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A new species of the genus *Niphargus* Schiödte, 1849 (Amphipoda: Niphargidae) from the subterranean lakes of the New Athos Cave, Abkhazia, Caucasus

Новый вид рода *Niphargus* Schiödte, 1849 (Amphipoda: Niphargidae) из подземных озер Новоафонской пещеры, Абхазия, Кавказ

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КЛЮЧЕВЫЕ СЛОВА: разнообразие, филогения, *Niphargus*, таксономия, пещерные озера, Кавказ.

ABSTRACT. A new species of the genus *Niphargus* Schiödte, 1849 (Amphipoda: Niphargidae), *Niphargus smyri* sp.n., is described based on female specimens from large subterranean lakes of New Athos Cave. Additionally, three closely related intraspecific populations (with *p*-distances not exceeding 5%) were recorded from nearby caves in the Gudauta–Sukhum area, including Mikhailovskaya Cave, Habyu Cave, the Bezdonnaya Yama stream (within New Athos Cave), and Duripshskaya Vodnaya Cave. Morphological characteristics of *Niphargus smyri* sp.n., particularly the elongation of ambulatory pereopods V–VII, probably, indicate its adaptation to permanent habitation in subterranean lakes, representing the first case of such ecological specialization (ectomorph) within the southern Caucasus region. Phylogenetic analyses demonstrate that the examined new species represent a distinct and cohesive lineage within the "*aquilex–tauri*" species group, being both morphologically and genetically well differentiated from all other Caucasian congeners. *Niphargus smyri* sp.n. can be readily distinguished from other Caucasian representatives of the genus by a combination of the following morphological features: (1) a single seta present on the dactyli of gnathopods I–II; (2) subrounded epimeral plates; (3) the presence of four long, well-developed spines on each postero-dorsolateral side of urosomite II; (4) five hooks retinacules of pleopods; and (5) elongated pereopods V–VII, representing a unique character combination within the "*aquilex–tauri*" species group. Morphologically, the most closely related species appears to be *Niphargus fongi* Fišer et Zagmajster, 2009, described from Slovenia, also sharing similar morphological features. However, molecular data for the latter species are currently unavailable in public genetic databases (e.g., GenBank (NCBI)), precluding direct phylogenetic comparison.

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РЕЗЮМЕ. Новый вид рода *Niphargus* Schiödte, 1849 (Amphipoda: Niphargidae), *Niphargus smyri* sp.n., описан на основе самок, собранных из крупных подземных озёр Новоафонской пещеры. Кроме того, четыре близкородственные внутривидовые популяции (с *p*-дистанциями, не превышающими 5%) отмечены в близлежащих пещерах района Гудаута–Сухум, включая Михайловскую пещеру, пещеру Хабю, ручей Бездонная Яма (внутри Новоафонской пещеры) и Дурипшскую Водную пещеру. Морфологические особенности *Niphargus smyri* sp.n., в частности удлиненные ходильные переоподы V–VII, вероятно, указывают на адаптацию к постоянному обитанию в подземных озёрах, представляя первый случай подобной экологической специализации (озерной экоморфы) в пределах южного Кавказа. Филогенетический анализ показал, что исследуемый новый вид представляет собой четко обособленную филогенетическую группу (lineage) в составе видовой группы "*aquilex–tauri*", чётко отличающуюся как морфологически, так и генетически от всех других кавказских представителей рода. *Niphargus smyri* sp.n. легко отличается от других кавказских представителей рода по совокупности следующих морфологических

признаков: (1) наличием одной щетинки на дактилях гнатопод I–II; (2) округлыми эпимеральные пластинками; (3) наличием четырёх длинных, хорошо развитых шипов на каждой постеро-дорсолатеральной стороне уросомита II; (4) наличием пяти крючков на ретинакулах плеопод; и (5) удлинёнными переоподами V–VII, что уникально для группы "*aquilex–tauri*". Морфологически наиболее близким видом является *Niphargus fongi* Fišer et Zagmajster, 2009 из Словении, обладающий сходными признаками. Однако молекулярные данные для данного вида в настоящее время отсутствуют в открытых генетических базах данных (например, GenBank (NCBI)), что исключает возможность прямого филогенетического сравнения.

Introduction

Hypogean amphipods of the genus *Niphargus* Schiödte, 1849 (Amphipoda: Niphargidae), are abundant and widespread in the water bodies and underground habitats, whose research in the Caucasus began in the 30s of the 20th century [Birštein, 1933, 1939; Derzhavin, 1939]. Currently, about 50 species have been described from the Ciscaucasus and Caucasus region, with a significant number of species identified and described from the subterranean habitats of the southern slope of the Greater Caucasus (e.g., Birštein [1940, 1941, 1952]; Derzhavin [1945]; Lagidze *et al*. [1954]; Karaman [1982, 2012]; Rendoša *et al*. [2021]; Marin, Palatov [2019, 2021, 2024]; Palatov, Marin [2021]). Nevertheless, the actual diversity of *Niphargus* in this region is assumed to be significantly underestimated. Most species described from this area are associated with hypogean environments such as springs, groundwater systems, and river hyporheic zones (e.g., Marin *et al*. [2021a, b]; Marin, Palatov [2025a–c]). However, no specialized species inhabiting subterranean lakes and exhibiting a typical "lake ectomorph" (see Trontelj *et al*. [2012]; Petković *et al*. [2015]) have yet been identified, despite the presence of extensive underground lacustrine systems in the southern Caucasus. Although, for example, such species are marked for the Crimean Peninsula [Petković *et al*., 2015].

One of the most prominent examples is New Athos Cave (= Novoafonskaya, Novy Afon Cave), one of the largest caves in Abkhazia, discovered on July 14, 1961, by an expedition led by Givi Smyr. The cave has an approximate volume of about 1.5 million m³, with up to 300,000 m³ of water flowing through it. It contains two large subterranean lakes: Lake Anatolia, with an area of approximately 1,000 m², a volume of about 290,000 m³, and a depth of 24–26 m; and the smaller Lake Bezymiannoe (Siphon), reaching depths of approximately 26 m. Investigations of the subterranean fauna associated with New Athos Cave system began even prior to its formal discovery. The hypogean atyid shrimp *Xiphocaridinella fagei* (Birštein, 1939) (Decapoda: Atyidae) was described from Psyrtskha Cave [Birštein, 1939], which serves as one of the discharge outlets of the New Athos Cave system. To date, several crustacean taxa have been recorded from the hypogean cave habitats, including the cyclopoid copepod *Diacyclops* cf. *bicuspidatus* (Claus, 1857) (Copepoda: Cyclopidae) [Chertoprud *et al*., 2016], the isopod *Proasellus* sp. (Isopoda: Asellidae) [Chertoprud *et al*., 2016], the crangonyctid amphipod *Synurella* sp. (Amphipoda: Crangonyctidae) [Chertoprud *et al*., 2016], the gammarid amphipod *Zenkevitchia karamani* Sidorov, 2018 (Amphipoda: Gammaridae) [Sidorov, 2018], and niphargid amphipod *Niphargus ablaskiri* Birštein, 1940 (Amphipoda: Niphargidae) [Skalski, 1980; Chertoprud *et al*., 2016].

Actually, the type material of *N. ablaskiri* was originally described from Achkhshe-Tyzgua (= Abrskila) Cave (entrance coordinates: 42°55′13.1″N, 41°33′15.8″E), located near Otapi village in the Ochamchira District of Abkhazia, with additional material reported from the New Athos Cave [Birštein, 1939, 1940]. However, recent detailed morphological examination and molecular analyses of *Niphargus* specimens from the subterranean lakes of the New Athos Cave demonstrate that they are not conspecific to *N. ablaskiri*, but instead represent a distinct and phylogenetically well-separated lineage (see Fig. 1a), corresponding to a new species described below. Moreover, the morphology of this species, particularly the elongation of the ambulatory pereopods V–VII, suggests an adaptation to permanent life in subterranean lakes, corresponding to the "lake ectomorph" (see Fišer *et al*. [2009]; Trontelj *et al*. [2012]; Petković *et al*. [2015]; Borko *et al*. [2021]), and represents the first documented case of such ecological specialization in the southern Caucasus.

Material and methods

SAMPLING. Amphipods were collected using a hand net in the subterranean lakes (Anatolia and Bezymannoe) of the New Athos Cave (the entrance — 43°05′25.4″N 40°48′37.3″E, see Fig. 1*b*), as well as different subterranean sources of the nearby caves and spring in the New Athos – Sukhum area, Abkhazia, Caucasus (see Fig. 1*b*). All collected amphipods were preserved in 90% ethanol for further DNA analysis. The type material is deposited at the collection of the Zoological Museum of Moscow State University, Moscow (ZMMU); other (additional) material is deposited in personal authors' collection in the A.N. Severtsov Institute of Ecology and Evolution of RAS, Moscow, Russia (LEMMI).

MORPHOLOGICAL STUDY. For the general view and alive coloration freshly collected specimens were relaxed in a clove oil and then photographed using Canon G16 digital camera. Fixed specimens were dissected under the stereomicroscope and then mounted on slides for examination and illustration The light microscopy photographs of the specimens were made with a digital camera Olympus ZX10 attached to the compound microscope Olympus CX21. The scanning electron microscopy (SEM) images were made at the Paleontological Museum of the Paleontological Institute of the Russian Academy of Sciences, Moscow, using Vega3 Tescan microscope. Amphipods were placed in 95% ethanol, cleaned in an ultrasonic cleaner then dehydrated with acetone, critical-point dried (CPD), fixed on specimen stubs with double-sided and coated with gold by sputtering using Polaron PS 100. The body length (bl., mm) was measured from the anterior margin of the cephalothorax to the posterior margin of the pleotelson.

MOLECULAR-GENETIC ANALYSIS. To enravel the cryptic diversity within the studied amphipods a fragment of

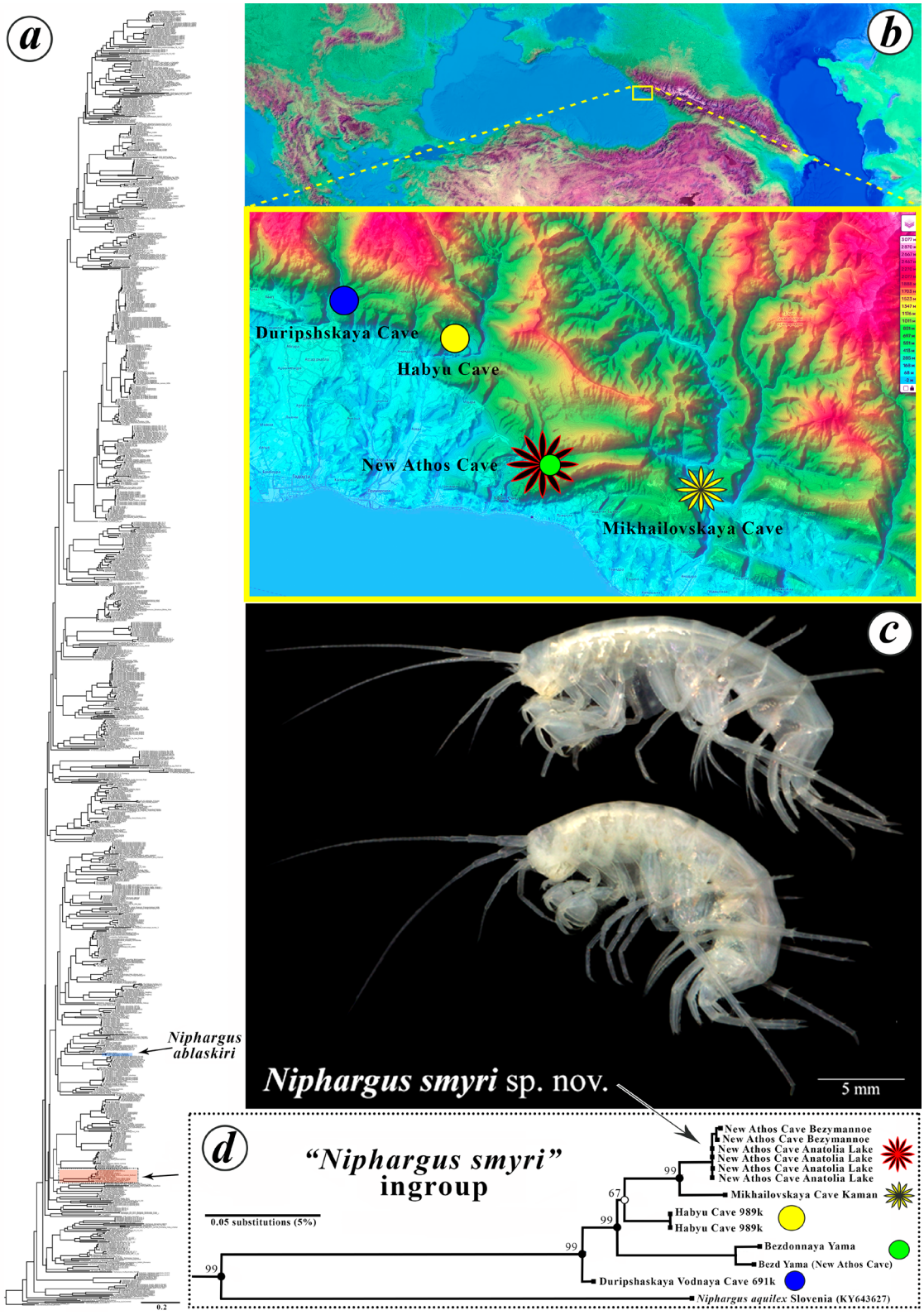


Fig. 1. General phylogenetic tree of the genus *Niphargus* based on COI mtDNA gene marker with the indication phylogenetic positions of *Niphargus ablaskiri* Birštein, 1940 and "*Niphargus smyri*" ingroup, the map of distribution of "*Niphargus smyri*" ingroup in the New Athos – Sukhum area (b), general view and alive coloration of *Niphargus smyri* sp.n. (c), and phylogenetic relationships within the "*Niphargus smyri*" ingroup.

Рис. 1. Общее филогенетическое древо рода Niphargus, основанное на генном маркере COI мтДНК, с указанием филогенетических позиций *Niphargus ablaskiri* Birštein, 1940 и ингруппы "*Niphargus smyri*", карта распространения ингруппы "*Niphargus smyri*" в районе Новый Афон – Сухум (b), общий вид и прижизненная окраска *Niphargus smyri* sp.n. (c) и филогенетические взаимоотношения внутри ингруппы "*Niphargus smyri*".

Table 1. Uncorrected pairwise genetic (COI mtDNA) distances (*p*-distances) (substitutions per 100 nucleotides±SE) with the "*Niphargus smyri*" ingroup.
Таблица 1. Нескорректированные попарные генетические дистанции (на основе митохондриальной ДНК COI) (*p*-дистанции) (количество замен на 100 нуклеотидов ± стандартная ошибка) для ингруппы "*Niphargus smyri*".

***Niphargus smyri* sp.n.** (New Athos Cave)		Mikhaylovskaya Cave	Habyu Cave	Bezdonnaya Yama stream (within New Athos Cave)
Mikhailovskaya Cave	0.023±0.006			
Habyu Cave	0.039±0.007	0.034±0.008		
Bezdonnaya Yama stream (within New Athos Cave)	0.041±0.007	0.046±0.009	0.030±0.006	
Duripshskaya Cave	0.044±0.010	0.042±0.009	0.019±0.006	0.022±0.006

cytochrome oxidase C subunit I (COI mtDNA) was used [Avise, 1994; Hebert *et al*., 2003]. Total genomic DNA was extracted from muscle tissue using the innuPREP DNA Micro Kit (AnalitikJena, Germany). The gene marker was amplified by using the universal primers LCO1490 (5'–GGTCAACAAATCATAAAGATATTGG–3') and HC02198 (5'–TAAACTTCAGGGTGACCAAAAAATCA–3') under the standard protocol conditions (Folmer et al., 1994). 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. Consensus dataset of aligned sequences, about 646 base pairs in length was obtained with MEGA 7.0. The best evolutionary substitution model was determined using MEGA 7.0 [Kumar *et al*., 2016] and jModeltest2.1.141 (Diego Darriba, Universidade da Coruña as part of the Computer Architecture Group (GAC), Coruña, Spain) on XSEDE via the CIPRES (Cyber Infrastructure for Phylogenetic Research) Science Gateway V. 3.3 (http://www.phylo.org/, accessed on 30 March 2026). A phylogenetic analysis was conducted on a single gene market (COI mt DNA) using PhyML 3.0 [Guindon *et al*., 2010] with several models based on BIC (Bayesian Information Criterion) and AIC (Akaike Information Criterion). The general dataset of sequences was used to establish the phylogenetic relationships of the described species, and is not visualized in the article.

Uncorrected pairwise genetic distances (*p*-distances±SE) were calculated based on available sequences using MEGA 7.0 with the Kimura 2-Parameter (K2P) model of evolution (Kimura, 1980).

Results

PHYLOGENETIC APPROACH. All phylogenetic reconstructions obtained using both ML and BI approaches yielded congruent topologies, consistently recovering the studied taxa as a distinct, well-isolated and well-supported phylogenetic lineage ((Bayesian–PP=1.00; ML–BS=95%). This lineage is assigned to the "*aquilex–tauri*" species group sensu Straškraba [1972]. It is also clearly phylogenetically separated from all other Caucasian representatives of the genus *Niphargus* and shows closest affinity only to *Niphargus* cf. *aquilex* Schiødte, 1855 from Slovenia (KY643627) (see Fig. 1*d*).

Based on our data, the lineage comprises several closely related populations from the foothill zone of the Gudauta–Sukhum area in central Abkhazia exhibiting low genetic divergence (p-distances ≤ 5%; see Table 1), including *Niphargus smyri* sp.n. (sensu stricto) from New Athos Cave (43°05′25.4″N 40°48′37.3″E), as well as four additional populations from Mikhaylovskaya Cave (43°03′38.1″N 41°02′12.8″E), Habyu Cave (43°11′32.3″N 40°47′28.2″E), Bezdonnaya Yama stream (within New Athos Cave), and Duripshskaya-Vodnaya Cave (43°11′13.6″N 40°38′21.9″E) (Fig. 1*b*, *d*). Phylogenetic relationships among these populations require further clarification based on more extensive sampling. Pending such analyses, we provisionally designate the "*Niphargus smyri*" ingroup, probably including undescribed species in the area.

TAXONOMIC ACCOUNT

Phylum Arthropoda von Siebold, 1848
Class Malacostraca Latreille, 1802
Order Amphipoda Latreille, 1816
Family Niphargidae Bousfield, 1977
Genus *Niphargus* Schiödte, 1849

***Niphargus smyri* sp.n.**

Figs 2–6.

MATERIAL EXAMINED. HOLOTYPE, ♀ (bl. 11.5 mm) (ZMMU Mb-1314), Abkhazia, Gudauta district, Lake Anatolia (approx. 43°05′54.51″N 40°48′43.68″E) in the Anakopia Hall, New Athos Cave (43°05′25.4″N 40°48′37.3″E, entrance), about 150 m a.s.l., coll. I. Marin & D. Palatov, 8 March 2026. PARATYPES, 4 ♀♀ (bl. 11.0 mm) (ZMMU Mb-1315), same data and locality as holotype.

ADDITIONAL MATERIAL: 10 ♀♀ (LEMMI), Abkhazia, Gudauta district, a small stream flowing out of the 'Bezdonnaya Yama' stream (43°05′56.44″N 40°48′45.65″E) in the Anakopia Hall, New Athos Cave, about 150 m a.s.l., coll. D. Palatov, 8 March 2026; 12 ♀♀ (LEMMI), Abkhazia, Gudauta district, a subterranean stream inside Habyu Cave, 43°11′29.35″N 40°47′26.69″E, about 218 m a.s.l., coll. D. Palatov, 8 May 2025; 9 ♀♀ (LEMMI), Abkhazia, Gudauta district, a subterranean stream inside Duripshskaya-Vodnaya Cave, 43°11′13.6″N 40°38′21.9″E, about 227 m a.s.l., coll. D. Palatov, 28 January 2020; 18 ♀♀ (ZMMU Mb-1316), Abkhazia, Sukhum district, a small subterranean stream inside Mikhaylovskaya Cave, 43°03′38.1″N 41°02′12.8″E, about 236 m a.s.l., coll. D. Palatov, 4 January 2019.

ETYMOLOGY. The species is named in honor of Givi Smyr (1945–2016), an Abkhazian artist and sculptor, discoverer of New Athos Cave, and its director from 2004 to 2016.

DIAGNOSIS. Only ♀♀ are known. Head without eyes or yellow pigmented spots on anterior lobe. Posteroventral corners of epimeral plates I–III rounded. Urosomite I with 1 slender long spine; urosomite II with 4 long slender spines on each side. Dactyli of pereopods III–VII very long, slender, with small ventral inner seta. Rami of uropod I slightly unequal in size. Pleopods with 5 hooks in retinacules. Telson clefted for approx. 70–75%, with 5–6 long distal spines on each lobe, with medium lateral long spines, accompanied by 1–2 small plumose setae on each side, and 2–3 simple short dorsal spines in proximal part of telson.

DESCRIPTION (holotype ♀). BODY: moderately slender, stygomorphic (Fig. 1*c*).

HEAD: large, without rostrum, without eyes or yellow spots on anterior lobe (Fig. 1*c*); with subrounded lateral cephalic lobes and excavated anteroventral sinus (Fig. 6*a*).

MESOSOMA: mesosomal segments smooth.

METASOMA: metasomal segments I–III with several short marginal setae on each posterodorsal margin.

EPIMERAL PLATES (Fig. 5*a–d*): epimeral plates I–III with rounded posteroventral corners. Epimeral plate I (Fig. 5*a*) with strongly oblique ventral margin, without ventrofacial setae; posterior margin slightly convex, bearing 4 short marginal setae; posteroventral corner subrounded, with 1 strong long seta. Epimeral plate II (Fig. 5*b*) with strongly convex ventral margin, with 4 ventrofacial setae; posterior margin concave, with 4 short marginal setae; posteroventral corner bluntly rounded, with 1 strong long seta. Epimeral plate III (Fig. 5*c*) with convex ventral margin, with 3 large and 1 tiny ventrofacial setae; posterior margin concave, with 4 short marginal setae; posteroventral corner rounded, with 1 strong long seta.

UROSOMITES (Fig. 6*e*,*f*): Urosomite I with 1 slender long spine, accompanied with small setae on each dorsolateral side; urosomite II with 4 simple strong spines on each dorsolateral side; urosomite III unarmed.

COXAE: coxae I–IV moderately large, with short ventromarginal setae: coxa I (Fig. 2*d*) nearly as long as broad, with subrounded anteroventral corner; coxa II (Fig. 2*g*) nearly as long as broad, with slightly convex anteroventral corner; coxae III–IV (Fig. 4) as short as broad; coxae V–VII smaller than coxa IV; coxa V and VI with 2 setae on anterior and 1 seta posterior lobes; coxa VII with 1 seta at posterior lobe.

COXAL GILLS: present on pereopods II–VI, ovoid, relatively large; gills/bases pereopod length ratio about 1/1; 0.7/1; 0.9/1; 0.8/1 and 0.6/1, respectively. Oostegites occur on pereopods II–V.

ANTENNA I (Fig. 2*a*): with relatively slender peduncular articles, with ratio about 1/0.8/0.6; main flagellum consisting of about 35 articles, most of them with 2 short aesthetascs each; accessory flagellum short, 2-articulated, with distal article about twice shorter than basal (Fig. 2*b*).

ANTENNA II (Fig. 2*c*): stout, peduncular article III slender; peduncular article V shorter than article IV, with several long setae along ventral margin, dorsal setae shorter than inner ones; flagellum is about 0.8× of peduncular articles IV+V, relatively short, consisting of about 13–14 articles with relatively short setae. Antennal gland cone blunt, not exceeding peduncular article III.

LABRUM (upper lip) (Fig. 3*a*): typical, entire, subrounded.

LABIUM (lower lip) (Fig. 3*b*): entire, broader than long, with entire outer lobes and developed inner lobes, not exceeding 1/3 of length of outer lobes.

MANDIBLES (Fig. 3*c*, *e*): incisor of left mandible with 5 teeth, lacinia mobilis with 4 teeth and row of 9 arcuate setae with lateral projections; incisor of right mandible with 4 teeth, lacinia mobilis bifurcate, pluritoothed and row of 7 arcuate setae with lateral projections; mandibular palp 3-articulated, with article ratio about 1.0/2.1/2.1 and represent 20, 40 and 40% of total length of palp, respectively; article I smooth with slightly pronounced neck; article II with 13 setae, palp article III subfalciform, equal to article II, with 19–20 marginal D-setae and 5 long distal E-setae; on outer face with 1 group of 5 A-setae, on inner face with 2 groups of B-setae, without C-setae (Fig. 6*b*).

MAXILLA I (Fig. 3g): inner plate with 1 distal seta, outer plate with 7 robust spines (only 3 spines with 1 strong lateral tooth each (0–0–0–1–1–1–0)) (Fig. 3*h*); palp 2-articulated, distal article with 8–9 simple setae distally.

MAXILLA II (Fig. 3*i*): with smooth well-developed plate armed with distolateral setae only, similar to other congeners.

MAXILLIPED (Fig. 3*j*): inner plate short, with 5 strong distal spines intermixed with 4–5 distal simple setae, outer plate reaching half of palpus article II and bearing row of 15–16 distolateral spines and distal setae; palpus article III with 1 distal bunch of setae at outer margin; palpus article IV with 1 median seta at outer margin; nail shorter than pedestal, with seta near basis.

GNATHOPOD I (Fig. 2*d*): with basis robust, expanded distally, about 2.5–3× longer than wide, with long simple setae along posterior and posterodistal margins; ischium almost quadrate, as long as wide, similar to merus, with posterior apical group of setae; merus rectangular, about 1.3× as long as wide, with row of setae along posterior margin; carpus subtrapezoid in shape, with several cluster of long setae along posterior margin; propodus (palm) large, nearly as long as broad, almost quadrate, with 7 groups of posterior marginal setae, with slightly convex palmar margin (Fig. 2*e*), covered with row of medium simple setae; defined on outer face by corner S-spine accompanied laterally by 3 serrate L-spines and 3 facial corner long M-setae, on inner face by 1 short subcorner R-spine (Fig. 2*f*); dactylus strong and sharp, reaching posterior margin of article VI, with 1 long simple seta along dorsal margin.

GNATHOPOD II (Fig. 2*g*): slightly larger than gnathopod I; basis about 3.5× as long as wide, with long simple setae along posterior and anterior margins; ischium quadrate, with 2 simple setae along posterior margin; merus rectangular, about 1.2× as long as wide, with row of setae along posteromedian margin; carpus subtrapezoid in shape, shorter than propodus, with several cluster of long setae along posterior margin; propodus (palm) large, subtrapezoid, nearly as long as broad, with posterior margin shorter than anterior, with about 10 groups of posterior marginal setae; palmar margin (Fig. 2*h*) almost straight, with row of medium simple setae; provided on outer face by 1 corner strong robust S-spine accompanied laterally by 2 smaller serrate L-spines and 2 corner long M-setae, on inner face by 1 short subcorner R-spine (Fig. 2*h*); dactylus strong and sharp, reaching posterior margin of article VI, with 1 simple setae along dorsal margin.

PEREOPODS III–IV (Fig. 4*a*, *c*): almost similar in size and shape, with relatively slender articles; basis about 5.3× as long as wide, with posterior and anterior margins bearing long marginal setae; ischium short, about as long as wide; merus about 4.9–5.6× as long as wide, with slender simple setae along posterior and anterior margins; carpus noticeably shorter than merus, slightly shorter than propodus, about 5.2–5.4× as long as wide; propodus about 6.5–7.2× as long as wide, with bunches of spines along ventral margin; dactylus (Fig. 4*b*) robust, relatively stout, curved, sharp distally, with 1 tiny ventral inner spine and 1 median short plumose seta at outer margin, with nail equal to pedestal.

PEREOPOD V (Fig. 4*e*): with basis wide, about 1.5× as long as broad, rectangular, with feebly marked posteroventral lobe, posterior margin slightly convex, with row of 12 slender marginal setae, anterior margin convex, with row of 10 marginal stout setae that distinctly longer than posterior and bunch of setae in distal part; ischium subquadrate, as long as wide; merus about 4.7× as long as wide, with bunches of slender spines along posterior and anterior margins; carpus slender, about 9.1× as long as wide, slightly shorter than propodus; propodus slender, about 12.2× as long as wide, with bunches of short spines; dactylus (Fig. 4*f*) short, with 1 small ventral inner spine and 1 median short plumose seta at outer margin.

PEREOPOD VI (Fig. 4*g*): slender, basis wide, about 1.5× as long as broad; with feeble posteroventral lobe and slightly convex posterior margin with row of 14 short marginal setae; anterior margin convex, with row of 7 longer marginal stout

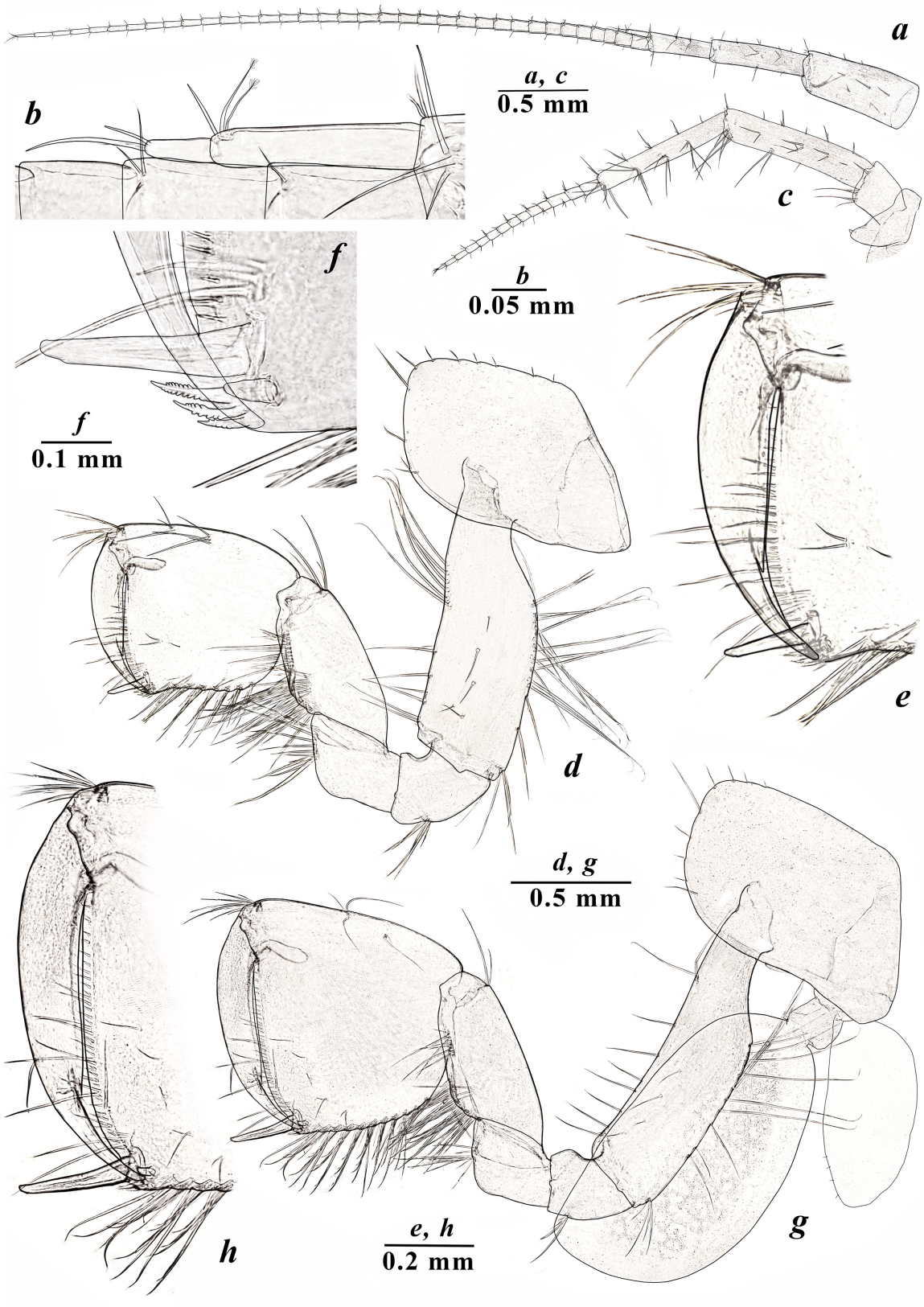


Fig. 2. *Niphargus smyri* sp.n., holotype ♀ (ZMMU Mb-1314), from Lake Anatolia, New Athos Cave, Abkhazia: *a* — antenna I; *b* — accessory flagellum of AI; *c* — antenna II; *d* — gnathopod I; *e*, *f* — palmar margin of chela of GnI; *g* — gnathopod II; *h* — palmar margin of chela of GnII.

Рис. 2. *Niphargus smyri* sp.n., голотип ♀ (ZMMU Mb-1314), из озера Анатолия, Новоафонская пещера, Абхазия: *a* — антенна I; *b* — добавочный жгутик AI; *c* — антенна II; *d* — гнатопода I; *e*, *f* — пальмарный край проподуса (клешни) гнатопода I; *g* — гнатопода II; *h* — пальмарный край проподуса (клешни) гнатопода II.

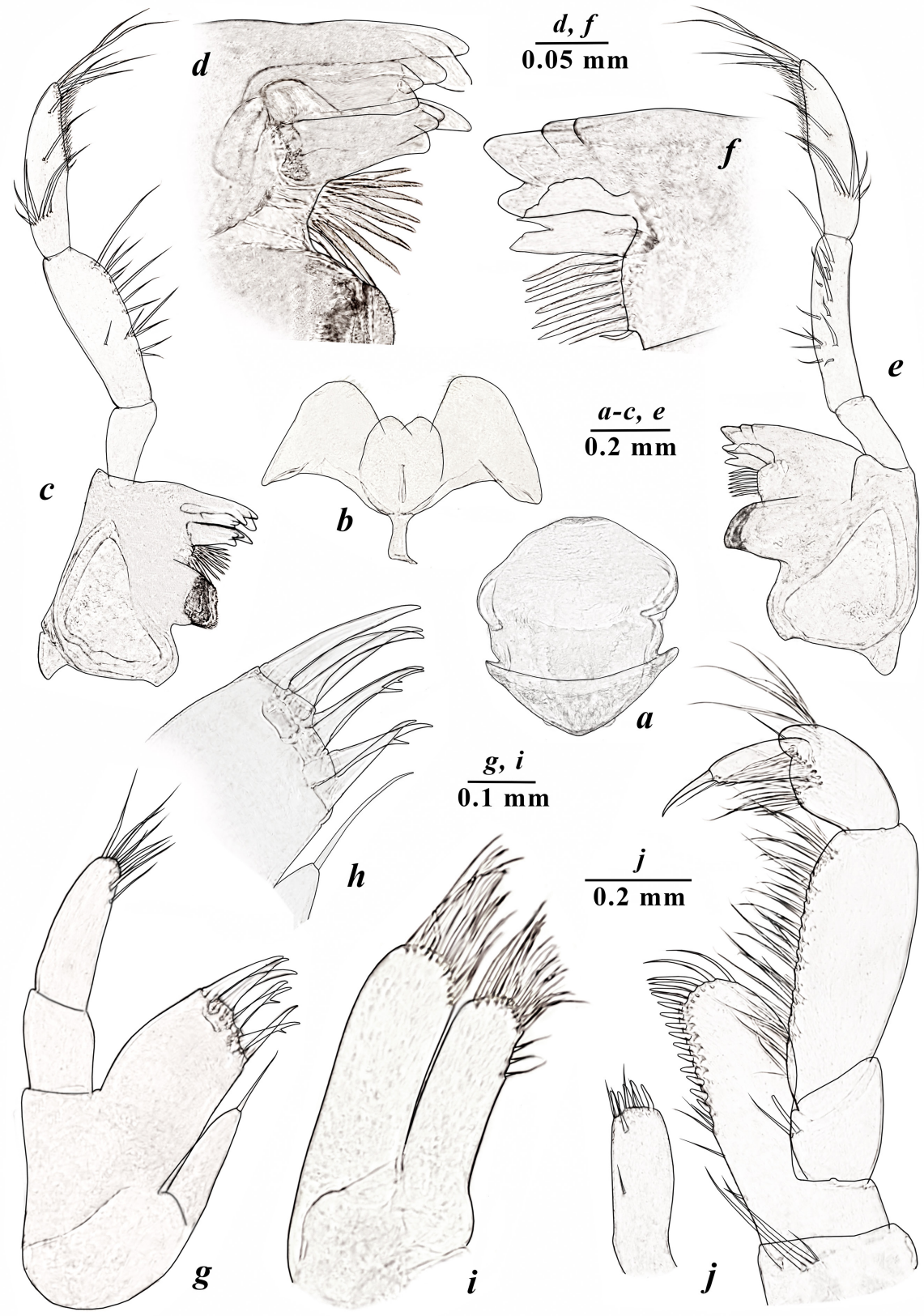


Fig. 3. *Niphargus smyri* sp.n., holotype ♀ (ZMMU Mb-1314), from Lake Anatolia, New Athos Cave, Abkhazia: *a* — upper lip; *b* — lower lip; *c*, *e* — mandibles; *d*, *f* — incisor process and pars incisiva; *g* — maxilla I; *h* — distal margin of upper endite; *i* — maxilla II; *j* — maxilliped.

Рис. 3. *Niphargus smyri* sp.n., голотип ♀ (ZMMU Mb-1314), из озера Анатолия, Новоафонская пещера, Абхазия: *a* — верхняя губа; *b* — нижняя губа; *c*, *e* — мандибулы; *d*, *f* — режущий отросток и pars incisiva; *g* — максилла I; *h* — дистальный край верхнего эндита; *i* — максилла II; *j* — максиллипеда.

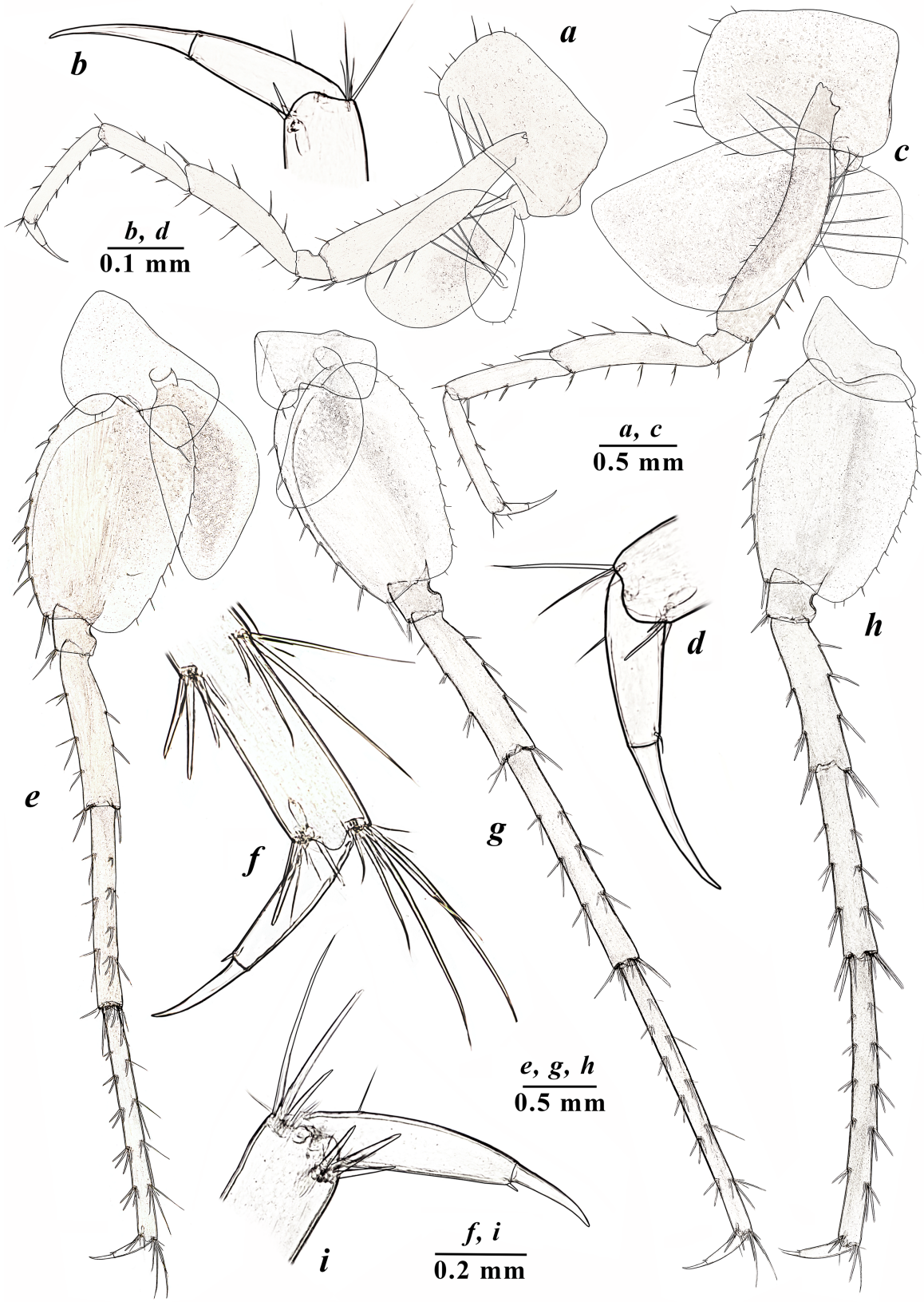


Fig. 4. *Niphargus smyri* sp.n., holotype ♀ (ZMMU Mb-1314), from Lake Anatolia, New Athos Cave, Abkhazia: *a* — pereopod III; *b* — dactylus of PIII; *c* — pereopod IV; *d* — dactylus of PIV; *e* — pereopod V; *f* — dactylus of PV; *g* — pereopod VI; *h* — pereopod VII; *i* — dactylus of PVII.

Рис. 4. *Niphargus smyri* sp.n., голотип ♀ (ZMMU Mb-1314), из озера Анатолия, Новоафонская пещера, Абхазия: *a* — переопода III; *b* — дактилус PIII; *c* — переопода IV; *d* — дактилус PIV; *e* — переопода V; *f* — дактилус PV; *g* — переопода VI; *h* — переопода VII; *i* — дактилус PVII.

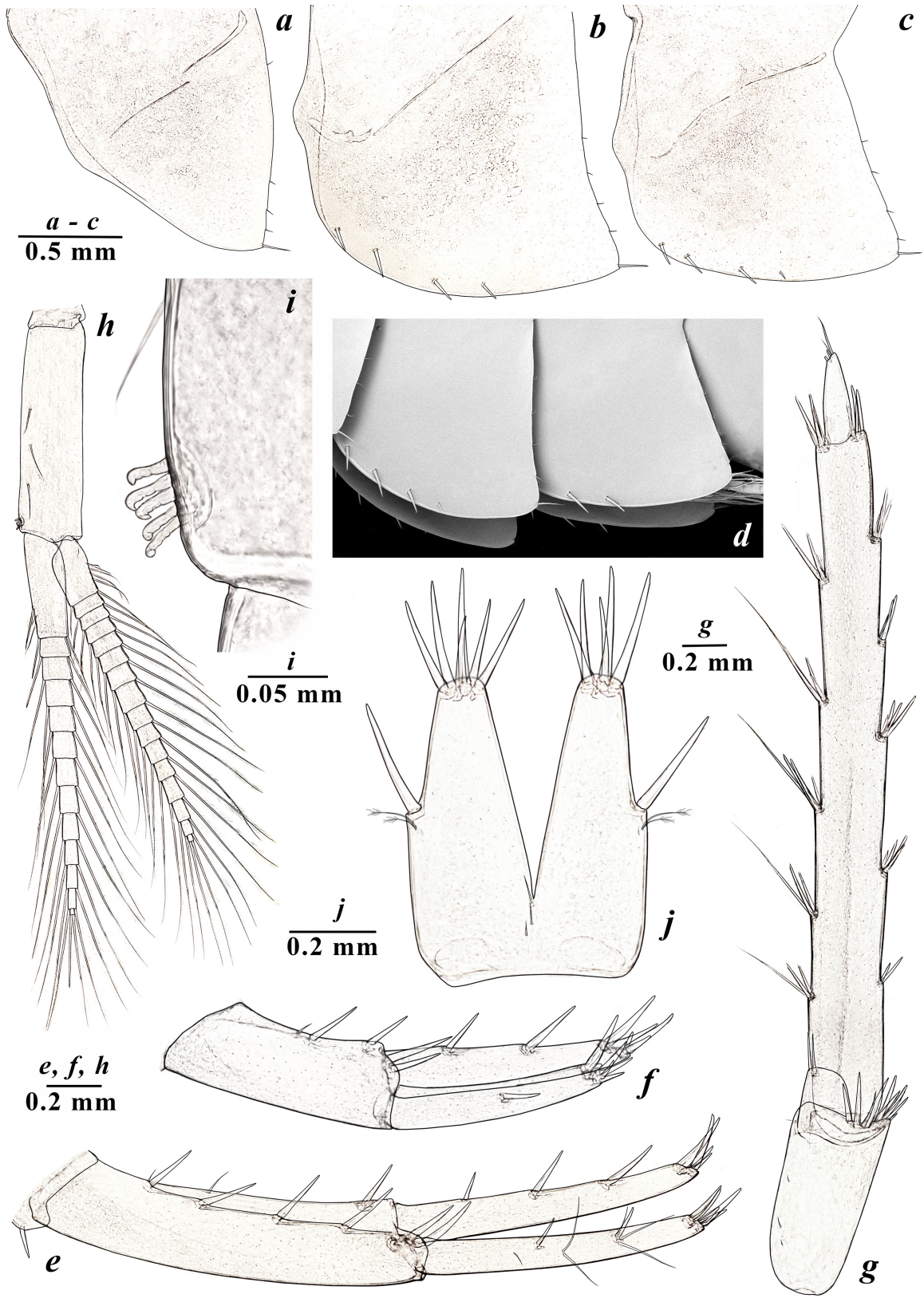


Fig. 5. *Niphargus smyri* sp.n., holotype ♀ (ZMMU Mb-1314), from Lake Anatolia, New Athos Cave, Abkhazia: *a–c* — epimeral plates I–III; *d* — epimeral plates I–II, SEM; *e* — uropod I; *f* — uropod II; *g* — uropod III; *h* — pleopod III; *i* — retinacules of pleopod III; *j* — telson.

Рис. 5. *Niphargus smyri* sp.n., голотип ♀ (ZMMU Mb-1314), из озера Анатолия, Новоафонская пещера, Абхазия: *a–c* — эпимеральные пластинки I–III; *d* — эпимеральные пластинки I–II, СЭМ; *e* — уропода I; *f* — уропода II; *g* — уропода III; *h* — плеопода III; *i* — ретинакула плеоподы III; *j* — тельсон.

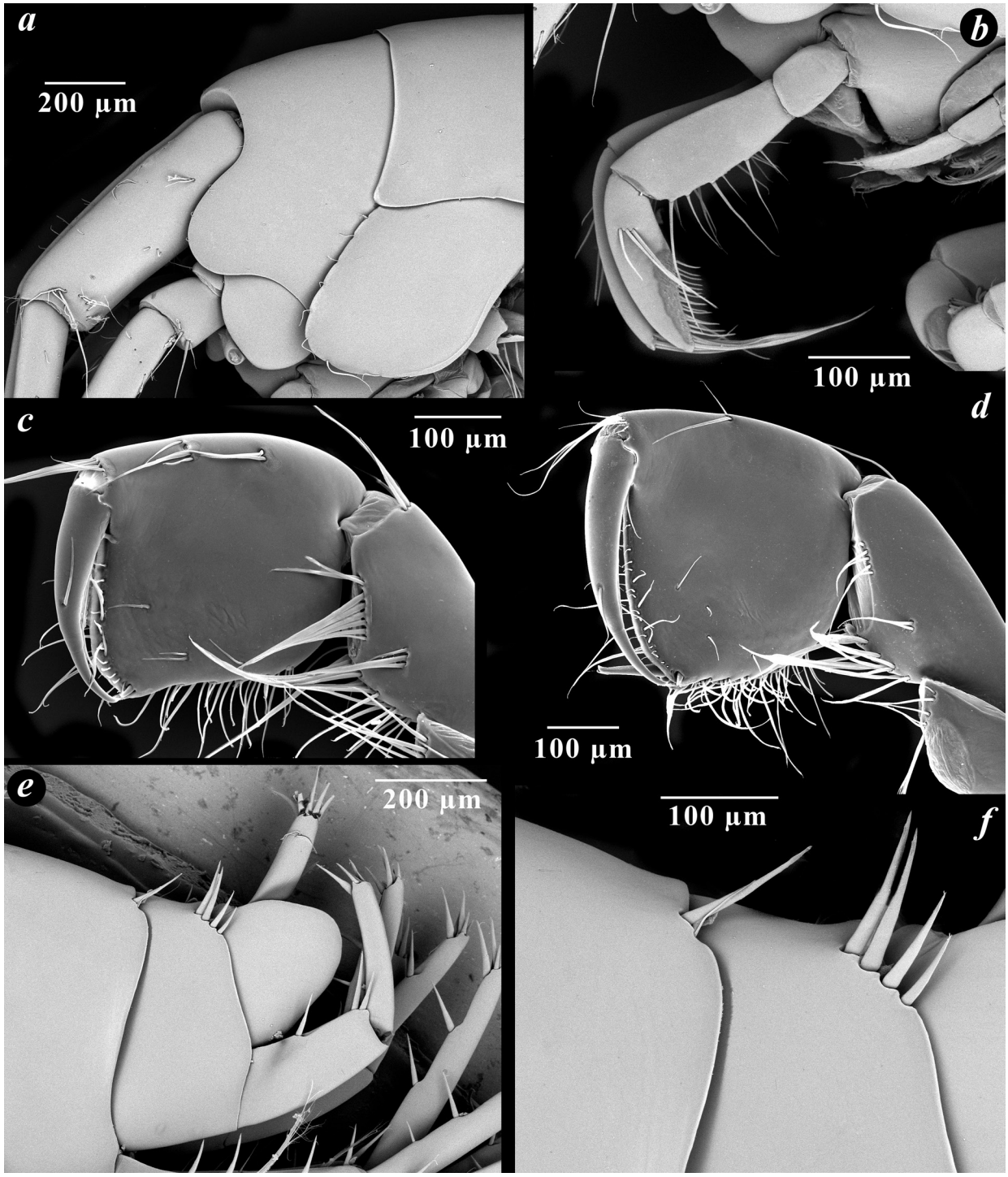


Fig. 6. *Niphargus smyri* sp.n., ♀ (LEMMI), from Lake Anatolia, New Athos Cave, Abkhazia, SEM: *a* — head; *b* — mandibular palp; *c* — propodus (palm) of gnathopod I; *d* — propodus (palm) of gnathopod II; *e* — urosomites I–III; *f* — armature of urosomites I–II.

Рис. 6. *Niphargus smyri* sp.n., ♀ (LEMMI), из озера Анатолия, Новоафонская пещера, Абхазия, СЭМ: *a* — голова; *b* — мандибулярный щупик; *c* — проподус (клешня) гнатопода I; *d* — проподус (клешня) гнатопода II; *e* — уросомиты I–III; *f* — вооружение уросомитов I–II.

setae and bunch of setae in distal part; ischium short, as long as wide; merus about 4.3× as long as wide, with bunches of short spines along dorsal and ventral margins; carpus slender, about 9.0× as long as wide, slightly shorter than propodus, with bunches of spines intermixed with single short setae; propodus slender, about 15.0–15.3× as long as wide, with several bunches of short spines; dactylus slender, with 1 small ventral inner spine and 1 short median plumose seta at outer margin, with nail much shorter than pedestal.

PEREOPOD VII (Fig. 4*h*): slender, basis about 1.4× as long as broad, with feeble posteroventral lobe, with convex posterior margin bearing 15 short marginal setae; anterior margin convex,

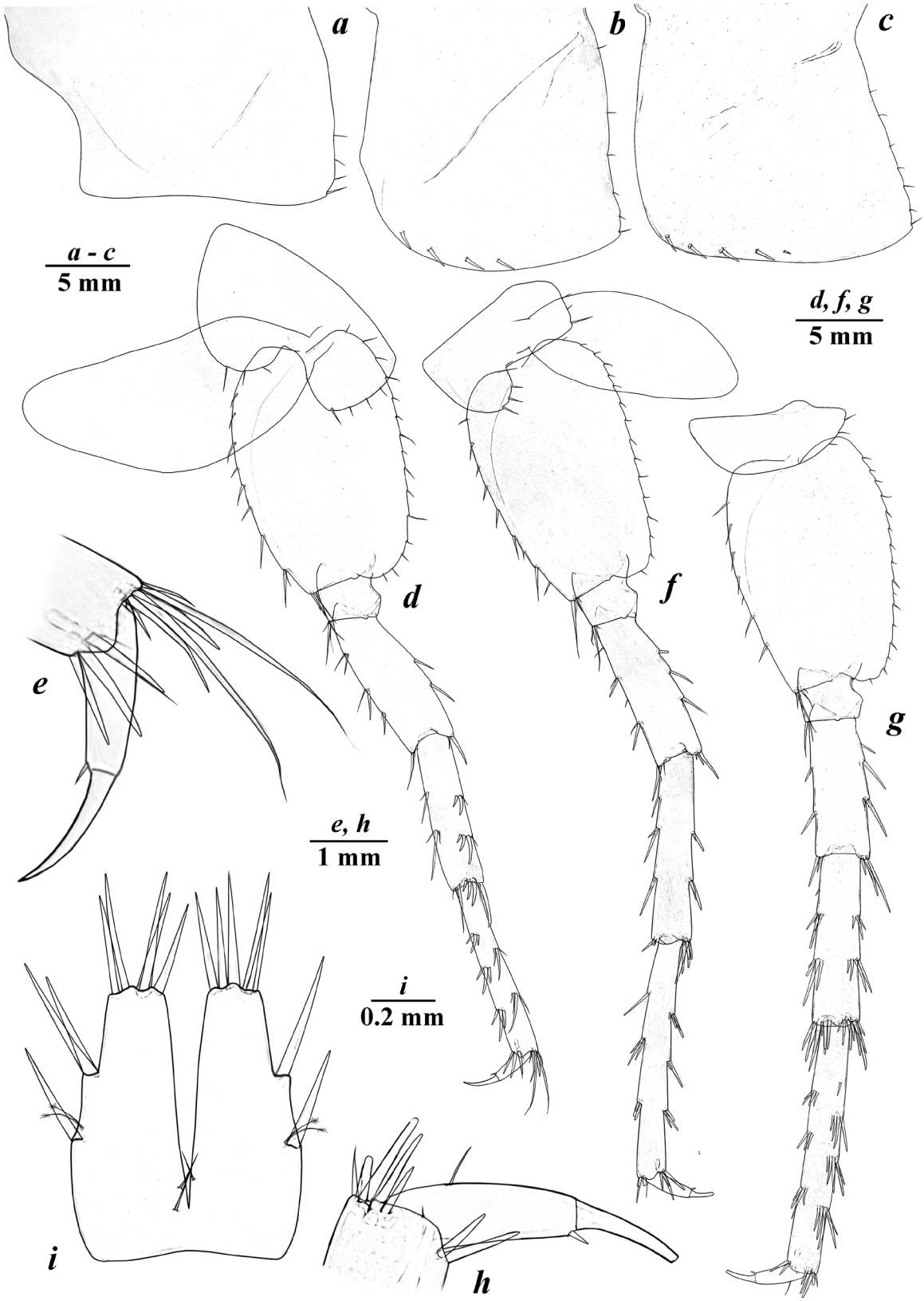


Fig. 7. *Niphargus smyri* sp.n., ♀ (ZMMU Mb-1316), from Mikhaylovskaya Cave, Abkhazia: *a–c* — epimeral plates I–III; *d* — pereopod V; *e* — dactylus of PV; *f* — pereopod VI; *g* — pereopod VII; *h* — dactylus of PVII; *i* — telson.

Рис. 7. *Niphargus smyri* sp.n., ♀ (ZMMU Mb-1316), из Михайловской пещеры, Абхазия: *a–c* — эпимеральные пластинки I–III; *d* — переопода V; *e* — дактилус PV; *f* — переопода VI; *g* — переопода VII; *h* — дактилус PVII; *i* — тельсон.

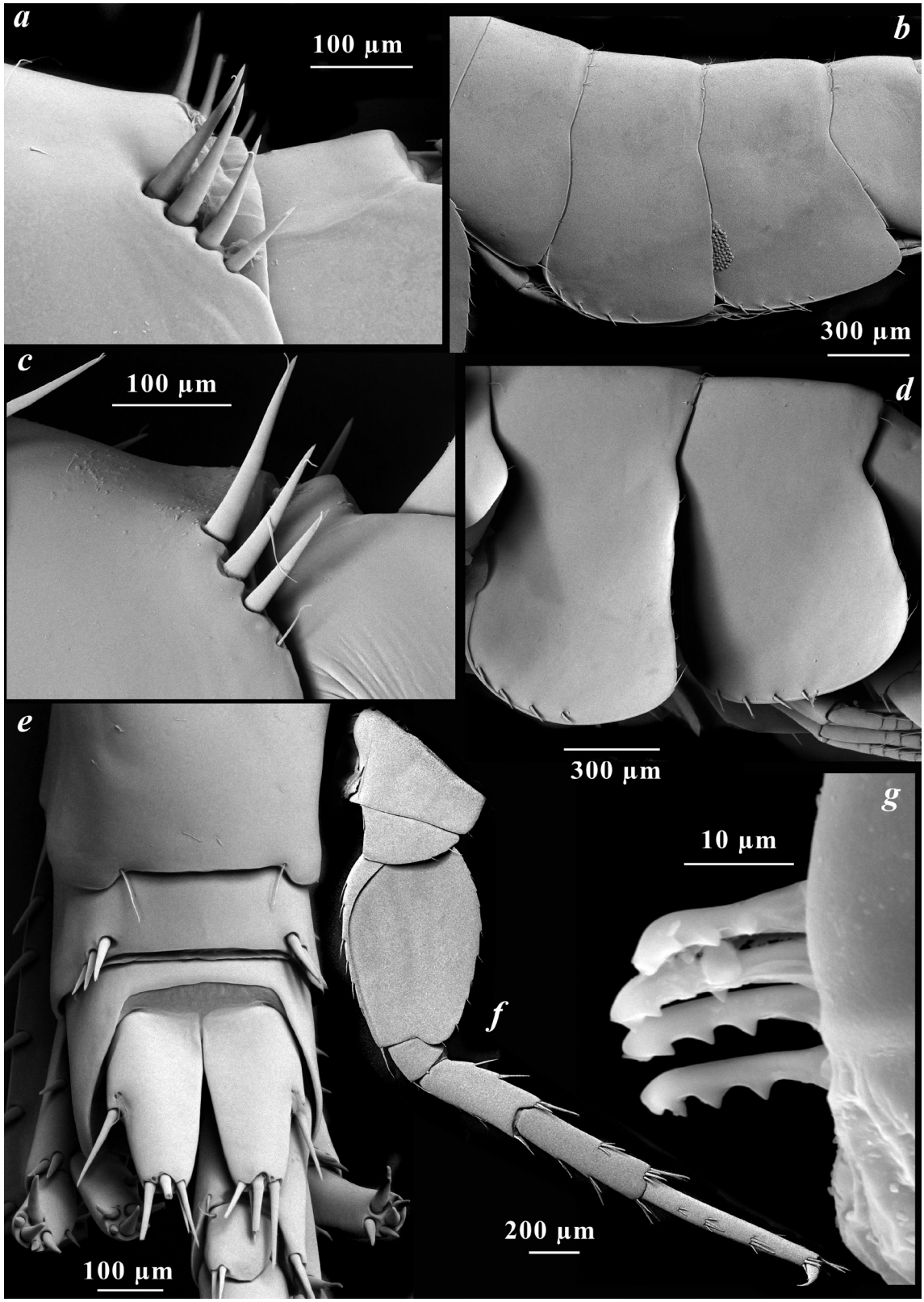


Fig. 8. *Niphargus smyri* sp.n., ♀ (LEMMI) from Mikhaylovskaya Cave, Abkhazia (*a*, *b*, *f*), and individuals from the related populations from Duripshskaya Vodnaya Cave (*c*, *d*, *g*) and Habyu Cave (*e*): *a*, *c* — armature of urosomite II; *b*, *d* — epimeral plates I–II; *e* — urosomites I–II and telson dorsally; *f* — pereopod VII; *g* — hooks in retinacula of pleopod III.

Рис. 8. *Niphargus smyri* sp.n., ♀ (LEMMI) из Михайловской пещеры, Абхазия (*a*, *b*, *f*), и представители родственных популяций из Дурипшской водной пещеры (*c*, *d*, *g*) и пещеры Хабю (*e*): а, *c* — вооружение уросомита II; *b*, *d* — эпимеральные пластинки I–II; *e* — уросомиты I–II и тельсоны дорсально; *f* — переопода VII; *g* — крючки в ретинакуле плеоподы III.

with row of 8 marginal stout setae; ischium short, as long as wide; merus about 4.0× as long as wide, with bunches of short spines along dorsal and ventral margins; carpus slender, about 6.0× as long as wide, slightly shorter than propodus, with bunches of spines intermixed with single short setae; propodus slender, about 10.0× as long as wide, with several bunches of short spines; dactylus (Fig. 4*i*) slender, with 1 median spine and 1 seta at inner margin, and 1 short median plumose seta at outer margin, with nail about twice shorter than pedestal.

PLEOPODS: basal segment (peduncle) of pleopods covered with numerous plumose setae, with 5 hooks in retinacules (Fig. 5*h*).

UROPOD I (Fig. 5*e*): protopodite (peduncle) about 4.5× longer than wide, slightly longer than outer ramus, with dorso-external row of 4 spines + 1–2 distal spine and spiniform setae, and dorso-internal row of 1 submarginal spiniform spine; rami equal in length, not paddle-like, about 8.8–9.0× as long as wide, with lateral and distal relatively robust spiniform setae and several pairs of long simple setae.

UROPOD II (Fig. 5*f*): protopodite (peduncle) nearly 2.6–2.7× longer than wide, slightly shorter than rami, outer ramus slightly longer than inner one, both rami with lateral and distal slender spines.

UROPOD III (Fig. 5*g*): with protopodite about 2.0× as long as wide, rami unequal, inner ramus (endopod) short, nearly 12× shorter than outer (exopod) ramus, bearing slender distal spine; outer ramus long, proximal article about 10.5× as long as wide; distal article about 8× of length of proximal article, with several short thin-flexible setae apically.

TELSON (Fig. 5*j*): relatively slender, elongated, about 1.3× as long as broad, ca 70% incised, lobes sloping distally, distal armature bearing usually 5–6 slender distal spines, reaching 0.35–0.37× of telson length; dorsal surface of telson with 1 large dorsal submarginal spine on each side, accompanying by 2 plumose setae and usually 2–3 simple short dorsal spines in proximal part of telson.

COLORATION. Body coloration of living animals is uniformly translucently white (Fig. 1*c*).

BODY SIZE. The largest collected ♀ has bl. 12.5 mm.

ACCESSION GENBANK NUMBERS. PZ440087 (Lake Anatolia (New Athos Cave)); PZ440088 (Lake Bezymannoe (New Athos Cave)); PZ440089 (‘Bezdonnaya Yama’ stream (New Athos Cave)); PZ440090 (Habyu Cave).

TAXONOMIC REMARKS. The newly discovered species belongs to the “*aquilex–tauri*” species group (after Straškraba [1972]), which includes mostly subterranean species. A striking and well-marked distinguishing feature of this species among the Caucasian representatives of the genus is the combination of several features, such as 1) a single seta on dactyli of gnathopods I–II (Fig. 2*d*, *e*, *g*, *h*), 2) subrounded epimeral plates (Fig. 5*a–d*), 3) the presence of 4 long and well-developed spines on each postero-dorsolateral side of urosomite II (Fig. 6*e*, *f*), 4) 5 hooks in retinacules (Fig. 5i) and 5) elongated ambulatory pereopods V–VII (Fig. 1*c*).

A comparatively high number of well-developed spines on urosomite II, together with numerous hooks in retinacules of pleopods, is characteristic of the western Georgian “*Niphargus borutzkyi*” ingroup. Specifically, 3 spines on urosomite II and 6–7 hooks in the retinacula in *N. rachalechkhumensis* Marin, Barjadze, Maghradze et Palatov, 2023; 4 slender spines and 7–10 hooks in *N. tvishiensis* Marin, Barjadze, Maghradze et Palatov, 2023; 4 spines and 7–8 hooks in *N. borutzkyi* Birštein, 1933; and 3 well-developed plus 1 slender spine, as well as 6–7 hooks, in *N. amirani* Marin, 2020 [Marin, 2020; Marin *et al*., 2023]. However, the “*Niphargus borutzkyi*” ingroup can be distinguished by a large, trapezoidal propodus (chela) of gnathopod I, the presence of numerous setae along the dorsal margin of the dactyli of gnathopods I–II, and a deeply cleft telson bearing two to three lateral spines (e.g., Marin *et al*. [2023]). A retinacular armature comprising 5hooks is also reported for several species from North Ossetia–Alania (northern slope of the Greater Caucasus), namely *N. alanicus* Marin et Palatov, 2021 (4–5 hooks), *N. ardonicus* Marin et Palatov, 2024 (5 hooks), *N. fiagdonicus* Marin et Palatov, 2024 (5 hooks), and *N. osseticus* Marin et Palatov, 2024 (5 hooks). However, these taxa differ in having only 2 spines in the dorsoposterior armature of urosomite II [Marin, Palatov, 2021, 2024]. Both of the aforementioned groups are phylogenetically distant from *Niphargus smyri* sp.n. (see Marin, Palatov [2021, 2024]; Marin *et al*. [2023]).

Among other *Niphargus* species, the new species phylogenetically related to the congeners from the “*aquilex–tauri*” species group, especially to species from Slovenia as far east to Turkey (Taurus Mountains), for example, *N. tauri* Schellenberg, 1933, *N. dobati* Sket, 1999, *N. fongi* Fišer et Zagmajster, 2009 and some others. Although the phylogenetic relationships have not been definitively confirmed and we have only a single sequence (KY643627, *Niphargus* cf. *aquilex* from Huda luknja pri Gornjem Doliču (46°24′50.4″N 15°10′26.4″E), Slovenia; see Fig. 1*d*) sister to the new “*Niphargus smyri*” ingroup, morphologically these species are also close. For example, *N. fongi* from Dolga Jama pri Koblarjih (45°42′43.9″N 14°49′48.2″E), Kocevje in Slovenia, also has subrounded epimeral plates, a single seta on dactyli of gnathopods I–II, 3–4 well-marked spines on urosomite II and 3–7 hooks in retinacules of pleopods, actually the unique feature within the “*aquilex-tauri*” species group (see Fišer & Zagmajster [2009]). The latter species is mostly morphologically similar to *Niphargus smyri* sp.n., and probably phylogenetically close, but its sequences are absent in the international genetic databases, for example GenBank (NCBI).

HABITAT AND ECOLOGY. The new species was discovered in large subterranean lakes (Anatolia and Bezymiannoe) inside New Athos Cave (entrance coordinates: 43°05′25.4″N 40°48′37.3″E; see Fig. 1*a*). All examined individuals were collected from the lake aquatic environment, including its rocky shores and muddy bottom substrates. The pronounced stygomorphic features of this species, including the absence of eyes, reduced body pigmentation, and the presence of yellow cephalic spots, indicate a fully subterranean mode of life. In addition, the elongation of pereopods V–VII, in comparison with other Caucasian representatives of the genus, likely reflects an adaptation to permanent habitation in large subterranean lakes of the New Athos Cave, corresponding to the “lake ectomorph” (after Fišer *et al*. [2009]; Trontelj *et al*. [2012]; Petković *et al*. [2015]; Borko *et al*. [2021]). At the same time, closely related populations have been found in other hypogeal resources, such as springs and streams (even inside New Athos Cave) (see above). This suggests that the “lake ectomorph” is more likely an ecological variation that occurs during prolonged habitation in large water bodies (= underground lakes).

BRIEF DESCRIPTION INDIVIDUALS FROM MIKHAYLOVSKAYA CAVE. The population from Mikhaylovskaya Cave is the most genetically and morphologically similar to the new species in the studied locations. The specimens from Mikhaylovskaya Cave differ mainly in the proportions of their ambulatory pereiopods (PpV–VII are much shorter) and in the presence of additional spines on the armament of telson. Additionally, their AI flagellum is shorter and urosomite II usually with 5, but some specimens with 4 simple strong spines on each dorsolateral side (see Fig. 8*a*). Epimeral plates I–III (Fig. 7*a–c*; 8*b*) with rounded posteroventral corners. Epimeral plate I (Fig. 7*a*) with slightly concave ventral margin, without ventrofacial

setae; posterior margin slightly convex, bearing 3 short marginal setae; posteroventral corner subrounded, with 1 strong long seta. Epimeral plate II (Figs 7*b*, 8*b*) with strongly convex ventral margin, with 4 ventrofacial setae; posterior margin concave, with 4 short marginal setae; posteroventral corner bluntly rounded, with 1 strong long seta. Epimeral plate III (Figs 7*c*, 8*b*) with convex ventral margin, with 4 large and 1 tiny ventrofacial setae; posterior margin concave, with 6 short marginal setae; posteroventral corner rounded, with 1 strong long seta. Coxal gills: present on pereopods II–VI, ovoid, relatively large; gills/bases pereopod length ratio about 1.3/1; 0.8/1; 1.2/1; 1.2/1 and 0.9/1, respectively. Oostegites on PpII–V. Pereopod V (Fig. 7*d*): with basis wide, about 1.5× as long as broad, rectangular, with feebly marked posteroventral lobe, posterior margin slightly convex, with row of 15 slender marginal setae, anterior margin convex, with row of 8 marginal stout setae that distinctly longer than posterior and bunch of setae in distal part; ischium subquadrate, as long as wide; merus about 2.8× as long as wide, with bunches of slender spines along posterior and anterior margins; carpus slender, about 4.1× as long as wide, slightly shorter than propodus; propodus slender, about 7.5× as long as wide, with bunches of short spines; dactylus (Fig. 7*e*) short, with 1 small ventral inner spine and 1 median short plumose seta at outer margin. Pereopod VI (Fig. 7*f*): slender, basis wide, about 1.6× as long as broad; with feeble posteroventral lobe and slightly convex posterior margin with row of 16 short marginal setae; anterior margin convex, with row of 9 longer marginal stout setae and bunch of setae in distal part; ischium short, as long as wide; merus about 3.2× as long as wide, with bunches of short spines along dorsal and ventral margins; carpus slender, about 5.0× as long as wide, slightly shorter than propodus, with bunches of spines intermixed with single short setae; propodus slender, about 8.2× as long as wide, with several bunches of short spines; dactylus slender, with 1 small ventral inner spine and 1 short median plumose seta at outer margin, with nail much shorter than pedestal. Pereopod VII (Figs 7*g*, 8*f*): slender, basis about 1.4× as long as broad, with feeble posteroventral lobe, with convex posterior margin bearing 16 short marginal setae; anterior margin convex, with row of 7 marginal stout setae; ischium short, as long as wide; merus about 2.7× as long as wide, with bunches of short spines along dorsal and ventral margins; carpus slender, about 3.8× as long as wide, slightly shorter than propodus, with bunches of spines intermixed with single short setae; propodus slender, about 7.6× as long as wide, with several bunches of short spines; dactylus (Fig. 7*h*) slender, with 1 median spine and 1 seta at inner margin, and 1 short median plumose seta at outer margin, with nail about twice shorter than pedestal. Pleopods with 4 (Fig. 8*g*) or 5 (usually) hooks in retinacules. Telson (Fig. 7*i*): relatively slender, elongated, about 1.2× as long as broad, ca 70% incised, lobes sloping distally, distal armature bearing usually 5–6 slender distal spines, reaching 0.45× of telson length; dorsal surface of telson with 2–3 large dorsal submarginal spines on each side, accompanying by 2 plumose setae and usually 2–3 simple short dorsal spines in proximal part of telson.

REMARKS ON DIFFERENCES AMONG STUDIED POPULATIONS. Due to the absence of large lakes in Mikhaylovskaya Cave and the fact that niphargids only inhabit small cave watercourses there, the morphology typical of the "lake ectomorph" is not observed there. The overall body size of the specimens from Mikhaylovskaya Cave is smaller than those from New Athos Cave, with the largest ♀ reaching only 7.5 cm in total body length (vs. 12.5 cm in New Athos Cave). The telson has two lateral spines instead of one, and the proportions of the merus and carpus in PpV–VII are different, being on average 1.5× shorter and sturdier. The relative size of the coxal gills is also larger, and the flagella of AI and AII are shorter by one segment.

It is likely that in smaller streams and seeps where these specimens live, there is less dissolved oxygen in the water, so the gill area has to be relatively larger. Ambulatory pereiopods are shorter and stronger to accommodate this environment. At the same time, in a large permanent cave lake (where there are no predators such as fishes), with much better oxygen conditions, it may be necessary for the gills to become shorter and the segments (merus–carpus) of the walking legs to become longer, while swimming in the water column.

The ambulatory pereopods of the specimens from Habyu and Duripshskaya-Vodnaya Cave (see Fig. 8*c*–*e*) are also relatively short and more clinging, as there are no lakes in these caves. All studied individuals from these caves have 4 spines on urosomite I and 5 hooks in the retinacules of pleopods.

Compliance with ethical standards

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

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

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