандибула; f — то же, режущий отросток и резцовая часть; g — максилла I; h — дистальный край внутренней пластины максиллы I; i — максилла II; j — максиллипод.

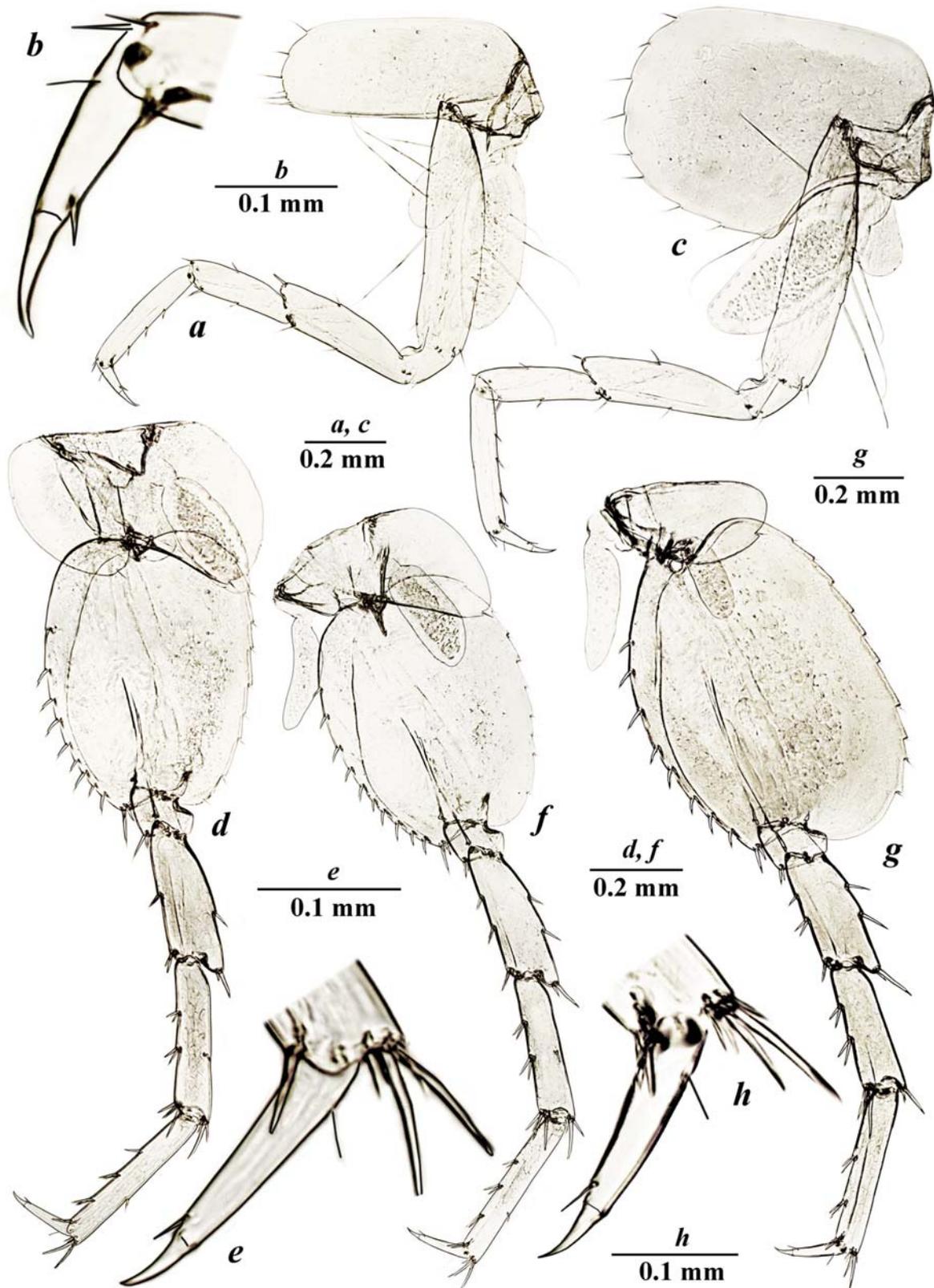


Fig. 35. *Synurella monteflumina* Palatov et Marin sp.n., ♀: a — pereopod III; b — dactylus of PIII; c — pereopod IV; d — pereopod V; e — dactylus of PV; f — pereopod VI; g — pereopod VII; h — dactylus of PVII.

Рис. 35. *Synurella monteflumina* Palatov et Marin sp.n., ♀: a — переопода III; b — дактилус PIII; c — переопода IV; d — переопода V; e — дактилус PV; f — переопода VI; g — переопода VII; h — дактилус PVII.

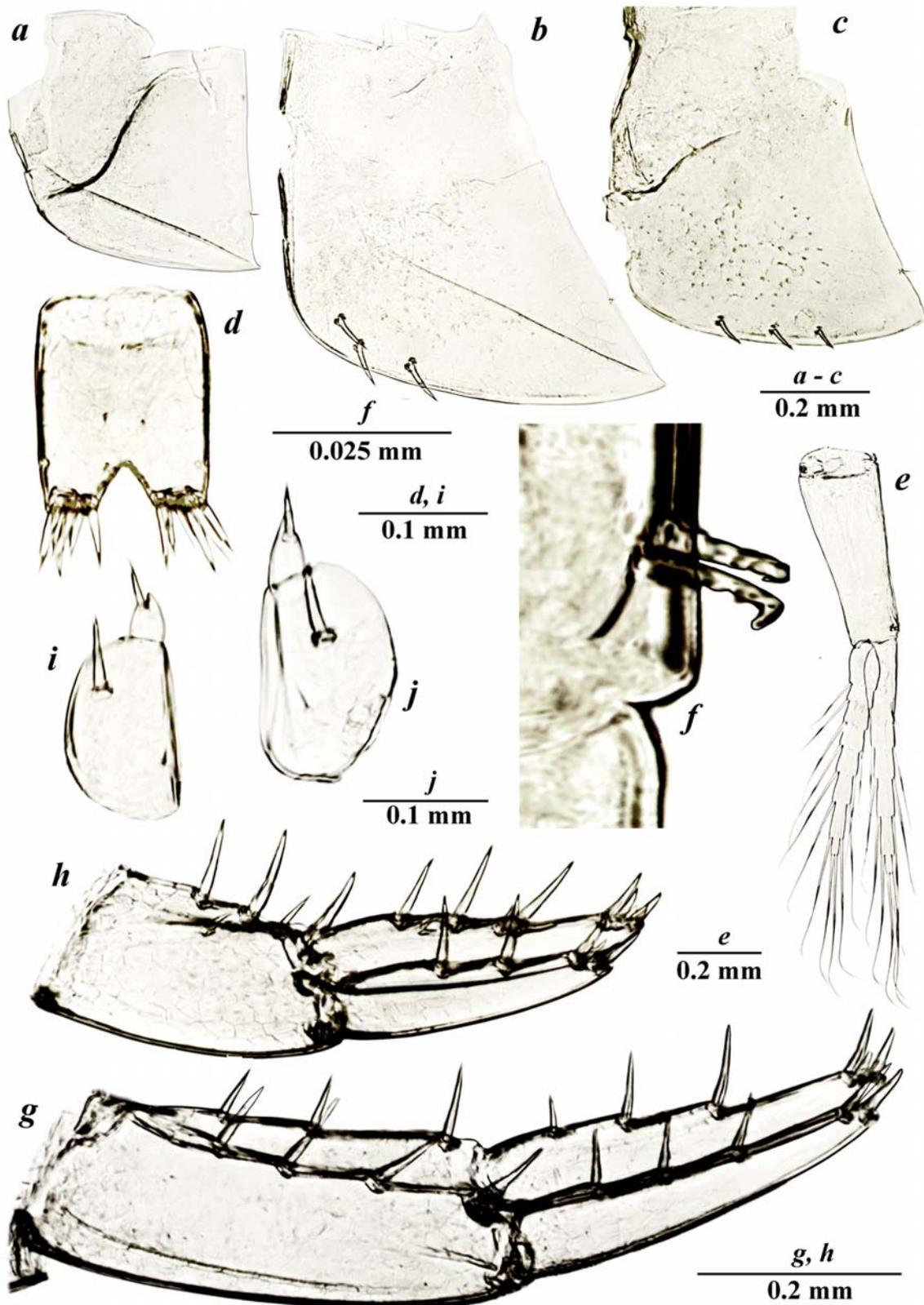


Fig. 36. *Synurella monteflumina* Palatov et Marin sp.n., ♀: *a* — epimeral plate I; *b* — epimeral plate II; *c* — epimeral plate III; *d* — telson; *e* — pleopod I; *f* — hooks of retinacula of pleopod II; *g* — uropod I; *h* — uropod II; *i, j* — uropod III.

Рис. 36. *Synurella monteflumina* Palatov et Marin sp.n., ♀: *a* — эпимеральная пластинка I; *b* — эпимеральная пластинка II; *c* — эпимеральная пластинка III; *d* — тельсон; *e* — плеопода I; *f* — крючки ретинакулы плеоподы II; *g* — уропода I; *h* — уропода II; *i, j* — уропода III.

Antenna II (Fig. 33c): gland clone distinct, distally pointed; peduncle about 1.8X longer than flagellum, with robust setae tightly covering articles 3 and 4, peduncle of article 4 about 1.1X longer than article 5; flagellum 6-articulated, without calceoli in females.

Mandible: left mandible (Fig. 34c) incisor 4-dentate, *lacinia mobilis* 5-dentate, with 4 robust plumose accessory setae; molar process with 1 seta (Fig. 34d). Right mandible (Fig. 34e) incisor 4-dentate, *lacinia mobilis* toothed, triturate, lobes with numerous protuberances; underlying with a row of 3 robust plumose setae; molar process similar to left mandible (Fig. 34f). Palp 3-articulated, article 2 with 5 setae; article 3 about 3.4X longer than wide, with convex margins, with 6 separate D-setae, 2 C-setae, 1 B-seta and 4 separate E-setae.

Lateralialia with 8 teeth.

Labrum (upper lip) (Fig. 34a): oval, apical margin with numerous small fine setae.

Labium (lower lip) (Fig. 34b): inner lobes feebly developed.

Maxilla I (Fig. 34h): inner plate with 5 plumose marginal setae, outer plate with 7 apical comb-spines; palp 2-articulated, distal article pubescent, about 3.4X of basal article, apical margin of distal article with 7–8 simple setae (Fig. 34i).

Maxilla II (Fig. 34g): 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 5 short plumose setae.

Maxilliped (Fig. 34j): inner plate much shorter than outer plate, with 1 robust spine, 2 robust plumose and 1 simple setae apically, and 2–3 robust plumose setae laterally; outer plate narrow, with a double row of 14 medial stiff simple setae of different length; palp 4-articulated, article I with 1 seta on outer margin, article II with a row of 16 simple setae on inner margin, article III sub-trapezoidal; dactylus with 1 seta on outer margin and with 2 thin setae at inner margin, nail long, slender, with 1 thin seta at hinge.

Gnathopod I (Fig. 33d) smaller than gnathopod II; coxal plate sub-rectangular, distally rounded, with 5 apical and numerous facial setae, width/depth ratio is 0.52/1; basis width/length ratio is 0.37/1, without setae on anterior margin, with 3–4 long setae on inner face and 5 long setae on posterior margin; merus with 10 distal setae; carpus is 0.46X of basis and 0.74X of propodus, with 14 serrated setae in inner margin and 4 simple setae in outer margin; propodus 1.6X longer than broad, with 5 simple anterior setae, 4 inferior medial and 7 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) (Fig. 33e) feebly developed, with 2 inner and 2 outer robust setae; dactylus with 1 outer seta.

Gnathopod II (Fig. 33f): coxal plate sub-rectangular, with 6 apical and numerous facial setae, width/depth ratio is 0.50/1; basis width/length ratio is 0.28/1, with 3 short setae inserted along posterior margin and with 2 long simple setae and 1 short seta in anterior margin; ischium with 1 short simple seta; merus with 3 distal setae; carpus is 0.63X of length of basis and 0.82X of propodus, with 1 anterior simple seta and 5 groups of plumose posterior setae; propodus 2.4X longer than broad, with 1 simple anterior seta, 5 superior medial, 3 inferior medial and 5 groups of posterior setae; palm oblique with a double row of 4 inner and 4 outer

bifurcate robust setae; palm groove (depression) (Fig. 33g) feebly developed, with 2 inner and 2 outer robust setae; dactylus without inner and with 1 outer seta.

Pereopod III (Fig. 35a): coxal plate sub-rectangular, with 6 apical and numerous facial setae, width/depth ratio is 0.40/1; basis about 2.5X as long as wide, with long anterior and posterior simple setae; merus about 0.60X of basis, about 1.34X of carpus and 0.90X of propodus in length; carpus about 0.91X of propodus in length; dactylus (Fig. 35b) about 0.42X of propodus, with 1 plumose seta on outer margin and 1 additional spine accompanying with 1 seta on ventral margin.

Pereopod IV (Fig. 35c): subequal to PIII in length; coxal plate expanded and broadly convex distally, posterior margin with shallow excavation, distal margin with 9 apical short setae and numerous facial setae, width/depth ratio is 1.37/1; basis about 4.2X as long as wide, with long anterior and posterior simple setae; merus about 0.62X of basis, about 1.35X of carpus and about 1.10X of propodus in length; carpus about 0.80X of propodus in length; dactylus about 0.41X of propodus, with 1 plumose seta on outer margin and 1 additional spine accompanying with 1 seta on ventral margin.

Pereopods V, VI, VII with the length ratio 1/1.10/0.93.

Pereopod V (Fig. 35d): coxal plate large, bilobate with distinct anterior and posterior lobes; posterior and anterior lobes with 1 margin simple seta each, with numerous facial setae; basis about 1.36X as long as wide, with numerous facial setae, posterior margin slightly convex, armed with 10 shallow serrations, with distal corner, anterior margin with 6 split-tipped robust and 4 distal setae; merus about 0.55X of basis, 0.96X of carpus and 0.88X of propodus in length; dactylus (Fig. 35e) approximately 0.43X of propodus, with 1 plumose seta on outer margin and 1 additional spine accompanying with 1 seta on ventral margin.

Pereopod VI (Fig. 35f): coxal plate bilobate, with distinct posterior and vestigial anterior lobes; anterior lobe without setae, posterior lobe with 1 margin seta, each with numerous facial setae; basis about 1.32X as long as wide, with numerous facial setae, posterior margin convex, armed with 9 shallow serrations, anterior margin with 10 split-tipped robust and 4 distal setae; merus about 0.58X of basis, subequal to carpus and about 0.90X of propodus in length; dactylus approximately 0.39X of propodus, with 1 plumose seta on outer margin and 1 additional spine accompanying with 1 seta on ventral margin.

Pereopod VII (Fig. 35g): coxal plate small, semi-lunar, with 1 posterior seta; basis about 1.40X as long as wide, with numerous facial setae, posterior margin convex, armed with 10 serrated setae and with wide distal lobe, anterior margin with 8 split-tipped robust and 3 distal setae; merus about 0.42X of basis, subequal to carpus and about 0.81X of propodus in length; dactylus (Fig. 35h) approximately 0.41X of propodus in length, with 1 plumose seta on outer margin and 1 additional spine accompanying with 1 seta on ventral margin.

Gills, brood plates (Fig. 35): coxal gills on somites II–VII, somites II–VII with lanceolate sternal gill on each. Coxal gills II–VII ovoid, gills/bases pereopod ratios are 0.77/1, 0.69/1, 0.69/1, 0.47/1, 0.43/1 and 0.26/1, respectively. Brood plates on somites II–V slender, setaceous, decreasing in size posteriorly.

Pleopods (Fig. 36e). Pleopod I peduncle with 2 coupling hooks in retinacula, without lateral setae; outer and inner rami with 6 and 8 articles, respectively. Pleopod II peduncle

with 2 coupling hooks in retinacula, without setae (Fig. 36f); outer and inner rami with 6 and 7 articles, respectively. Pleopod III peduncle with 2 coupling hooks in retinacula, without lateral setae; outer and inner rami with 6 articles each.

Epimera. Epimeral plate I (Fig. 36a) distally produced and sharpened, ventral margin without spines, posterior margin with 1 seta. Epimeral plate II (Fig. 32b) distally produced and sharpened, ventral margin armed with 3 spines, posterior margin with 1 seta. Epimeral plate III (Fig. 36c) distally produced, ventral margin armed with 3 spines, posterior margin with 1 seta.

Urosomites completely fused, smooth.

Uropod I (Fig. 36g): peduncle about 3.0X as long as wide, with dorsoexternal row of 3 robust spines, 1 subdistal spine and 3 dorsointernal robust spines; exopodite slightly shorter than endopodite; endopodite not paddle-like, with 3 dorsolateral, 4 apical spines and 1 ventral seta; exopodite with 3 dorsolateral and 4 apical spines.

Uropod II (Fig. 36h): peduncle about 0.82X of endopodite in length, with 3 dorsal robust spines; exopodite about 0.85X of endopodite in length, with 3 dorsal and 5 apical robust spines; endopodite with 3 dorsal and 4 apical robust spines.

Uropod III (Fig. 36i, j): uniramous, peduncle oval, about 1.6X as long as wide, with a weak spine and 1 seta; apical margin of ramus armed with a weak spine.

Telson (Fig. 36d): close to rectangular, about 1.3X as long as broad; distal margin with V-shaped distal notch, reaching about 1/5 of its length, each lobe armed with 6 robust spines, with 2 additional submarginal plumose setae.

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

GENBANK ACCESSION NUMBERS. OP312988–OP312990.

TAXONOMIC REMARKS. The new species distinctly belong to the “*behningi*” species complex (Figs 1, 2). The new species can be clearly separated from *Synurella behningi* by the following features: 1) inner lobes of lower lip (labium) mostly reduced (Fig. 34b); 2) palm (propodus) of GnII longer, about 2.5X as long as wide (Fig. 33f) (vs. about 2.3X as long as wide (see Fig. 16f)); 3) ventrally produced EpII with 3 ventral spines (Fig. 36b) (vs. medium EpII with 4 ventral spines (Fig. 17b)); 4) EpIII with mostly triangular distoventral margin (Fig. 36c) (vs. sharply produced posteroventral tooth (Fig. 17c)); and 5) short distal article of UIII (see Fig. 36f).

The new species can be clearly separated from *Synurella gizmavi* sp.n. by the following features: 1) inner lobes of lower lip (labium) mostly reduced (Fig. 34b); 2) ventrally produced EpII with 3 ventral spines (Fig. 36b) (vs. medium EpII with 4 ventral spines (Fig. 21b)); and 3) EpIII with mostly triangular distoventral margin (Fig. 36c) (vs. sharply produced posteroventral tooth (Fig. 21c)).

The new species can be clearly separated from *Synurella praemontana* sp.n. by the following features: 1) inner lobes of lower lip (labium) mostly reduced (Fig. 34b); 2) ventrally produced EpII with 3 ventral spines (Fig. 36b) (vs. medium EpII with 6 ventral spines (Fig. 26b)); 3) EpIII with mostly triangular distoventral margin with 3 ventral spines (Fig. 36c) (vs. sharply produced posteroventral tooth with 4 ventral spines (Fig. 26c)); and 4) telson with deeper distal notch (Fig. 36d).

The new species can be clearly separated from *Synurella adegoyi* sp.n. by the following features: 1) inner lobes of lower lip (labium) mostly reduced (Fig. 34b); 2) EpII with 3 ventral spines (Fig. 36b) (vs. with 4 ventral spines (Fig. 31b)); and 3) telson with deeper distal notch (Fig. 36d).

DISTRIBUTION AND ECOLOGY. Hypogean (stygobiotic) species, which is presently known only from a single spring (well) in the upper stream of the Olkhovka River.

## Discussion

The presented study significantly expands our knowledge about the Palaearctic species of the genus *Synurella*, especially about its Caucasian and Ciscaucasian diversity. At the same time, the described species comprise the only first insight and we believe that the diversity of the genus is far from being fully studied in the region. Caucasian region due to its history, geology, climate and heterogeneity is a well-known refugium for the different taxa, including numerous and diverse amphipods [Marin, 2020; Marin, Palatov, 2021b, c, d; Marin *et al.*, 2021, 2022; Palatov, Marin, 2021b].

The hypogean “*behningi*” clade was previously assigned to the isolated subgenus *Boruta* Wrześniowski, 1888 (after Birštein [1948]), which was suggested for *Synurella tenebrarum* (Wrześniowski, 1888), known from wells in Zakopane (Poland) [Wrześniowski, 1888]. Currently, *S. tenebrarum* is considered as a junior synonym of *S. ambulans* and probably belongs to the “*ambulans*” or “*intermedia*” clades [Skalski, 1988], but it is impossible to verify its phylogenetic position as molecular genetic data on this species are not available in genetic databases. At the same time, we can confidently conclude that the species does not belong to the Caucasian “*behningi*” clade, and similar morphological features were formed in different clades under the influence of the same conditions, namely the underground lifestyle.

All species of the genus *Synurella* can be divided into epigeal (living in surface waters) and hypogean (living in groundwater (subterranean water resources) forms. Such separation is also supported phylogenetically (see Figs 1–3). The species with a very narrow habitat range are found mainly among hypogean species (their range is usually restricted to a single known spring/well (e.g., *S. adegoyi* sp.n., *S. praemontana* sp.n., *S. monteflumina* sp.n.) or cave (e.g., *S. behningi*, *S. gizmavi* sp.n.), while epigeal species are usually widespread (e.g., *S. ambulans* and *S. taurica*).

Epigeal species usually differ in a more masking body coloration (green or greenish grey), and presence of a bright yellow spot on the head, which presumably helps to distinguish light from darkness (see Fig. 4). They are also able to curl up into a ball when in danger, sinking deep into the substrate (pers. observ.), which apparently is a protective mechanism against attacks of large predators. These species usually live in streams that are deviated from springs, but at the same time, they are rarely found in large water bodies, such as lakes inhabited by vertebrate predators (e.g., fishes).

The question of the dispersion of these species independently rests on the fact that currently all epigeal species are found only in surface water resources devoid of large predators, such as fishes, etc. Thus, their

self-propagation over long distances should be limited by the presence of predators, but such effect is not studied. Therefore, this question remains open as before. Their wide distribution over large territories also could suggest their dispersion by other animals, for example, waterbirds, as is known for cladocerans (e.g., Figuerola, Green [2002]), *Artemia* (Anostraca: Branchiopoda) [Vanhaecke *et al.*, 1987] and false scorpions (Arachnida: Pseudoscorpiones) [Christophoryová *et al.*, 2011]. Such wide ranges are also characteristic of epigeal niphargids (Amphipoda: Niphargiidae) [Copilaş-Ciocianu *et al.*, 2014, 2015, 2017; Palatov, Marin, 2021a], whereas for most hypogean, they are very narrow [Marin *et al.*, 2021]. It is also believed that the dispersal of such species is mediated by floods or seasonal river flooding (passive long-range dispersal events) [van Leeuwen *et al.*, 2013; Copilaş-Ciocianu *et al.*, 2018].

Finally, in the presented article, we tried to characterize the role of the Caucasian refugee, the Colchis Lowland and the southern slope of the Greater Caucasian Ridge, in the evolution and distribution of this genus during the Pliocene-Pleistocene times. According to our data (see Fig. 2), the ancestral form appeared in the Caucasus during the Pliocene and the diversity of the “*behningi*” clade was formed in the Caucasian region. The ancestral forms from the “*ambulans*” clade also probably originated in the Caucasus refugee during the Pliocene. The representatives of the clade survived there the cold times during the Pleistocene, and lately spread widely to the north, occupying almost the entire territory of modern Europe and southwestern Russia; two modern species (*S. taurica* and *S. inkiti* sp.n.) are still living there. The lifestyle switching from hypogean to epigeal (and probably vice versa during the early Pliocene), was one of the most important events in the evolution and distribution of the genus *Synurella*. At least, it is obvious that such ability allowed the species of the “*ambulans*” clade to spread widely to the north during the late Pleistocene.

**Supplementary data.** The following Table is available online at <http://kmkjournals.com/journals/AS>.

Supplementary Table 1. The list of nucleotide sequences of the studied species of the genus *Synurella*, other crangonyctid and outgroup sequences used for molecular-genetic analysis taken from GenBank (NCBI).

#### Compliance with ethical standards

CONFLICTS OF INTEREST: The authors declare that they have no conflicts of interest.

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