

Crustacean “cave fishes” from the Arabika karst massif (Abkhazia, Western Caucasus): new species of stygobiotic crustacean genera *Xiphocaridinella* and *Niphargus* from the Gegskaya Cave and adjacent area

«Пещерные рыбы» карстового массива Арабика (Абхазия, Западный Кавказ): новые виды стигобионтных ракообразных родов *Xiphocaridinella* и *Niphargus* из Гегской пещеры и прилегающих районов

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KEY WORDS: Crustacea, Malacostraca, *Xiphocaridinella*, Atyidae, *Niphargus*, Niphariidae, stygobiotic, new species, Gegskaya Cave, Arabika, Abkhazia, Caucasus.

КЛЮЧЕВЫЕ СЛОВА: Crustacea, Malacostraca, *Xiphocaridinella*, Atyidae, *Niphargus*, Niphariidae, стигобионты, новые виды, Гегская пещера, Арабика, Абхазия, Кавказ.

ABSTRACT. Stygobiotic animals washed from various groundwater sources from the Arabika karst massif (Abkhazia, Western Caucasus) were studied. As a result, new species of stygobiotic crustacean genera *Xiphocaridinella* and *Niphargus* were described based on DNA (COI mtDNA gene marker) and morphological studies in the Gegskaya (Gega) Cave. These crustaceans are probably the legendary cave-dwelling “fishes” which were previously reported from the Arabika karst massif. At the same time, during the study, no real cave fish or any evidence of their presence was found. Genetic delimitation thresholds for Caucasian *Niphargus* species are also discussed in the paper.

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РЕЗЮМЕ. В работе представлены описания стигобионтных животных, вымытых из различных подземных источников разгрузки карстового массива Арабика (Абхазия, Западный Кавказ). На основе анализа ДНК и исследования морфологии из Гегской пещеры описаны новые виды стигобионтных ракообразных родов *Xiphocaridinella* и *Niphargus*. Эти ракообразные, вероятно, представляют собой

легендарных «пещерных» рыбок, которых ранее видели в подземных озерах карстового массива Арабика. В то же время в ходе исследования не было обнаружено ни одной истинной пещерной рыбы или какого-либо подтверждения их присутствия. В статье также впервые обсуждаются пороги (thresholds) генетического разделения видов для кавказских видов рода *Niphargus*.

Introduction

Cave fishes are very diverse, being an important component of almost all tropical subterranean environments (e.g. Jeffery, 2001; Romero, 2001; Romero, Paulson, 2001; Culver, Pipan, 2009; Borowsky, 2018). *Troglocobitis starostini* (Parin, 1983) (Nemacheilidae), the only true cave-dwelling fish species presently known within the former USSR, including Europe and Central Asia, was described from the Köytendag ridge (37°55'N 66°23'E), Chardzhou province, Turkmenistan [Parin, 1983]. The only known European stygobiotic fish is presented by the underground population of the loach genus *Barbatula* Linck, 1790 (Nemacheilidae), recently discovered in the Donau-Aach underground karst water system in the southern Germany [Behrmann-Godel *et al.*, 2017] (provisionally named European cave loach). The population is morphologically and genetically differentiated from the common loach *Barbatula barbatula* (Linnaeus, 1758), living in the adja-

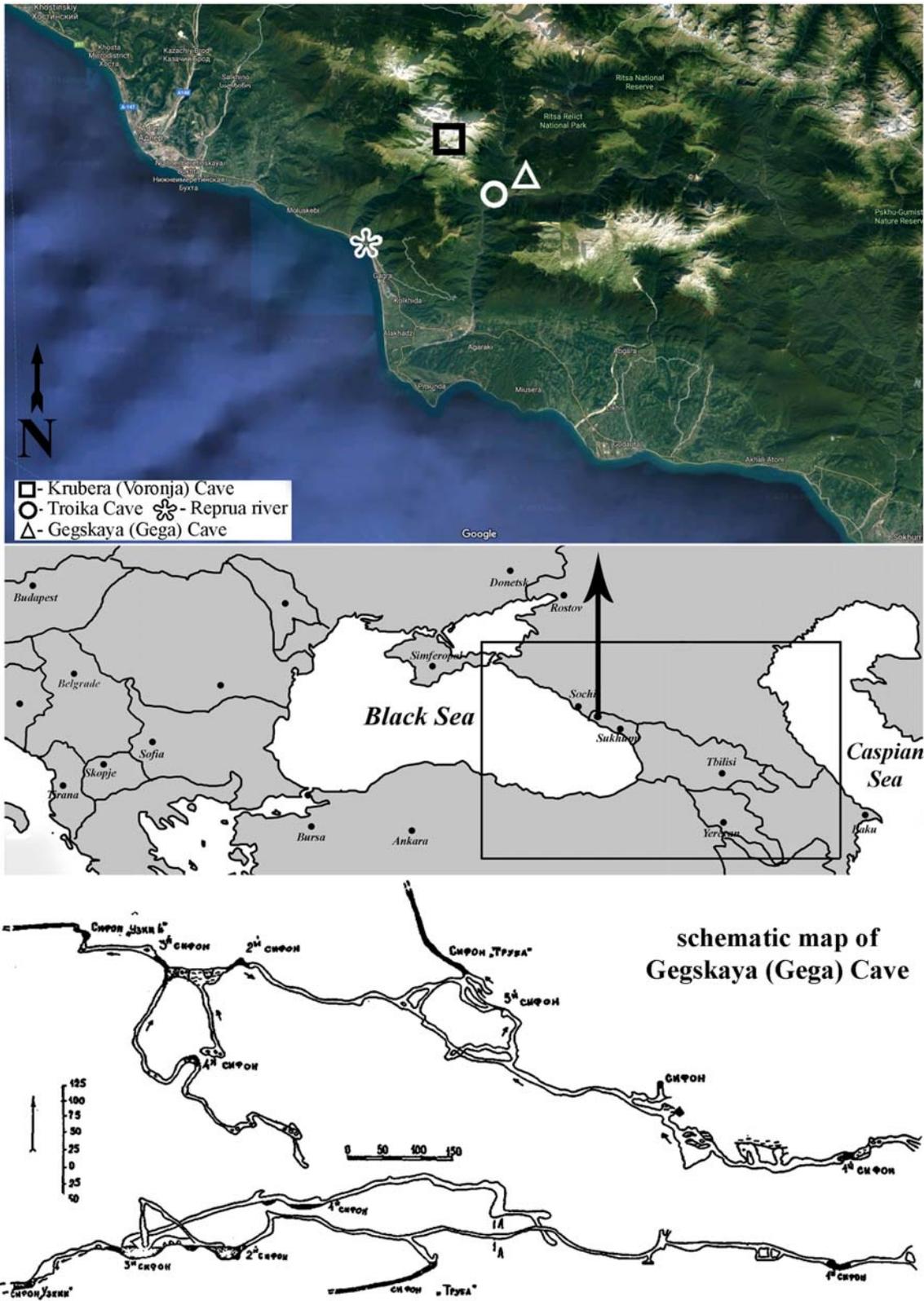


Fig. 1. Map of distribution of caves and rivers of the Arabika karst massif (Abkhazia, Western Caucasus) where crustaceans were collected; with schematic map of the Gegskaya (Gega) Cave.

Рис. 1. Карта размещения пещер и источников карстового массива Арабика (Абхазия, Западный Кавказ), где были собраны ракообразные; со схематической картой Гегской пещеры.

cent surface waters, but not in the status of the separate species. To date, neither cave fish nor underground populations of common species have been described in karst systems in the Western Caucasus [Romero, Paulson, 2001], which is the second (after the Balkan Peninsula) region of the Western Palearctic in the size and diversity of karst landscapes.

At the same time, information about the possible occurrence of blind and translucent cave fishes inside the Arabika karst massif, namely inside the deepest world cave – Krubera (Voronya) Cave [Samokhin, Bizoukin, 2018] and Diaklaz siphon in Gegskaya (Gega) Cave [Anonymous, 2018], was noticed by cave divers and published for several times on the Internet. Genady Samokhin, a famous cave diver, noted after the diving in the “Two Captains” sump (–2144 m) inside the Krubera-Voronya Cave in August 2016 Expedition: “... lying in the crack, I observed a school of small, translucent fish with flat elongated bodies and tail fins. Why I haven’t seen them before? Most likely, I focused on the morphology of the sump and did not notice them ...” [Samokhin, Bizyukin, 2018]. There is a legend that any “small transparent” fishes live in underground lakes inside caves of the Arabika karst massif. Unfortunately, scientists have never collected or researched samples of such mysterious Caucasian cave fishes. At the same time, it is known that a unique endemic fauna lives in the Arabika karst massif [e.g., Sidorov, 2014; Sidorov *et al.*, 2015, 2018; Sidorov, Samokhin, 2016] and some interesting animals are expected to be discovered from there.

The hydrogeology of the groundwater flow in the Arabika karst massif with the highest point of the Arabika mountain (43°25′06.3″N 40°21′23.5″E), located on the Gagra Range of the Western Caucasus, is represented by several springs (rivers), such as Reprua (river), Kholodnaya Rechka (Cold River), the Gega waterfall and the Gegskaya (Gega) Cave in the Bzyb Canyon, springs in the Goluboe (Blue) Lake as well as several small sources around the Gagra City (e.g., Kiknadze, 1979; Klimchuk, 1990, 2006). The author collected material from various sources of karst water discharge from the massif, and also took samples in some underground environments, including large underground lakes. As a result, numerous specimens of *Xiphocaridinella* and *Niphargus* were found in the studied springs and lakes, probably representing these legendary small transparent cave “fish” (see Fig. 2a, b), and the author photographed them *in situ* in a large subterranean lake inside the Gegskaya Cave (43°23′43.7″N 40°27′28.4″E). A study of DNA markers and morphology of both collected *Xiphocaridinella* and *Niphargus* samples showed that they belong to distinct species described herewith as new to science. At the same time, during the study, no real cave fish were found. However, *in situ* photographs of representatives of the genus *Xiphocaridinella* showed a clear resemblance to blind and transparent swimming fishes (see Fig. 2b).

Material and methods

Specimens of *Xiphocaridinella* were collected by hand net from the Gegskaya (Gega) Cave (43°23′43.7″N 40°27′28.4″E) and the Verevkina Cave (43°24′56.0″N 40°21′23.0″E) while *Niphargus* specimens — from the Gegskaya (Gega) Cave and Reprua River (43°19′52.0″N 40°12′16.8″E; 0 m above sea level) (see Fig. 1). Alive specimens of *Xiphocaridinella* and *Niphargus* were photographed *in situ* using Pentax digital camera. In addition, in the laboratory, live specimens of *Xiphocaridinella* and *Niphargus* were relaxed with clove oil and photographed using a Canon G16 camera. All collected specimens were preserved and stored in 96% solution of ethanol for further DNA analysis. Postorbital carapace length (pcl., in mm), the length from posterior orbit to the posterodorsal margin of carapace, and total body length (tbl., in mm), dorsal length from tip of rostrum till the distal margin of telson for *Xiphocaridinella* shrimps and dorsal length from the distal margin of head to the distal margin of telson (tbl., in mm) for *Niphargus*, are used as standard measurements. Type material is deposited in the collection of the Zoological Museum of Moscow State University, Moscow (ZMMU), and additional material is in the collection of the Zoological Institute of the Russian Academy of Sciences (ZIN), St-Petersburg, Russia and the Laboratory of Ecology and Evolution of Marine Invertebrates (LEMMI) of A.N. Severtzov Institute of Ecology and Evolution of the Russian Academy of Sciences, Moscow, Russia.

To study molecular genetic barcode, a fragment of the mitochondrial gene coding for cytochrome c oxidase subunit I (COI mtDNA) gene marker was amplified, sequencing and compared. Total genomic DNA was extracted from abdominal and pereopod muscle tissue using the innuPREP DNA Micro Kit (AnalytikJena, Germany) following the manufacturer’s protocol. The gene marker was amplified with the help of the universal primers LCO1490 (5′-ggtaacaatcat-aaagatattgg-3′) and HC02198 (5′-taaacctcagggtgacccaaaaatca-3′) [Folmer *et al.* 1994]. PCR products were performed on amplifactor 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 10uL of reaction mixture contained 1uL of total DNA, 2uL of 5xPCR mix (Dialat, Russia) and 1uL 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 Analyzer ABI 3500 (Applied Biosystems Inc.) and BigDye 3.1 (Applied Biosystems Inc.) with direct and reverse primers. Uniformity of obtained sequences was processed using the program BioEdit v. 5.0.9. A dataset of COI mtDNA gene markers used in the study are presented in previously published data on *Xiphocaridinella* (see Marin, 2018a, b) as well as were taken from GenBank (NCBI) (see Appendix 1). The aligned sequences of COI mtDNA gene markers, 658 base pairs in length, were analyzed for pairwise sequence divergence (uncorrected *p*-distances) and used to construct the phylogenetic relations. The best evolutionary substitution model was determined using MEGA 7.0. and jModeltest2.1.141. Phylogenetic analysis was performed using MrBayes v.3.2.6 for Bayesian analysis (BA) using NKY+I+G evolutionary model and MEGA 7.0 for Maximum-Likelihood (ML), Neighbour-Joining (NJ), UPGMA (unweighted pair group method

with arithmetic mean) analyses using Kimura-2-parameter (K2P) model. Bayesian analysis was carried out by sampling one tree every 1,000 generations over 1,000,000 generations. Values of confidence >50% are presented for ML, NJ and BA analyses (bootstraps); the divergence of pairwise genetic distances (p-distances) was calculated using the Kimura-2-parameter (K2P) model in MEGA 7.0. The species delimitation is carried out according to the latest understanding of the interspecific distances at cave crustaceans [Zakšek *et al.*, 2009, 2019; Copilas-Ciocianu *et al.*, 2017; Delia *et al.*, 2017; Marin, 2017b, 2018a, b].

Systematic account

Order **Decapoda** Latreille, 1802

Family **Atyidae** De Haan, 1849

Genus ***Xiphocaridinella*** Sadowsky, 1930

***Xiphocaridinella dbari* sp.n.**

Figs. 2–5.

MATERIAL EXAMINED. Holotype: 1 male (pcl. 7.5 mm, tbl. 24.0 mm), ZMMU Ma3574, Abkhazia, Gagry region, Bzyb River Canyon, Gegskaya (Gega) Cave, 43°23'43.7"N 40°27'28.4"E, about 273 m above sea level, in cave lake, coll. I. Marin, 17 Sept. 2017; 5 non-ovigerous females, 5 males, (LEMMI), same locality and date as holotype; 1 non-ovigerous females, LEMMI, Abkhazia, Gagry region, Arabika karst massif, Verevkina Cave, 43°24'56.0"N 40°21'23.0"E, about –400 m from of the cave entrance, in cave lake, unknown date, unknown collector; 1 non-ovigerous females, LEMMI, Verevkina Cave, coll. Natalia and Andrey Sizikov, 10–15 Sept. 2018.

DESCRIPTION. Medium-sized shrimp with swollen, smooth, subcylindrical body (Fig. 2e–g). Carapace swollen, smooth, with small dorsal carina in frontal part (Fig. 3a–d). Rostrum (Fig. 3a–d) short, robust, slender, not reaching the distal margin of basal antennular segment, triangular in shape, dorsally and ventrally unarmed, sharply pointed distally, with tip turned forward, broad proximally, with developed lateral lamina (Fig. 3a–d).

Abdominal somites smooth, unarmed; tergites non-carinate, without dorsal lobes, not posteriorly produced; pleura of pleomeres I–IV posteroventrally and ventrally rounded; pleomere V small, with feebly developed pleura; distal and distoventral margins of pleomere VI sharply produced posterodorsally. Telson (Fig. 3e) relatively slender, smooth, about 3 times as long as wide proximally, tapering distally, with 2 pairs of slender dorsal spines, each about 0.08 of telson length, situated at about 0.45 and 0.75 telson length respectively; distal margin convex, with 4–5 pairs of distal spines, including a pair of short lateral spines, a pair of long intermediate spines and 2–3 pairs of slender medial marginal spines.

Eyes (Fig. 3a–d) partly reduced, subcylindrical, covered by carapace; cornea rounded, reduced and feebly marked, without pigment; eyestalk stout, swollen, cylindrical, about as long as wide.

Antennula (Fig. 3a–d, f) with stout unarmed articles, basal peduncular segment robust, about twice as long as proximal width, without ventromedial tooth, distolateral angle with broadly produced blunt projection (Fig. 3f); stylocerite stout, sharpening distally, overreaching the midlength of basal segment; second and third segments stout, unarmed; second segment about 1.5–2 times as long as wide and about 1.5–2 times as long as distal segment; distal segment about as long as wide.

Antenna (Fig. 3g) with basicerite stout, about 1.5 times as wide as long, with distolateral margin unarmed; caropocrite robust, about 1.5 times as long as wide, not reaching midlength of scaphocerite; scaphocerite well developed, broad, with small but well marked distolateral tooth, lamella bluntly rounded distally.

Mouthparts typical for the genus and were not dissected. Maxilliped III (Fig. 4a) with slender segments; epipodite stout, bluntly rounded; arthrobranch reduced; exopodite slender, overreaching the distal margin of antepenultimate segment; antepenultimate segment slender, about 6–7 times as long as wide; penultimate segment about 6–7 times as long as wide, with straight lateral margins; ultimate (distal) segment slender, equal to penultimate segment, about 6–7 times as long as wide, tapering distally, with tufts of short simple stick-like setae along ventral and lateral margins, with several tufts of long setae dorsally.

Pereiopods I equal in size and similar in shape, and similar in females (Fig. 4b) and males (Fig. 4g), with smooth unarmed segments; coxa with well-developed slender epipodite and tuft of long simple setobranchs; basis about as long as wide, with well-developed exopodite overreaching carpo-meral articulation; ischium about 2–3 times longer than wide, with straight margins; merus slender, about 3 times as long as wide, equal to ischium, with straight margins; carpus relatively stout, significantly widening distally, equal to merus, about as 1.5 times as long as maximal width; palm relatively stout, about as long as wide, subcylindrical in cross-section, smooth; fingers relatively slender, subcylindrical, smooth, with blunt distal margins, about 3 times as long as proximal width, armed with a row of stout strong plumose setae distally.

Pereiopods II (Fig. 4c, h) equal in size and similar in shape, similar in males and females and almost similar to pereiopod I, with relatively stouter basal smooth unarmed segments; coxa with well-developed slender epipodite and tuft of setobranchs; basis about as long as wide, with well-developed exopodite overreaching carpo-meral articulation; ischium about 3 times as long as wide, with straight margins, unarmed; merus slender, about 4 times as long as wide, usually equal to ischium or lightly longer, with straight margins; carpus slender, about 4–5 times as long as wide, slightly widening distally, longer than merus; palm relatively stout, similar to palm of pereiopod I, about as long as wide, subcylindrical in cross-section, smooth; fingers relatively slender, subcylindrical, smooth tapering distally, about 4 times as long as proximal width, with simple and straight cutting edges, with broad blunt distal margin, armed with a row of stout strong plumose setae distally.

Pereiopod III in females (Fig. 4d) with rectangular coxa, about as long as wide, with tuft of long simple setobranchs, with small epipodite; basis about as long as wide, with well-marked exopodite almost reaching the midlength of merus; ischium about 2 times as long as wide, with well-marked distoventral spine; merus about 7 times as long as wide, with straight margins, with 2 well marked spines along ventral margin; carpus relatively slender, about 6 times as long as wide, slightly widening distally, about 1.5–2 times shorter than merus and slightly longer than half of the length of propodus, with bluntly projecting distodorsal margin overlapping carpo-propodal articulation; propodus about 10 times as long as wide, with straight margins, armed with 7–8 spines along proximal half of ventral margin (Fig. 4d); dactylus (Fig. 5g) about 3 times longer than wide, biunguiculate, ventral margin armed with 6–7 small spines, main

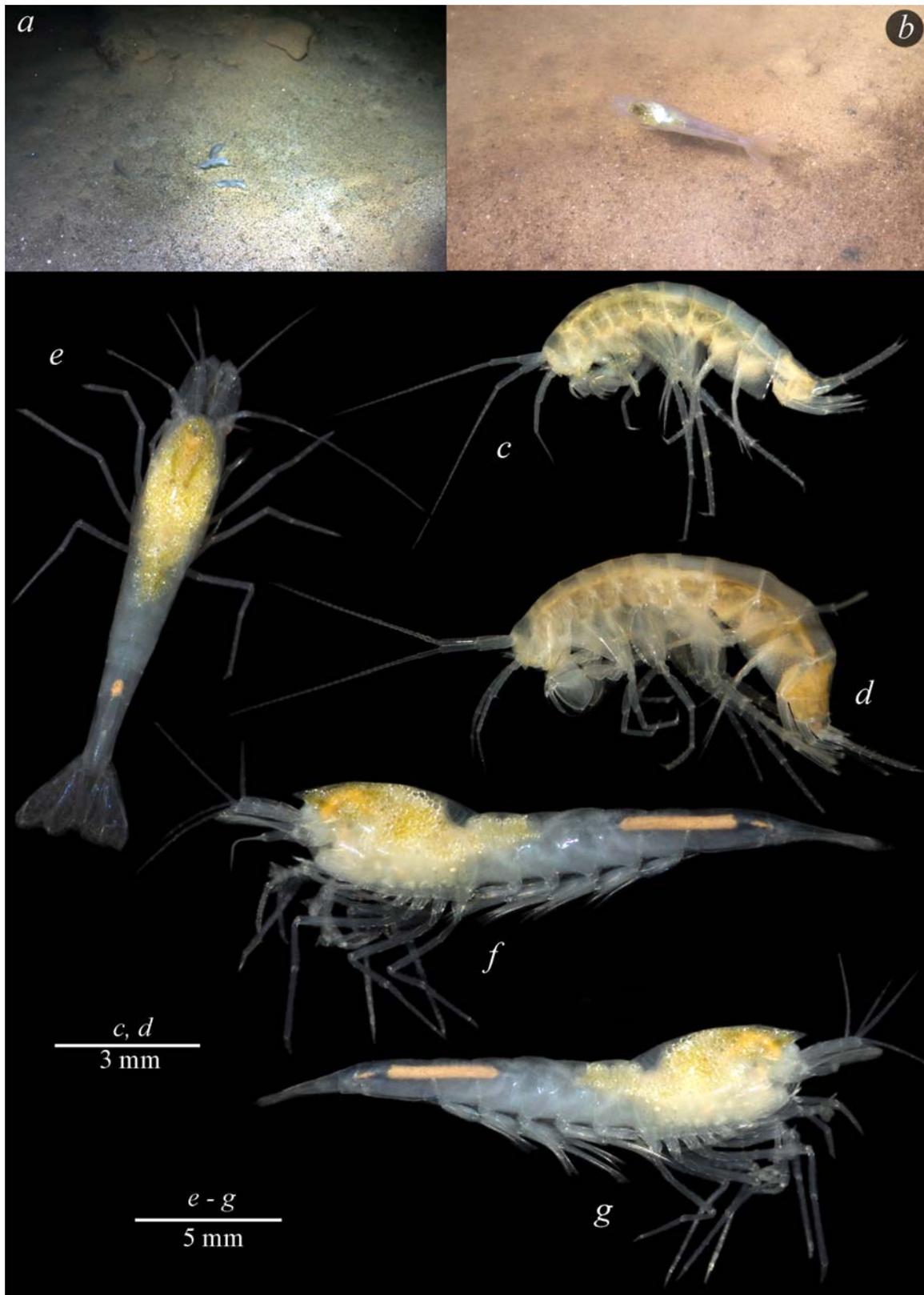


Fig. 2. Photo of *Niphargus* (a) and *Xiphocaridinella* (b) *in situ* and alive coloration of *Niphargus gegi* sp.n. (c, d) and *Xiphocaridinella dbari* sp.n. (e–g) from the Gegskaya (Gega) Cave, Arabika karst massif.

Рис. 2. Фотографии представителей рода *Niphargus* (a) и *Xiphocaridinella* (b) *in situ* и прижизненная окраска *Niphargus gegi* sp.n. (c, d) и *Xiphocaridinella dbari* sp.n. (e–g) из Гегской пещеры, карстовый массив Арабика.

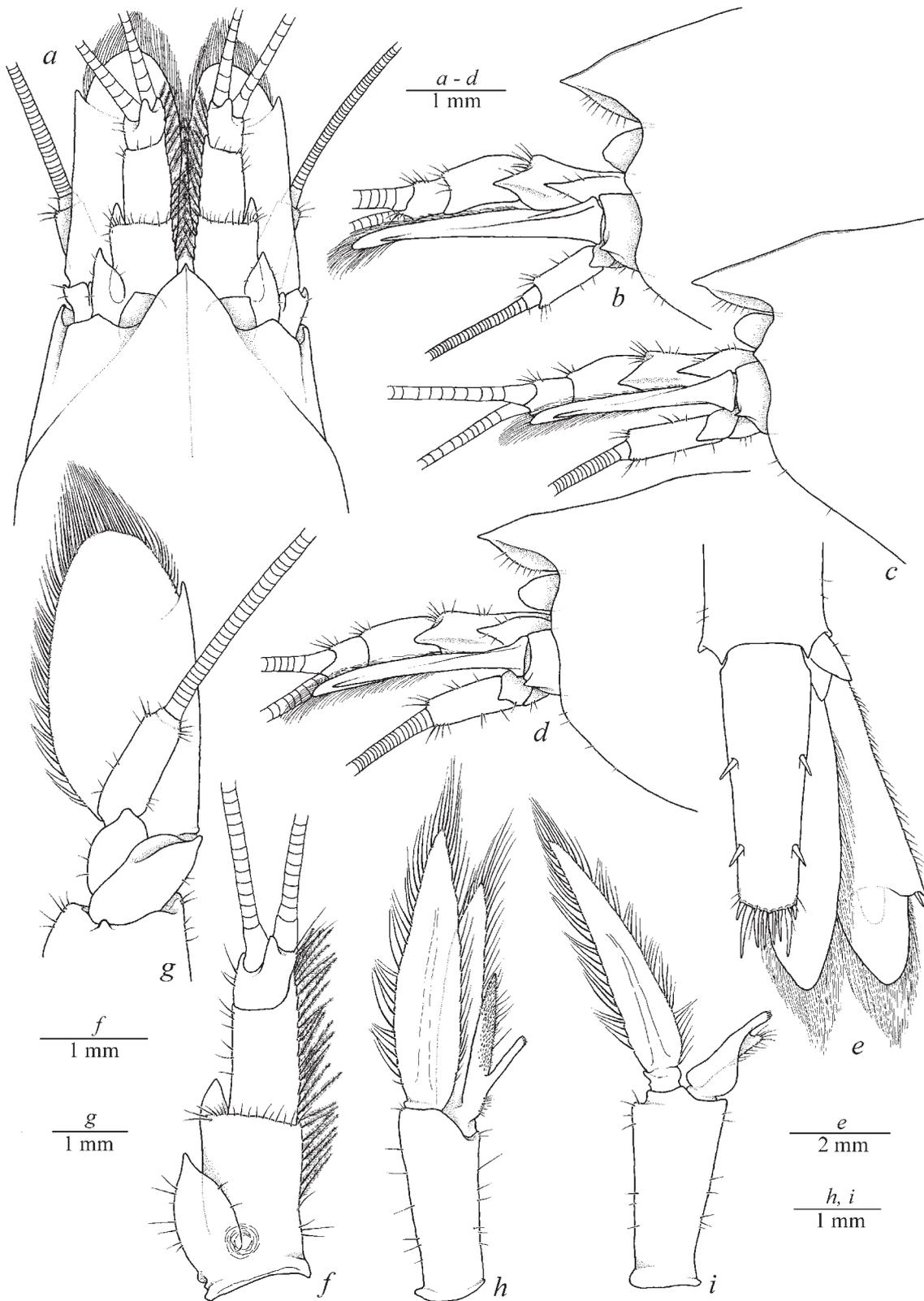


Fig. 3. *Xiphocaridinella dbari* sp.n., LEMMI, female (a, d-g), male (b, c, h, i), Gegskaya (Gega) Cave, Arabika karst massif: a — front of carapace, dorsal view; b-d — front of carapace, lateral view; e — telson; f — antennula; g — antenna; h — pleopod I; i — pleopod II.

Рис. 3. *Xiphocaridinella dbari* sp.n., LEMMI, самка (a, d-g), самец (b, c, h, i), Гегская пещера (Gega), карстовый массив Арабика: a — передняя часть карапакса, вид сверху; b-d — передняя часть карапакса, вид сбоку; e — тельсон; f — антеннула; g — антенна; h — плеопода I; i — плеопода II.

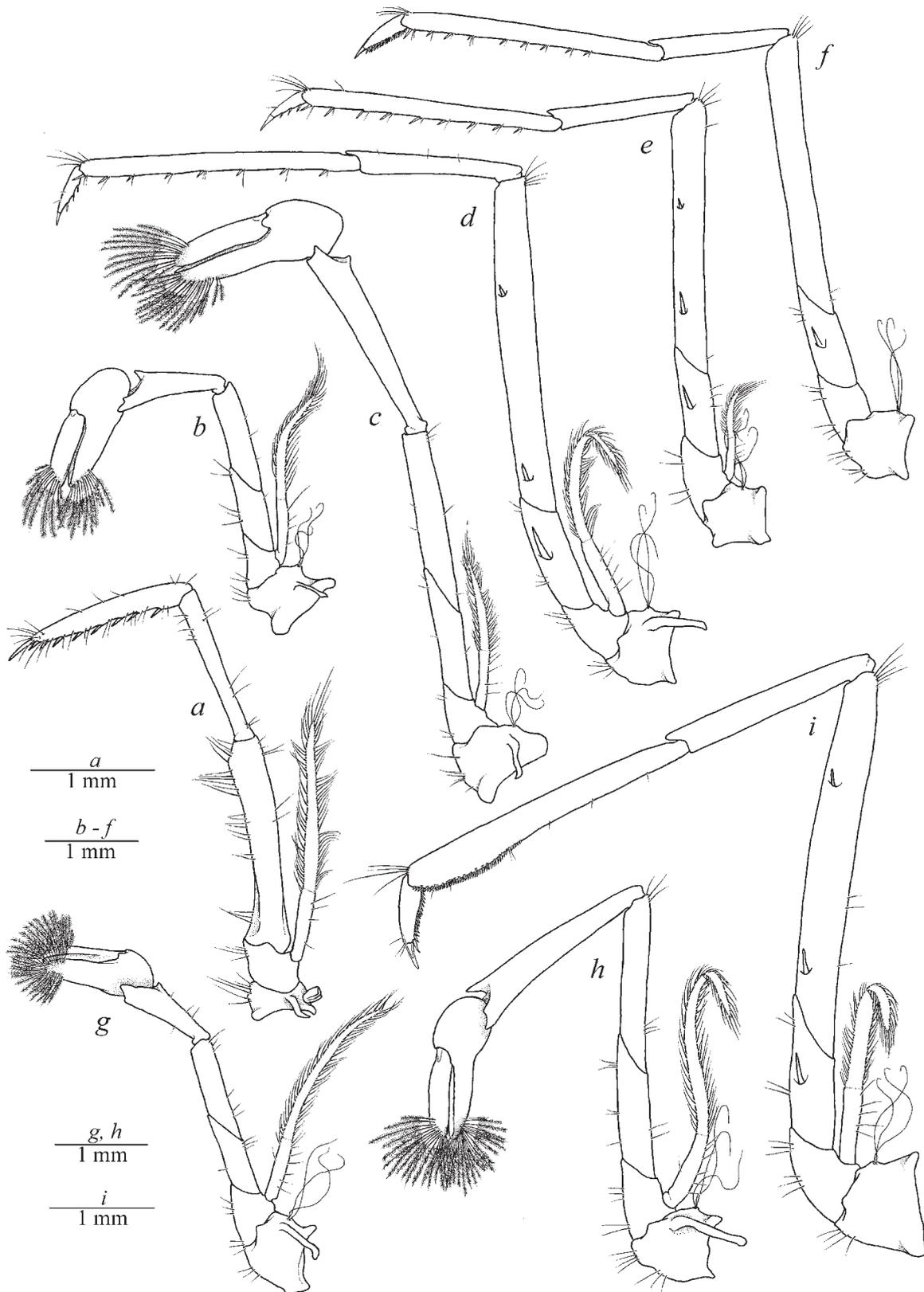


Fig. 4. *Xiphocaridinella dbari* sp.n., LEMMI, female (a-f), male (g-i), Gegskaya (Gega) Cave, Arabika karst massif: a — maxilliped III; b, g — pereopod I; c, h — pereopod II; d, i — pereopod III; e — pereopod IV; f — pereopod V.

Рис. 4. *Xiphocaridinella dbari* sp.n., LEMMI, самка (a-f), самец (g-i), Гегская пещера, карстовый массив Арабика: a — максиллипеда III; b, g — переопода I; c, h — переопода II; d, i — переопода III; e — переопода IV; f — переопода V.



Fig. 5. *Xiphocaridinella dbari* sp.n., LEMMI, male (a-f, h), female (g), Gegskaya (Gega) Cave, Arabika karst massif: a — pleopod I; b — same, *appendix interna*, apical part; c — same, *appendix interna*, distal part; d — distal part of *appendix masculina*; e — pleopod II; f — distal part of *appendix masculina*; g, h — dactylus of pereopod III.

Рис. 5. *Xiphocaridinella dbari* sp.n., LEMMI, самец (a-f, h), самка (g), Гегская пещера, карстовый массив Арабика: a — плеопод I; b — то же, *appendix interna*, апикальная часть; c — то же, *appendix interna*, дистальная часть; d — дистальная часть *appendix masculina*; e — плеопод II; f — дистальная часть *appendix masculina*; g, h — дактилус переопода III.

unguis smooth, curved and sharp; accessory unguis triangular, sharp, larger than ventral teeth, about twice shorter than main unguis. Pereiopod IV in females (Fig. 4e) generally similar to pereiopod III; merus armed with 2 spines, carpus without spine; exopodite smaller than in pereiopod III. Pereiopod V in females (Fig. 4f) generally similar to pereiopods III and IV, but without armature on basal segments and exopodite on basis; segments covered with simple setae dorsally and ventrally; propodus about 9–10 times as long as wide, with straight margins, armed with 8–10 long spines along ventral margin and pair of long slender spines at distoventral angle; dactylus with ventral margin armed with a dense “brush” consisting of small simple sharp setae; without accessory unguis, main unguis curved, triangular, sharp distally.

Morphological differences between males and females lead in the structure of distal part of propodi and dactyli of pereiopods III (Figs 4d, i, 5g, h). Pereiopod III in males (Fig. 4i) with relatively slender segments; coxa rectangular, about as long as wide, with tuft of long simple setobranchs, with epipodite; basis about as long as wide, with well-marked exopodite overreaching the distal margin of ischium; ischium about 1.5 times as long as wide, with well-marked distoventral spine; merus about 6 times as long as wide, with straight margins, with 2 well marked spines along ventral margin; carpus relatively slender, about 5–6 times as long as wide, slightly widening distally, about twice shorter than merus and 1.5 times shorter than propodus, with bluntly projecting distodorsal margin slightly overlapping carpopropodal articulation, without subdistal spine; propodus about 8 times as long as wide, with straight margins, distal third of propodus widening and armed with a series of small spines along its ventral margin; dactylus (Fig. 5h) about 3 times as long as wide, with single unguis, ventral margin armed with small relatively stout sharp teeth, main unguis smooth, curved and sharp.

Pleopods I and II in females normal, characteristic for the genus without specific differentiating features. Pleopod I in males with endopod bearing well marked *appendix interna* (Fig. 5e). Pleopod II in males (Fig. 5a) with well-developed *appendix interna* and *appendix masculina* (Fig. 5j); *appendix interna* with small cincinnuli distally (Fig. 5d, f); *appendix masculina* covered with numerous small sharp stout simple spines (Fig. 5b, c).

Uropods (Fig. 3e) relatively stout, remarkably exceeding telson; lateral margin of uropodal exopodite article 1 straight, with sharp triangular distolateral angle; dieresis simple, with 1 spine.

COLORATION. Body and appendages of shrimps transparent whitish and yellowish; cornea of eyes albescent; internal organs (gonads and hepatopancreas) whitish or yellowish; numerous small transparent fat granules can be seen through carapace (Fig. 2e–g).

BODY SIZE. The largest collected female has pcl. 7.5 mm, tbl. 24.0 mm; the largest collected male has pcl. 6.0 mm, tbl. 20.0 mm.

GENBANK ACCESSION NUMBER. MK875787.

DISTRIBUTION. The species is known from an underground lake inside the Gegskaya Cave, 43°23'43.7"N 40°27'28.4"E, Abkhazia, Western Caucasus (the type locality) and from the Verevkina Cave (43°24'56.0"N 40°21'23.0"E) at a depth –2100 m (from the upper entrance), where a small population differing for 1% by COI mtDNA gene marker (0.01 substitutions per 100 nucleotide positions (n=1)) was found in 2017 and only a single female was collected and sequenced for this study (see Appendix 1). It can be assumed that the same species also live in the deep underground lakes of the neighboring Krubera-Voronya Cave (43°24'35"N 40°21'44"E), where have already been reported about cave shrimp from water siphon at a depth –2140 m [Sendra, Reboleira, 2012] but shrimp specimens from there were not available for our study.

ETYMOLOGY. The species is dedicated to Dr. Roman Saidovich Dbar, a famous Abkhazian zoologist, in recognition of his long-time studies on the diversity of the animal world of Abkhazia and a leading role in organization of biological research in this area of Caucasus. Roman Zbar is the head of the Institute of Ecology of the Academy of Sciences of Abkhazia, a member of the Government of the Republic of Abkhazia, and the chairman of the State Committee of the Republic of Abkhazia on ecology and environmental management.

TAXONOMIC REMARKS. The new species morphologically differs from the Caucasian congeners by relatively long and distally sharp, but unarmed rostrum. Rostrum features are relatively constant (Fig. 3a–d). Based on genetic barcoding data (see Table 1; Fig. 10), *Xiphocaridinella jusbaschjani*, known from the Agura river (39°48'40.54"E 43°

Table 1. Pairwise interspecific genetic (COI mtDNA) distances (p -distance \pm SE) between known Caucasian species of the genus *Xiphocaridinella* and *Xiphocaridinella dbari* sp.n. from the Gegskaya Cave (n=5).

Таблица 1. Попарные межвидовые генетические (COI мтДНК) дистанции (p -distance \pm SE) между известными кавказскими видами рода *Xiphocaridinella* и *Xiphocaridinella dbari* sp. nov. из Гегской пещеры (n=5).

<i>Xiphocaridinella dbari</i> sp.n. from Verevkina Cave (n=2)	0.012 \pm 0,004
<i>Xiphocaridinella fagei</i> (n=3)	0.062 \pm 0,010
<i>Xiphocaridinella jusbaschjani</i> (n=3)	0.068 \pm 0,011
<i>Xiphocaridinella kumistavi</i> (n=9)	0.107 \pm 0,014
<i>Xiphocaridinella ablaskiri</i> (n=5)	0.112 \pm 0,015
<i>Xiphocaridinella otapi</i> (n=5)	0.113 \pm 0,015
<i>Xiphocaridinella shurubumu</i> (n=5)	0.115 \pm 0,015
<i>Xiphocaridinella osterlofi</i> (n=5)	0.121 \pm 0,015
<i>Xiphocaridinella kutaissiana</i> (n=6)	0.122 \pm 0,016

32°57.26′N) in Sochi area of the Russian Federation, and *Xiphocaridinella fagei*, known from the Anatolia Lake inside the New Athos (Novo-Afonskaya) Cave (43°5′44″N 40°48′53″E) in Abkhazia, are the most closely relative within Caucasian *Xiphocaridinella*. These species are also characterized by short unarmed rostrum, but can be morphologically distinguished from the new species as following. *Xiphocaridinella jusbaschjani* clearly differs from the new species by shorter rostrum, slightly overreaching the distal margins of cornea of eye (see Marin, Sokolova, 2014: figs 2a–c), blunt stylocerite (see Marin, Sokolova, 2014: fig. 2a, h), the different position of dorsal spines on telson (see Marin, Sokolova, 2014: fig. 2d, f) and more robust ambulatory pereopods, especially pereopods II and III (see Marin, Sokolova, 2014: fig. 4b, c, d). At the same time, *Xiphocaridinella fagei* can be separated from *Xiphocaridinella dbari* mostly by long and distally pointed unarmed rostrum, reaching the distal margin of basal antennular segment (see Marin, Sokolova, 2014: fig. 14a–h).

The genetic divergence (*p*-distances) of COI mtDNA gene marker between *Xiphocaridinella dbari* and other Caucasian *Xiphocaridinella* species correspond to characteristic interspecific values calculated for Decapoda and cave shrimps (Fig. 10; Table 1) (after Knowlton *et al.*, 1993; Knowlton, Weigt, 1998; Hebert *et al.*, 2003; Sites, Marshall, 2004; Zakšek *et al.*, 2007, 2009; Lefébure *et al.*, 2006a, b; Marin, 2017b, 2018a, b).

Order Amphipoda Latreille, 1816
Family Niphargidae Bousfield, 1977
Genus *Niphargus* Schiödte, 1849
Niphargus gegi **sp.n.**
 Figs. 2a, b, 3–7.

MATERIAL EXAMINED. Holotype: 1 male (tl. 18.0 mm), ZMMU Mb1147, Abkhazia, Gagry region, Bzyb River Canyon, Gegskaya Cave, 43°23′43.7″N 40°27′28.4″E, about 273 m above sea level, in subterranean lake, coll. I. Marin, 17 Sept. 2017; 5 non-ovigerous females, 5 males, (LEMMI), same locality and date as neotype. 1 female, 1 damaged specimen (LEMMI), Abkhazia, Gagry region, Reprua river, 43°19′52″N 40°12′17.6″E, 0–4 m above sea level, in river flow, coll. I. Marin & S. Sinelnikov, 10 Aug. 2016.

DESCRIPTION. Body moderately slender. Head (Fig. 6a) large, vaulted, without rostrum and with subrounded lateral cephalic lobes and excavated antero-ventral sinus (Figs 2c, d, 6a), eyes absent. Mesosomal and metasomal segments smooth, without specific features (Fig. 2c, d); coxae moderately large, with short ventro-marginal setae (Fig. 8f). Pereonites I–VI without setae; pereonites V–VII with 1–2 postero-ventral setae each. Pleonites I–III with several setae along postero-dorsal margin. Epimeral plate I with blunt postero-ventral corner (Fig. 8f). Epimeral plate II with ventral margins convex and blunt postero-ventral corner. Epimeral plate III ventral margin sinusoid postero-ventral corner triangular, distally. Urosomite I with one seta on each dorsolateral side, and with one postero-ventral spine near the basis of uropod I. Urosomites II–III unarmed. Coxal gills ovoid, of moderate size, never reaching the distal tip of pereopod article 2.

Antenna 1 (Fig. 6a) slender, overreaching half of the body (Fig. 2c, d); peduncular articles moderately slender, ratio: 1:1.3:1 (Fig. 6a); flagellum consisting of about 30 articles, most of them with two short aesthetascs each; accessory flagellum short, 2-articulated.

Antenna 2 (Fig. 6a) moderately slender, peduncular article 3 equal to article 2, both articles bearing long setae along

ventral margin; flagellum relatively slender, consisting of 9–10 articles bearing relatively short setae (Fig. 6a).

Mouthparts. Labrum (Fig. 6b) entire, broader than long, with entire outer lobes and developed inner lobes exceeding half of the outer lobes. Mandibles (Figs 6c, 9b) with incisor process and *pars incisiva* similar to other *Niphargus* species; mandibular palp with 3 articles: article 1 smooth; article 2 with numerous setae, article 3 subfalciform, equal to article 2, with numerous marginal and long distal setae, with several setae on the inner surface. Maxilla 1 (Fig. 6d) with: inner plate with 6 distal setae, outer plate with 7 spines armed with 1–2 small lateral teeth each (Fig. 9a); palp 2-articulated, distal article with 9–10 simple setae distally. Maxilla 2 (Fig. 6e) with smooth well developed lobes armed with distolateral setae only. Maxilliped (Fig. 6f) with short inner plates, left plate with 8–10 distal simple spines; outer plate reaching the half of palp article 2, with a row of inner lateral spines; palp 4-articulated (Fig. 9e).

Gnathopods moderately large, with segment 6 slightly larger than corresponding coxae. Gnathopod 1 (Figs 7a, c; 9f) with article 2 long, about 3 times as long as wide, with long simple setae along the posterior and postero-distal margins; article 3 quadrate, as long as wide, similar to article 4; article 4 quadrate, about as long as wide, with a row of setae along posterior margin; article 5 triangular in shape, shorter than article 6; article 6 (propodus) large, nearly as long as broad, trapezoid, with 8 groups of posterior marginal setae; palmar margin poorly convex, slightly serrated, with medium simple setae, defined on the outer face by one strong corner spine accompanied laterally by 2 short serrate small spines (Fig. 9f); dactylus strong and sharp, not reaching the posterior margin of article 6.

Gnathopod II (Fig. 7b, d) remarkably larger than gnathopod I; article 2 long, about 4 times as long as wide, with long simple setae along the posterior and postero-distal margins; article 3 quadrate, with one median group of setae along posterior margin; article 4 quadrate, about 1.5 times as long as wide, with a row of setae along postero-median margin; article 5 triangular in shape, shorter than article 6; article 6 (propodus) large, subtrapezoid, nearly as long as broad, with 6–8 groups of posterior marginal setae; palmar margin poorly convex, oblique almost 2/3 of propodus length, with medium simple setae, defined on the outer face by one strong corner spine without accompanying smaller spines (Fig. 9g); dactylus strong and sharp, reaching the posterior margin of article 6.

Ambulatory pereopods slender, covered with clusters of short setae, characteristic for “*Niphargus ablaskiri*” species group. Pereopods II (Fig. 8a) with slender poorly setose articles; article 2 about 7 times as long as wide, with the posterior margin bearing long marginal setae; articles 3 short, about as long as wide; article 4 about 4 times as long as wide, with small setae along dorsal and ventral margins; articles 5–6 almost equal, about 3–4 times as long as wide, with bunches of short spines along the ventral margin; dactylus stout, curved, sharp distally; outer margin of dactylus with one median short plumose seta.

Pereopods IV (Fig. 8b) similar to pereopod III, with slender poorly setose articles; article 2 about 7 times as long as wide, with the posterior margin bearing long marginal setae; articles 3 short, about as long as wide; article 4 about 4 times as long as wide, with small setae along dorsal and ventral margins; articles 5–6 almost equal, about 3–4 times as long as wide, with bunches of short spines along ventral margin; dactylus (Fig. 9h) stout, curved, sharp distally; outer margin of dactylus with one median short plumose seta.

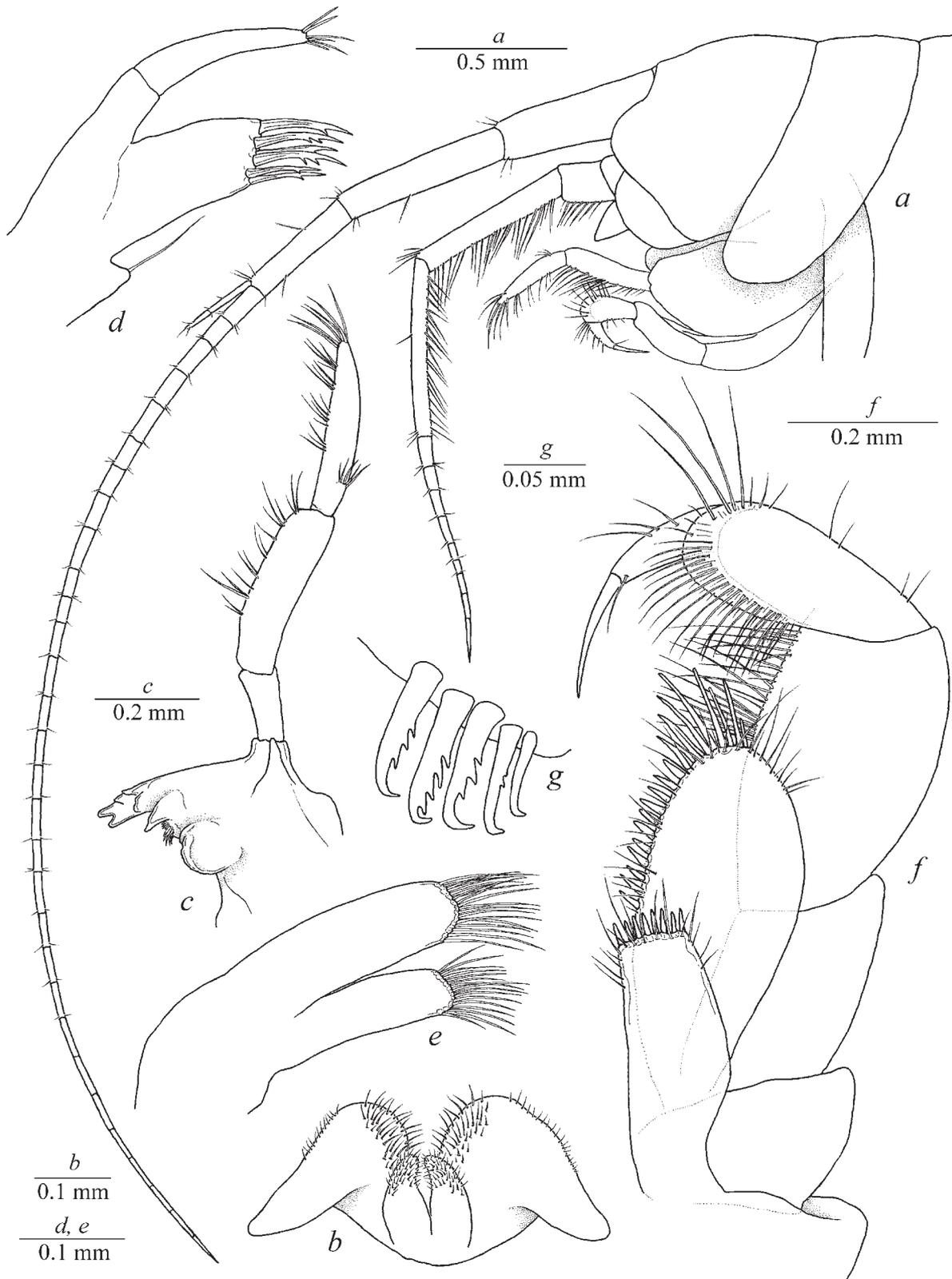


Fig. 6. *Niphargus gegi* sp.n., LEMMI, male, Gegskaya (Gega) Cave, Arabika karst massif: *a* — head; *b* — labrum; *c* — mandible; *d* — maxilla I; *e* — maxilla II; *f* — maxilliped; *g* — setae of pleopod.

Рис. 6. *Niphargus gegi* sp.n., LEMMI, самец, Гегская пещера, карстовый массив Арабика: *a* — голова, *b* — верхняя губа (лабрум); *c* — мандибула; *d* — максилла I; *e* — максилла II; *f* — максиллипеда; *g* — щетинки плеопод.

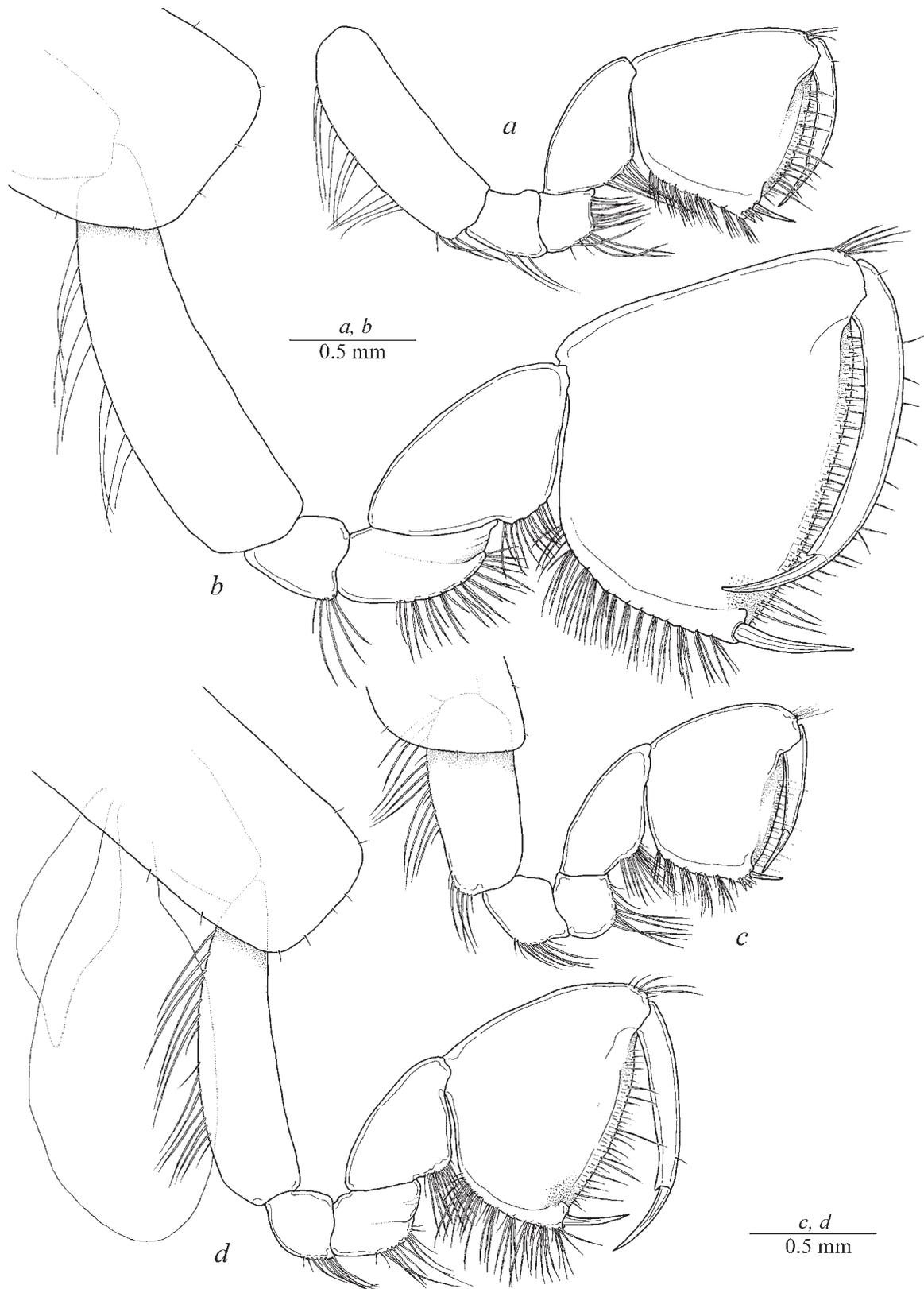


Fig. 7. *Niphargus gegi* sp.n., LEMMI, male (*a, b*), female (*c, d*), Gegskaya (Gega) Cave, Arabika karst massif: *a, c* — gnathopod I, *b, d* — gnathopod II.

Рис. 7. *Niphargus gegi* sp.n., LEMMI, самец (*a, b*), самка (*c, d*), Гегская пещера, карстовый массив Арабика: *a, c* — гнатопода I; *b, d* — гнатопода II.

Pereiopod V (Fig. 8c) with article 2 subrectangular, widening proximally, with feebly marked ventro-posterior lobe, posterior margin barely concave in the middle, bearing a row of 9–10 posterior short marginal setae, anterior margin of article 2 is slightly convex, with a row of slender marginal setae that slightly longer than posterior; article 3 subquadrate, as long as wide; article 4 about 3 times as long as wide, with bunches of short spines along dorsal and ventral margins; article 5 slender, about 4 times as long as wide, slightly longer than article 3 and shorter than article 5; article 6 slender, about 4 times as long as wide, bunches of short spines; dactylus slender, with a tiny median spine at the inner margin and one short median setae at the outer margin.

Pereiopods VI–VII (Fig. 8d, e) almost similar, moderately slender, with article 2 narrow, slightly shorter twice as long as broad, without a distinct ventro-posterior lobe and with a concave posterior margin bearing a row of 10–11 short posterior marginal setae; anterior margin convex, with a row of longer marginal setae; articles 3 short, as long as wide; article 4 about 5 times as long as wide, with bunches of short spines along dorsal and ventral margins; article 5 slender, about 3 times as long as wide, slightly longer than article 3 and shorter than article 5, with bunches of spines intermixed with single short setae; article 6 slender, about 10–11 times as long as wide, bunches of short spines; dactylus (Fig. 9i) slender, with a tiny median spine at the inner margin and one short median setae at the outer margin.

Pleopods normal, without specific features, with 4 retinacles.

Uropod I with protopodite (peduncle) about 3.5 times as long as wide, slightly longer than rami, with a dorso-external and dorso-internal row of slender spines; rami straight and equal in length, both rami with lateral and distal slender spines (Fig. 8f). Uropod II with protopodite (peduncle) about 2.5–3 times as long as wide, slightly shorter than rami, inner ramus barely shorter than the outer one, both rami with lateral and distal slender spines. Uropod III (Figs 8f, g, 9j) with protopodite about 1.5–2 times as long as wide, rami unequal, inner ramus short bearing several small distal spines; outer ramus long, proximal article about 9–10 times as long as wide, about 4–5 times longer than distal article, distal article about 2 times as long as wide, both article armed with setae and clusters of small setae (Fig. 8f, g).

Telson (Figs 8h, 9c, d) about 1.5 times as long as broad, ca 70% incised, lobes obtuse and rounded distally, bearing 3–4 long distal and 1–2 subdistal spines; without lateral seta; distal and subdistal spines reaching the half length of the telson.

COLORATION. Body, appendages and internal organs whitish or yellowish (Fig. 2a, b) characteristic to all stygobiotic representatives of the genus *Niphargus*.

BODY SIZE. The largest collected female has tbl. 18.0 mm; the largest collected male has tbl. 16.0 mm.

GENBANK ACCESSION NUMBER. MK875788.

DISTRIBUTION. The species is known from an underground lake inside the Gegskaya Cave, 43°23'43.7"N 40°27'28.4"E, Abkhazia, Western Caucasus (the type locality). It can also be assumed (see Discussion) that the same species can live in underground lakes inside the Krubera-Voronya Cave as specimens differing from population from the Gegskaya Cave for about 12% by COI mtDNA gene marker (about 0.12 substitutions per 100 nucleotide positions (n=2)) were collected in a stream of the Reprua river (e.g. Kiknadze, 1979; Klimchouk, 1990, 2006). Moreover, the specimen differing by about 12% (about 0.12 substitutions per 100

nucleotide positions (n=1)) was described by Sidorov [2014] from the Troika Cave (43°23'00.0"N 40°22'00.0"E) (see Tab. 2; Figs. 1, 10; see below). It is possible that the same species also inhabit the underground lake inside the Ver-evkina Cave (43°24'56.0"N 40°21'23.0"E) at a depth –400 m (Turbanov, pers. comm.).

ECOLOGY. *Niphargus gegi* sp.n. seems to be a lake dweller. All collected specimens were found in the underground lake and small pools inside the Gegskaya Cave. The specimens sampled in a stream of the Reprua river were dead and partly destroyed, being probably washed out of the Arabika karst massif system.

ETYMOLOGY. The species is named after the Gegskaya (Gega) Cave (43°23'43.7"N 40°27'28.4"E), where it was firstly found.

TAXONOMIC REMARKS. The new species clearly belongs to the Caucasian “*Niphargus ablaskiri*” species group that is a part of the “*carpathicus*” group (after Straškraba, 1972), including *Niphargus ablaskiri* Birstein, 1940 and *N. inermis* Birstein, 1940 described from the Abrskil Cave (42°55'14.0"N 41°33'17.0"E) and the Lower Shakuran (=Nizhne-Shakuranskaya) Cave (43°01'47.8"N, 41°20'02.0"E), *N. vadi-mi* Birstein, 1961 from Crimean Peninsula, Iranian *N. dani-ali* Esmaeili-Rineh et Sari, 2013 and two European species, *N. ambulator* G. Karaman, 1975 and *N. gebhardti* Schellenberg, 1934 (Fig. 10; Table 2), respectively. Taxonomic features of the group are: 1) unequal gnathopods I and II; 2) different carpal segments (in form and shape) of pereiopods I and II; 3) elongated deeply dissected with long distal, subdistal and lateral long simple spines; 4) simple dactyli of pereiopod III–VII without ventral spines and 5) short distal article of uropod III [Birstein, 1940]. The new species has all these morphological features (Figs 6–9). The detected genetic differences (about 12%) between specimens from the Gegskaya Cave, the Troika Cave and the Reprua river (Table 2) may indicate the presence of several cryptic species inside these neighboring but isolated karst systems. However, the present-day genetic knowledge on the Caucasian *Niphargus* species is poor and insufficient for a more accurate taxonomic revision. Moreover, such a revision is beyond the scope of this study and will be performed later when additional genetic data became available.

The most morphologically similar and genetically close *N. inermis*, known from the Lower Shakuran (=Nizhne-Shakuranskaya) Cave (43°01'47.8"N, 41°20'02.0"E), can be reliably separated from *Niphargus gegi* by less numerous spines on telson with 3 distal spines on each lobe of the new species (Figs 8h, 9c, d) (vs. 5–6 distal spines on each lobe of telson in *N. inermis* [Birstein, 1940: fig. 3g]). The new species can be reliably differed from *N. ablaskiri* known from Abrskil Cave (Achkshe-Tyz-Gua Cave, 42°55'14.0"N 41°33'17.0"E), by morphological features of telson — *N. ablaskiri* has several lateral long simple spines and 5 distal spines on each lobe of telson (see Birstein, 1940: fig. 2f) vs. only 1 lateral and 3 distal spines on each lobe of telson in *Niphargus gegi* (Figs 8h, 9c, d). Moreover, the genetic *p*-distances between the new species and the related Caucasian species, *N. ablaskiri* and *N. inermis*, exceed 15% (0.15 substitutions per 100 nucleotide position) (Tab. 1; Fig. 10), which makes it possible to separate it as a valid biological species (see Hebert *et al.*, 2003; Copilas-Ciocianu *et al.*, 2017; Delić *et al.*, 2017; Zakšek *et al.*, 2019; see Discussion).

The new species can be separated from *N. daniali*, known from Danial cave (36°39'51.2"N 51°10'51.4"E) in Iran, by

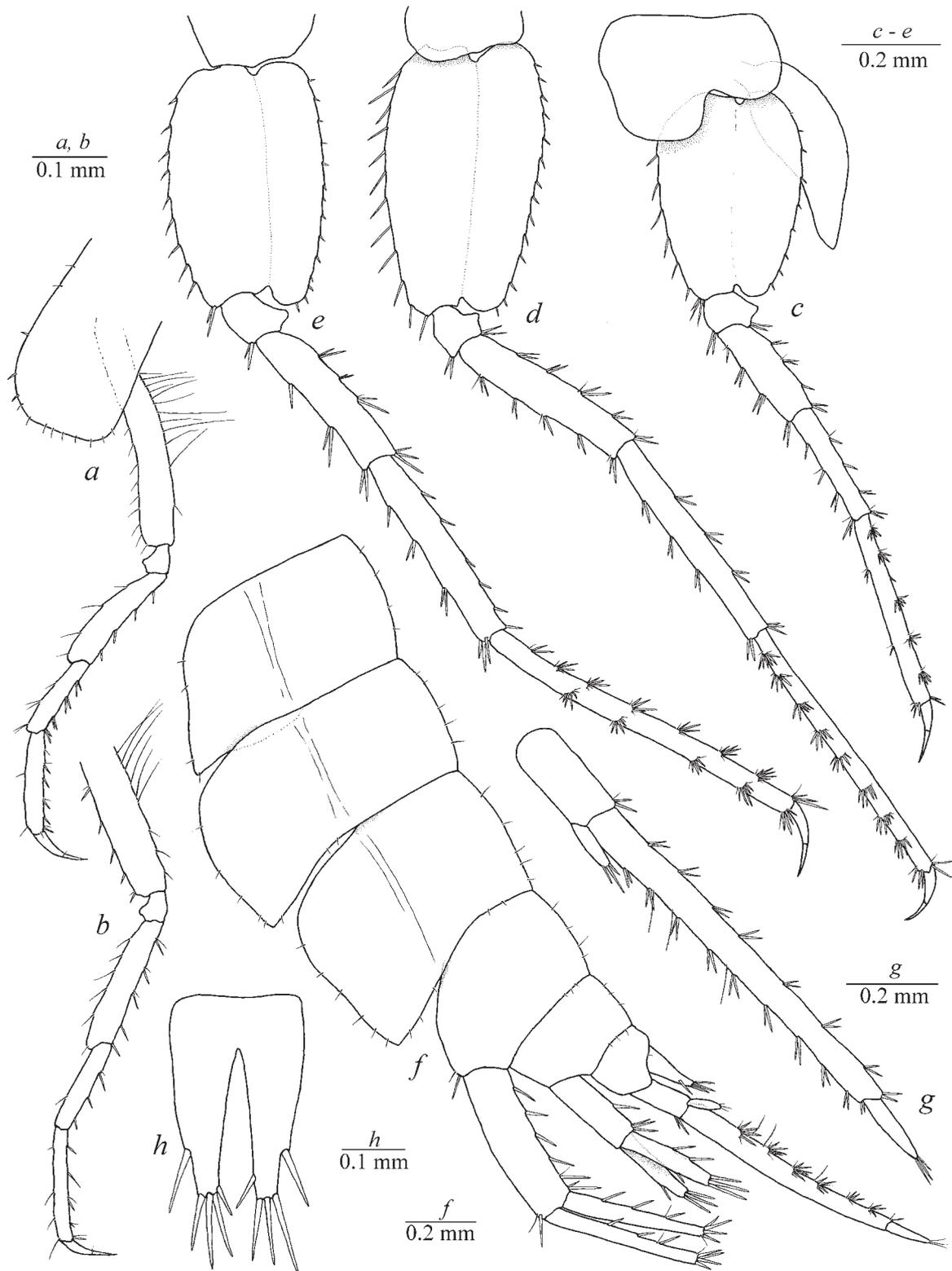


Fig. 8. *Niphargus gegi* sp.n., LEMMI, male, Gegskaya (Gega) Cave, Arabika karst massif: *a* — pereopod III; *b* — pereopod IV; *c* — pereopod V; *d* — pereopod VI; *e* — pereopod VII; *f* — urosomites and uropods; *g* — uropod 3; *h* — telson.

Рис. 8. *Niphargus gegi* sp.n., LEMMI, самец, Гегская пещера, карстовый массив Арабика: *a* — переопода III; *b* — переопода IV; *c* — переопода V; *d* — переопода VI; *e* — переопода VII; *f* — уросомиты и уроподы; *g* — уропода III; *h* — тельсон.

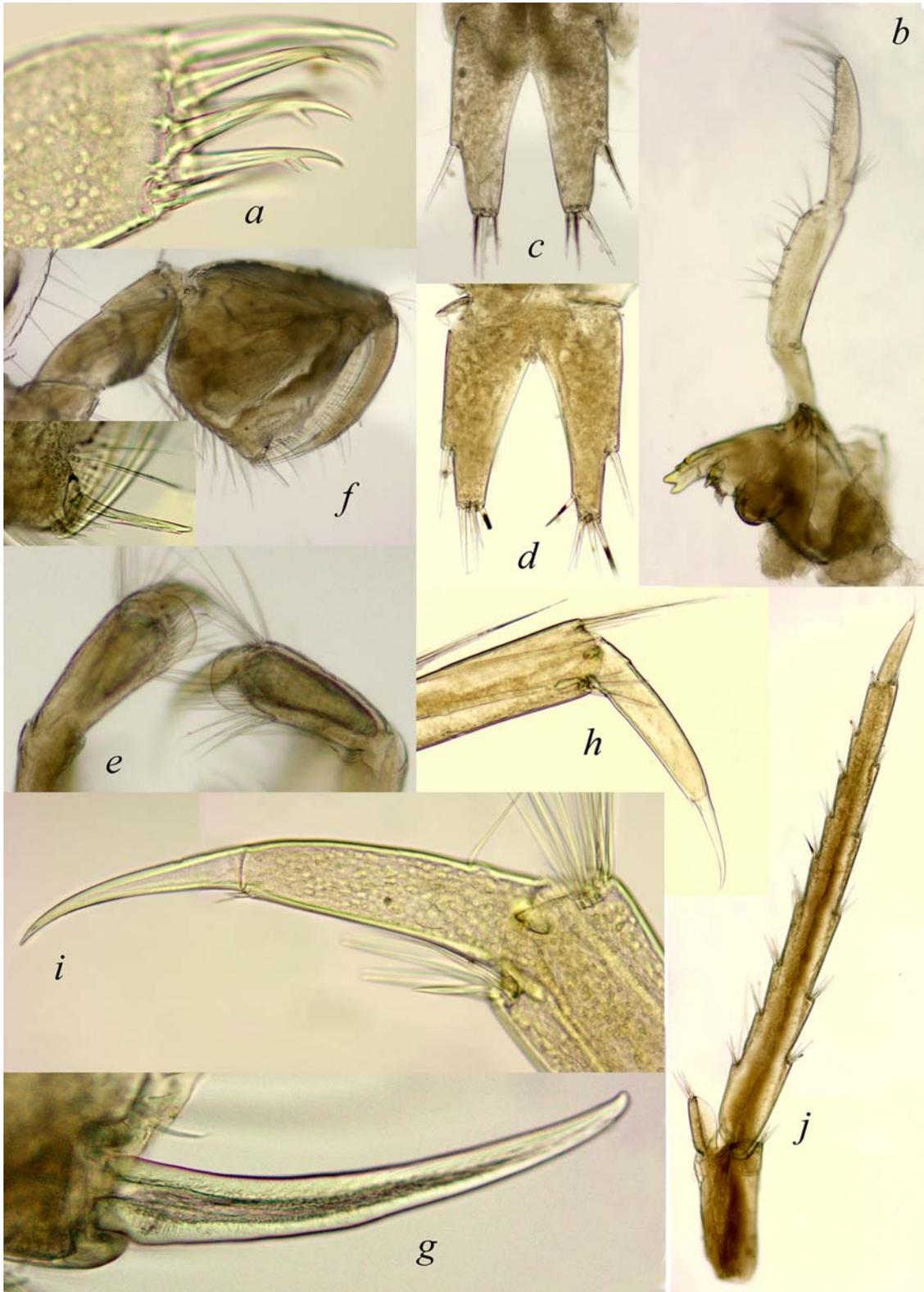


Fig. 9. *Niphargus gegi* sp.n., LEMMI, female (a-f, i), male (g, j), Gegskaya (Gega) Cave, Arabika karst massif: a — outer plate of maxilla I; b — mandible; c, d — telson; e — distal article of maxilliped; f — gnathopod II; g — corner palmar spine of gnathopod II; h — dactylus of pereopod III; i — dactylus of pereopod VII; j — uropod III.

Рис. 9. *Niphargus gegi* sp.n., LEMMI, самка (a-f, i), самец (g, j), Гегская пещера, карстовый массив Арабика: a — наружная пластина максиллы I; b — мандибула; c, d — тельсон; e — дистальная часть максиллипод; f — гнатопода II; g — угловой пальмарный шип гнатоподы II; h — дактилус переоподы III; i — дактил переопод VII; j — уropоды III.

Table 2. Pairwise interspecific genetic (COI mtDNA) distances (p -distance \pm SE) between *Niphargus gegi* sp.n. from Gegskaya (Gega) Cave (n=3) and other *Niphargus* known from the Caucasus, Crimean Peninsula and neighboring area. Таблица 2. Попарные межвидовые генетические (COI мтДНК) дистанции (p -distance \pm SE) между *Niphargus gegi* sp.n. из Гегской пещеры (n=3) другими видами рода *Niphargus* с Кавказа, Крыма и близлежащих регионов.

<i>Niphargus gegi</i> sp.n. from Troika Cave, Caucasus (n=1) (identified as “ <i>N. inermis</i> ” [after Sidorov, 2014])	0.121 \pm 0.014
<i>Niphargus gegi</i> sp.n. from Reprua, Caucasus (n=2)	0.125 \pm 0.015
<i>Niphargus bihorensis</i> (Europe)	0.187 \pm 0.019
<i>Niphargus timavi</i> (Italy)	0.181 \pm 0.020
<i>Niphargus julius</i> (Italy)	0.185 \pm 0.020
<i>Niphargus daniali</i> (Iran)	0.196 \pm 0.020
<i>Niphargus gebhardti</i> (Europe)	0.202 \pm 0.021
<i>Niphargus inermis</i> (Nizhne-Shakuranskaya Cave, Caucasus)	0.213 \pm 0.025
<i>Niphargus ambulator</i> (Europe)	0.221 \pm 0.021
<i>Niphargus molnari</i> (Europe)	0.247 \pm 0.022
<i>Niphargus vadimi</i> (Crimean Peninsula)	0.212 \pm 0.020
<i>Niphargus tauricum</i> (Crimean Peninsula)	0.235 \pm 0.022
<i>Niphargus dimorphus</i> (Crimean Peninsula)	0.225 \pm 0.022

the presence of a single strong corner spine without accompanying short spines (Fig. 9g) (vs. the presence on 2 accompanying spines in *N. daniali* [Esmacili-Rineh, Sari, 2013: fig. 8C, D]; a more slender uropod III with article 2 about 7–8 times as long as wide in males (Figs 8g, 9j) and about 5 times as long as wide in females (see Sidorov, 2014: fig. 20) (compared to robust uropod III with article 2 about 4 times as long as wide in *N. daniali* [Esmacili-Rineh, Sari, 2013: fig. 10F]) and more slender telson armed with only 1 lateral spine (vs. cluster of several simple lateral spines in *N. daniali* [Esmacili-Rineh, Sari, 2013: fig. 10G]).

In addition, the new species clearly differs from *N. ambulator* and *N. gebhardti* in the presence on 1 strong corner spine without accompanying smaller spines (Fig. 9g) (vs. the presence on 2–3 accompanying small spines in both males and females in *N. gebhardti* [Angyal *et al.*, 2015: fig. 13] and *N. ambulator* [Karaman, 1975: fig. 9F]; similar uropod III with short distal article (Figs 8g, 9j) in both males and females (vs. longer distal segment in males in *N. gebhardti* [Angyal *et al.*, 2015: fig. 16] and *N. ambulator* [Karaman, 1975: fig. 7H, I] and telson only 1 lateral spine (Figs 8h, 9c, d) (vs. 2 pairs in *N. gebhardti* [Angyal *et al.*, 2015: fig. 16] and *N. ambulator* [Karaman, 1975: fig. 8D, I]). The species are geographically isolated as *N. gebhardti* is described from Abaliget Cave (46°08'14.2"N 18°06'59.2"E) in Hungary and *N. ambulator* is recorded from the Province of Como in Italy. Genetic difference of the new species from *N. gebhardti* and *N. ambulator* by COI mtDNA gene marker is more than 20% (see Tab. 2) as well as p -distances between *Niphargus gegi* and other neighboring *Niphargus* species is more than 15% (0.15 substitutions per 100 nucleotide positions), which allow separating it as a distinct biological species (see Tab. 1; Fig. 10) (e.g. Copilas-Ciocianu *et al.*, 2017; Delić *et al.*, 2017; Zakšek *et al.*, 2019).

Discussion

The atyid shrimp genus *Xiphocaridinella* Sadowsky, 1930 (Crustacea: Decapoda: Atyidae) currently includes 8 valid species described in the stygobiotic habitats of the Caucasus (e.g. Sadowsky, 1930; Birstein, 1939, 1948; Juzbaš'jan, 1940; Marin, Sokolova, 2014; Marin, 2017a, b, 2018a, b). The present study increases the number up to 9 species while the real diversity of the genus is possibly richer and comparable to the combined diversity of relative Dinaric stygobiotic genera *Troglocaris* Dormitzer, 1853 and *Spelaeocaris* Matjašič, 1956. At the same time, the morphological similarity of the Caucasian representatives of the genera *Xiphocaridinella* and *Niphargus* creates a number of taxonomic problems with intra- and interspecific delimitation. Thus, additional non-morphological information, i.e., geographic origin and distribution of the species, sequences of gene markers, is usually used for the species identification. For example, Marin [2017a, b, 2018a, b] mentioned that all known Caucasian

Xiphocaridinella species are strictly restricted to certain karst cave ecosystem, showing a genetic divergence of at least 5% (COI mtDNA), allowing to describe them as separate species [after Lefébure *et al.*, 2006a, b]. However, these estimates are essentially approximate. The species delimitation within subterranean crustacean “lake dwellers” is probably correlated due to salting and changes of the sea level and the following events in geological history (e.g. Delić *et al.*, 2017; Guy-Haim *et al.*, 2018). The time of the origin of

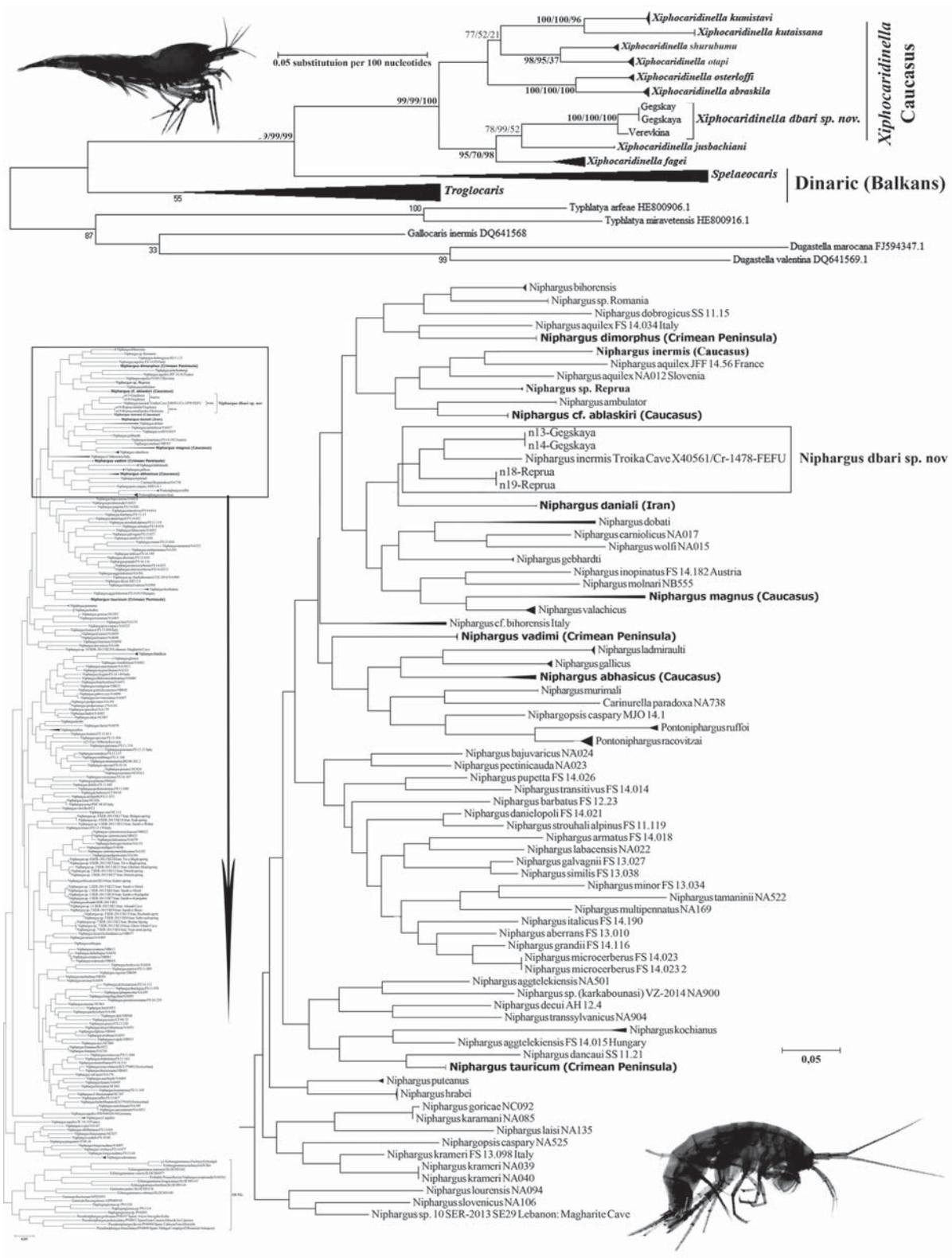


Fig. 10. Phylogenetic reconstruction (COI mtDNA gene marker) of studied Western Caucasian *Xiphocaridinella* (upper with BA/ML/NJ algorithms) and *Niphargus* (lower) species (ML algorithm). The clade of related taxa is enlarged for *Niphargus* (lower right).

Рис. 10. Филогенетическая реконструкция (на основе генного маркера COI мтДНК) изученных видов западно-кавказских видов родов *Xiphocaridinella* (сверху, с помощью алгоритмов BA/ML/NJ) и *Niphargus* (снизу, ML алгоритм). Клада родственных таксонов увеличена для *Niphargus* (внизу справа).

some subterranean lake-dwelling *Niphargus* lineages (e.g. Delić *et al.*, 2017) and the genera splits in *Troglocaris*-like cave shrimps coincide with the period of the Dinaric orogenesis and salting of the Mediterranean basin (10–23MYA) [Popov *et al.*, 2004; Sket, Zakšek, 2008] similar to the major epigeal *Gammarus* species diversifications [Hou *et al.*, 2011, 2014; Copilaş-Ciocianu, Petrušek, 2015, 2016; Mamos *et al.*, 2016]. Besides, the splitting of species within *Xiphocaridinella*, *Spelaecaris* and *Troglocaris* is probably correlated with the Messinian salinity crisis (5.96–5.33 MYA) and the Pleistocene glacial maxima (or the Quaternary glaciation) (2MYA–10.000YA) [Colantoni *et al.*, 1979; Gargani, Rigollet, 2007; Garcia-Castellanos *et al.*, 2009], when the process of isolation of cave shrimp lineages within the certain karst systems occurred, which enabled them to survive in previously flooded caves.

Data on “molecular clocks” used in *Troglocaris*-like cave shrimps, including Caucasian *Xiphocaridinella*, as a sequence (COI mtDNA) divergence rate about 1.4–2.4% of substitutions per site on 1MYA [Knowlton *et al.*, 1993; Knowlton, Weigt, 1998; Zakšek *et al.*, 2007; Jugovic *et al.*, 2012] calculating the splitting time within the Caucasian lineages/species from ~2.0 to ~10.0MYA) (see Marin, 2017b; Table 1). Using known data, it is possible to assume two separate divergence events within Dinaric–Caucasian *Xiphocaridinella* lineages (genera) occurred about 9–15MYA (ancestor of *Troglocaris* separated from *Spelaecaris*–*Xiphocaridinella*) and about 8–13MYA (ancestor taxon diverged for Dinaric *Spelaecaris* and Caucasian *Xiphocaridinella* [Marin, 2017b]). It is difficult to compare this time with any geological events, and the divergence rates should be revised upwards in the percentage of substitutions by 1MYA [Marin, in prep.].

At the same time, similar genetic criteria for the species delimitation were never determined for the Caucasian representatives of the genus *Niphargus*. Modern molecular studies have shown that many widely distributed species of the genus *Niphargus* include a number of almost morphologically identical, but genetically different species, so called “cryptic species” [Lefébure *et al.*, 2006a, b, 2007; Väinölä *et al.*, 2008; Trontelj *et al.*, 2009; Meleg *et al.*, 2013; McInnery *et al.*, 2014; Fišer *et al.*, 2018]. Uncovering cryptic diversity is important for understanding species distribution, the levels of endemism and ecology (e.g. Oliver, 2011). The minimum *p*-distances (COI mtDNA) between *Niphargus* species deposited in GenBank (NCBI) is about 0.009 substitutions per 100 nucleotide positions in *Niphargus gabrovceci* S. Karaman, 1952 vs. *Niphargus novomestanus* S. Karaman, 1952 probably representing one species. The maximal is about 0.310 substitutions per 100 nucleotide positions (e.g. *Niphargus gegi* sp.n. vs. *Niphargus kochianus*). At the same time, the total average *p*-distance (\pm SE) (COI mtDNA) between data on 200+ species of the genus presented in GenBank (NCBI) is calculated as 0.214 \pm 0.016 substitutions per 100 nucleotide positions. Genetic *p*-dis-

tances with other genera slightly exceed the total overall average between species within the genus: 0.307 \pm 0.021 with the genus *Echinogammarus* Stebbing, 1899 (Gammaridae), 0.296 \pm 0.023 with the genus *Haploglymus* Mateus et Mateus, 1958 (Niphargidae) and 0.256 \pm 0.025 with the genus *Gammarus* Fabricius, 1775 (Gammaridae) (own calculations).

With regard to the genus *Niphargus*, the attempts to determine the genetic delimitation threshold, including cryptic species, had already been made. For example, Švara *et al.* [2015] identified a genetic distance between Croatian *N. zagorae* and *N. boskovici* at about 14%, which is presumably close to the reproductive barrier found in interbreeding experiments [Cothran *et al.*, 2013; Lagrue *et al.*, 2014]. At the same time, the morphological differences between these species are insignificant and are determined only by the setal ornamentation on urosomite III and pereopods III–IV as well as the different proportions in gnathopods II and pereopods V–VII [Švara *et al.*, 2015]. Recent molecular genetic studies suggest that most of *Niphargus* species have a limited distribution, being mostly narrow endemics [Fišer *et al.*, 2008; Delić *et al.*, 2017], while widespread taxa are complexes of cryptic species even for epigeal species [Lefébure *et al.*, 2006, 2007; Delić *et al.*, 2017]. Delić *et al.* [2017] used a threshold value of 0.16 substitutions per site to separate species within “*Niphargus arbiter* – *Niphargus salonitanus*” species complex, belonging to “lake giants” from the Dinaric Karst, where all species overlap significantly in morphology and cannot be uniquely separated without help molecular markers. This most conservative 0.16-threshold (patristic distances) approach is confirmed by other researches (after Lefébure *et al.*, 2006a). Lefébure *et al.* [2006b] found that 95% of the observed intraspecific divergences in the studied population of *Niphargus virei* Chevreux, 1896 were below 0.2 substitutions per site, and that the 0.16-threshold could be used to differentiate inter- from intraspecific distances with reasonable success (about 87% of success on the entire data set and 99% of success when cryptic species and a peculiar genus were removed).

Thus, it is possible to assume a threshold of 0.15 substitutions per site for delimitation of the species within the Caucasian *Niphargus ablaskiri* species complex from neighboring caves of the Arabika karst massif and other relative Caucasian species (see Table 2), that is even rather conservative according to recent investigations [Copilaş-Ciocianu *et al.*, 2017; Delić *et al.*, 2017; Zakšek *et al.*, 2019]. This threshold also makes it possible to separate species using the characteristics of their geographical distribution and the possible connection between adjacent karst massifs. Although, divergence rates need to be corrected in the future using additional genetic data obtained for the Caucasian niphargids.

Molecular clock calibration for peracarid crustaceans for COI mtDNA gene marker was proposed to be 1.25% of substitutions per 1MYA by Ketmaier *et al.*

[2003] and 0.34 to 0.76% of substitutions per 1MYA according to Lefébure *et al.* [2006b] (see review in Gay-Haim *et al.*, 2018). The splitting time calculated for *Xiphocaridinella* and *Troglocaris*-like shrimps from the same karst systems exceed the time of splitting between the Caucasian *Niphargus* lineages by at least for 2–3 times and also need to be studied using new genetic data and other gene markers. At the same time, nuclear genomics (single nucleotide polymorphism and microsatellites) should also be used to analyze the restriction of gene flow, in order to confirm the species isolation, since the allopatric speciation in the hypogean aquatic fauna under different effective populations can also be associated with several evolutionary molecular genetic processes.

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Appendix 1. The list of nucleotide sequences of genera *Xiphocaridinella*, *Troglocaris* and *Niphargus*, used for molecular-genetic analysis.

Приложение 1. Список нуклеотидных последовательностей родов *Xiphocaridinella*, *Troglocaris* и *Niphargus*, используемых для молекулярно-генетического анализа.

Species	GenBank (NCBI) reference
<i>Xiphocaridinella dbari</i> sp.n. from the Gegskaya (Gega) Cave, Abkhazia, Western Caucasus	MK875787
<i>Xiphocaridinella kutaissiana</i>	MF287657, MF287655, MF287656
<i>Xiphocaridinella kumistavi</i>	MF287654, MF287652, MF287653
<i>Troglocaris anophthalmus</i>	FJ426022
<i>Niphargus gegi</i> sp.n. from the Gegskaya (Gega) Cave, Abkhazia, Western Caucasus	MK875788
<i>Niphargus gegi</i> sp.n. from Troika Cave, Caucasus (as <i>Niphargus inermis</i> voucher X40561/Cr-1478-FEFU)	KJ415376
<i>Niphargus daniali</i> (<i>Niphargus</i> sp. 12 SER-2013 isolate SE28)	KF581080
<i>Niphargus dimorphopus</i>	KX379138
<i>Niphargus vadimi</i>	KR905817
<i>Niphargus tauricus</i>	KR905823
<i>Niphargus bihorensis</i>	KY706873, KY706930, KF218661-KF218666
<i>Niphargus timavi</i>	KY706810
<i>Niphargus julius</i>	KY706723, KY706739, KY706780, KY706914, KY706943
<i>Niphargus gebhardtii</i>	KP967553, KP967554, KY706947
<i>Niphargus ambulator</i>	KX379125, KY706884, KY706897
<i>Niphargus molnari</i>	KP967552, KY643567