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A new minute species of the genus *Palearcticarellus* Palatov et Marin, 2020 (Crustacea: Amphipoda: Crangonyctidae) from a high-altitude mountain spring of the Altai Mountains (Russia)

Новый миниатюрный вид рода *Palearcticarellus* Palatov et Marin, 2020 (Crustacea: Amphipoda: Crangonyctidae) из высокогорного родника Алтайских гор (Россия)

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КЛЮЧЕВЫЕ СЛОВА: Стигобионты, разнообразие, филогения, Евразия, Палеарктика.

ABSTRACT. A new minute species of the genus *Palearcticarellus* Palatov et Marin, 2020 (Crustacea: Amphipoda: Crangonyctidae) is described from a high-altitude mountain spring located in a drainage basin of a small mountainous river in the Ulagan District of the Altai Mountains, a tributary of Bashkaus River flowing into Lake Teletskoye. The species differs well from its relatives both morphologically and genetically. This is the seventh described species of the genus *Palearcticarellus*, and the fifth known from the mountainous areas of Altai, Russia.

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РЕЗЮМЕ. Новый миниатюрный вид рода *Palearcticarellus* Palatov et Marin, 2020 (Crustacea: Amphipoda: Crangonyctidae) описан из высокогорного родника, расположенного в бассейне небольшой горной реки в Улаганском районе Алтайских гор, притока реки Башкаус, впадающей в Телецкое озеро. Вид хорошо отличается от своих сородичей как морфологически, так и генетически. Это седьмой описанный вид рода *Palearcticarellus,* и пятый известный с горных районов Алтая, Россия.

Introduction

The family Crangonyctidae Bousfield, 1973 (Crustacea, Amphipoda) currently consists of 14 valid genera with about 280 described species of predominantly freshwater amphipods, distributed in groundwater or epigean water bodies throughout the Holarctic [Bousfield, 1973; Holsinger, 1978; Lowry, Myers, 2013, 2017; Zhang, Holsinger, 2003; Horton *et al.*, 2023; Marin, Palatov, 2022a, b, 2023; Palatov, Marin, 2020, 2023]. Among them, 49 known species from 10 described genera have been described from the Palearctic [Marin, Palatov, 2023]. However, our knowledge of the true diversity of these amphipods is still very limited, especially in the mountainous areas of the eastern Palaearctic.

Currently, six crangonyctid species referring to the genus *Palearcticarellus* Palatov et Marin, 2020 are reported from the mountain regions of the southern Siberia and Central Asia (see Marin, Palatov [2023]): *P. pusillus* (Martynov, 1930) is known from the deep-water zone of Lake Teletskoye (Altai Republic, Russia) [Martynov, 1930; Holsinger, 1987; Sidorov *et al.*, 2010]; *P. kazakhstanica* (Kulkina, 1992) — from a

Fig. 1. Habitus of *Palearcticarellus pusillus* (Martynov, 1930) (upper) and *Palearcticarellus ulagani* sp.n. (lower). Scale bar 1 mm.
Рис. 1. Общий вид *Palearcticarellus pusillus* (Martynov, 1930) (сверху) и *Palearcticarellus ulagani* sp.n. (снизу). Масштаб 1 мм.

small spring in the foothills of the western Tien Shan (Zhambyl region, Kazakhstan) [Kulkina, 1992]; *P. anastasiae* (Sidorov, Holsinger et Takhteev, 2010) — from several springs near Baikal Lake (Irkutsk region, Russia) [Sidorov *et al.*, 2010]; *P. mikhaili* (Sidorov, Holsinger et Takhteev, 2010) — from the springs in the valley of the Chuya River in the Kuray mountain steppe (Altai Republic, Russia) [Sidorov *et al.*, 2010]; *P. smirnovi* Palatov et Marin, 2020 — from various spring reservoirs (rheokren/gelokren) in the drainage basins of Biya and Katun rivers in the foothills (up to 400 m above sea level (a.s.l.)) of the Altai Mountains (Altai Republic, Russia) [Marin, Palatov, 2020]; and *P. sapozhnikovi* Palatov et Marin, 2020 — in spring reservoirs (rheokrens) around Lake Kureevo in the drainage basins of Biya River in the foothills (about 350 m a.s.l.) of the Altai Mountains (Altai Republic, Russia) [Marin, Palatov, 2020]. An unidentified and possibly undescribed species of the genus *Palearcticarellus* was recently discovered in the Kök-Tash Cave (Shebalinsky district, Altai Republic, Russia), the deepest known cave in Siberia [Turbanov *et al.*, 2019].

All species of the genus *Palearcticarellus* are characterized by troglomorphic features (troglomorphy), such as complete depigmentation, absence of eyes, while all abovementioned species, except *P. smirnovi* and *P. sapozhnikovi*, are also characterized by extremely small body size, not exceeding 3.8–5 mm. It was suggested [Palatov, Marin, 2020] that such small body size is associated with rather extreme conditions of highland mountain habitats, as well as possible neotenic origin.

The mountainous territory occupies a significant area of Southern Siberia, and, most likely, a large number of hitherto undescribed representatives of the family Crangonyctidae live in the underground habitats of this area. In this paper, we describe a new tiny species of the genus *Palearcticarellus* collected from a high-altitude mountain spring located at 1278 m a.s.l. in the Altai mountains, currently representing one of the highest altitudinal record and probably the smallest species of the genus. Unfortunately, due to the rarity and complexity of sampling in the high-altitude springs, the presented description is based only on two small-sized females, which, however, differ well from their congeners both morphologically and genetically (barcoding).

Material and methods

Amphipods were collected using a hand net, and then fixed in 90% solution of ethanol. Morphological photographs were made with a digital camera attached to light microscope Olympus ZX10 and Olympus CX21.

The body length (bl., mm), the dorsal length from the distal margin of head to the posterior margin of telson, without uropod III and both antennas, is used as a standard measurement. The type material is deposited at the collection of Zoological Museum of Moscow State University, Moscow, Russia (ZMMU).

Since the mitochondrial cytochrome oxidase c subunit I (COI mtDNA) gene has proven extremely informative in previous studies at both population and species level in the family Crangonyctidae [Avise, 1993; Palatov, Marin, 2020; Marin, Palatov, 2021a, b, 2022a, b], it was sequenced in this study as well. Total genomic DNA was extracted from muscle tissue using the innuPREP DNA Micro Kit (AnalitikJena, Germany). The gene marker was amplified by using the universal primers LCO1490 (5'–GGTCAACAAATCATAAAGATATTGG–3') and HC02198 (5'–TAAACTTCAGGGTGACCAAAAAATCA–3') under the standard protocol conditions [Folmer *et al*., 1994]. PCR products were then sequenced using Genetic Analyzer ABI 3500 (Applied Biosystems, USA) and BigDye 3.1 (Applied Biosystems, USA) with forward and reverse primers. Consensus dataset of aligned sequences, about 617 base pairs in length was obtained with MEGA 7.0. The best evolutionary substitution model was determined using MEGA 7.0 and jModeltest2.1.141. A phylogenetic analysis was conducted using PhyML 3.0 [Guindon *et al*., 2010] with several models based on BIC (Bayesian Information Criterion) and AIC (Akaike Information Criterion). All obtained trees were used only to satisfy the phylogenetic position of the genus within the family Crangonyctidae (not presented in the article).

Pairwise genetic divergences (*p*-distances) was calculated based on available sequences using MEGA 7.0 [Kumar *et al.,* 2016] with the Kimura 2-Parameter (K2P) model of evolution [Kimura, 1980].

Results

Order Amphipoda Latreille 1816
Infraorder Gammarida Latreille 1802
Family Crangonyctidae Bousfield 1973
Genus *Palearcticarellus* Palatov et Marin 2020
Palearcticarellus ulagani **sp.n.**
Figs 2–5.

MATERIAL EXAMINED. Holotype, ♀ (bl. 2.2 mm), ZMMU Mb-1264, Russian Federation, Altai Republic, Ulagan District, about 7 km southwest of the village Ulagan, 50°36′2.57″N 87°52′34.49″E, 1278 m a.s.l., in a small spring in a drainage basin of a small mountainous river, a tributary of Bashkaus River flowing into Lake Teletskoye, coll. S.A. Ostroukhova, 24 June 2022.

Additional material. ♀ (bl. 2.0 mm), same locality and data as for holotype (mostly used for DNA analysis).

ETYMOLOGY. The new species is named after Ulagan District, the Altai Republic, Russia, where the new species was discovered.

DIAGNOSIS. Stygobiotic species; only females are currently known. Eyeless, unpigmented. Flagellum of antenna II is 3-articulated. Gnathopods I and II well developed, without a row of setae along palmar margins. Coxal gills present on coxal segments II–VI. Pleopods I–III with 2 hooks in retinacules, with reduced number of segments in rami (2–3). Uropod III with peduncle about thrice longer than ramus, ramus with 3 apical spines. Telson subrectangular, about 1.2X wider than long; distal margin with shallow U-shaped distal notch, each lobe armed with 4 distal spines and some plumose submarginal setae.

DESCRIPTION. Female ♀ 2.2 mm long, eyeless, unpigmented (Fig. 1). Inter-antennal lobe wide, bluntly rounded anteriorly (Fig. 2*a*).

Antenna I (Fig. 2*a*) is about 45% of the body length, 1.8X longer than antenna II; primary flagellum with 9 articles, with aesthetascs on distal article, shorter than respective articles; accessory flagellum 2-articulated, approximately equal article of main flagellum in length (Fig. 2*b*).

Antenna II (Fig. 2*c*): gland clone distinct; peduncle 2.3X longer than flagellum, with several thin setae tightly covering articles III and IV, peduncle of article IV subequal to ones of article V in length; flagellum 3-articulated.

Mandible (Fig. 3*c*, *d*): left mandible incisor 5-dentate, lacinia mobilis 4-dentate, with 3–4 robust plumose accessory setae; molar process with 1 seta. Right mandible incisor 4-dentate, lacinia mobilis triturative, both lobes with numerous protuberances; underlying with a row of 3 robust plumose setae; molar process similar to left mandible. Palp 3-aticulated, article II with 1 long seta; article III oval, with straight posterior margin, with 1 A-seta, 3 separate D-setae and 3 separate E-setae.

Upper lip (Fig. 3*a*): oval, elongated, apical margin of labrum with numerous fine setae.

Lower lip (Fig. 3*b*): inner lobes poorly developed.

Maxilla I (Fig. 3*f*): inner plate with 3 plumose marginal setae, outer plate with 7 apical comb-spines; palp 2-aticulated, distal article pubescent, apical margin of distal article with 3 robust and 1 simple subdistal setae.

Maxilla II (Fig. 3*e*): inner, outer plates covered in pubescent setae; outer plate subequal than inner plate in length, almost not narrowing distally, with 7–8 apical setae; inner plate narrowing distally, with group of dense short setae on apex, with oblique row of 2 short plumose setae.

Maxilliped (Fig. 3*g*): inner plate much shorter than outer plate, armed with 3 spines along apical margin accompanied

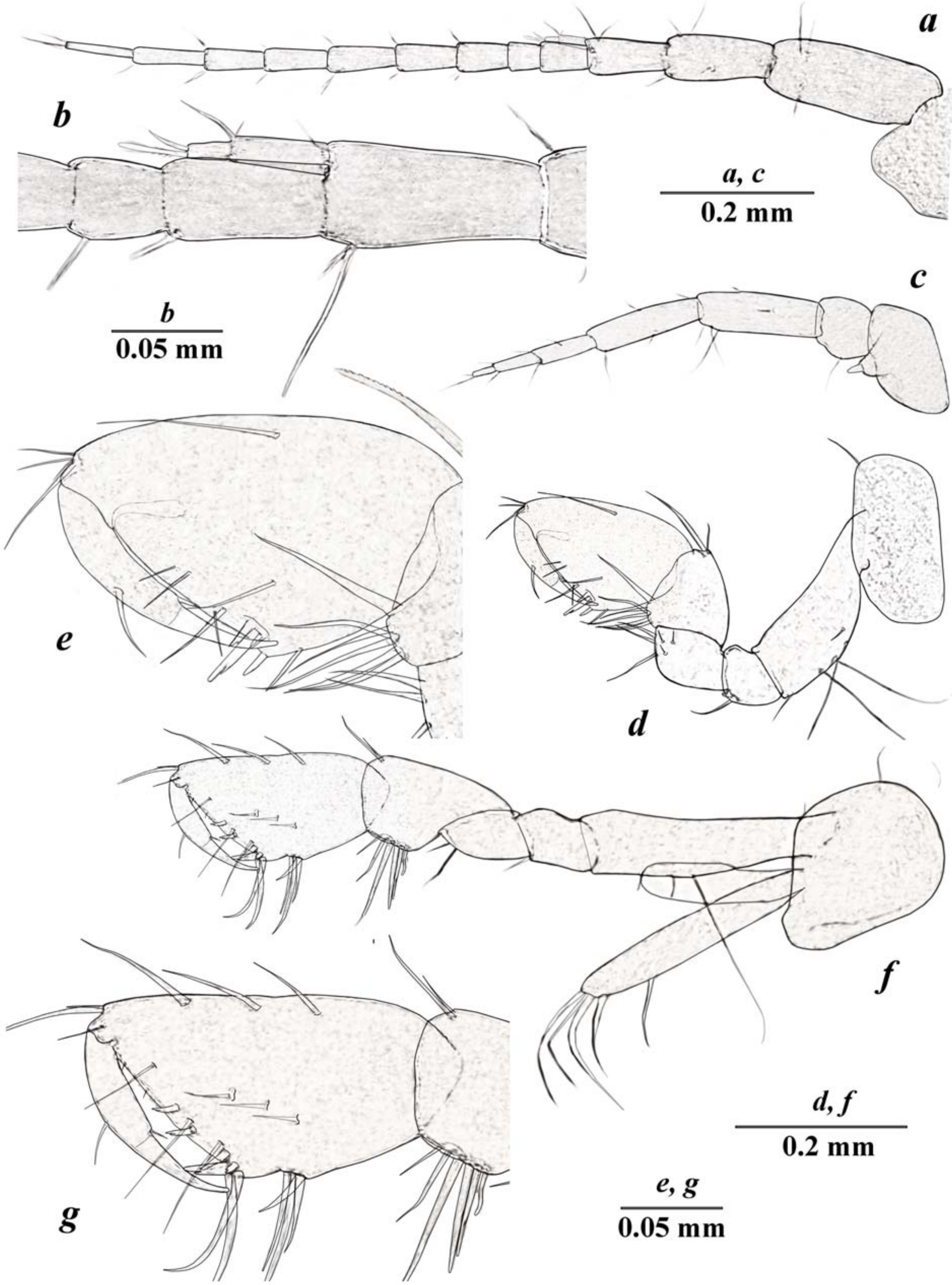

Fig. 2. *Palearcticarellus ulagani* sp.n., holotype ♀: a — antenna I; b — accessory flagellum of antenna I; c — antenna II; d — gnathopod I; e — distoventral margin of chela of GnI; f — gnathopod II; g — palmar margin of chela of GnII.

Рис. 2. *Palearcticarellus ulagani* sp.n., голотип ♀: *a* — антенна I; *b* — дополнительный жгутик антенны I; *c* — антенна II; *d* — гнатопод I; *e* — дистовентральный край клешни GnI; *f* — гнатопод II; *g* — дистовентральный край клешни GnII.

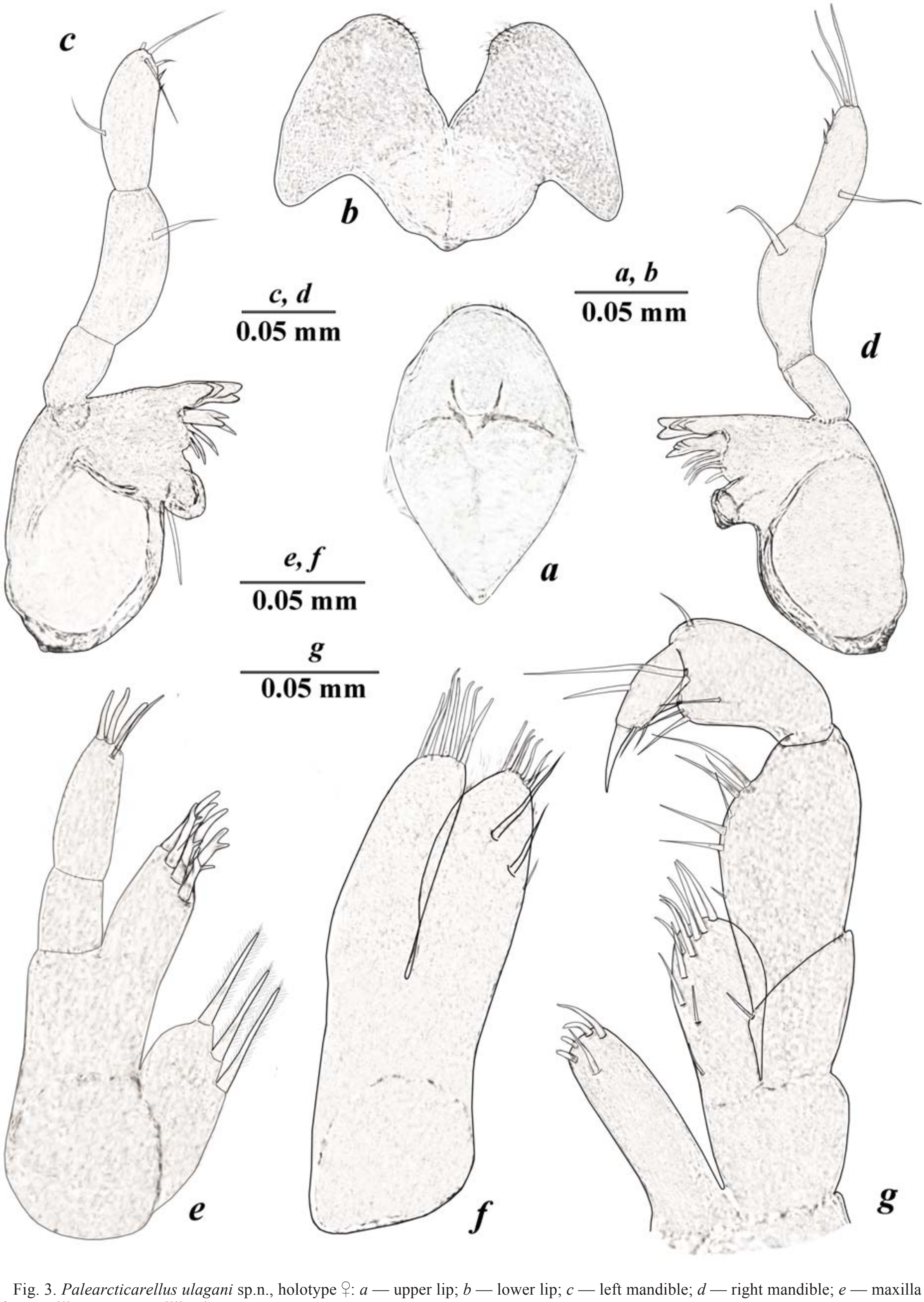

Fig. 3. *Palearcticarellus ulagani* sp.n., holotype ♀: *a* — upper lip; *b* — lower lip; *c* — left mandible; *d* — right mandible; *e* — maxilla I; *f* — maxilla II; *g* — maxilliped.

Рис. 3. *Palearcticarellus ulagani* sp.n., голотип ♀: *a* — верхняя губа; *b* — нижняя губа; *c* — левая мандибула; *d* — правая мандибула; *e* — максилла I; *f* — максилла II; *g* — максиллипеда.

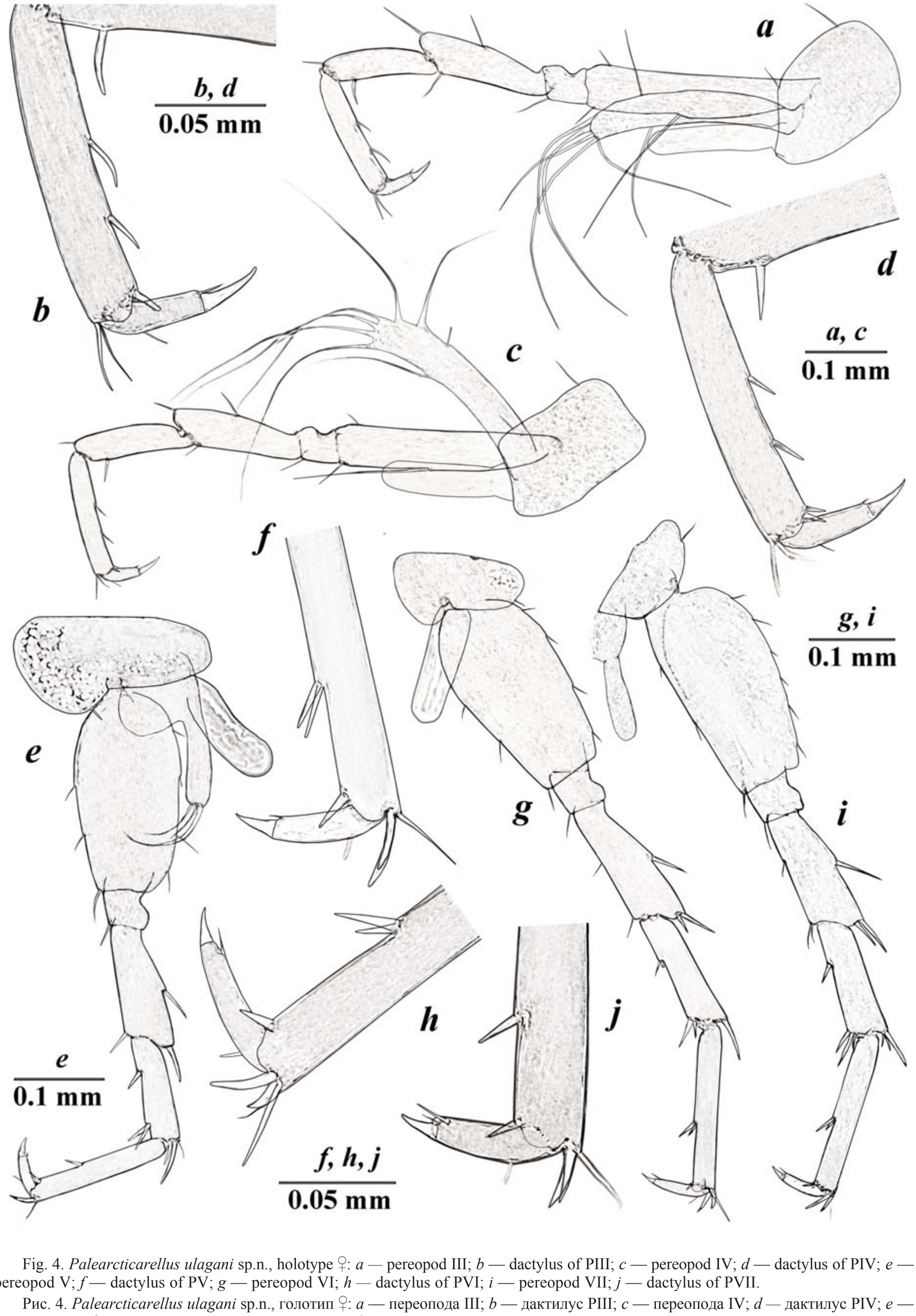

Fig. 4. *Palearcticarellus ulagani* sp.n., holotype ♀: *a* — pereopod III; *b* — dactylus of PIII; *c* — pereopod IV; *d* — dactylus of PIV; *e* — pereopod V; *f* — dactylus of PV; *g* — pereopod VI; *h* — dactylus of PVI; *i* — pereopod VII; *j* — dactylus of PVII.

Рис. 4. *Palearcticarellus ulagani* sp.n., голотип ♀: *a* — переопода III; *b* — дактилус PIII; *c* — переопода IV; *d* — дактилус PIV; *e* — переопода V; f — дактилус PV; *g* — переопода VI; *h* — дактилус PVI; *i* — переопода VII; *j* — дактилус PVII.

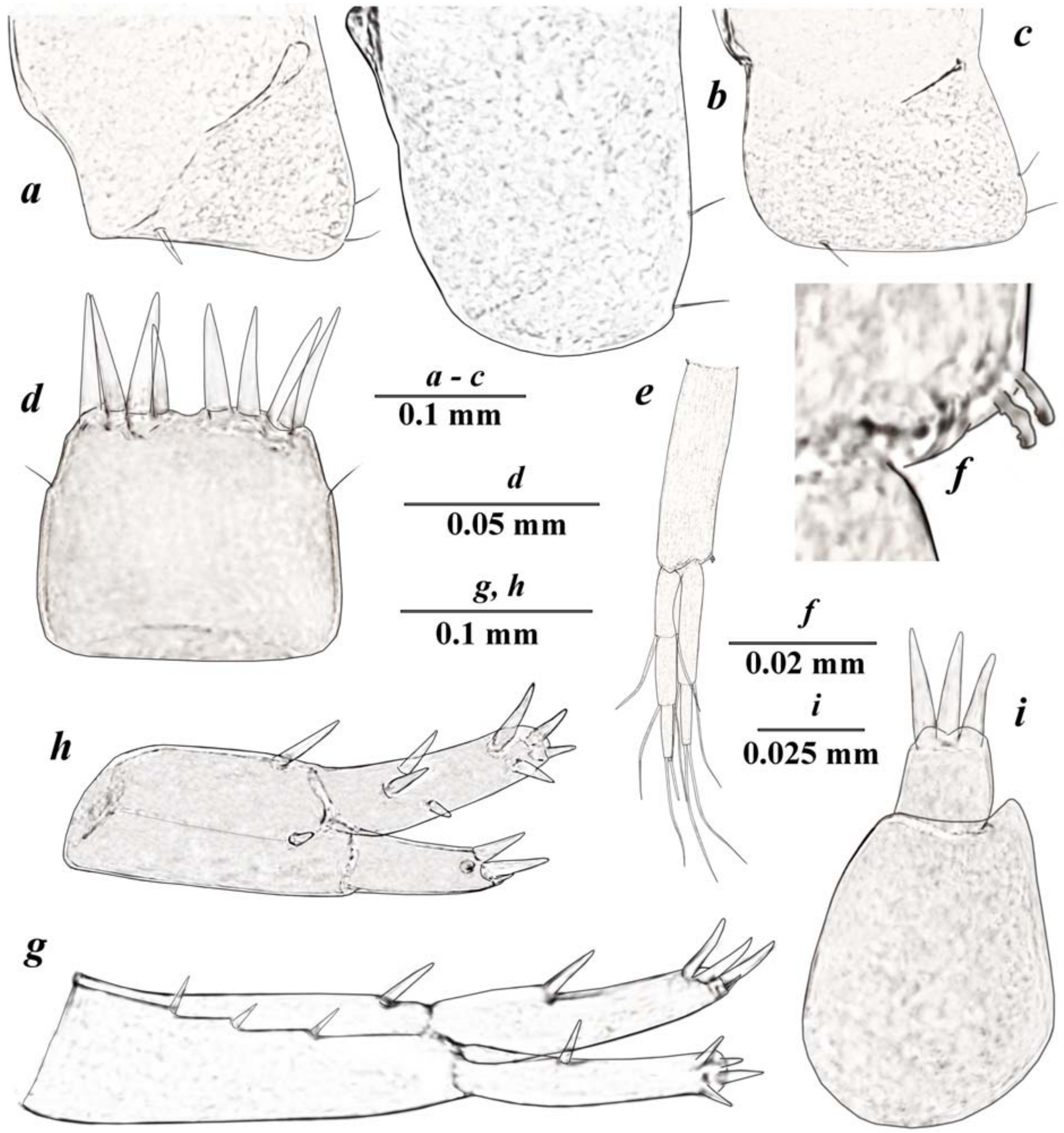

Fig. 5. *Palearcticarellus ulagani* sp.n., holotype ♀: *a–c* — epimeral plates I–III; *d* — telson; *e* — pleopod II; *f* — retinacle of pleopod II; *g* — uropod I; *h* — uropod II; *i* — uropod III.

Рис. 5. *Palearcticarellus ulagani* sp.n., голотип ♀: *a–c* — эпимеральные пластинки I–III; *d* — тельсон; *e* — плеопода II; *f* — ретинакула плеоподы II; *g* — уропода I; *h* — уропода II; *i* — уропода III.

1 plumose and 1 simple submarginal setae, surface of plate covered in fine pubescence; outer plate with 10 setae; palp 4-articulated, article I with 1 seta, article II with 7 marginal setae, article III setaceous with numerous marginal/submarginal setae; dactylus with 1 outer and 2 thin inner setae.

Gnathopod I (Fig. 2*d*, *e*): slightly smaller than gnathopod II; coxal plate oval, not narrowing distally, with 1 apical seta; basis with 3–4 long setae inserted along posterior margin and 1 short seta on medial margin; ischium with 1 plumose seta; merus with 5–6 distal setae; carpus about 45% of length of propodus, with groups of serrated setae on anterior and posterior margins; propodus 1.7X longer than broad, with 1 inferior medial seta; palm oblique with double row of long and short simple setae; palm groove (depression) where dactylus enters, with 2 inner robust, 1 large and 1 smaller outer robust setae (Fig. 2*e*); dactylus with a single outer seta.

Gnathopod II (Fig. 2*f*, *g*): coxal plate rounded, with 2 apical setae; basis with 2–3 short or long setae inserted along posterior margin; ischium with 1 short simple seta; merus with 2–3 distal setae; carpus about 75% of the length of propodus, with 2 anterior and 7 posterior setae; propodus 2.0X longer than broad, with 3 anterior, 3 inferior medial and 2 groups of posterior setae; palm oblique with a row of 2 inner bifurcate robust setae and numerous simple setae; palm groove with 2 inner and 1 outer robust setae (Fig. 2*g*); dactylus with a single outer seta.

Pereopod III (Fig. 4*a*, *b*): coxal plate oval, with 2 apical setae; basis with numerous anterior (1 long and 1 short) and single posterior setae; merus and propodus 1.2–1.3X longer than carpus; dactylus about 46% of length of propodus, with plumose seta on outer margin and stout seta on distal corner of inner margin (Fig. 4*b*).

Pereopod IV (Fig. 4*c*, *d*): subequal to pereopod 3 in length; coxal plate subrectangular, with 2 apical setae; basis with numerous anterior (1 long and 1 short) and single posterior setae; merus and propodus 1.1X longer than carpus; dactylus approximately 47% of length of propodus, setation similar to pereopod III (Fig. 4*d*).

Pereopod V (Fig. 4*e, f*): coxal plate large, bilobate, with distinct anterior and posterior lobes, anterior lobe with a single seta; basis with posterior margin straight, armed with row of 4 short setae, without distal corner; anterior margin with row of 2 naked setae and 2 short setae distally; propodus 1.3X longer that carpus; dactylus approximately 38% of length of propodus, setation similar to that of other pereopods (Fig. 4*f*).

Pereopod VI (Fig. 4*g*, *h*): coxal plate bilobate, posterior lobe with a single apical seta; basis with posterior margin slightly convex, armed with row of 4 short setae, with poorly developed distal corner; anterior margin with row of 2 naked setae and 2 short setae distally; propodus 1.3X longer that carpus; dactylus approximately 42% of length of propodus, setation similar to that of other pereopods (Fig. 4*h*).

Pereopod VII (Fig. 4*i*, *j*): coxal plate small, semilunar, with a single posterior seta; basis with posterior margin convex, armed with row of 6 short naked setae, with weakly convex distal corner; anterior margin with row of 2 naked setae and 2 short setae distally; propodus 1.4X longer that carpus; dactylus approximately 36% of length of propodus, setation similar to that of other pereopods.

Gills, brood plates (Fig. 4): coxal gills on somites II–VI, somite VII with small oval sternal gill. Slender, setaceous brood plates on somites II–V, decreasing in size posteriorly.

Pleopods I–III (Fig. 5*e*, *f*): peduncle with 2 hooks in retinacules; outer and inner rami with 3 and 2 segments, respectively; basal segment of outer ramus lacking clothes–pin setae.

Epimera (Fig. 5*a*–*c*): epimeron I with a single robust seta on ventral margin, posterior margin with 2 setae. Epimeron II with ventral margin distinctly convex, without setae, posterior margin with 2 setae. Epimeron III with ventral margin straight, armed with a single seta, posterior margin with 2 setae.

Urosome with free smooth segments, with sparse setae covering dorsal surface.

Uropod I (Fig. 5*g*): peduncle about 1.5X of length of rami, with 3 outer and 1 inner robust spines; inner ramus 1.1X longer that outer ramus, with 1 dorsal and 4 apical robust spines; outer ramus with 1 dorsal and 4 apical robust spines.

Uropod II (Fig. 5*h*): peduncle about 1.2X of length of inner ramus, with 1 outer and 1 inner robust spines; outer ramus is about 68% of length of inner ramus, with 4 apical robust spines; inner ramus with 3 dorsolateral and 4 apical robust spines.

Uropod III (Fig. 5*i*): small, subequal to telson in length, uniramous; peduncle about twice longer than ramus in length, without spines, with terminal "pointed knob"; ramus with 3 apical robust spines.

Telson (Fig. 5*d*): subrectangular, about 1.2X wider than long; distal margin with shallow U-shaped distal notch, each lobe armed with 4 distal spines and some 2 plumose submarginal setae.

BODY SIZE. The largest collected ♀ has bl. 2.2 mm.

GENBANK ACCESSION NUMBERS. OR413827.

TAXONOMIC REMARKS. The new species clearly belongs to the group of small-sized species of the genus *Palearcticarellus*, being distinguished from the large-sized *P. smirnovi* and *P. sapozhnikovi* (after Palatov, Marin [2020]) by 1) the presence of 2 hooks in retinacules; 2) rectangular telson with very shallow notch; 3) the shape of palms of both gnathopods without a double row of setae on propodus (palm); and 4) the absence of subapical group of spines on proximal article of the outer ramus of uropod III (vs. apical spines present only on distal article of outer ramus, while proximal article is unarmed).

The new species can be separated from the closely related *P. pusillus* and *P. mikhaili* (after Sidorov et al. [2010]) by 1) the inner lobe of the lower lip is poorly developed (vs. well developed); 2) flagellum of antenna II consists of 3 articles (vs. 4 articles); 3) coxal plate of pereopod IV is narrow and rectangular (vs. wide and rounded); 4) rami of pleopods I–III with a reduced number of segments (2–3) (vs. with 5–4 (rarely 3)); 5) peduncle of uropod III with a pointed terminal "knob" (vs. without terminal "knob"); and 6) epimeron I with a single strong bristle on the abdominal margin (vs. without bristle).

From *P. anastasiae* (after Sidorov *et al*. [2010]), it can be separated by 1) inner planes of lower lips is poorly developed (vs. well developed); 2) telson subrectangular, wider than long (vs. longer than broad, tapering distally); 3) epimeron I with a single robust seta on ventral margin (vs. without setae on ventral margin); and 4) epimeron III with a single robust seta on ventral margin (vs. without seta on ventral margin).

From *P. kazakhstanica* (after Kulkina [1992]), the new species can be easily separated by 1) absence of calceoli on antenna II; 2) absence of ventral setae on epimeral plates I–III; 3) different shape of palm of gnathopods I–II; and 4) the absence of subapical group of spines on proximal article of outer ramus of uropod III.

PHYLOGENY. The molecular genetic analysis clearly confirmed the validity of the newly described species. The interspecific genetic divergence by COI mtDNA gene marker of the new species and other congeners (see Table 1) is estimated at over 27%, showing a long-time genetic isolation.

The estimated divergence time based on COI mtDNA gene marker of the new species from the congeners is about 10.8 (4.8–35.06) Mya (the average as 2.5%Mya^{-1}; minimal as 0.77%Mya^{-1}; and maximal as 5.16%Mya^{-1} (after Guy-Haim *et al*. [2018])), and 15.22 Mya, respectively (about 1.773% Mya^{-1} for COI mtDNA gene marker (according to Copilaş-Ciocianu *et al*. [2019])).

DISTRIBUTION AND ECOLOGY. Presently, the species is currently known exclusively from a single small spring (50°36′2.57″N 87°52′34.49″E) located at the altitude 1278 m a.s.l. in a drainage basin of a small mountainous river, a tributary of the Bashkaus River flowing into Lake Teletskoye. The bed of the studied spring was shaded, the substratum consisted mainly of gravel and pebbles, and about 15% of the surface of the substratum was covered with moss; water temperature was about 6°C

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Table 1. Comparison of uncorrected pairwise genetic (COI mtDNA) distances (*p*-distances) (substitutions per 100 nucleotides±SE) between the studied species of the genus *Palearcticarellus*.
Таблица 1. Сравнение попарных генетических (COI mtDNA) дистанций (*p*-distances) (замен на 100 нуклеотидов±SE) между изучаемыми видами рода *Palearcticarellus*.

Palearcticarellus ulagani sp.n.		*P. mikhaili*	*P. pusillus*	*P. smirnovi*
P. mikhaili	0.2700±0.0260			
P. pusillus	0.2743±0.0252	0.0926±0.0101		
P. smirnovi	0.2773±0.0234	0.2138±0.0203	0.2168±0.0199	
P. anastasiae	0.3384±0.0291	0.2712±0.0281	0.2779±0.0238	0.2906±0.0257

References

Avise J.C. 1994. Molecular markers, natural history and evolution. Chapman and Hall, New York. 511 pp. http://dx.doi.org/10.1007/978-1-4615-2381-9

Bousfield E.L. 1973. Shallow-water gammaridean Amphipoda of New England. Ithaca: Cornell University Press. 312 p.

Copilaş-Ciocianu D., Sidorov D.A., Gontcharov A. 2019. Adrift across tectonic plates: molecular phylogenetics supports the ancient Laurasian origin of old limnic crangonyctid amphipods // Organisms Diversity & Evolution. Vol.19. P.191–207. https://doi.org/10.1007/s13127-019-00401-7

Folmer O., Black M., Hoeh W., Lutz R., Vrijenhoek R. 1994. DNA primers for amplification of mitochondrial cytochrome c oxidase subunit 1 from diverse metazoan // Molecular Marine Biology and Biotechnology. Vol.3. No.5. P.294–299.

Guindon S., Dufayard J.F., Lefort V., Anisimova M., Hordijk W., Gascuel O. 2010. New algorithms and methods to Estimate Maximum–Likelihood Phylogenies: Assessing the Performance of PhyML 3.0 // Systematic Biology. Vol.59. No.3. P.307–321. https://doi.org/10.1093/sysbio/syq010

Guy-Haim T., Simon-Blecher N., Frumkin A., Naaman I., Achituv Y. 2018. Multiple transgressions and slow evolution shape the phylogeographic pattern of the blind cave-dwelling shrimp *Typhlocaris* // PeerJ. Vol.6. Art.e5268. https://doi.org/10.7717/peerj.5268

Holsinger J.R. 1978. Systematics of the subterranean amphipod genus *Stygobromus* (Gammaridae). Part II: Species of the eastern United States // Smithsonian Contributions to Zoology. Vol.266. P.1–144.

Holsinger J.R. 1987. Redescription of the stygobiont amphipod crustacean *Stygobromus pusillus* (Crangonyctidae) from the Soviet Union, with comments on taxonomic and zoogeographic relationships // Journal of Crustacean Biology. Vol.7. P.249–257. https://doi.org/10.1163/193724087X00207

Horton T., Lowry J., De Broyer C., Bellan-Santini D., Copilas-Ciocianu D., Corbari L., Costello M.J., Daneliya M., Dauvin J.-C., Fišer C., Gasca R., Grabowski M., Guerra-García J.M., Hendrycks E., Hughes L., Jaume D., Jazdzewski K., Kim Y.-H., King R., Krapp-Schickel T., LeCroy S., Lörz A.-N., Mamos T., Senna A.R., Serejo C., Souza-Filho J.F., Tandberg A.H., Thomas J.D., Thurston M., Vader W., Väinölä R., Vonk R., White K., Zeidler W. 2023. World Amphipoda Database. Crangonyctidae Bousfield, 1973. Accessed through: World Register of Marine Species at: https://marinespecies.org/aphia.php?p=taxdetails&id=430454 [accessed on 2023-07-23].

Kimura M. 1980. A simple method for estimating evolutionary rates of base substitutions through comparative studies of nucleotide sequences // Journal of Molecular Evolution. Vol.16. No.2. P.111–120. https://doi.org/10.1007/BF01731581

Kulkina L.V. 1992. [*Stygobromus kazakhstanica* sp. n. (Amphipoda, Crangonyctidae) from underground waters of Tien Shan] // Zoologicheskyi Zhurnal. Vol.71. P.40–45 [in Russian with English abstract].

Kumar S., Stecher G., Tamura K. 2016. MEGA7: molecular evolutionary genetics analysis version 7.0 for bigger datasets // Molecular Biology and Evolution. Vol.33. No.7. P.1870–1874. https://doi.org/10.1093/molbev/msw054

Lowry J.K., Myers A.A. 2013. A phylogeny and classification of the Senticaudata subord. nov. (Crustacea: Amphipoda) // Zootaxa. Vol.3610. P.1–80. https://doi.org/10.11646/zootaxa.3610.1.1

Lowry J.K., Myers A.A. 2017. A phylogeny and classification of the Amphipoda with the establishment of the new order Ingolfiellida (Crustacea: Peracarida) // Zootaxa. Vol.4265. P.1–89. https://doi.org/10.11646/zootaxa.4265.1.1

Marin I.N, Palatov D.M. 2021a. *Volgonyx* gen.n. and *Pontonyx* gen.n., two new genera of the family Crangonyctidae (Crustacea: Amphipoda) from the southeastern Europe // Arthropoda Selecta. Vol.30. No.1. P.43–61. http://doi.org/10.15298/arthsel.30.1.05

Marin I.N., Palatov D.M. 2021b. The hidden diversity of the genus *Lyurella* Derzhavin, 1939 (Crustacea: Amphipoda: Crangonyctidae): four new species from the subterranean habitats of the northwestern Caucasus, Russia // Zootaxa. Vol.5006. No.1. P.127–168. https://doi.org/10.11646/zootaxa.5006.1.17

Marin I.N., Palatov D.M. 2022a. *Uralocrangonyx* gen.n. (Amphipoda: Crangonyctidae) from the Southern Ural, Russia // Arthropoda Selecta. Vol.31. No.2. P.183–195. https://doi.org/10.15298/arthsel.31.2.07

Marin I.N., Palatov D.M. 2022b. Lifestyle switching and refugee availability are the main factors in the evolution and distribution of the genus *Synurella* Wrześniowski, 1877 (Amphipoda: Crangonyctidae) // Arthropoda Selecta. Vol.31. No.4. P.393–448. https://doi.org/10.15298/arthsel.31.4.04

Marin I.N., Palatov D.M. 2023. A revision of the genus *Pontonyx* Palatov et Marin, 2021 (Amphipoda: Crangonyctidae), with an overview of crangonyctid diversity in the Palaearctic // Arthropoda Selecta. Vol.32. No.2. P.173–196. https://doi.org/10.15298/arthsel.32.2.04

Martynov A.V. 1930. [Amphipodous fauna of Teletskoye Lake and its origin] // Izvestiya Gosudarstvennogo Gidrologicheskogo Instituta. Vol.29. P.95–128 [in Russian with English abstract].

Palatov D.M., Marin I.N. 2020. A new genus of the family Crangonyctidae (Crustacea, Amphipoda) from the Palaearctic, with descriptions of two new species from the foothills of the Altai Mountains // Zoologicheskyi Zhurnal. Vol.99. No.10. P.1160–1186.

Palatov D.M., Marin I.N. 2023. Diversity of the Caucasian genus *Diasynurella* Behning, 1940 (Amphipoda: Crangonyctidae) with description of four new species // Arthropoda Selecta. Vol.32. No.1. P.23–55. https://doi.org/10.15298/arthsel.32.1.03

Sidorov D.A., Holsinger J.R., Takhteev V. 2010. Two new species of the subterranean amphipod genus *Stygobromus* (Amphipoda: Crangonyctidae) from Siberia, with new data on *Stygobromus pusillus* (Martynov) and remarks on morphology and biogeographic relationships // Zootaxa. Vol.2478. P.41–58. https://doi.org/10.11646/zootaxa.2478.1.2

Turbanov I.S., Schwartz D.B., Shelepin A.L. 2019. [Kok-Tash Cave] // Shelepin A.L. (ed.). Atlas peshcher Rossii. Moscow: Russian Geographical Society, Russian Union of Speleologists. P.490–493 [in Russian].

Zhang J., Holsinger J.R. 2003. Systematics of the freshwater amphipod genus *Crangonyx* (Crangonyctidae) in North America // Virginia Museum of Natural History Memoir. Vol.6. P.1–274. https://doi.org/10.1163/156854008X354894

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