

Distribution of the genus *Volgonyx* Marin et Palatov, 2021 (Crustacea: Amphipoda: Crangonyctidae) in groundwater habitats along the Lower Volga with a description of a new species

Распространение рода *Volgonyx* Marin et Palatov, 2021 (Crustacea: Amphipoda: Crangonyctidae) в стигобионтных местообитаниях вдоль Нижней Волги с описанием нового вида

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КЛЮЧЕВЫЕ СЛОВА: Разнообразие, Crustacea, Amphipoda, Crangonyctidae, новый вид, подземные, Нижняя Волга, Россия.

ABSTRACT. A detailed study of spring habitats in the eastern Volga Upland, located north of Saratov, was conducted to explore the ecology of representatives of the genus *Volgonyx* Marin et Palatov, 2021 (Crustacea: Amphipoda: Crangonyctidae). As a result, the known distribution area of *Volgonyx dershavini* (Behning, 1928) has been significantly expanded north to Ulyanovsk; the known area of distribution of this species currently extends along the right (upper) bank of the Lower Volga for more than 350 km. A new species, *Volgonyx behningi* sp.n., has also been discovered in the Zhiguli Mountains, which differs from the previously known *V. dershavini* in the structure of antennae, epimeral plates, uropods and telson, as well as genetically. The article also discusses the known diversity of crangonyctid amphipods in the Volga River basin, possible ways of gene flow between different populations and the mechanisms of their isolation.

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РЕЗЮМЕ. Проведено детальное изучение родниковых местообитаний восточной части Приволжской возвышенности, расположенных к северу от Саратова, с целью поиска новых локаций для представителей рода *Volgonyx* Marin et Palatov, 2021 (Crustacea: Amphipoda: Crangonyctidae). В результате известный ареал *Volgonyx dershavini* (Behning, 1928) значительно расширен вдоль на север до Ульяновска; известный ареал распространения этого вида в настоящее время простирается вдоль правого (верхнего) бе-

рега Нижней Волги более чем на 350 км. Кроме того, в Жигулевских горах был обнаружен новый генетически изолированный вид, *Volgonyx behningi* sp.n., который отличается от ранее известного *V. dershavini* строением антенн, эпимеральных пластинок, уropод и тельсона, а также генетически. В статье обсуждается известное разнообразие амфипод-крангониктид в бассейне Волги, возможные пути дрейфа генов между различными популяциями и механизмы их изоляции.

Introduction

The Holarctic family Crangonyctidae Bousfield, 1973 (Crustacea: Amphipoda: Gammarida) is represented by a very ancient group of amphipods that appeared at the beginning of the Cretaceous in Laurasia [Copilaş-Ciocianu *et al.*, 2019]. The family is closely related to the East Asian freshwater family Pseudocrangonyctidae Holsinger, 1989 and the Iceland monotypic family Cymostygiidae Kristjánsson et Svavarsson, 2004 [Kornobis *et al.*, 2011; Kristjánsson, Svavarsson 2004; Copilaş-Ciocianu *et al.*, 2019]. Modern representatives of the main clades of the family Crangonyctidae are scattered across the divergent areas of Nearctic [Koenemann, Holsinger, 2001; Zhang, Holsinger, 2003; Gibson *et al.*, 2021; Cannizzaro *et al.*, 2021] and Palearctic [Sidorov, Holsinger, 2007; Svavarsson, Kristjánsson, 2006; Copilaş-Ciocianu *et al.*, 2019; Palatov, Marin, 2020, 2021a, b; Marin, Palatov, 2021b, 2023a, b], and are currently most well studied in North America (Nearctic), where more than 150 species have been described [Cannizzaro *et al.*, 2021; Sisco, Sawicki, 2023]. The known diversity of the family in the Palearctic is currently presented by 51 known species from 10 described genera, with the majority of species

known from Russia [Marin, Palatov, 2023, 2024; Marin *et al.*, 2023].

Most of the stygobiotic crustaceans are strictly endemic, usually living in one isolated underground (subterranean) basin, and well adapted to strict environmental conditions (stenobiotic) [Galassi *et al.*, 2009; Fišer *et al.*, 2008; Eme *et al.*, 2017; Borko *et al.*, 2021]. In addition, crangonyctid amphipods are usually characterized by an ancient (relict) distribution, which does not change for a long time [Sidorov, Holsinger, 2007; Svavarsson, Kristjánsson, 2006; Copilaș-Ciocianu *et al.*, 2019]. At the same time, there are some exceptions in stygobiotic amphipods when some species move to inhabit surface waters (e.g., epigean crangonyctids *Synurella ambulans* (F. Müller, 1846) and some species of the genus *Pontonyx* Palatov et Marin 2021 (Amphipoda: Crangonyctidae), as well as niphargid amphipod *Niphargus hrabei* S. Karaman, 1932 and *Niphargus potamophilus* Birštein, 1954 (Amphipoda: Niphargidae) and some others), and then their distribution expands significantly [Copilaș-Ciocianu *et al.*, 2014, 2017, 2018; Palatov, Marin, 2021a, b; Marin, Palatov, 2022a]. According to the suggested hypothesis, the dispersal of epigean species is mediated by floods or seasonal river flooding (passive long-range dispersal events) [van Leeuwen *et al.*, 2013; Copilaș-Ciocianu *et al.*, 2018]. At the same time, large distribution ranges of strictly stygobiotic species are extremely rare, and in most cases the conditions allowing them to spread over significant distances remain unknown. In some cases, for example for *Niphargus utrishensis* Marin et Palatov, 2021, it is assumed that there are large underground basins or a network of connected basins, where gene flow takes place [Marin *et al.*, 2021].

The crangonyctid genus *Volgonyx* Marin et Palatov 2021 was proposed after the revision of the so called “*Synurella dershavini*”-group suggested by Sidorov & Kovtun [2015] (see Marin & Palatov [2015]). Prior to the present study, the only known species of the genus, *Volgonyx dershavini* (Behning, 1928), has been known as endemic to the Volga Upland, distributed in several wells and springs along the upper (right) bank of the Volga River in the vicinity of the city of Saratov, Russia [Behning, 1928; Marin, Palatov, 2021]. At the same time, the subterranean fauna of the Volga Upland has been studied extremely poorly, including due to its large area.

During our study in August 2023, we have tried to examine in detail a part of the Volga Upland, located north of Saratov (see Fig. 1), in order to find new locations for representatives of the genus *Volgonyx*. As a result, the known distribution area of *V. dershavini* was significantly expanded along the Lower Volga to north, and a new species, which is described below as new to science, was discovered in the Zhiguli Mountains (Samara Luka).

The Zhiguli Mountains (the elevated part of the Samara Luka) are the only mountains of tectonic origin on the Russian Plain, a manifestation of the Zhiguli Fault, which arose in the late Miocene, about 5–7 Mya, rising in the form of a lopsided fold, and growing to the present. They are represented by an elevated massif of carboniferous and permian rocks formed about 240–300 Mya.

Approximately 3.4–1.8 Mya (Pliocene–Pleistocene) the Zhiguli Mountains were an isolated island in the so-called Akchagyl Sea (apparently brackish), which was part of the modern Caspian Sea [Milanovsky, 1940; Emelyanov, 1955; Obedientova, 1953, 1977, 1988].

Material and Methods

Amphipods were collected using a hand net in various epigean water resources along the Lower Volga River in August 2023 (see Fig. 1). All collected animals were fixed in 90% solution of ethanol. Morphological photographs were made with a digital camera attached to Olympus CX21 light microscopes. Photographs of alive coloration of animals *in situ* were made using a Canon G16 digital camera. The body length (bl., in mm), the dorsal length from the distal margin of head to the distal margin of telson, without the length of uropod III and both antennae, is used as a standard measurement. The type and collected material are deposited in the collection of Zoological Museum of Moscow State University, Moscow, Russia (ZMMU) and author’s collection in A.N. Severtsov Institute of Ecology and Evolution of Russian Academy of Sciences, Moscow, Russia (LEMMI).

Cytochrome c oxidase subunit I (COI) mtDNA was used as one of the most informative gene markers for genetic studies at population and species level to confirm the phylogenetic relationships of the studied species [Avice, 1993; Hebert *et al.*, 2003]. Total genomic DNA was extracted from muscle tissue using the innuPREP DNA Micro Kit (AnalytikJena, Germany). The COI mtDNA gene marker was amplified with the help of the universal primers LCO1490 (5′-GGTCAACAAATCATA-AAGATATTGG-3′) and HC02198 (5′-TAAACTTCAGGGT-GACCAAAAATCA-3′) under standard protocol conditions [Folmer *et al.*, 1994]. 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 the Genetic Analyzer ABI 3500 (Applied Biosystems, USA) and BigDye 3.1 (Applied Biosystems, USA) with direct and reverse primers. Dataset of aligned sequences of the COI gene marker, about 586 base pairs in length, taken from GenBank (NCBI) and author’s database were used in the phylogenetic study. Consensus of complementary sequences was obtained with MEGA 7.0 [Kumar *et al.*, 2016].

The best evolutionary substitution model was determined using MEGA 7.0. and jModeltest2.1.141 on XSEDE via the CIPRES (Cyber Infrastructure for Phylogenetic Research) Science Gateway V. 3.3 (<http://www.phylo.org/>). Phylogenetic analysis was performed on single gene marker dataset (COI mtDNA) using PhyML 3.0 [Guindon *et al.*, 2010] using GTR+G+I model for Maximum-Likelihood (ML) analysis. Median joint network of haplotypes [Bandelt *et al.*, 1999] was reconstructed with PopArt (Population Analysis with Reticulate Trees) software [Leigh, Bryant, 2015].

Pairwise genetic divergences (*p*-distances) were 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 the discovered and studied locations of the widely distributed *Volgonyx dershavini* (Behning 1928) along the Lower Volga River is relatively low, being about 0.0075±0.0022 substitutions per 100

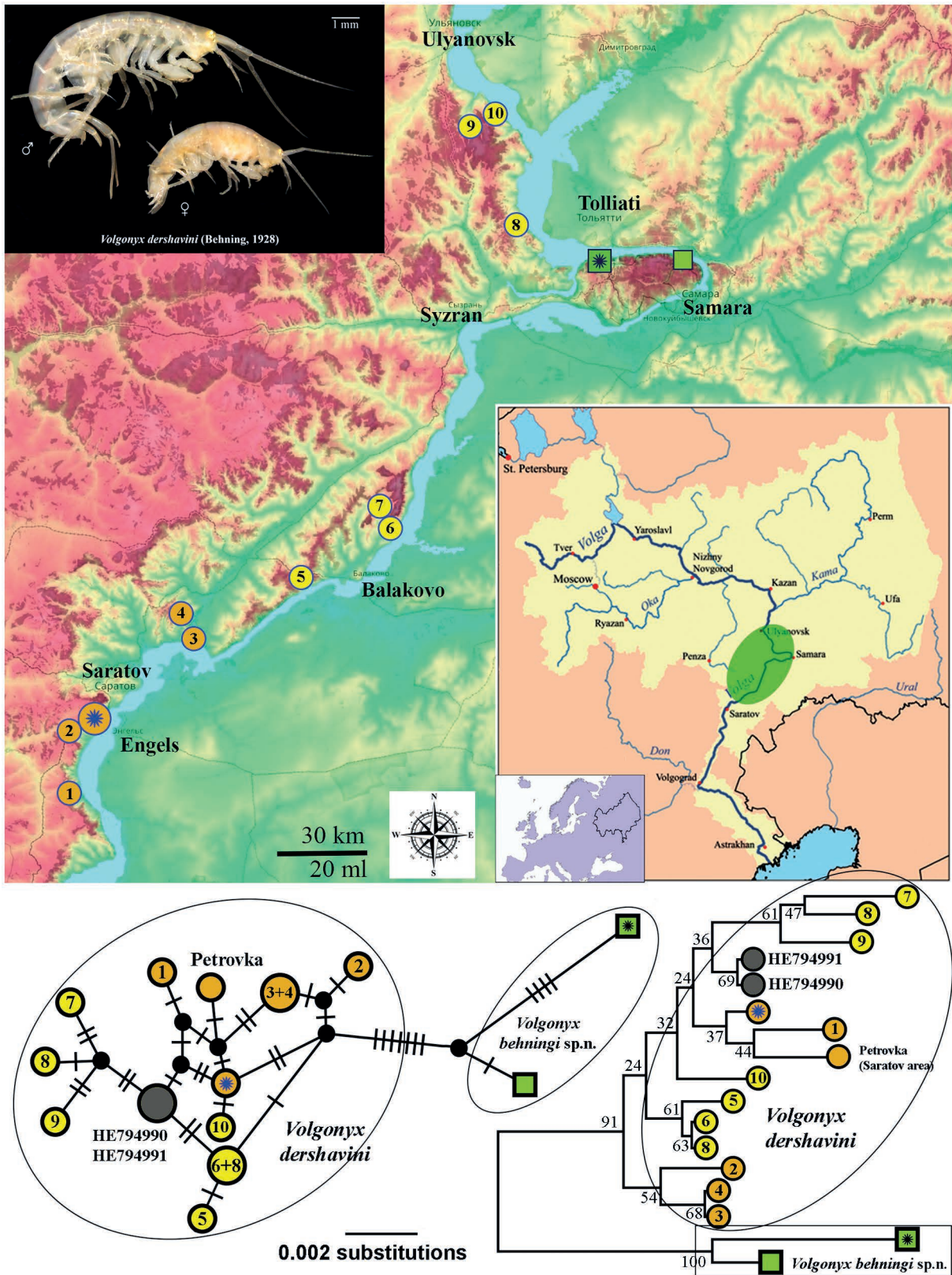


Fig. 1. The map of distribution, MJ network of haplotypes (TSC) and reconstruction of phylogenetic relationships (based on COI mtDNA gene marker) of the representatives of the genus *Volgonyx* Marin et Palatov 2021 along the Lower Volga River. Green color showing the studied area. Yellow and brown circles represent new and previous records of *Volgonyx dershavini* (Behning, 1928), respectively [Behning, 1928; Marin, Palatov, 2021]. Quadrates shows the records of *Volgonyx behningi* sp.n. in Zhiguli Mountains. Figures with stars represent type localities of each species. Topographic maps are taken from Mineeva *et al.* [2021] and topographic-map.com.

nucleotides (0.8%) (n=11). The data obtained probably show that genetically populations from fairly remote populations, for example, the environs of Saratov, Samara and Ulyanovsk, are currently not genetically isolated (see Fig. 1).

At the same time, the specimens of the new species discovered in the Zhiguli Mountains (Samara Luka), an isolated mountainous massive in the eastern part of the Volga Upland (see Discussion), shows the genetic divergence (*p*-distances) from *V. dershavini* for about 0.021±0.005 substitutions per 100 nucleotides (2.1%) (n=2). Similar genetic distances (about 2.3% or 0.023±0.0106 substitutions per 100 nucleotides) are known between widely distributed Western European *Synurella ambulans* (F. Müller, 1846) and Crimea–Western Caucasian *S. taurica* Martynov, 1931 (after Marin, Palatov [2022a]).

Such genetic isolation is well supported (Bayesian–PP=1.00; ML–BS=99%) and relatively high within the family Crangonyctidae. The estimated min. (5.16%/Mya⁻¹) and max. (as 0.77% per Mya⁻¹) divergence time is calculated after Guy-Haim *et al.* [2018], with the average divergence time (as 2.5% per Mya⁻¹), calculated after Lefébure *et al.* [2006], Copilas-Ciocianu & Petrussek [2015], reveal the genetic isolation from 2.77 to 0.4 Mya, with the average divergence time for about 0.84 Mya. According to Copilas-Ciocianu *et al.* [2019] (1.773% per Mya⁻¹), the genetic divergence between the species can be calculated as 1.18 Mya.

TAXONOMIC PART

Order Amphipoda Latreille, 1816
 Infraorder Gammarida Latreille, 1802
 Family Crangonyctidae Bousfield, 1973
 Genus *Volgonyx* Marin et Palatov, 2021
Volgonyx dershavini (Behning, 1928)

MATERIAL EXAMINED. Russian Federation, Ulyanovsk Region: 6♂♂, 15♀♀, LEMMI, Lysukha Mountain, Cemzavod, in a spring, 54°00'14.8"N 48°43'19.7"E, 13.08.2023, coll. I. Marin & D. Palatov; 15♀♀, LEMMI, in Bogomolnii Spring, 53°58'34.4"N 48°31'44.3"E, 13.08.2023, coll. I. Marin & D. Palatov; Samara Region: 1♂, 5♀♀, LEMMI, Novodevichiy, in a spring, 53°36'03.3"N 48°50'29.7"E, 28.08.2023, coll. I. Marin & D. Palatov; Saratov Region: 5♂♂, 7♀♀, LEMMI, Khvalynskiy Region, near Khvalynsk, in a forest spring, 52°28'33.3"N 48°03'34.4"E, 27.08.2023, coll. I. Marin & D. Palatov; 5♂♂, 17♀♀, LEMMI, Khvalynskiy Region, near Alekseevka, in a spring near road Syzran–Balakovo, 52°21'16.4"N 47°56'42.1"E, 27.08.2023, coll. I. Marin & D. Palatov; 5♂♂, 5♀♀, LEMMI, Volsk, in a spring in city park, 52°03'06.4"N 47°23'25.9"E, 27.08.2023, coll. I. Marin & D. Palatov.

DIAGNOSIS. Relatively large amphipods (up to 10.0 mm) with troglomorphic yellowish body. Head with mostly reduced ommatidia and well-marked yellow spots. Antenna I with relatively stouter peduncular articles, which are 3/3.5/2.5X longer than wide, respectively. Accessory flagellum of antenna II with basal article about 3.5X longer than wide, with distal article short, about 2X shorter than basal one. Basis of pereopod V about 2X longer than wide. Basis of pereopod VII with distinctly convex posterior margin. Epimeral plates I and II with slightly convex posterior margins. Outer ramus of uropod I in ♂♂ about 3X longer than inner one. Uropod III small, shorter than telson, uniramous; peduncle about 4X longer than ramus in length, ramus with 3 apical robust spines. Pleopods with 3–4 (in ♀♀) and

7–8 (in ♂♂) coupling hooks in retinacles of pleopods. Telson rectangular, with U-shaped distal notch relatively shallow, less than 1/5–1/6 of telson length.

COLORATION. The body and appendages yellowish transparent; with small pigmented spots on the anterior lobe of head (see Marin & Palatov [2021]).

BODY SIZE. The largest collected ♂ has bl. 11.0 mm, ♀– 8.0 mm.

GENBANK ACCESSION NUMBERS. MT231260, MT231261, PP431257–PP431257.

DISTRIBUTION AND ECOLOGY. Widely distributed crangonyctid species, presently known from numerous wells and springs of the eastern part of the Volga Upland along coastal line of the upper (right) bank of the Lower Volga River from Ulyanovsk to Saratov (see Fig. 1) [Behning, 1928; Marin, Palatov, 2021]. The species was found together with such spring dwelling insect larvae, such as *Baetis rhodani* (Pictet, 1843) (Ephemeroptera: Baetidae), *Nemoura cinerea* (Retzius, 1783) (Plecoptera: Nemouridae), *Leuctra fusca* (Linnaeus, 1758) (Plecoptera: Leuctridae), *Plectrocnemia conspersa* (Curtis, 1834) (Trichoptera: Polycentropodidae), *Pedicia rivosa* (Linnaeus, 1758) (Diptera: Pediciidae) [Marin, Palatov, 2024].

Volgonyx behningi sp.n.

Figs 2–5.

MATERIAL EXAMINED. Holotype, ♂ (bl. 12.5 mm), ZMMU Mb-1280, Russian Federation, Samara Region, Zhiguli Mountains, Zhigulevsk, inside a small spring-well (Morkshavinskiy Well), 53°24'55.8"N 49°32'15.5"E, 14.08.2023, coll. I. Marin & D. Palatov.

Paratypes. ♀ (bl. 8 mm), ZMMU Mb-1281, same locality and data as holotype.

Additional material. ♀ (bl. 8 mm), LEMMI, same locality and data as holotype; ♂ (bl. 9 mm), LEMMI, Zhiguli Mountains, Shiryaev, 53°24'33.5"N 50°00'47.4"E, in small mountainous spring (Vinniy Spring), hand net sampling, 15.08.2023, coll. I. Marin & D. Palatov.

ETYMOLOGY. The new species is named in honor of Dr. Arvid Liboryevich Behning (1890–1943), a famous Russian and Soviet scientist (hydrobiologist, ichthyologist and zoologist), for a long time headed the Volga Biological Station, carefully studying the fauna of the Volga and its main tributaries. He conducted first biodiversity studies of the biocenoses of the Volga River, the Aral and Caspian Seas, as well as the Caucasus, including the study of the diversity of stygobiotic crustaceans.

DIAGNOSIS. Relatively large amphipods (up to 12.5 mm) with strongly troglomorphic unpigmented body. Head with mostly reduced ommatidia and feebly marked yellow spots. Antenna I with relatively stouter peduncular articles, which are 2.5/3/2X longer than wide, respectively. Accessory flagellum of antenna II with basal article about 4.5X longer than wide, with distal article short, about 3X shorter than basal one. Basis of pereopod V about 2.5X longer than wide. Basis of pereopod VII rectangular, with almost straight posterior margin. Epimeral plates I and II with strongly convex posterior margins. Outer ramus of uropod I in ♂♂ about 4X longer than inner one (vs. 3X only). Uropod III small, shorter than telson, uniramous; peduncle about 4.5X longer than ramus in length, ramus with 3 apical robust spines. Pleopods with 4 (in ♀♀) and 8 (in ♂♂) coupling hooks in retinacles of pleopods. Telson rectangular, with V-shaped distal notch deep, about ¼ of telson length.

Рис. 1. Карта распространения, сеть гаплотипов (TSC) и реконструкция филогенетических взаимоотношений (на основе генного маркера COI мтДНК) представителей рода *Volgonyx* Marin et Palatov 2021 вдоль Нижней Волги. Зеленым цветом отмечена изученная территория. Желтые и коричневые кружки обозначают новые и предыдущие находки *Volgonyx dershavini* (Behning, 1928), соответственно [Behning, 1928; Marin, Palatov, 2021]. Квадратами обозначены находки *Volgonyx behningi* sp.n. в Жигулевских горах. Фигуры со звездочками представляют типовые области каждого вида. Топографические карты взяты из Mineeva *et al.* [2021] и topographic-map.com.

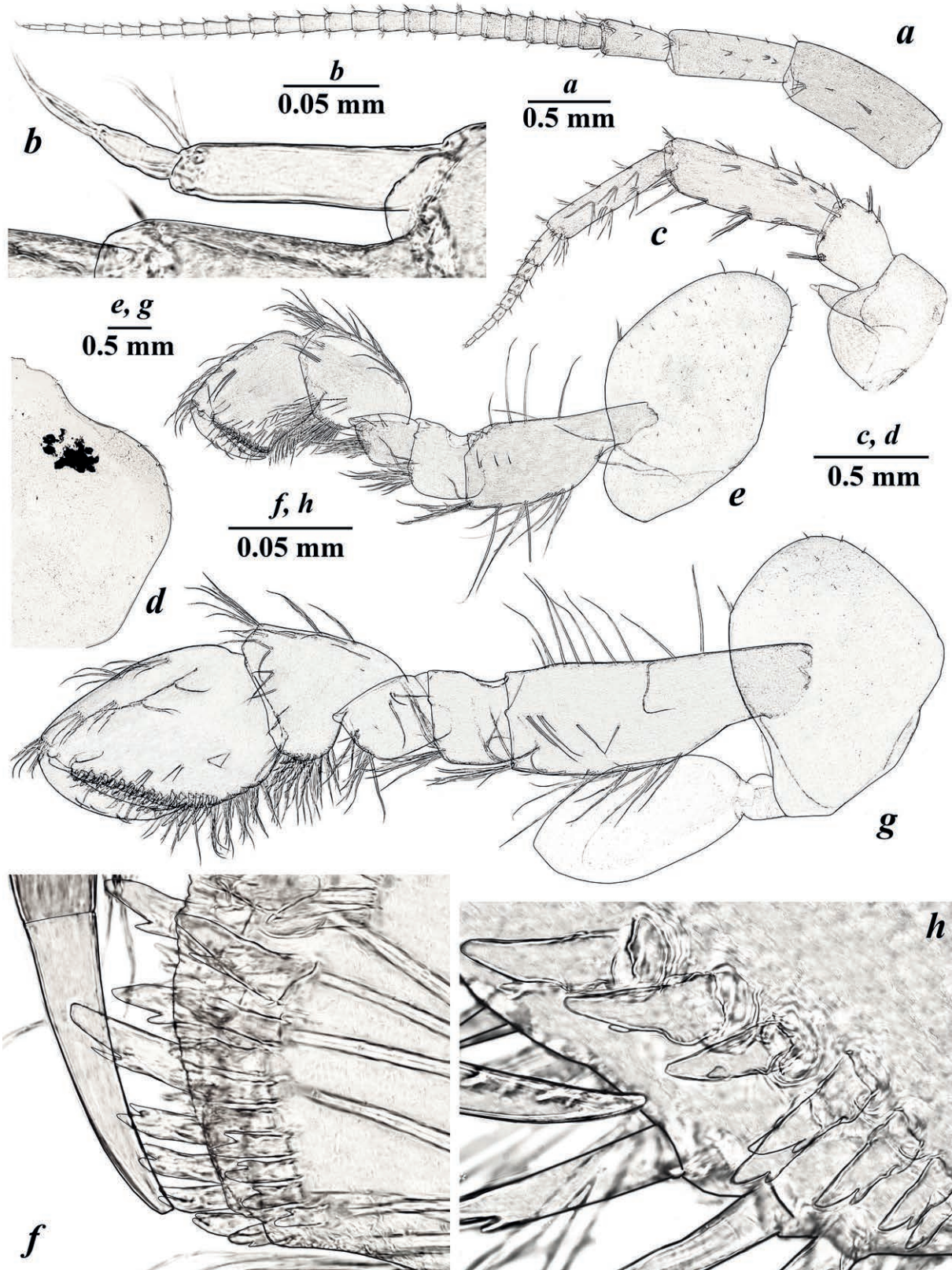


Fig. 2. *Volgonyx behningi* sp.n., ♂: a — antenna I; b — accessory flagellum of antenna I; c — antenna II; d — head; e — gnathopod I; f — distoventral corner of propodus (chela) of GnI; g — gnathopod II; h — distoventral corner of propodus (chela) of GnII.

Рис. 2. *Volgonyx behningi* sp.n., ♂: a — антенна I; b — дополнительный жгутик антенны I; c — антенна II; d — голова; e — гнатопода I; f — дистовентральный угол проподуса (клешни) GnI; g — гнатопода II; h — дистовентральный угол проподуса (клешни) GnII.

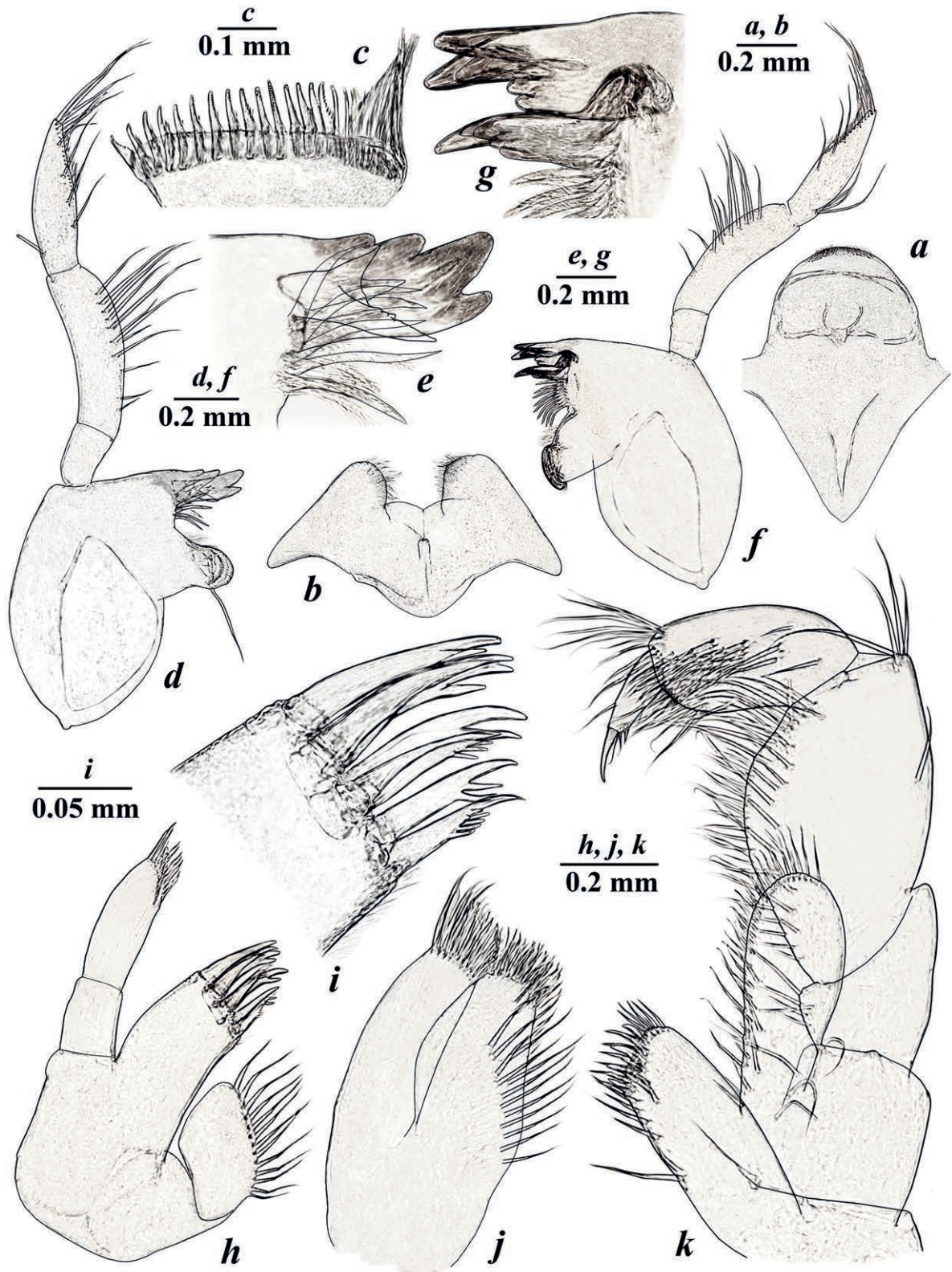


Fig. 3. *Volgonyx behingi* sp.n., ♂: a — upper lip; b — lower lip; c — laterallia; d — left mandible; e — same, incisor process and pars incisiva; f — right mandible; g — same, incisor process and *pars incisiva*; h — maxilla I; i — distal margin of inner plate of maxilla I; j — maxilla II; k — maxilliped.

Рис. 3. *Volgonyx behingi* sp.n., ♂: a — верхняя губа; b — нижняя губа; c — латералия; d — левая мандибула; e — режущий отросток и *pars incisiva* (резец) мандибулы; f — правая мандибула; g — то же, режущий отросток и *pars incisiva* (резец) мандибулы; h — максилла I; i — то же, дистальный край наружной доли; j — максилла II; k — максиллипеда.

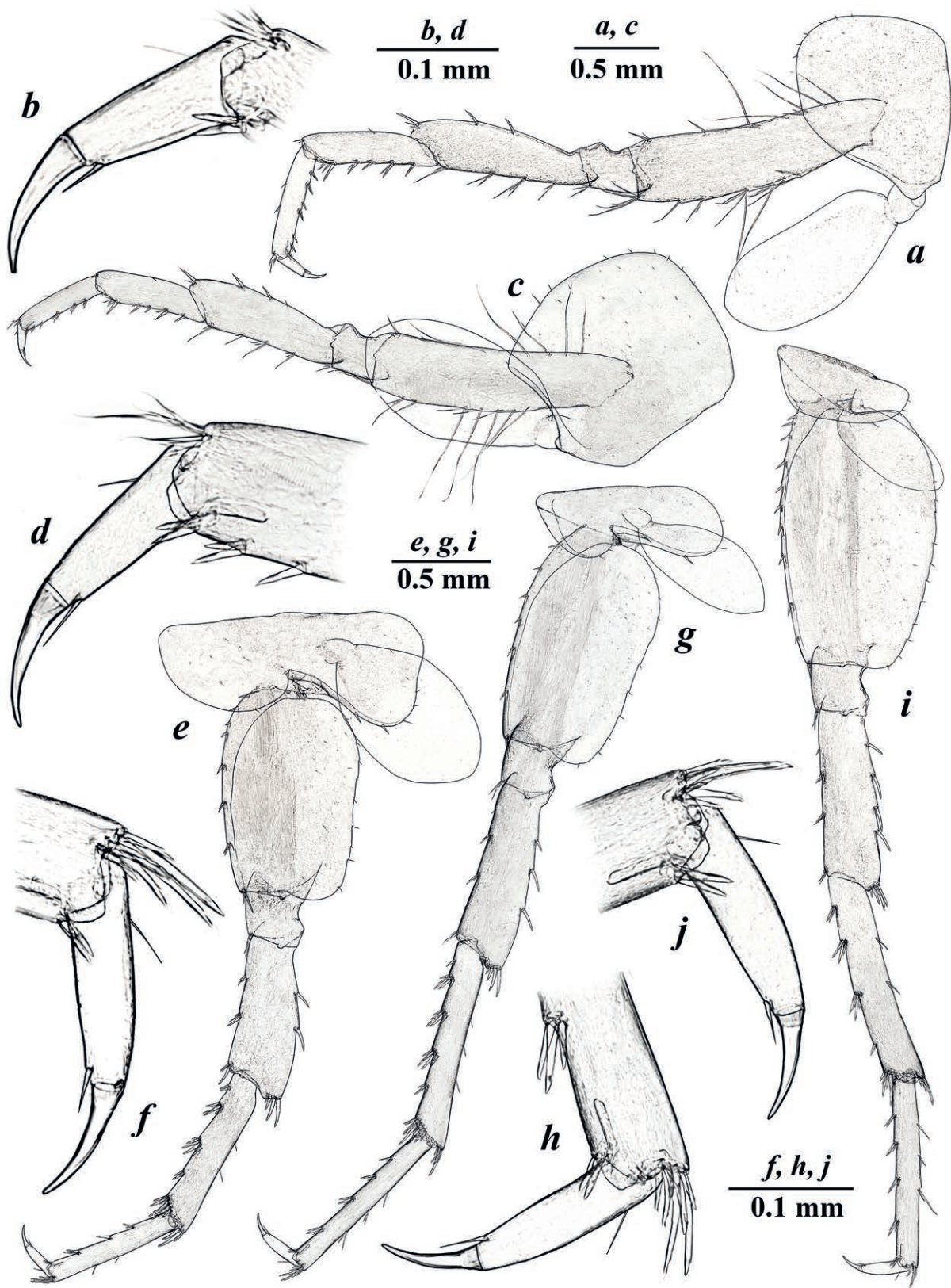


Fig. 4. *Volgonyx behingii* sp.n., ♂: *a* — pereopod III; *b* — dactylus of PIII; *c* — pereopod IV; *d* — dactylus of PIV; *e* — pereopod V; *f* — dactylus of PV; *g* — pereopod VI; *h* — dactylus of PVI; *i* — pereopod VII; *j* — dactylus of VII.

Рис. 4. *Volgonyx behingii* sp.n., ♂: *a* — переопода III; *b* — дактилус PIII; *c* — переопода IV; *d* — дактилус PIV; *e* — переопода V; *f* — дактилус PV; *g* — переопода VI; *h* — дактилус PVI; *i* — переопода VII; *j* — дактилус VII.

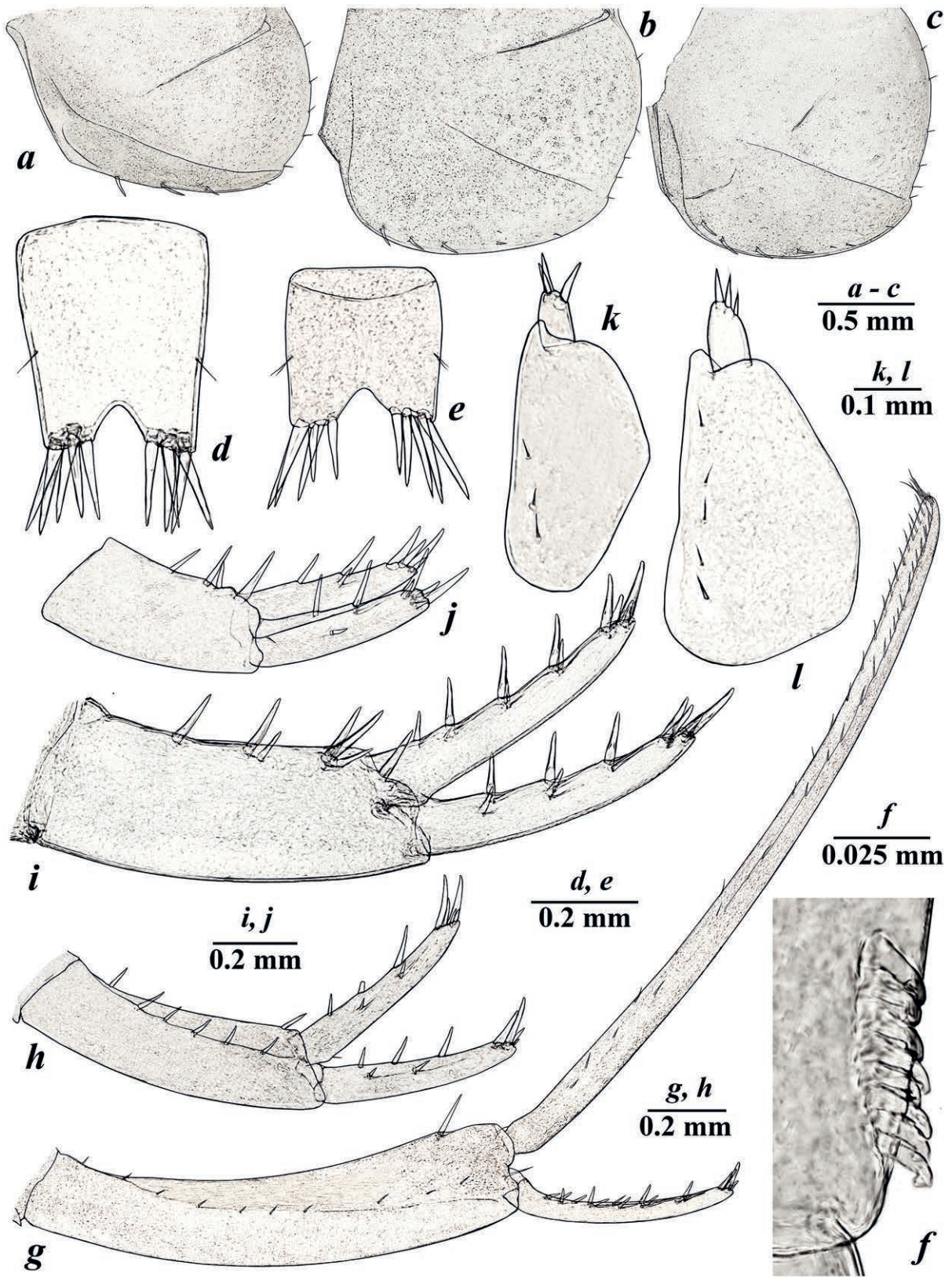


Fig. 5. *Volgonyx behngi* sp.n., ♂ (*a-d, f, g, i, l*), ♀ (*e, h, j, k*): *a-c* — epimeral plates I-III; *d, e* — telson; *f* — hooks of retinacula of pleopod III; *g, h* — uropod I; *i, j* — uropod II; *k, l* — uropod III.

Рис. 5. *Volgonyx behngi* sp.n., ♂ (*a-d, f, g, i, l*), ♀ (*e, h, j, k*): *a-c* — эпимеральные пластинки I-III; *d, e* — тельсон; *f* — крючки ретинакулы плеоподы III; *g, h* — уропода I; *i, j* — уропода II; *k, l* — уропода III.

DESCRIPTION. Body unpigmented, troglomorphic. Head with inter-antennal lobe wide, bluntly rounded anteriorly (Fig. 2d); eyes (ommatidia) reduced, invisible in alive specimens and well seen in fixed specimens (Fig. 2d); yellow pigmented spots visible on head *in-situ*, invisible in fixed specimens.

Antenna I (Fig. 2a) is about 60–70% of body length, about 2.0X longer than AII; primary flagellum with 26–27 articles in ♂♂ and 18–20 in ♀♀, aesthetascs on distal articles, shorter than respective articles; accessory flagellum 2-articulated (Fig. 2b), basal article about 4.5X longer than wide, distal article about 3X shorter than basal one.

Antenna II (Fig. 2c) with distinct gland clone; peduncle about 2.0X longer than flagellum, with robust setae tightly covering articles III–IV; flagellum 7-articulated in ♀♀ or 9-articulated in ♂♂; calceoli absent on peduncle and flagellum both in ♀♀ and ♂♂.

Mandible (Fig. 3d–g): left mandible incisor 5-dentate, *lacinia mobilis* 5-dentate, with 8–9 robust plumose accessory setae (Fig. 3e); molar process with 1 long simple seta (Fig. 3d). Right mandible (Fig. 3f) incisor 4-dentate, *lacinia mobilis* tritritative, both lobes with numerous protuberances; underlying with 1 row of 8–9 robust plumose setae (Fig. 3g); molar process similar to left mandible. Palp 3-articulated, article II with 11–12 setae; article III about 3–3.5X longer than wide, with convex margins, with 12–15 separate D-setae, 4 separate E-setae, 3–4 separate C-setae and 1–3 separate A-setae, lacking both B-setae.

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

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

Lateralialia (Fig. 3c): with 15 serrated teeth.

Maxilla I (Fig. 3h): inner plate with 13 plumose marginal setae, outer plate with 7 apical comb-spines (Fig. 3i); palp 2-articulated, distal article pubescent, about 2X of length of basal article, apical margin of distal article with 2 rows of 10 simple setae in each and 2 subdistal robust setae.

Maxilla II (Fig. 3j): inner and outer plates covered in pubescent stiff setae; outer plate subequal than inner plate in length, almost not narrowing distally, with numerous apical setae; inner plate narrowing distally, with group of dense long setae on apex, with oblique row of 12–13 long plumose stiff setae.

Maxilliped (Fig. 3k): inner plate much shorter than outer plate, with 3 spines, 14–15 plumose setae along apical margin and row of 3 simple submarginal setae, surface of plate covered with fine pubescence; outer plate with 24–26 marginal and 8–10 submarginal simple setae; palp 4-articulated, article I with 4 setae, article II with distinctly convex inner margin, armed with 33–35 marginal setae, article III setaceous with numerous marginal/submarginal setae; dactylus with 2–3 inner setae.

Gnathopod I smaller than GnII (ratio of GnI/II about 0.7/1) (Fig. 2e): coxal plate bluntly expanded distally, with 7–8 apical and numerous facial setae; width/depth ratios is about 1.4; basis about 2X longer than wide, with numerous long simple setae inserted along posterior and anterior margins; ischium quadrate, with tuft of numerous plumose setae distoventrally; merus short, about as long as wide, with tuft of distal simple setae; carpus about 1.3X longer than wide, about 0.58X length of basis and 0.9X length of propodus, with numerous groups of serrated setae along anterior margin and several groups of serrated setae distoventrally; propodus close to quadrate, about 1.2–1.3X longer than broad, with several groups of simple setae (with 2–3 setae each) along anterior and posterior margins, palmar margin almost straight, slightly oblique, with double row of 8 inner and 7 outer bifurcate robust setae; palm groove (depression) with 8 inner robust setae, 1 large and 4 smaller robust outer setae (Fig. 2f); dactylus with 2–3 outer and 5 inner setae. Gnathopod I in ♀♀ are generally similar to ♂♂.

Gnathopod II (Fig. 2g): coxal plate short, bluntly rounded, with 4–5 apical and several facial setae, about 1.1X longer than wide; basis about 32.5X longer than wide, with numerous long setae inserted along posterior and anterior margins; ischium quadrate, with tuft of long simple setae distoventrally; merus short, as long as wide, with tuft of distal setae; carpus triangular, about 0.45X length of basis and 0.6X length of propodus, with several groups of anterior and plumose posterior setae; propodus teardrop-shaped, about 1.4X longer than broad, palmar margin distinctly oblique with double-row of 9 inner and 12 outer bifurcate robust setae; palm groove (depression) with 7–8 inner robust setae (Fig. 2h); dactylus with 3 outer and 9 inner setae. Gnathopod II in ♀♀ are generally similar to ♂♂.

Pereopod III (Fig. 4a): coxal plate bluntly rounded, weakly narrowing distally, with 6–7 apical and numerous facial setae; basis about 3.7X longer than wide, with long anterior and posterior simple setae; ischium short, about as long as wide; merus about 3.5X longer than wide, about 1.2X longer than carpus; carpus about 3.8X longer than wide, with spines along posterior margin, anterior margin with 1 small median and several setae anterodistally; propodus about 4.5X longer than wide, equal to carpus, with 6 double setae along posterior margin and couple of strong setae distoventrally, anterior margin with 2 small setae; dactylus (Fig. 4b) slender, about 0.4X length of propodus, with single long plumose seta on outer margin and stout long seta on distal corner of inner margin.

Pereopod IV (Fig. 4c) subequal to PIII in length: coxal plate bluntly rounded, with 8–9 apical and numerous facial setae; basis about 4.0X longer than wide, with long anterior and posterior simple setae; ischium short, about as long as wide; merus about 3.5X longer than wide, about 1.2X longer than carpus; carpus about 3.2X longer than wide, with spines along posterior margin, anterior margin with 1 small median and several setae anterodistally; propodus about 4.0X longer than wide, equal to carpus, with 5 double setae along posterior margin and couple of strong setae distoventrally, anterior margin with 1–2 small setae; dactylus (Fig. 4d) slender, about 0.4X length of propodus, with single long plumose seta on outer margin and stout long seta on distal corner of inner margin.

Pereopods V–VII (Fig. 4e, g, i): length ratio of PpV/VI/VII is 1/1.34/1.36 (in ♂♂) and 1/1.30/1.32 (in ♀♀).

Pereopod V (Fig. 4e): coxal plate large, bilobate, with distinct bluntly rounded anterior and posterior lobes, anterior with 2 small setae, posterior with 2 spines and 5 small setae; basis with posterior margin slightly convex, armed with row of short spine-like setae, anterior margin almost straight, with row of strong small setae, with feebly marked bluntly produced distal corner; ischium quadrate, as long as wide, unarmed; merus stout, about 2.2X longer than wide, slightly shorter than carpus, with strong spines along anterior and posterior margins, with 3–4 strong curved spines anterodistally; carpus elongated, about 4.4X longer than wide, with strong spines along posterior margin, anterior margin with several small setae; propodus about 5.0X longer than wide, equal to carpus, with 3 double setae along posterior margin and couple of strong setae in distoventral angle; dactylus (Fig. 4f) slender, about 0.4X length of propodus, with single long plumose seta on outer margin and stout long seta on distal corner of inner margin.

Pereopod VI (Fig. 4g): coxal plate medium, bilobate, with distinct bluntly rounded anterior and posterior lobes, anterior with 2 small setae, posterior with 1 spine and 4 small setae; basis with posterior margin slightly convex, armed with row of short spine-like setae, anterior margin almost straight, with row of strong small setae, with feebly marked bluntly produced distal corner; ischium quadrate, as long as wide, unarmed; merus relatively stout, about 3.0X longer than wide, slightly shorter

than carpus, with strong spines along anterior and posterior margins, with 3–4 strong curved spines anterodistally; carpus elongated, about 5.0X longer than wide, with strong spines along posterior margin, anterior margin with several small setae; propodus about 5.5X longer than wide, equal to carpus, with 4 double setae along posterior margin and couple of strong setae in distoventral angle; dactylus (Fig. 4h) slender, about 0.3X length of propodus, with single long plumose seta on outer margin and stout long seta on distal corner of inner margin.

Pereopod VII (Fig. 4i): coxal plate small, semilunar, with 4 small posteroventral setae; basis with posterior margin slightly convex, armed with row of short spine-like setae, anterior margin convex, armed with row of strong small setae, with feebly marked rounded distal corner; ischium quadrate, as long as wide, unarmed; merus relatively stout, about 3.0X longer than wide, slightly shorter than carpus, with strong spines along anterior and posterior margins, with 3–4 strong curved spines anterodistally; carpus elongated, about 5.0X longer than wide, with strong spines along posterior margin, anterior margin with several small setae; propodus about 5.5X longer than wide, equal to carpus, with 4 double setae along posterior margin and couple of long strong setae in distoventral angle; dactylus (Fig. 4j) slender, about 0.35X length of propodus, with single long plumose seta on outer margin and stout long seta on distal corner of inner margin.

Gills, brood plates: coxal gills on somites II–VII, somite V–VII with lanceolate sternal gill. Coxal gills II–VII ovoid, ratio of lengths of gills/bases pereopod are 0.70/1, 0.74/1, 0.77/1, 0.87/1, 0.66/1 and 0.46/1, respectively. Slender, setaceous brood plates on somites II–V, decreasing in size posteriorly.

Pleopods I–III almost similar, with peduncle with 7–8 coupling hooks in retinacles in ♂♂ and with 4 hooks in ♀♀, and large lateral plumose seta; outer and inner rami almost equal in length, with 13 and 10 articles, respectively; basal article of outer ramus with clothes-pin seta.

Epimeron. Epimeral plate I (Fig. 5a) distally rounded, ventral margin with 3 long spines, posterior margin distinctly convex, with 5 setae. Epimeral plate II (Fig. 5b) without subdistal protrusion, ventral margin armed with 4–5 spines, posterior margin convex, with 5–7 small setae. Epimeral plate III (Fig. 5c) with small subdistal rounded protrusion, ventral margin convex, armed with 6–7 spines, posterior margin slightly convex, with 5–6 small setae.

Urosome with completely fused urosomites, sutures visible, with sparse setae covering dorsal surface.

Uropod I (Fig. 5g, h): greatly dissimilar in ♂♂ and ♀♀. Male (Fig. 5g): peduncle about 5X as long as wide, with dorsointernal row of 10 small and slender spines, 1 subdistal slender and with 1 dorsoexternal strong spines; outer ramus (endopodite) about 4X of length of inner one; endopodite paddle-like, with 2 dorsal rows of 20–22 slender spines each; exopodite with 5–6 groups of spines dorsally and medially, and group of 3 apical spines. Female (Fig. 5h): peduncle about 4X as long as wide, with dorsointernal row of 6 robust spines, 1 subdistal spine and 1 dorsoexternal robust spine; outer ramus subequal inner ramus in length; endopodite not paddle-like, with 3–4 dorsolateral and 5 apical spines; exopodite with 3 dorsolateral, 2 mesial and 3–4 apical spines.

Uropod II (Fig. 5i, j): peduncle subequal in length to rami, with 5 outer robust and no inner robust spines, 1 subdistal robust spine; rami equal in length, outer ramus with 4 outer robust, 3–4 small medial and 3–4 apical robust spines, without inner robust spines; inner ramus with 4 outer robust and 4–5 apical spines.

Uropod III (Fig. 5k, l): small, equal or smaller than telson, uniramous; peduncle about 4–4.5X of length of ramus, with 3–5 medial spines; ramus with 3 apical robust spines.

Telson (Fig. 5d, e) rectangular, about 1.3X longer than broad in ♂♂, and quadrate, about 1X in ♀♀; distal margin with relatively deep V-shaped distal notch, reaching ¼ of telson length, each lobe armed with 4–5 robust spines, with 1–2 additional submarginal plumose setae.

COLORATION. The body, antenna and appendages whitish-yellowish transparent; with small pigmented spots on the anterior lobe of the head; generally similar to *V. derzhavini* (see Marin & Palatov [2021]).

BODY SIZE. The largest collected ♂ has bl. 12.5 mm, ♀ — 8.0 mm.

TAXONOMIC REMARKS. The new species can be easily separated from *V. derzhavini* by 1) stouter peduncular articles of antenna I (see Fig. 2a); 2) longer basal article of accessory flagellum of antenna II, which is about 4.5X longer than wide (vs. 3.5X); 3) significantly shorter distal article of accessory flagellum of antenna II, which is about 3X shorter than basal article (vs. 2X shorter); 4) slightly elongated basis of pereopod V, which is about 1.5X longer than wide (vs. less than 1.3–1.4X); 5) basis of pereopod VII is about 1.4X longer than distal width, with almost straight posterior margin (vs. about 1.6X longer than distal width, with distinctly convex posterior margin); 6) more convex posterior margins in epimeral plates I and II; 7) longer outer ramus of uropod I in ♂♂, with is about 4X longer than inner one (vs. 3X only) and 8) deeper V-shaped distal notch on telson.

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DISTRIBUTION AND ECOLOGY. The species is presently known only from two neighboring locations, Morkshavinskiy Well in Zhigulevsk (53°24'55.8"N 49°32'15.5"E) and the Vinny Spring in Shiryaevo (53°24'33.5"N 50°00'47.4"E), in a mountainous area of the Zhiguli Mountains (Samara Luka), Samara Region, Russia.

In the type locality, a small well in the city of Zhigulevsk, it has been observed that these amphipods avoid sunlight and hide under various shelters (boulders, stones and bricks) during the day. At darkness and night time, it was noticed that they were grouped, and apparently fed on different dead arthropods that fell into the well, such as insects (Insecta), spiders (Arachnida: Araneae) and harvestmens (Arachnida: Opiliones). During the sampling, they actively avoided the net and hid in the crevices, which indicates that they are very well oriented in the biotope and are able to actively avoid predators.

The species was found together with such spring dwelling insect larvae, such as *Metriocnemus hygropetricus* (Kieffer, 1911), *Pseudodiamesa gr. nivosa* (Goetghebuer, 1928) (Diptera: Chironomidae), *Nemoura cinerea* (Retzius, 1783) (Plecoptera: Nemouridae) and *Plectrocnemia conspersa* (Curtis, 1834) (Trichoptera: Polycentropodidae), and mollusks *Ampullaceana balthica* (Linnaeus, 1758) (Gastropoda: Lymnaeidae) and *Euglesa casertana* (Poli, 1791) (Bivalvia: Sphaeriidae). In the Vinny Spring, the new species was found together with other crangonyctid *Uralocrangonyx zhiguliensis* Marin et Palatov, 2024 (Amphipoda: Crangonyctidae) (see Marin & Palatov [2024]).

Discussion

Currently, 3 genera with 5 species of crangonyctid amphipods (Amphipoda: Crangonyctidae) are known in the Volga River basin. They are: epigeal *Synurella ambulans* (F. Müller, 1846) currently described from various surface and underground water sources in Vladimir, Moscow, Ryazan and Kaluga areas [Sidorov, Palatov, 2012; Marin, Palatov, 2022a]; stygobiotic *Uralocrango-*

nyx chlebnikovi (Borutzky, 1928), which is known from cave (subterranean) water reservoirs and wells of Kungur, Orda and Suksun districts of Perm Krai, the Southern Ural Mountains [Sidorov *et al.*, 2012; Marin, Palatov, 2022]; recently described stygobiotic *Uralocrangonyx zhiguliensis* Marin et Palatov, 2024, which is currently known from a single spring in Zhiguli Mountains (Samara Luka), Samara Region [Marin, Palatov, 2024]; as well as the two species of the genus *Volgonyx* Marin et Palatov, 2021, described above from the Lower Volga (present study). It is obvious, the diversity of crangonyctid amphipods is much higher in the area, even if two representatives of the family were recently discovered in the Zhiguli Mountains during one specialized scientific expedition (present study; Marin, Palatov [2024]). In general, the groundwater fauna of mountainous area of the entire Russian Plain has been studied very poorly so far, while there are a very large number of springs and wells on this territory, among which only some have been carefully examined. The question arises why such large crustaceans as *Volgonyx* and *Uralocrangonyx* have not been found before – it is very likely that they were simply identified as representatives of the genus *Gammarus* Fabricius, 1775 (Amphipoda: Gammaridae).

As described above, for absolutely the majority of stygobiotic crangonyctid amphipods, very small (strict) distribution areas are known, which are usually associated with a single underground water system (see above). Nevertheless, the most important question that this study has revealed is how the gene flow in the population of *V. dershavini* is maintained in such a large area. Currently, the range of this species is stretched over 340 km, representing one of the widest distribution areas among stygobiotic crangonyctid species (see above), and strictly confined to the eastern part of the Volga Upland, which is characterized by shallow groundwater and a large number of springs. In many areas of the Upland, significant strata are formed by limestones and gypsum, and where they lie close to the surface and are subject to the dissolving action of groundwater, karst area are common. From a geological point of view, the Volga Upland is relatively young: its age is the Late Paleogene, about 30 Mya (e.g., Milkov [1953]; Obedientova [1957]).

According to the obtained molecular genetic data, the interspecific genetic distance between populations of *V. dershavini* is very low (about 0.8%) and well corresponds to intraspecific for most of the studied species of the family Crangonyctidae (e.g., Marin & Palatov [2022a]). It is very likely that the drift of genes is supported by the presence of a common extensive underground basin in the eastern part of the Volga Upland, from which the sources in which the studied animals were found already flow. This species is able to live for some time in the terrestrial part of the springs (pers. observ.), however, have never been detected at a significant distance from springs in surface waters. Therefore, surface propagation, as for example it is known for *S. ambulans* (e.g., Marin & Palatov [2022a]), can be easily excluded.

At the same time, the newly discovered species in the Zhiguli Mountains is genetic isolated from *V. dershavini*

since 1.18–0.84 Mya, which is in good agreement with the flushing of the channel by the Volga River in the western part of the Zhiguli Mountains, and the subsequent flooding of this area by brackish/salty waters of the Akchagyl Sea in the Pliocene–Pleistocene (3.4–1.8 Mya) (e.g., Esin *et al.* [2019]; Naidina, Richards [2020]). It is very likely that these geological events led to the isolation of *V. behningi* sp.n., as well as the recently described endemic stygobiotic *U. zhigulensis*, in the Zhiguli Mountains.

Compliance with ethical standards

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

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

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