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The Quaternary speciation in the Caucasus: a new cryptic species of stygobiotic amphipod of the genus *Niphargus* (Crustacea: Amphipoda: Niphargidae) from the Kumistavi (Prometheus) Cave, Western Georgia

Четвертичное видообразование на Кавказе: новый криптический вид стигобионтных амфипод рода *Niphargus* (Crustacea: Amphipoda: Niphargidae) из пещеры Кумистави (Прометей), Западная Грузия

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KEY WORDS: Crustacea, Amphipoda, Niphargidae, *Niphargus*, new species, stygobiotic, Western Georgia, Caucasus.

КЛЮЧЕВЫЕ СЛОВА: Crustacea, Amphipoda, Niphargidae, *Niphargus*, новый вид, стигобионты, Западная Грузия, Кавказ.

ABSTRACT. A new cryptic species of stygobiotic amphipod of the genus *Niphargus* Schiödte, 1849 (Amphipoda: Niphargidae) is described from underground stream and lakes in the Kumistavi (Prometheus) Cave, Tskaltubo–Kumistavi, Imereti region of the Western Georgia, Caucasus, based on morphology and DNA analysis. The new species belongs to the "*carpathicus*" species complex with the representatives in Europe, Caucasus and Iran, but clearly differs from all Caucasian congeners by stout telson, which is about as long as wide (vs. about not less than 1.5 times in other related species); relatively stout basal part of dactyli of pereopods V–VII, which is about as long as wide (vs. usually more than 1.5 times as long as wide in other related species); and almost rectangular palm of gnathopods I and II with straight distal margin (vs. usually sloped distal margin in other related species). The sister species *N. borutzkyi* Birštein, 1933, inhabiting the neighboring, but isolated underground karst system, including of the Sataplia, Sapichkhia and Tskaltsitela caves, differs from the new species in some minor morphological features and genetically (about 10% or 0.1 substitutions per 100 nucleotides by COI gene marker). The phylogenetic analysis of available genetic data (COI mtDNA) shows that karsts regions in the vicinity of Kutaisi are currently inhabited by closely related *Niphargus* species descended from the ancestral taxon in the Quaternary as a result of geological processes that caused fragmentation of the ancestral range.

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РЕЗЮМЕ. Новый криптический вид стигобионтных амфипод рода *Niphargus* Schiödte, 1849 (Amphipoda: Niphargidae) описан из подземного ручья и озер в пещере Кумистави (Прометея), Цхалтубо-Кумистави, Имеретинская область Западной Грузии, Кавказ, на основе морфологии и анализа ДНК. Новый вид принадлежит к видовому комплексу "*carpathicus*", в который входят представители рода, обитающие в Европе, на Кавказе и в Иране, но явно отличается от всех кавказских сородичей более коротким тельсоном, который примерно такой же длины как и ширины (у других родственных видов он примерно в 1,5 раза длиннее); относительно толстой базальной частью дактилусов переопод V–VII, длине которой примерно равна ширине (у родственных видов эта часть дактилуса более чем 1,5 раза длиннее, чем шире); и почти прямоугольная пальмарной частью гнатопод I и II с прямым дистальным краем (он обычно скошен у других родственных видов). Наиболее родственный вид *N. borutzkyi* Birљtein, 1933, обитающий в соседней, но изолированной подземной карстовой системе, включающей пещеры Сатаплия, Сапичхия и Цхалицитела, отличается от нового вида некоторыми незначительными морфологическими признаками и генетически (около 10% или 0,03 замен на 100 нуклеотидов по генетическому маркеру

COI мтДНК). Филогенетический анализ имеющихся генетических данных (COI мтДНК) показывает, что в карстовых районах окрестностей Кутаиси в настоящее время обитает группа близкородственных видов рода *Niphargus*, произошедшие от единого предкового таксона в Четвертичном периоде в результате геологических процессов, которые привели к фрагментации предкового ареала.

Introduction

The Caucasus is a hotspot of biodiversity, characterized by a unique and very rich fauna, formed by local separation of ecological niches and microhabitats [Myers *et al.*, 2000; Krever *et al.*, 2001]. Diverse stygobiotic fauna, including numerous crustacean species, is recently described as new to science from the region (e.g., Marin, Sokolova, 2014; Sidorov *et al.*, 2015a, b, 2018; Sidorov, Samokhin, 2016; Marin, 2017a, b, 2018a, b, 2019a, b, 2020; Marin, Sinelnikov, 2017; Turbanov, Marin, 2017; Marin, Palatov, 2019), showing that the real diversity of the region is far to be well known. It is obvious that the fauna of the region has been studied unevenly, and it is very likely that a large number of new species will be described in the future.

The genus *Niphargus* Schiödte, 1849 (Crustacea: Amphipoda: Niphargidae) is one of the largest freshwater amphipod genus, comprising over 400 described species, inhabiting various subterranean and epigean aquatic habitats such as deep cave lakes, wells, small pores in the epikarst, helocrene of springs and hyporeic zone of rivers in the West Palearctic [Fišer *et al.*, 2006, 2014; Väinölä *et al.*, 2008; Fišer, 2012; Horton *et al.*, 2017]. During the speleological survey along karst systems of Imereti region of the Western Georgia in September 2017 numerous specimens of the genus *Niphargus* were discovered in subterranean cave streams and lakes in Kumistavi (=Prometheus, Gliani) Cave (42°22′35.8″N 42°36′03.2″E), Tskaltubo-Kumistavi, in the Imereti region of the Western Georgia, Caucasus. The only known stygobiotic species from this region is *Niphargus borutzkyi* Birštein, 1933 (Malacostraca: Amphipoda: Niphargidae), originally described from the Tskaltsitela (=Iazoni) Cave in Kutaisi [Birštein, 1933, 1950] and lately reported from the neighboring the Sapichkhia (=Rionhesi) Cave and the Sataplia I Cave (after Barjadze *et al.*, 2015). Careful examination of the specimens collected from the Kumistavi (Prometheus) Cave and their morpho-genetic comparison with the topotypic material of *N. borutzkyi* from the Tskaltsitela Cave, Kutaisi (the type locality of the species) showed that they belong to genetically and morphologically well separated species described herewith as a new to science.

Material and methods

Amphipods were collected by hand net in subterranean cave streams and lakes within the Kumistavi (=Prometheus, Gliani) Cave, Tskaltubo–Kumistavi (42°22′35.8″N 42°36′03.2″E) and the Tskaltsitela (=Iazoni) Cave (42°16′19.62″N 42°44′1.63″E) in Kutaisi, Western Georgia, Caucasus, in 2017–2018. The study does not include endangered or protected species. All collected specimens were preserved in 90% solution of ethanol for further DNA analysis. Body length (bl., in mm), dorsal length from the tip of rostrum till distal margin of telson, is used as standard measurements. The type material is deposited in the collection of Zoological Museum of Moscow State University, Moscow (ZMMU) and the Laboratory of Ecology and Evolution of Marine Invertebrates of A.N. Severtsov Institute of Ecology and Evolution of the Russian Academy of Sciences, Moscow, Russia (LEMMI). All obtained sequences are deposited in the GenBank (NCBI) database.

A fragment of the mitochondrial gene coding for cytochrome c oxidase subunit I gene marker (COI) was amplified, sequencing and compared to resolve the cryptic diversity. Total genomic DNA was extracted from abdominal and pereiopod muscle tissue using the innuPREP DNA Micro Kit (AnalitikJena, Germany) following the manufacturer's protocol. The mitochondrial marker COI was amplified with the help of the universal primers LCO1490 (5'–ggtcaacaaatcataaagatattgg–3') and HC02198 (5'–taaacttcagggtgaccaaaaaatca–3') [Folmer *et al.*, 1994]. PCR products were performed on amplificator T100 (Bio-Rad, USA) under the following conditions: initial denaturation at 96 °C for 1.5 min followed by 42 cycles of 95 °C for 2 min, 49°C for 35 seconds, and 72 °C for 1.5 min, followed by chain extension at 72 °C for 7 min. The volume of 10 uL of reaction mixture contained 1 uL of total DNA, 2 uL of 5x PCR mix (Dialat, Russia) and 1 uL of each primer. 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. DNA nucleotide sequences were determined using Genetic Analizer ABI 3500 (Applied Biosystems, USA) and BigDye 3.1 (Applied Biosystems, USA) with direct and reverse primers. Uniformity of obtained sequences was processed using the program BioEdit v. 5.0.9. Uniformity of obtained sequences was processed using the program BioEdit v. 5.0.9. The resulting markers of COI gene of mtDNA with 620+ nucleotide long sections were registered in GenBank (NCBI) and used for further phylogenetic analysis. A dataset of COI gene of mtDNA of our specimens and sequences from GenBank (NCBI) were assembled for phylogenetic analysis (see Fig. 1). The aligned sequences of COI gene, 658 base pairs in length, were analyzed and verified with MEGA 7.0. The best evolutionary substitution model was determined using MEGA 7.0. and jModeltest 2.1.141. The received nucleotide alignments of COI mtDNA gene marker were used to reconstruct the phylogenetic relations (tree) in (http://www.atgc-montpellier.fr/phyml/) [Guindon *et al.*, 2020] using GTR+G+I model for Maximum–Likelihood analysis

Table 1. Pairwise genetic (COI mtDNA) distances (*p*-distances) *Niphargus amirani* sp.n. from the Kumistavi (Prometheus) Cave (n=4) and other related cave-dwelling *Niphargus*, known from the Northern Caucasus, the Crimean Peninsula and Europe (from GenBank (NCBI) database).

Таблица 1. Попарные генетические (COI мтДНК) дистанции (*p*-дистанции) *Niphargus amirani* sp.n. из пещеры Кумистави (Прометей) (n=4) и других родственных пещерных представителей рода *Niphargus*, известных с Северного Кавказа, Крымского полуострова и Европы (из базы данных GenBank (NCBI)).

Niphargus borutzkyi (Tskaltsitela Cave, Northern Caucasus)	0.092±0.013
Niphargus sp. (cave between Gumbrini and Khomouli (=Sataplia I Cave), Northern Caucasus)	0.095±0.015
Niphargus sp. (Shaori water reservoir, Northern Caucasus)	0.161±0.024
Niphargus inermis (Nizhne-Shakuranskaya Cave, Northern Caucasus)	0.169±0.022
Niphargus cf. *latimanus* Birštein 1952 (Partizanskaya Cave, Northern Caucasus)	0.171±0.025
Niphargus dimorphus (Crimean Peninsula)	0.172±0.026
Niphargus bihorensis (Meziad, Romania)	0.173±0.023
Niphargus glontii (Tskhratskaro, Northern Caucasus)	0.176±0.023
Niphargus vadimi (Crimean Peninsula)	0.182±0.027
Niphargus gebhardti (Europe)	0.185±0.027
Niphargus daniali (Iran)	0.194±0.028
Niphargus ambulator (Northern Italy)	0.194±0.028
Niphargus gegi (Northern Caucasus)	0.197±0.023
Niphargus abraskili (Northern Caucasus)	0.203±0.028
Niphargus krasnodarus (Fanagoriyskaya Cave, Northern Caucasus)	0.209±0.028
Niphargus molnari (Europe)	0.244±0.030

Table 2. Comparison of pairwise genetic (COI mtDNA) distances of *Niphargus* species from the vicinity of Kutaisi, Imereti region of the Western Georgia, Northern Caucasus.

Таблица 2. Сравнение попарных генетических дистанций (COI mtDNA) видов рода *Niphargus* из окрестностей г. Кутаиси, Имеретинский регион Западной Грузии, Северный Кавказ.

	Niphargus amirani sp.n. (n=4)	*Niphargus borutzkyi* (n=4)	*N.* cf. *borutzkyi* (n=1) (Gumbrini–Khomouli)
Niphargus borutzkyi (n=4) (Tskaltsitela Cave)	0.092±0.013		
Niphargus cf. *borutzkyi* (n=1) (Gumbrini–Khomouli, probably, Sataplia I Cave)	0.095±0.015	0.036±0.008	
Niphargus sp. (n=1) (Shaori water reservoir)	0.161±0.024	0.153±0.021	0.154±0.021

(ML). Pairwise genetic divergences (*p*-distances) was calculated based on COI sequences using MEGA 7.0 with the Kimura 2-Parameter (K2P) model of evolution [Kimura, 1980].

Results

PHYLOGENETIC APPROACH. The calculated intraspecific pairwise genetic distances *p*-distances in studied populations of *Niphargus* from the Kumistavi (Prometheus) Cave (n=4) and the Tskaltsitela Cave (n=4) are very low, being 0.01 and 0.0 substitutions pre 100 nucleotides (0.1% and 0%), respectively.

The interspecific genetic distances allowing to separate specimens from the Kumistavi (Prometheus) Cave as a new species (*Niphargus amirani* sp.n.) generally increase the thresholds used for separation of crustaceans and different invertebrates (see Table 1, 2; Fig. 1) (see below; Lefébure et al., 2006a, b, 2007; Cothran *et al*., 2013; Lagrue *et al*., 2014; Kekkonen *et al*., 2015; Delić *et al*., 2017; Grabowski *et al*., 2017; Gay-Haim *et al*., 2018; Jazdzewska *et al*., 2020).

The genetic data from GenBank (NCBI) (KT 180185), based on the specimen of *Niphargus* sp., collected in "Georgia: cave between Gumbrini and Khamali (=Khomouli)" probably belong to the species from the Sataplia I Cave (see Fig. 6). This specimen represents an isolated population of *N. borutzkyi*, which differs from the typical population from the Tskaltsitela Cave by the minimal genetic differences (about 3.6%

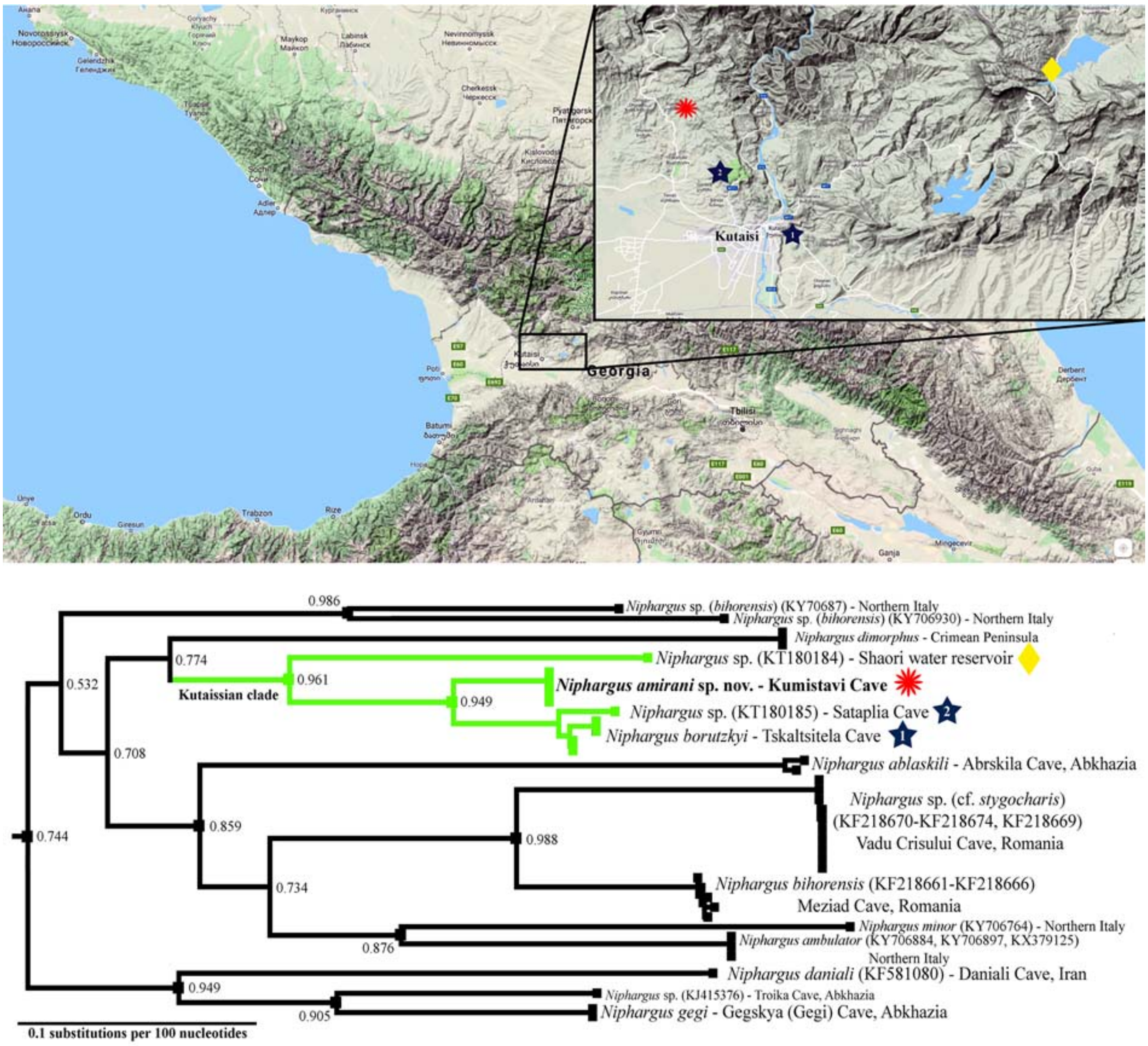

Fig. 1. The area of sampling in the Western Georgia, Caucasus (above), and the reconstruction of phylogenetic relations (below) of cave-dwelling species related to *Niphargus amirani* sp.n. based on COI mtDNA gene marker (ML algorithm, GTR+G+I model). The sequences of the related species were taken from the GenBank (NCBI) database.

Рис. 1. Карта отбора проб в Западной Грузии, Кавказ (сверху), и реконструкция филогенетических отношений (снизу) пещерных видов рода, наиболее родственных *Niphargus amirani* sp.n., на основе маркера гена COI мтДНК (алгоритм ML, модель GTR+G+I). Последовательности родственных видов взяты из базы данных GenBank (NCBI).

or 0.03 substitutions per 100 nucleotides by COI mtDNA) (see Table 2).

The specimen from the Shaori water reservoir (KT180184) is represented a sister taxon to the clade "*Niphargus borutzkyi–Niphargus amirani* sp.n." (Tables 1, 2; Fig. 1).

TAXONOMIC PART

Order Amphipoda Latreille, 1816
Family Niphargidae Bousfield, 1977
Genus *Niphargus* Schiödte, 1849

Niphargus amirani **sp.n.**
Figs 2–7, 8*a*.

MATERIAL EXAMINED. Holotype: female (bl. 10.0 mm), ZMMU Mb-1167: Caucasus, Western Georgia, Imereti region, Tskaltubo–Kumistavi, Kumistavi (Prometheus) Cave, 42°22′35.8″N 42°36′03.2″E, in subterranean stream, about 100 meters above the sea level, coll. I. Marin, 15 Sept. 2016.

Paratypes: 1 female (bl. 9.0 mm), ZMMU Mb-1168; 4 females, 2 males, LEMMI: same locality and date as holotype.

DIAGNOSIS. Urosomite II with 3 spine-like setae in dorso-proximal angle. Epimeral plates subangular, with rounded ventro-posterior corner. Maxilla 1 with inner plate armed with 7+ setae, outer plate with 7 spines. Gnathopods I–II moderate, palm almost rectangular, with straight distal margin, dactylus with row of several setae along outer margin. Dactyli of pereopods III–VII with relatively stout basal (proximal part), at inner margin with 1 spine or seta near basis of nail. Pleopods with 4 hooks in retinacle of pleopods. Uropod III elongated, article 2 of outer ramus long,

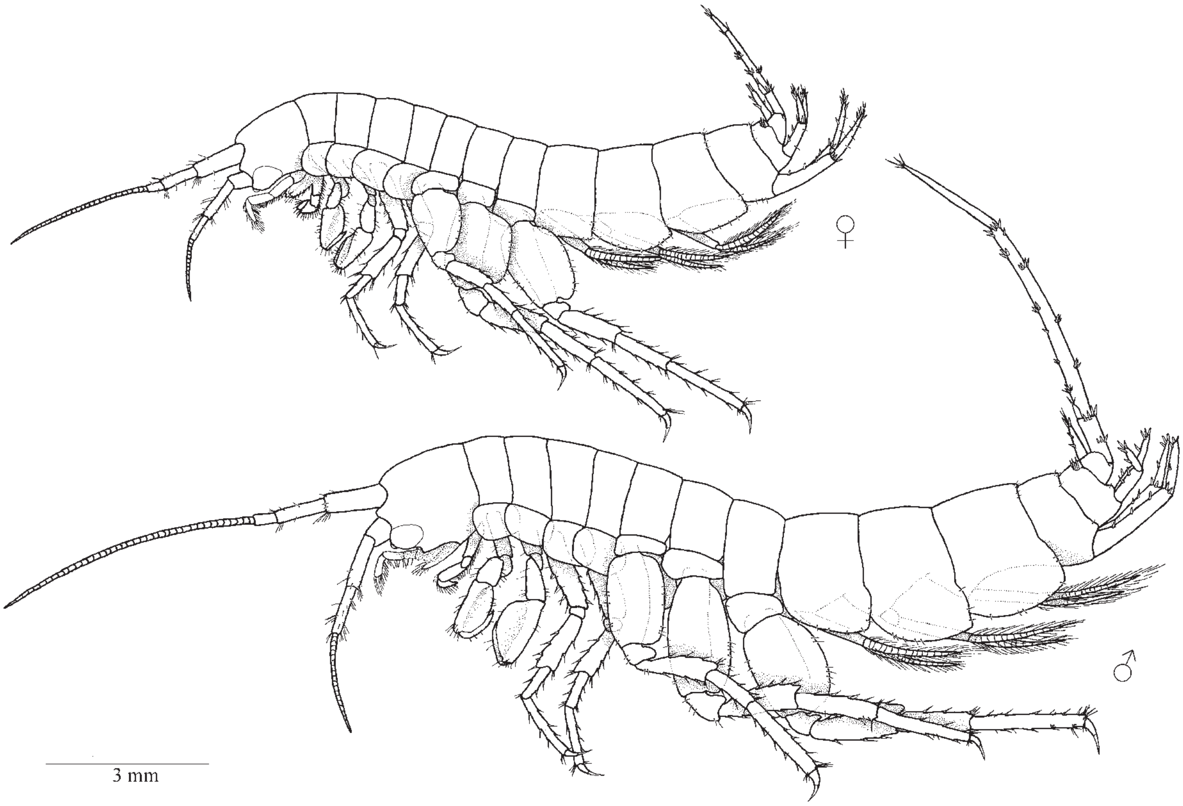

Fig. 2. *Niphargus amirani* sp.n., general view, the Kumistavi (Prometheus) Cave, Tskaltubo–Kumistavi, Western Georgia, Caucasus.
Рис. 2. *Niphargus amirani* sp.n., общий вид, пещера Кумистави (Прометея), Цхалтубо–Кумистави, Западная Грузия, Кавказ.

article 1 (distal) about 4–4.5 times as long as wide in females. Telson short and relatively stout, deeply incised, each lobe with 4–5 long distal spines and 2 outer marginal spines, facial spines absent.

DESCRIPTION. Body medium in size, moderately slender. Head without rostrum, with subrounded lateral cephalic lobes and excavated antero-ventral sinus; eyes or pigmented spots absent. Epimeral plates I–III with pointed postero-ventral corners (Figs 2, 8*a*). Urosomites I and III unarmed; dorso-proximal angle of urosomite II with 3 large slender spines on each side (Fig. 8*a*). Coxal gills ovoid, of moderate size, reaching and overreaching distal tip of article 2 of ambulatory pereopods.

Antenna I (Fig. 3*a, b*) slender, long; peduncular articles moderately slender, ratio 1:0.7:0.35; flagellum consisting of about 20+ articles, most of them with 2 short aesthetascs each; accessory flagellum (Fig. 3*b*) short, 2-articulated.

Antenna II (Fig. 3*c, d*) with peduncular article 3 almost equal to article 2, about 4 times as long as wide, with separate rare tufts of long setae along distoventral margin; article 2 about 6 times as long as wide; article 1 about 1.5 times as long as wide; flagellum relatively short, consisting of about 10–11articles bearing relatively short setae.

Mouthparts. Labrum entire, broader than long, with entire outer lobes and developed inner lobes exceeding half of outer lobes. Mandibles (Fig. 3*e*) with incisor process (Fig. 3*f*) and *pars incisiva* similar to other *Niphargus* species; mandibular palp (Fig. 3*e*) with 3 articles: article 1 about 2 times as long as wide, smooth; article 2 about 4 times as long as wide, with numerous setae, article 3 subfalciform, about 3 times as long as wide, slightly shorter than article 2, with numerous marginal and long distal setae, with row of small setae along inner surface. Maxilla I (Fig. 3*g*) with: inner plate with relatively short 3–4 distal setae, outer plate with 7 robust spines armed with 1–2 small lateral teeth each; palp 2-articulated, distal article with a tuft of long simple setae distally. Maxilla II (Fig. 3*h*) with smooth well-developed lobes armed with numerous distolateral setae, distal margins with long simple setae. Maxilliped (Fig. 3*i*) with short inner plates, left plate with 10+ distal simple spines; outer plate reaching half of palp article 2, with row of inner lateral spines; palp 4-articulated, distal article with large spine.

Gnathopods moderate, similar in size, with segment 6 slightly smaller than corresponding coxae (Fig. 2). Gnathopod I (Figs 4*a*, 5*a*) with article 2 robust, about 2–2.5 times as long as wide, with long simple setae along posterior and postero-distal margins; article 3 almost quadrate, as long as wide, similar to article 4; article 4 quadrate, about as long as wide, with row of long setae along posterior margin; article 5 trapezoid in shape, about 1.5 times as long as wide; article 6 (propodus) large, nearly as long as broad, trapezoid, with 7–8 groups of ventral marginal setae; palmar margin poorly convex, almost straight, with medium simple setae, defined on outer face by one strong large corner spine accompanied laterally by 3 stout distally serrated robust spine spines (Figs 4*b*, 5*b*); dactylus strong and sharp, reaching posterior margin of article 6, with a row of small numerus setae along dorsal margin.

Gnathopod II (Figs 4*c*, 5*c*) with article 2 relatively slender, about 3 times as long as wide, with long simple setae along posterior and postero-distal margins; article 3 almost

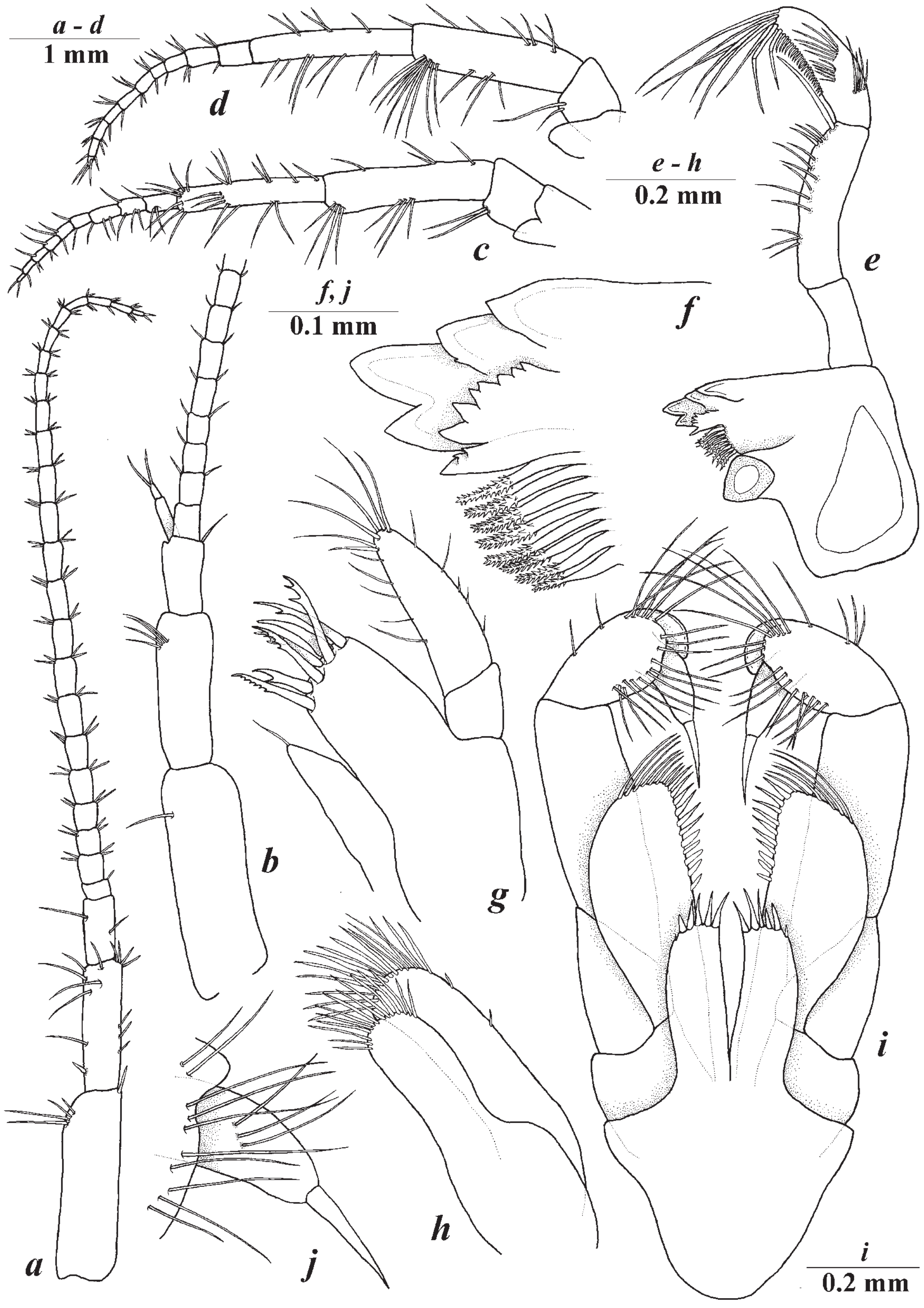

Fig. 3. *Niphargus amirani* sp.n., the Kumistavi (Prometheus) Cave, Tskaltubo–Kumistavi, Western Georgia, Caucasus (*a, c, d–j* — female; *b, d* — male): *a, b* — antenna I; *c, d* — antenna II; *e* — mandible (right); *f* — incisor process and *pars incisiva* of right mandible; *g* — maxilla I; *h* — maxilla II; *i* — maxilliped; *j* — distal article of maxilliped.

Рис. 3. *Niphargus amirani* sp.n., пещера Кумистави (Прометея), Цхалтубо–Кумистави, Западная Грузия, Кавказ (*a, c, d–j* — самка; *b, d* — самец): *a, b* — антенна I; *c, d* — антенна II; *e* — мандибула (правая); *f* — режущий отросток и *pars incisiva* правой мандибулы; *g* — максилла I; *h* — максилла II; *i* — максиллипед; *j* — дистальный членик максиллипед.

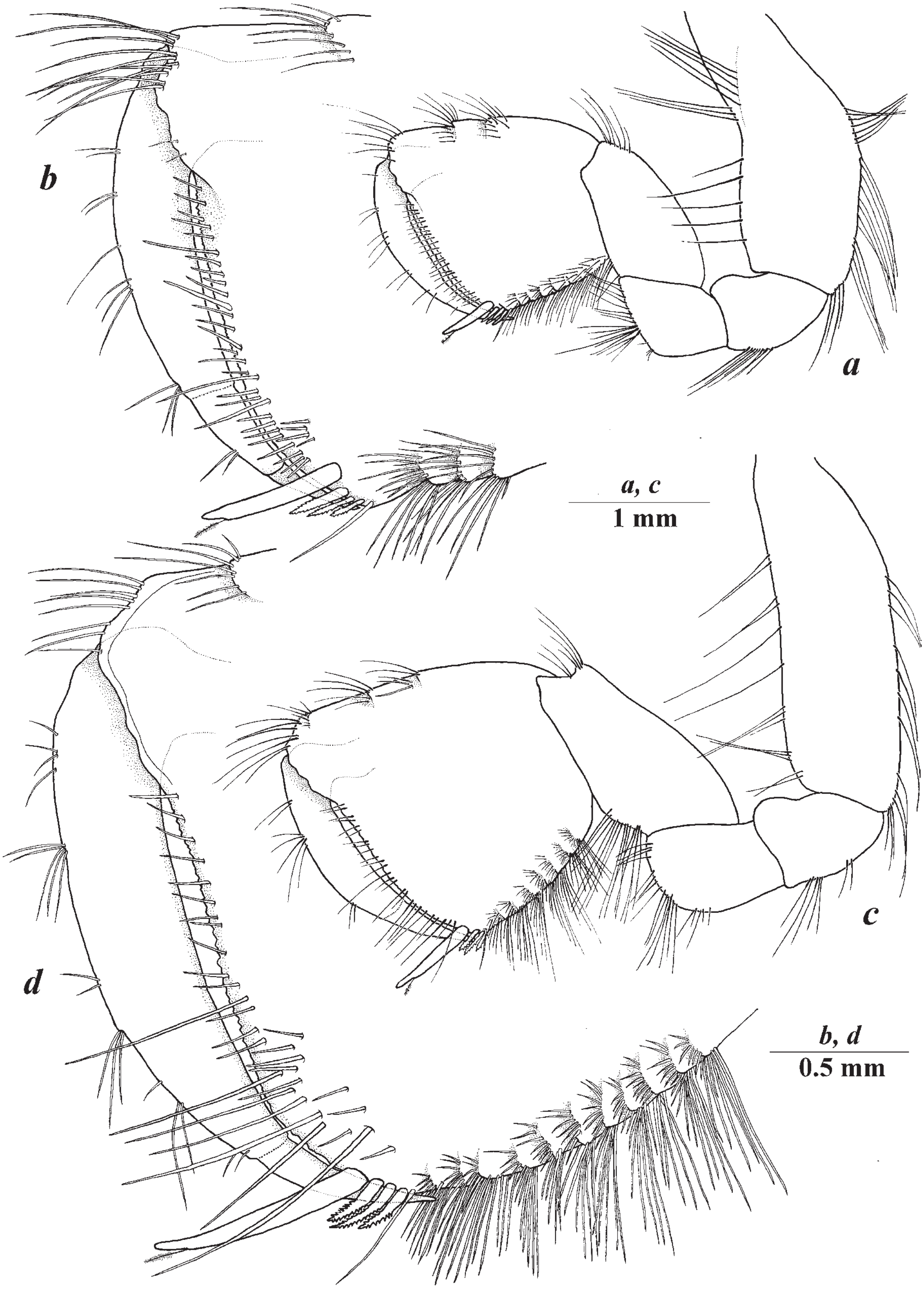

Fig. 4. *Niphargus amirani* sp.n., the Kumistavi (Prometheus) Cave, Tskaltubo–Kumistavi, Western Georgia, Caucasus, female: *a* — gnathopod I; *b* — same, distal palmar margin and dactylus; *c* — gnathopod II; *d* — same, distal palmar margin and dactylus.

Рис. 4. *Niphargus amirani* sp.n., пещера Кумистави (Прометея), Цхалтубо–Кумистави, Западная Грузия, Кавказ, самка: *a* — гнатопод I; *b* — то же, дистальный край клешни и дактилус; *c* — гнатопод II; *d* — то же, дистальный край клешни и дактилус.

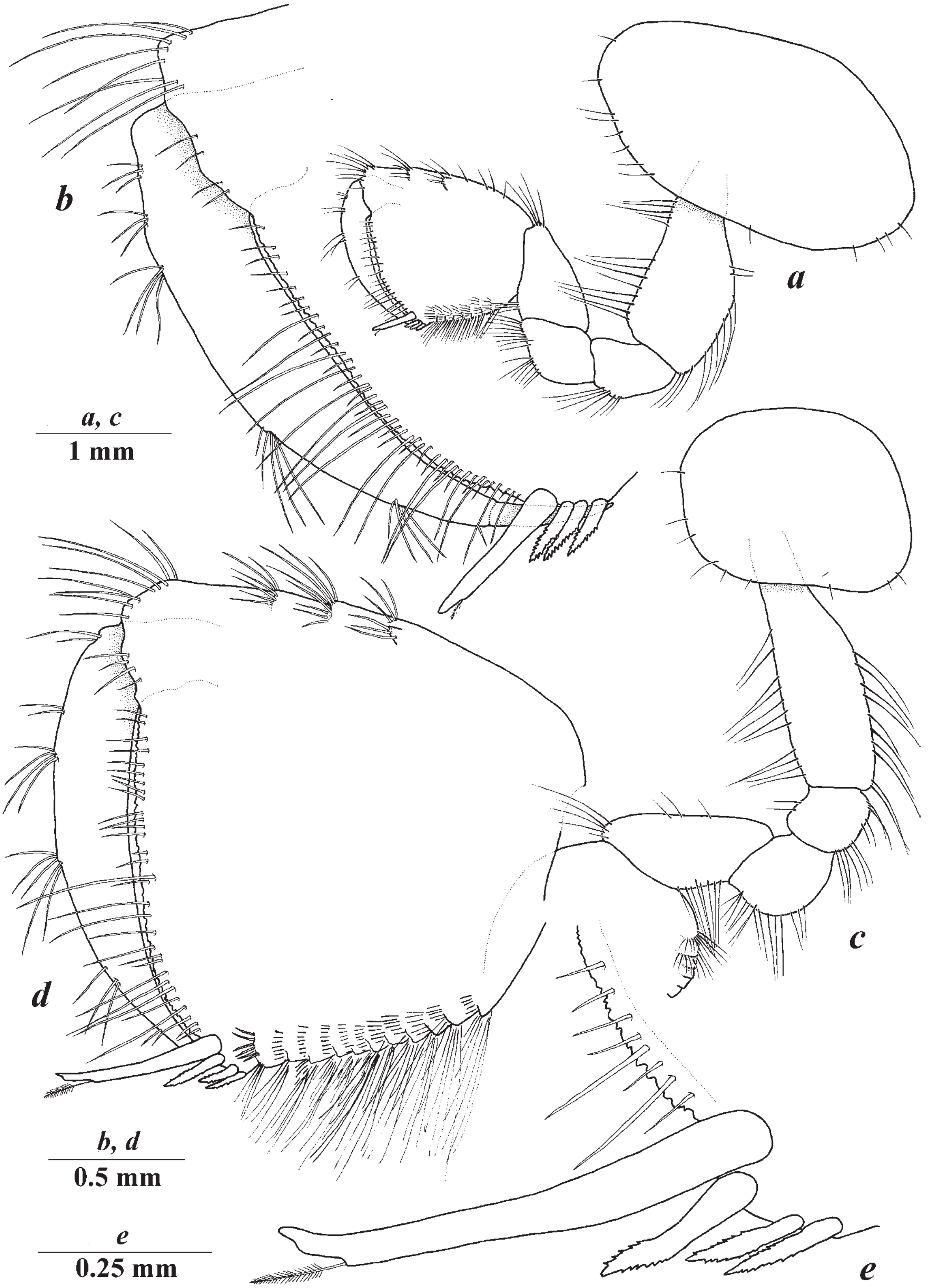

Fig. 5. *Niphargus amirani* sp.n., the Kumistavi (Prometheus) Cave, Tskaltubo–Kumistavi, Western Georgia, Caucasus, male: *a* — gnathopod I; *b* — same, distal palmar margin and dactylus; *c* — proximal segments of gnathopod II; *d* — palm and dactylus (chela) of gnathopod II; *e* — disto-ventral palmar margin of gnathopod II.

Рис. 5. *Niphargus amirani* sp.n., пещера Кумистави (Прометея), Цхалтубо–Кумистави, Западная Грузия, Кавказ, самец: *a* — гнатопод I; *b* — то же, дистальный край клешни и дактилус; *c* — проксимальные сегменты гнатопод II; *d* — пальмарная часть клешни и дактилус гнатопод II; *e* — дисто-вентральный край клешни гнатопода II.

about as long as wide, similar to article 4; article 4 subquadrate, about 1.5 times as long as wide, with row of long setae along posterior margin; article 5 trapezoid in shape, about 2 times as long as wide; article 6 (propodus) large, nearly as long as broad, trapezoid, with 6–7 groups of ventral marginal setae; palmar margin (Figs 4*d*, 5*d*) poorly convex, almost straight, with medium simple setae, defined on outer face by one strong large corner spine accompanied laterally by 3 stout distally serrated robust spine spines (Fig. 5*e*); dactylus strong and sharp, reaching posterior margin of article 6, with a row of small numerus setae along dorsal margin.

Ambulatory pereopods relatively robust, armed with single long simple setae. Pereopods III–IV (Fig. 6*a–c*) almost similar in size and shape; article 2 about 5–6 times as long as wide, with posterior margin bearing long marginal setae; articles 3 short, about as long as wide; article 4 about 4 times as long as wide, with simple setae along dorsal and ventral margins; articles 5 shorter than article 6, about 3–3.5 times as long as wide; article 6 about 6–7 times as long as wide, with small simple spines along ventral margin; dactylus (Fig. 6*b*) relatively slender, curved, sharp distally, with small ventral median spine.

Pereopods V–VI (Fig. 6*d, e*) with article 2 almost subrectangular, about twice as long as wide, widening proximally, with feebly marked ventro-posterior lobe, posterior margin barely concave in middle, anterior margin of article 2 slightly convex, with a row of slender marginal setae that slightly longer than posterior; article 3 small, subquadrate, as long as wide; article 4 about 3–3.5 times as long as wide, with short setae along dorsal and ventral margins; article 5 robust, about 3–3.5 times as long as wide, almost equal to article 4; article 6 relatively slender, about 6–7 times as long as wide, armed with short simple spines; dactylus slender, curved, sharp distally, with additional ventral median spine.

Pereopod VII (Fig. 6*f*) moderately slender, with article 2 narrowly rectangular, twice as long as broad, anterior and posterior margins slightly convex; articles 3 small and short, as long as wide; article 4 about 3 times as long as wide, with short spines along dorsal and ventral margins; article 5 about 4–4.5 times as long as wide, shorter than article 6, armed with simple setae; article 6 slender, about 12 times as long as wide, armed with small single setae along margins; dactylus slender, curved, sharp distally, without additional ventral median spine.

Pleopods normal, without specific features, with 4 hooks in retinacle of pleopods (Fig. 7*g*).

Uropod I (Fig. 7*c*) with protopodite (peduncle) about 5 times as long as wide, longer than rami, with a dorso-external row of slender simple spines; rami about 5 times as long as wide, equal in length, armed with armed with lateral and distal relatively robust simple spines.

Uropod II (Fig. 7*d*) with protopodite (peduncle) about 2–2.5 times as long as wide, equal to rami; rami almost equal in size, with lateral and distal slender spines.

Uropod III (Fig. 7*e, f*) different in males and females. Uropod III in females (Fig. 7*e*) with protopodite about 2 times as long as wide, rami unequal, inner ramus short, about 7–7.5 times shorter than outer one, bearing several small distal and lateral spines; outer ramus long, proximal article about 10–10.5 times as long as wide, distal article about 3 times shorter than previous article, about 4–4.5 times as long as wide, with several small distal simple setae. Uropod III in males (Fig. 7*f*) with protopodite about 2 times as long as wide, rami unequal, inner ramus short, about 5–5.5 times shorter than outer one, bearing several small distal and lateral spines; outer ramus long, proximal article about 14 times as long as wide, distal article about 1.5 times shorter than previous article, about 20–21 times as long as wide, with several small distal simple setae.

Telson (Fig. 7*b*) about as long as broad, ca 80% incised, lobes obtuse and sloping distally. Armature of telson is variable, bearing 4–6 long distal spines, and 2 outer marginal spines on each side; distal and marginal spines relatively long and slender, reaching about 0.5–0.7 of length of telson.

COLORATION. Body and appendages are completely white.

BODY SIZE. The largest collected female has bl. 10 mm; the largest male has bl. 11.5 mm.

GENBANK ACCESSION NUMBER. MW014293–MW014296.

ETYMOLOGY. The species is named after the Caucasian ethnic hero Amirani. The legend says, "*Amirani, like Prometheus, angered the Gods and was punished. Days and nights eagle tormented him eating his liver; however, in contrast to the Greek giant, cruel Gods chained Amirani not to the rock, but somewhere inside a huge cave (presumably, in Kumistavi Cave)*". This legend fits very well with the situation with a new species, which remained "chained" in the Kumistavi Cave after the separation of the ancestral area into separate karst massifs.

TAXONOMIC REMARKS. The new species clearly belongs to the cave-dwelling group of species, native to the Caucasus (sometimes called "*ablaskiri*" species complex), and related to the "*carpathicus*" species complex (after Straškraba, 1972). The presently known Caucasian and neighboring representatives of the groups are *Niphargus borutzkyi* Birštein, 1933 (Malacostraca: Amphipoda: Niphargidae) described from the Tskaltsitela (=Iazoni) Cave (42°16"03.7"N 42°43"50.0"E) near Kutaisi [Birštein, 1933, 1950], *N. ablaskiri* Birštein, 1940 described from the Abrskil Cave (42°55"14.0"N 41°33"17.0"E), Abkhazia [Birštein, 1940]; *N. inermis* Birštein, 1940 known from the Lower Shakuran (=Nizhne-Shakuranskaya) Cave (43°01"47.8"N, 41°20"02.0"E), Abkhazia [Birštein, 1940]; *N. vadimi* Birštein, 1961 from the Skelskaya Cave (44°27"45.6"N 33°52"11.8"E) and *N. dimorphus* Birštein, 1961 from the vicinity of Sorokino (Perevalnoe) (the Crimean Peninsula) [Birštein, 1961] and recently described *N. dbari* Marin, 2019 from the Gegskaya (Gega) Cave (43°23"43.7"N 40°27"28.4"E), Abkhazia [Marin, 2019a]. The related taxa from the neighboring regions are Iranian *N. daniali* Esmaeili-Rineh et Sari, 2013 and 2 European species, *N. ambulator* G. Karaman, 1975 and *N. gebhardti* Schellenberg, 1934. Taxonomic features of the group are elongated and deeply dissected telson with long distal, subdistal and lateral long simple spines and relatively short distal article of uropod III (see Birštein, 1940).

From mostly related *N. borutzkyi*, the new species can be separated by the presence of 3 spine-like setae on dorso-proximal angle of urosomite II (Fig. 8*a*) (vs. always 4 spine-like setae in *N. borutzkyi* (Fig. 8*b*)); and longer distal segment of uropod III in females, which is more than 4 times as long as wide in the new species (Fig. 7*e*) (vs. about 3 times as long as wide in *N. borutzkyi* (Fig. 8*f*)). These morphological features are minor but permanent and allow separating the species in the museum collections. At the same time, these species can be separated from the related species by stout telson, which is about as long as wide (vs. about not less than 1.5 times in other related species); relatively stout basal part of dactyli of pereopods III–VII, which is about as

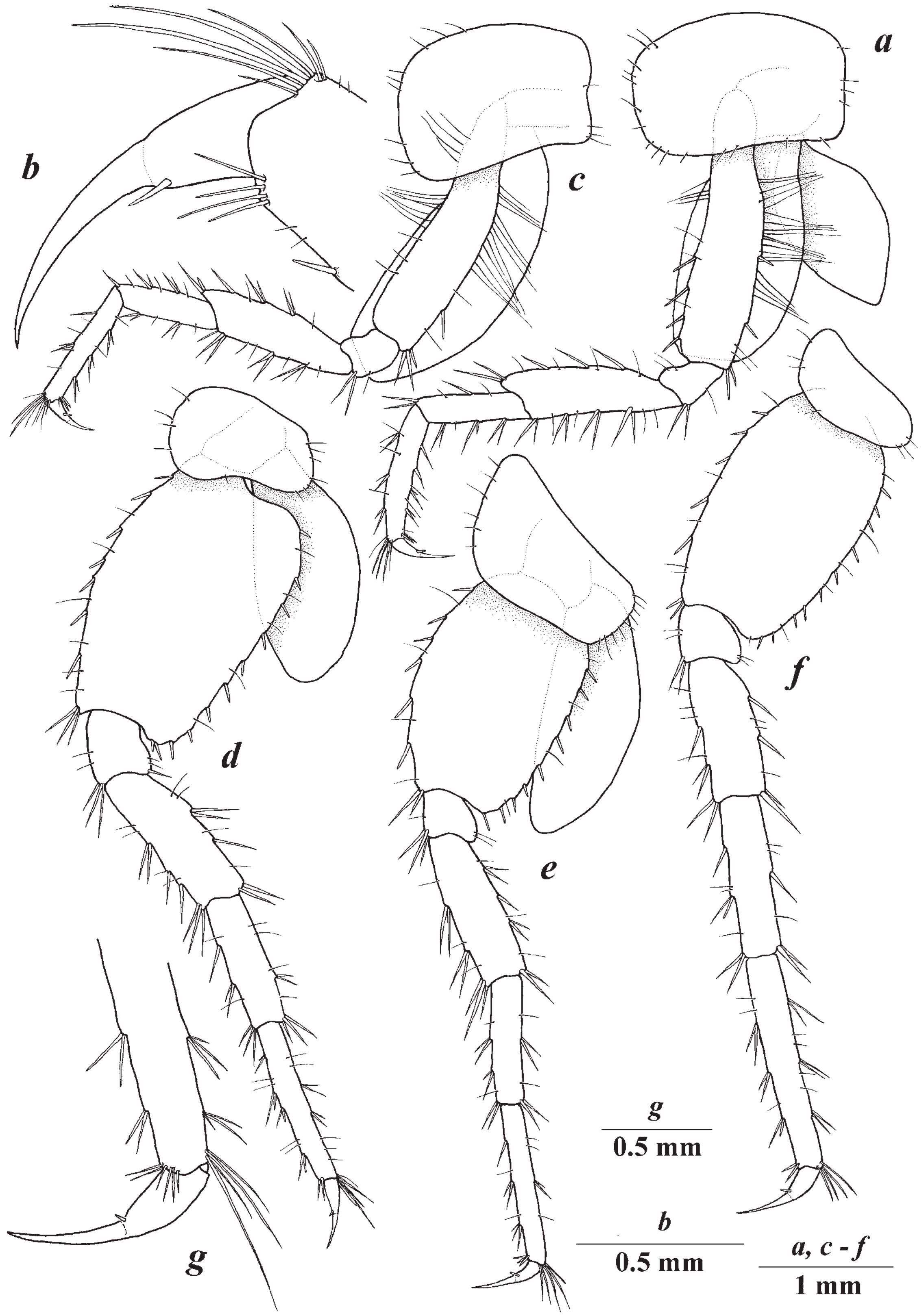

Fig. 6. *Niphargus amirani* sp.n., the Kumistavi (Prometheus) Cave, Tskaltubo–Kumistavi, Western Georgia, Caucasus, female: *a* — pereopod III; *b* — same, dactylus; *c* — pereopod IV; *d* — pereopod V; *e* — pereopod VI; *f* — pereopod VII; *g* — same, dactylus.

Рис. 6. *Niphargus amirani* sp.n., пещера Кумистави (Прометея), Цхалтубо–Кумистави, Западная Грузия, Кавказ, самка: *a* — переопода III; *b* — тоже, дактилус; *c* — переопода IV; *d* — переопода V; *e* — переопода VI; *f* — переопода VII; *g* — тоже, дактилус.

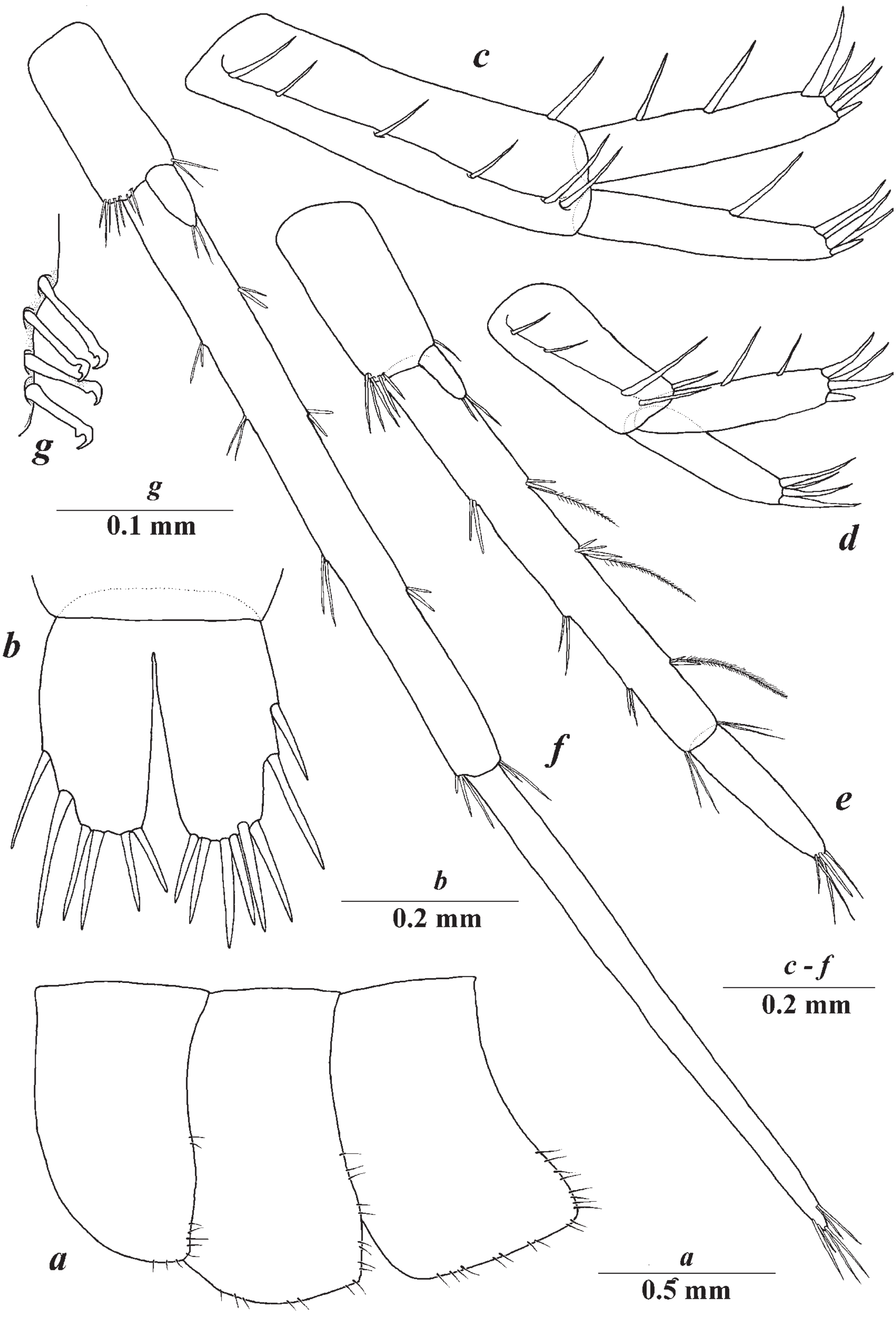

Fig. 7. *Niphargus amirani* sp.n., the Kumistavi (Prometheus) Cave, Tskaltubo–Kumistavi, Western Georgia, Caucasus, female (*a–e*) and male (*f*): *a* — pleonites and epimeral plates I–III; *b* — telson; *c* — uropod I; *d* — uropod II; *e, f* — uropod III; *g* — retinacule of pleopod I.

Рис. 7. *Niphargus amirani* sp.n., пещера Кумистави (Прометея), Цхалтубо-Кумистави, Западная Грузия, Кавказ, самка (*a–e*) и самец (*f*): *a* — плеониты и эпимеральные пластинки I и III; *b* — тельсон; *c* — уроподы I; *d* — уроподы II; *e, f* — уроподы III; г — ретинакула плеопод I.

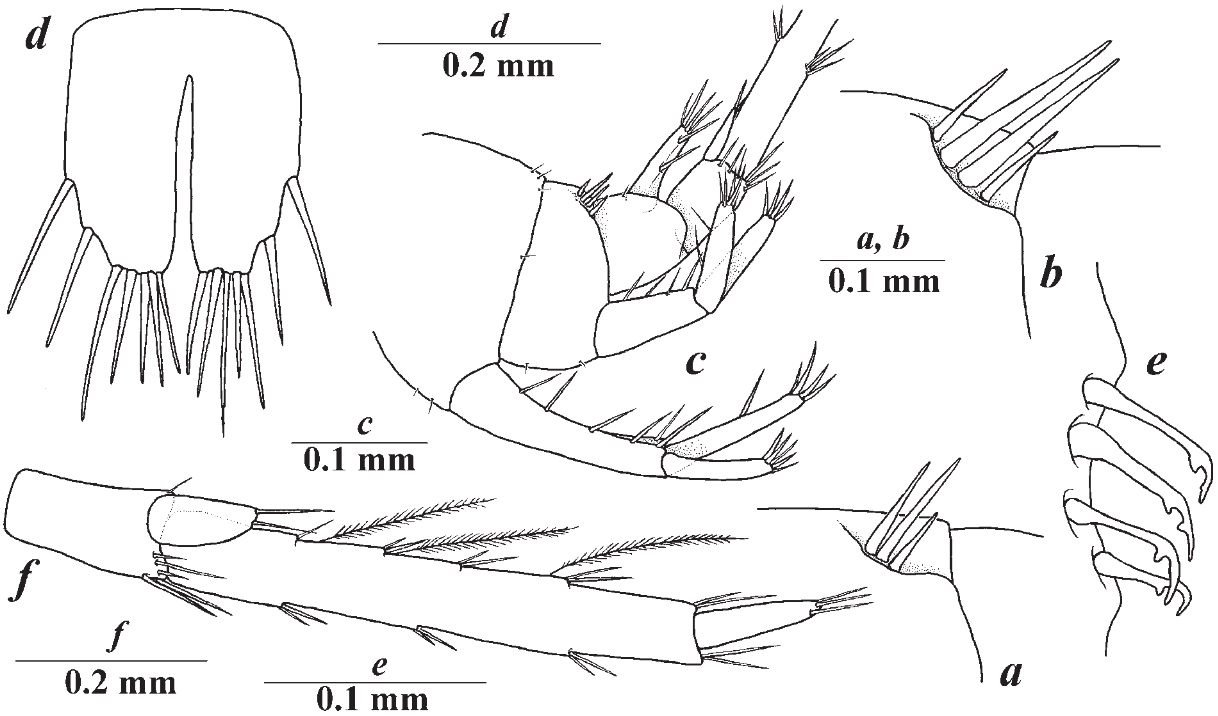

Fig. 8. *Niphargus amirani* sp.n., female from the Kumistavi Cave (*a*) and *N. borutzkyi* Birštein, 1933 from the Tskaltsitela (=Iazoni) Cave, female (*b–f*), Imereti region of the Western Georgia, Caucasus: *a, b* — dorso-proximal angel of urosomite II; *c* — urosomites I–III; *d* — telson; *e* — retinacule of pleopod I; *f* — uropod III.

Рис. 8. *Niphargus amirani* sp.n., самка из пещеры Кумистави (Прометея) (*a*) и *N. borutzkyi* Birъtein, 1933 из пещеры Цхалицитела (=Язони), самка (*b–f*), Имеретинский район Западной Грузии, Кавказ: *a, b* — дорсо-проксимальный угол уросомита II; *c* — уросомиты I–III; *d* — тельсон; *e* — ретинакула плеопод I; *f* — уропод III.

long as wide (vs. usually more than 1.5 times as long as wide in other related species); and almost rectangular palm of gnathopods I–II with straight distal margins (vs. usually sloped distal margin in other related species).

From *N. gegi*, the new species can be clearly separated by shorter telson with 2 outer marginal spines on each side; stouter basal part of dactyli of pereopods III–VII; and shorter outer ramus of uropod III in females.

From *N. ablaskiri*, the new species can be separated by shorter telson with 2 outer marginal spines on each side; almost straight distal margin of palm of gnathopods I–II, which is significantly sloped in *N. ablaskiri*; and stouter basal part of dactyli of pereopods III–VII.

From *N. inermis*, the new species can be separated by shorter telson, almost straight distal margin of palm of gnathopods I and II, and the presence of well-marked additional spine on dactyli of pereopods III–VII, which is mostly very small and reduced in *N. inermis*.

ECOLOGY AND DISTRIBUTION. *Niphargus amirani* sp.n. is presently known from the type locality only, inhabiting subterranean stream and small lakes inside the Kumistavi (Prometheus) Cave (42°22′35.8″N 42°36′03.2″E), Tskaltubo–Kumistavi, Imereti region of the Western Georgia, Caucasus. The other stygobiotic crustacean species known from the same cave system is *Xiphocaridinella kumistavi* Marin, 2017 (Crustacea: Decapoda: Atyidae) [Marin, 2017a]. The known subterranean fauna of the cave consists of 21 terrestrial species, including diplurans, insects, millipedes, mites, mollusks and springtails (see Barjadze *et al*., 2015).

Niphargus borutzkyi Birštein, 1933
Fig. 8*b–f*.

MATERIAL EXAMINED. 1 female (bl. 10.0 mm), 3 females, LEMMI, Caucasus, Western Georgia, Imereti region, Kutaisi, Tskaltsitela (=Iazoni) Cave, 42°16′03.7″N 42°43′50.0″E, in subterranean stream, about 120 meters above the sea level, coll. I. Marin, 25 Jan. 2018.

DIAGNOSIS. Urosomite II with 4 spine-like setae in dorso-proximal angle. Epimeral plates subangular, with rounded ventro-posterior corner. Maxilla I with inner plate armed with 7+ setae, outer plate with 7 spines. Gnathopods I–II moderate, palm almost rectangular, with straight distal margin, dactylus with row of several setae along outer margin. Dactyli of pereopods III–VII with relatively stout basal (proximal part), at inner margin with 1 spine or seta near basis of nail. Pleopods with 4 hooks in retinacle of pleopods. Uropod III elongated, article 2 of outer ramus long, article 1 (distal) about 3 times as long as wide in females. Telson short and relatively stout, deeply incised, each lobe with 4–5 long distal spines and 2 outer marginal spines, facial spines absent.

COLORATION. Body and appendages are completely white.

BODY SIZE. The largest collected female has bl. 10 mm.

GENBANK ACCESSION NUMBER. MW014297–MW014300.

REMARKS. The type series of *Niphargus borutzkyi* Birštein, 1933 from the Tskaltsitela (=Iazoni) Cave, including about 95 specimens, is deposited in ZMMU (ZMMU

Mb-128). The specimens are in poor condition, have been dried for a long time, which does not allow for a thorough morphological study, and due to long-term storage, molecular-genetic analysis of the samples is also currently unavailable.

ECOLOGY AND DISTRIBUTION. The species is known from subterranean stream of the Tskaltsitela (=Iazoni) Cave (42°16′19.62″N 42°44′1.63″E) (the type locality of the species), the subterranean lakes of Sataplia Cave (42°18′56.9″N 42°40′24.3″E) and, probably, Sapichkhia (=Sapichxia, Rionhesi) Cave (see Barjadze *et al.*, 2015; present data), which are represented the same karst system (Mtsvanekvavila–Sapichkhia–Godora karst massif) (after Jinjikhadze & Chkheidze, 2018). The other stygobiotic crustacean species known from the same cave system is *Xiphocaridinella kutaissiana* Sadowsky, 1930 (Crustacea: Decapoda: Atyidae), also described from the Tskaltsitela Cave [Marin, 2017a]. The known subterranean fauna of this karst cave system consists of more than 30 terrestrial species, including annelids, centripeds, insects, isopods, false scorpions, harvestmans, maxillopods, millipedes, mollusks, seed shrimps, springtails and spiders (see Barjadze *et al.*, 2015).

Discussion

All known genetic data, based on specimens of the genus *Niphargus* from the vicinity of Kutaisi, Imereti region of the Western Georgia, shows a monophyletic origin of the clade from the common ancestor (see Fig. 1). The phylogenetically related species, based on GenBank (NCBI) database, are *N. dimorphus* from the Crimean Peninsula (see Fig. 1). Moreover, minimal genetic distances show the relation of this clade of cave-dwelling species to some species from the Northern Caucasus, Europe and, even, Iran. Most of these species belong to the "*carpathicus*" species group (after Straškraba, 1972). At the same, the genetic divergence (*p*-distances more than 15% or 0.15 substitutions per 100 nucleotides by COI mtDNA) of the clade from the related species shows its isolation for more than 2–4 Mya (see review in Gay-Haim *et al*. [2018] for molecular clock calibration for peracarid crustaceans for COI mtDNA gene marker). The speciation within the clade occurred during the Quaternary period and is, probably, associated with the mountain formation of the Great Caucasus and the separation of karst massifs in this region (e.g., Jinjikhadze, Chkheidze, 2018). Meleg *et al.* [2013] showed that the habitat heterogeneity can promote speciation and that speciation events can be predicted from species' distributions. Different drainage systems in mountain regions as well as karst sectors can be inhabited by the sets of distinct species if these environments are isolated for some time [Meleg *et al.*, 2013].

The separation of the new species is based on the genetic difference (see Table 2) that is close to the interspecific threshold [Lefébure *et al.*, 2006a, b, 2007; Cothran *et al.*, 2013; Lagrue *et al.*, 2014; Deliæ *et al.*, 2017], the presence of minimal but permanent morphological features (see below), and the modern separation of karst massif inhabited by the species (see Jinjikhadze & Chkheidze, 2018). The karst massifs, inhabited by the new species and *N. borutzkyi*, are isolated (e.g., Jinjikhadze & Chkheidze, 2018) and not presently connected that appears in genetic isolation of other stygobiotic inhabitants (see Marin, 2017a). It is important to note that such conclusions are preliminary and based on the available genetic data only, with the receipt of new data, their correction is possible.

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