Ruthenica, 2025, vol. 35, No. 3: 143-156.
Published online July 1, 2025

A new species of the family Bithyniidae (Gastropoda: Littorinimorpha) from Russia, with remarks on some genera of this family

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ABSTRACT. A new species of the bithyniid snails, *Opisthorchophorus* ***confusus*** Andreeva sp. nov., is described based on molecular and morphological data. A COI phylogeny inferred on the material of newly obtained sequences and those accessible through the GenBank has releaved the species distinctness of *O.* ***confusus*** sp. nov. as well as the full genus status for *Codiella* Monterosato, 1894 and *Opisthorchophorus* Beriozkina et Starobogatov, 1995. The genus *Pseudobithynia* Glöer et Pešić, 2006, on the other hand, has been revealed as paraphyletic, but the proper status of this taxon is unclear, since no genetic information is available on its type species distributed in Iran. The new species is widely distributed in Russia; its genetically confirmed localities are situated in Krasnodar Krai (south of European Russia) and Western Siberia. Based on morphologically identified specimens, the range of *O.* ***confusus*** sp. nov. embraces European Russia, southern parts of Western and Eastern Siberia as well as Northern and Central Kazakhstan. The new genus is conchologically and molecularly distinct from the species *Opisthorchophorus troschelii* (Paasch, 1842) [known also as *Bithynia transsilvanica* Bielz, 1853]. The nomenclatural issues related to the name *Bihynia troschelii* are discussed.

Zoobank registration: urn:lsid:zoobank.org:pub:A8C8CEE0-1D40-4325-9BB9-C03D9FA94071

https://doi.org/10.35885/ruthenica.2025.35(3).3

Новый вид семейства Bithyniidae (Gastropoda: Littorinimorpha) из России с замечаниями о некоторых родах этого семейства

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РЕЗЮМЕ. На основании молекулярных и морфологических данных описывается новый вид брюхоногих моллюсков семейства Bithyniidae – *Opisthorchophorus* ***confusus*** Andreeva sp. nov. Филогенетическая реконструкция, основанная на последовательностях гена COI, как заимствованных из GenBank, так и вновь полученных в ходе данного исследования, позволила показать видовую самостоятельность *O.* ***confusus*** sp. nov. и подтвердить родовой статус *Codiella* Monterosato, 1894 и *Opisthorchophorus* Beriozkina et Starobogatov, 1995. Род *Pseudobithynia* Glöer et Pešić, 2006, напротив, оказывается парафилетическим, но его статус остается неясен, поскольку отсутствует генетическая информация о его типовом виде, обитающем в Иране. Новый вид широко распространен в России; его генетически подтвержденные местообитания расположены в Краснодарском крае (юг европейской части России) и Западной Сибири. Судя по особям, идентифицированным на основе морфологических признаков, ареал *O.* ***confusus*** sp. nov. охватывает Европейскую Россию, южные районы Западной и Восточной Сибири, а также Северный и Центральный Казахстан. Новый вид конхологически и молекулярно отличается от вида *Opisthorchophorus troschelii* (Paasch, 1842) [известного также как *Bithynia transsilvanica* Bielz, 1853]. Обсуждаются номенклатурные вопросы, связанные с применимостью названия *Bihynia troschelii*.

Introduction

The family Bithyniidae J.E. Gray, 1857 is one of the most practically significant and widespread families of freshwater snails in the Old World. Numerous publications have been devoted to both taxonomy and ecology of bithyniid snails, and the number of literary sources on this topic is constantly growing [e.g., Ponder, 2019; Sitnikova, Bazova, 2019; Andreeva, 2023; Wilke *et al*., 2023; Ng, Tan, 2024; Zhang *et al*., 2024, 2025]. For a long time, the classification of the family was built solely on shell traits [Westerlund, 1886; Geyer, 1927; Zhadin, 1952]. In the second half of the last century, taxonomists began to use characters of the reproductive system for this purpose, trying to use them to build a system at both the species and the generic level [Anistratenko, Stadnichenko, 1995; Beriozkina *et al.*, 1995; Ponder, 2003]. However, the use of the same set of morphological characters (shells, soft body anatomy, operculum) did not lead to a unity of views on the family system. The classifications proposed by different authors varied greatly both in the number of species identified and in the number of genera. For example, a system developed in the 1980-1990s in Russia by Starobogatov and his co-authors [Starobogatov, Zatravkin, 1987; Zatravkin *et al*., 1989; Beriozkina *et al*., 1995; Starobogatov *et al*., 2004] recognizes several genera of bithyniid snails in the fauna of Europe and Northern Asia. On the other hand, taxonomists of West and Central Europe usually tend to accept a single genus *Bithynia* s. l., embracing all diversity of bithyniids in this area [i. e., Falniowski, 1989; Falkner et al., 2001; Glöer, 2002a; Welter-Schultes, 2012]. In 2006, a new genus, *Pseudobythinia* Glöer et Pešić, 2006, was erected; its difference from the genus *Bithynia* s. l. lies in the distinct structure of the male copulatory organ [Glöer, Pešić, 2006; Glöer, 2019].

The use of molecular methods for the study of taxonomy and phylogeny of freshwater molluscs has already formed a standard in current systematic malacology. Unfortunately, the family Bithyniidae has largely been neglected in this respect, and we still lack a system of this group based on an approach that would integrate genetic and morphological data. The most intensive studies of the bithyniids by molecular methods are currently performing by South-East malacologists, focused on freshwater snails that serve as intermediate hosts of various trematodes of medical importance [e.g. Tantrawatpan *et al*., 2020; Bunchom *et al*., 2020, 2021a, b, 2025]. Recent studies by Wilke *et al*. [2023] and Zhang *et al*. [2024] has solved the aenigma of the genus *Helicostoa* Lamy, 1926, a relict sessile snail of the South China malacofauna. Zhang *et al*. [2025] made a molecular revision of the bithyniids inhabiting Lake Inle in Myanmar.

The knowledge on the genetic and taxonomic diversity of the bithyniids of Europe and Northern Asia remains unsatisfactory. Some data on this subject were presented by Wilke *et al*. [2023], who included some European species of the genera *Bithynia* s. l. and *Pseudobithynia* in their phylogenetic reconstruction. They demonstrated that the family Bithyniidae can be divided into four or more subfamilies, some of which remain undescribed formally. The European representatives form a separate cluster on the cladogram, corresponding to the subfamily Bithyniinae Gray, 1857. Another publication, albeit not a peer-reviewed one, is that by Katokhin *et al*. [2017]. The authors presented a molecular analysis of two species of the genus *Boreoelona* Starobogatov et Streletzkaja, 1967 from Eastern Siberia and demonstrated their genetic distinctness. Unfortunately, the gene sequences obtained during this study, as well during the next research of the same team [Katokhin *et al*., 2019], have not been submitted to GeneBank, which makes them virtually inaccessible for other malacologists.

Therefore, most of the recent publications on bithyniid snails of Eastern Europe and Northern Asia, including Siberia, are based on the typological approach to species delineation, based on the combined use of shell morphology and (often, but not always) reproductive anatomy of these mollusks [Lazutkina *et al*., 2014; Kołodziejczyk, Lewandowski, 2016; Andreeva *et al*., 2018; Sitnikova, Bazova, 2019; Andreeva, 2023; Andreeva, Grebennikov, 2023]. Genetic information on the bithyniids of this area is only beginning to accumulate.

The initial point of the present research was the finding of a presumably undescribed species of the family Bithyniidae in samples collected in Eastern Europe (Russia), the Urals, Western Siberia, and Central Kazakhstan. It is characterized as having low-conical, almost globose shell, with short spire and convex whorls. The morphology of its shell and reproductive organs allowed to place it in the genus *Boreoelona*, which is widely distributed in Eastern Siberia, the Russian Far East, and some regions of Central Asia [Izzatullaev, 1982; Starobogatov et al., 2004; Vinarski, Kantor, 2016]. However, the presence of a species of *Boreoelona* in the East Europe waterbodies would raise great doubts since it can hardly be explained zoogeographically. A molecular genetic analysis of these snails has allowed us to determine the exact place of the new species in the system. Below, we provide a formal description of this species alongside with a discussion of some debatable questions of the European bithyniid phylogeny and classification.

Material and methods

The primary material for this study was collected by the authors in different parts of Russia and Central Kazakhstan or donated to us by colleagues. In addition, we examined some uncatalogued samples kept in the Museum of the Institute of Plant and Animal Ecology, the Ural Branch of the Russian Academy of Sciences (Yekaterinburg). The type materials of some species of bithyniid snails kept in the Zoological Institute of the Russian Academy of Sciences in St.-Petersburg (ZIN, hereafter) have been studied as well.

In total, 419 specimens of snails from 51 localities, belonging to a new species have been studied (for the list of samples and locations see Supplementary Info, Table S1), 76 of them were dissected to examine the structure of the copulatory apparatus. Shell measurements were made according to the standard scheme [Starobogatov *et al*., 2004], by means of an ocular-micrometer with an accuracy to the nearest 0.1 mm. The shell photos were taken using a Canon EOS 500D camera, a Canon EF 100 mm f/2.8 Macro USM lens, as well as an Olympus SZ61 with a Progress Gryphax Jenoptik.

To study the morphology of egg-clusters of snails of the undescribed species, in June 2022, live individuals were collected from an impoundment on the Maly Uchug River, and the Atachka River (Omsk Region, Western Siberia, Russia). Under laboratory conditions, snails were kept singly in plastic cups with a small amount of water. The egg-clusters and separate egg capsules were studied and measured using an MBS-10 microscope. For each cluster, its length and width were measured, the number of rows and egg capsules was counted, and the length (dimension along the egg-cluster) and width (dimension across the egg-cluster) of each egg capsule were measured.

The molecular genetic analysis was carried out in the Russian Museum of Biodiversity Centers at the N. Laverov Federal Center for Integrated Arctic Research of the Ural Branch of the Russian Academy of Sciences (Arkhangelsk, RMBH hereafter), sequencing was performed at the Genome Research Center at the V. Engelhardt Institute of Molecular Biology, Russian Academy of Sciences (Moscow).

Total genomic DNA was extracted from 96% ethanol-preserved foot tissues of bithyniid snails using the DNeasy Blood & Tissue Kit (QIAGEN GmbH, Germany), following the manufacturer's protocol. The performed molecular genetic analysis included amplification and sequencing of the mitochondrial cytochrome c oxidase subunit I gene (COI marker). The COI sequences were amplified by polymerase chain reaction (PCR) using the following primers: LCO1490 and HCO2198 [Folmer *et al*., 1994]. The PCR mix contained approximately 200 ng of total cell DNA, 10 pmol of each primer, 200 µmol of each dNTP, 2.5 µl of PCR buffer (with 10 × 2 mmol $MgCl_2$), 0.8 units Taq DNA polymerase (SibEnzyme Ltd., Novosibirsk, Russia), and H_2O was added for a final volume of 25 µl. Thermocycling was implemented with markers-specific PCR programs as follows: 95 °C (4 min), followed by 28 cycles at 94 °C (50 sec), 49 °C (50 sec), 72 °C (50 sec) and a final extension at 72 °C (5 min). Forward and reverse sequencing were performed on an automatic sequencer (ABI PRISM3730, Applied Biosystems, USA) using the ABI PRISM BigDye Terminator v. 3.1 reagent kit. The resulting sequences were checked using a sequence alignment editor BioEdit v. 7.2.5 [Hall, 1999].

8 new sequences of COI gene have been obtained during this study and placed in the NCBI GenBank under accession numbers PV037647–PV037654 (Table S2 in Supplementary Info). A set of other 46 COI sequences of bithyniid species belonging to the genera *Bithynia, Boreoelona, Pseudobithynia, Gabbia* Tryon, 1865*,* and *Wattebledia* Crosse, 1886 was obtained from the NCBI GenBank to be used in molecular genetic analysis (Table S2 in Supplementary Info).

Sequence alignment was performed using the MUSCLE algorithm implemented in MEGA X [Kumar et al. 2018], with subsequent checking via a p-distance matrix (we used uncorrected pairwise genetic distances). The Maximum likelihood phylogenetic analyses were based on the COI data set of the Bithyniidae species with 49 unique haplotypes. These analyses were carried out with an online version of IQ-TREE v1.6.11 [Trifinopoulos *et al*., 2016] using an ultrafast bootstrap algorithm [Hoang *et al*., 2017] and an automatic identification of the most appropriate substitution models [Kalyaanamoorthy

Table 1. Genetic divergences (mean uncorrected *p*-distances, %) between various *Opisthorchophorus* and *Codiella* species based on the sequences of the mitochondrial COI gene.

Табл. 1. Показатели генетической дивергенции (средние некорректированные p-расхождения, %) между различными вилами родов *Opisthorchophorus* и *Codiella*, рассчитываемые на основе последовательностей митохондрального гена COI.

Genus		*O.* ***confusus*** sp. nov.	*B. troschelii*	*B. transsilvanica*	*P. pentheri*	*B. leachii*	*P. panetolis*
Opisthorchophorus	*Opisthorchophorus* ***confusus*** sp. nov.						
	Bithynia troschelii	4.5					
	Bithynia transsilvanica	5.9	4.8				
	Pseudobithynia pentheri	10.7	12.2	11.4			
Codiella	*Bithynia leachii*	12.5	13.3	12.4	11.3		
	Pseudobithynia panetolis	10.9	11.2	11.1	11.8	7.7	
	Pseudobithynia trichonis	10.8	11.2	11.0	11.6	7.7	0.0

et al., 2017]. Sequences of *Bythiospeum acicula* (Held, 1838) [Gastropoda: Moitessieriidae] and *Colligyrus* sp. [Gastropoda: Amnicolidae] were used as the outgroups.

Results

The molecular analysis based on COI gene sequences has shown that the sequenced individuals of various bithyniid snails form several distinct and highly supported clades, which can be identified with several genera, described in the past on the ground of shell morphology and reproductive anatomy (Fig. 1). As many as 8 groups of generic rank have been delineated as an outcome of our analysis. The specimens of a suspected bithyniid species form a separate cluster on a cladogram falling within the genus *Opisthorchophorus* Beriozkina et Starobogatov in Anistratenko et Stadnichenko, 1995 together with a sequence belonged to '*Bithynia troschelii*' from Republic of Bashkortostan, Russia (GenBank accession No. MW138394) (Fig. 1). However, this specimen is not very close genetically to snails identified as '*Bithynia troschelii*' from West Russia and to '*Bithynia transsilvanica*' from Germany [the names *B. transsilvanica* and *B. troschelii* refer, most probably, to the same species; see Glöer, 2004; Welter-Schultes, 2012].

The genetic distance between this suspected species and its closest relatives of the genus *Opisthorchophorus* is rather prominent and is equal to 4.5–5.9% (Table 1).

Thus, in our opinion, the available genetic data confirm the existence of at least two species of *Opisthorchophorus*, one of which is known from Germany and the western regions of European Russia (Table S2) and must retain the name *O. troschelii* (Paasch, 1842) [type locality: Germany, lakes in vicinity of Berlin], whereas the application of the alternate name, *Opistorchophorus transsilvanica* (Bielz, 1853), is questionable (see further remarks on this topic below, in 'Discussion' section). The type locality of the latter is situated in Romania, and one needs to study topotypic individuals genetically in order to be able to determine their exact taxonomic position. It is important, that both species mentioned above cannot be classified within the genus *Bithynia*, as it is accepted by most of recent researchers [Falkner *et al*., 2001; Glöer, 2002a, b, 2004, 2019; Welter-Schultes, 2012; Kołodziejczyk, Lewandowski, 2016; Sitnikova *et al*., 2017]. The genetic distance between species of *Opisthorchophorus* and *Bithynia* s. str. is so considerable that warrants their placement in two distinct genera, as it was proposed by Beriozkina *et al*. [1995] and accepted by some subsequent Russian and Ukrainian researchers [Anistratenko, Stadnichenko, 1995; Starobogatov *et al*., 2004; Andreeva, 2023].

The question arises whether the newly identified member of *Opisthorchophorus* can be assigned to any of the previously described species, or should it be established as a new taxon for science?

Beriozkina *et al*. [1995], in their revision of the East European bithyniid snails, erected the genus *Opisthorchophorus* and placed four nominal species

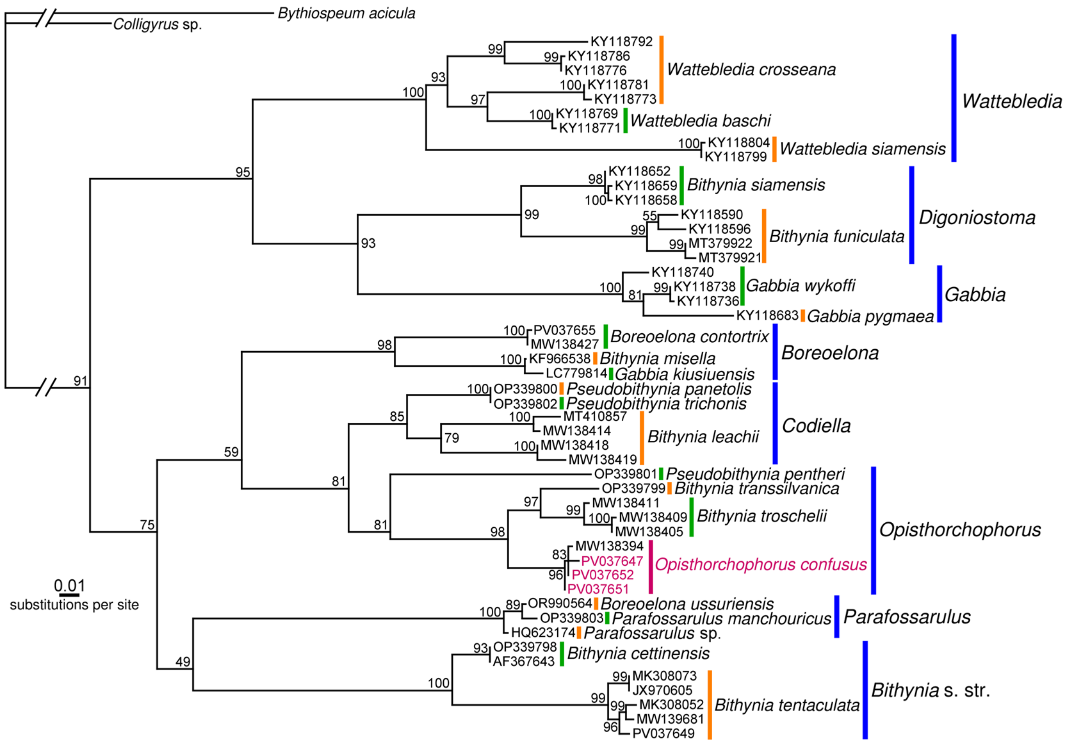

FIG. 1. Maximum likelihood tree inferred from COI sequences of 53 bithyniid snails belonging to different genera. The sequences of *Bythiospeum acicula* and *Colligyrus* sp. were chosen as outgroups.

РИС. 1. Дерево на основе последовательностей COI 53 особей битиниид, принадлежащих к разным родам, полученное методом максимального правдоподобия. В качестве внешних группы были выбраны последовательности COI *Bythiospeum acicula* и *Colligyrus* sp.

into it. Six years later, the fifth species, *O. abakumovae* Andreeva et Starobogatov, 2001, was described [Andreeva, Starobogatov, 2001]. Out of these five species, two, *O. troschelii* and *O. abakumovae*, cannot be identified with the newly discovered species because of significant conchological differences between them. Both these species have highly turreted shell, with tall spire and relatively small body whorl. Two other species, listed by Beriozkina *et al*. [1995] as members of *Opisthorchophorus*, were described from West Europe. One of them was identified by Beriozkina *et al*. [1995] as the species *Bithynia hispanica* Servain, 1880, which is known only in the Mediterranean coast of Spain [Jaume-Ramis, Martínez-Ortí, 2021]. The identification of this South European species with that distributed in Russia, eastward to Siberia, is highly problematic, and seems to us practically impossible. Another species, originally included to *Opisthorchophorus*, *O. baudonianus* (Gassies, 1859), was described from Southern France, and it has been absent from all most recent surveys and check-lists of the Bithyniidae of Western Europe [Falkner *et al*., 2001; Glöer, 2002a, 2019; Welter-Schultes, 2012]. Recently, Boeters and Falkner [2017], by examining the type material of Gassies, showed that this snail is not a bithyniid and should be assigned to the genus *Mercuria* Boeters, 1971 (Hydrobiidae: Mercuriinae).

At last, a species described by Beriozkina *et al*. [1995] as *Opisthorchophorus valvatoides*, must be considered. Its type locality is situated in Saratov Region of European Russia, in the Lower Volga basin. We studied the paratypes of *O. valvatoides* kept in ZIN (holotype is illustrated by Sitnikova *et al*. [2017]). This species has a high-conical shell, conchologically it much resembles *O. troschelii* and may represent its junior synonym.

Thus, we cannot surely identify the specimens examined by us with any of the species previously placed in the genus *Opisthorchophorus*, and we describe them below as a new taxon for science.

Opisthorchophorus ***confusus*** Andreeva, sp. nov.

Figs 2; 3 A–D

Zoobank registration: urn:lsid:zoobank.org:act:0ED7D867-0CED-4CB2-9980-C967EEDA67A0

? = *Opisthorchophorus baudonianus* sensu Beriozkina *et al.* [1995], non Gassies, 1859 (partim).

? = *Opisthorchophorus hispanicus* sensu Beriozkina *et al.* [1995], non Servain, 1880.

Type locality. Russia, Western Siberia, Tomsk Region, vicinity of Tomsk City, a temporary waterbody in the Tom’ River floodplain. Collected by

Table 2. A comparative characteristic of shells of *Opisthorchophorus* ***confusus*** sp. nov. from localities of the floodplains of the Western Siberia rivers. The mean value ± standard deviation as well as the extent of variation, min–max (in parentheses) are provided.

Табл. 2. Сравнительная характеристика раковин *Opisthorchophorus* ***confusus*** sp. nov. из пойменных водоемов рек Западной Сибири. Приводятся среднее значение ± стандартное отклонение и размах вариации (min–max).

Character	Locality		
	Type locality (n = 11)	Omsk City, the Irtysh River floodplain near bus station, 12.06.2005 (n = 8)	Tyumen Region, Bolshoy Balyk River, 20.08.2019 (n = 4)*
Shell height (SH), mm	9.74±1.41; (7.2–11.7)	7.94±0.80; (6.5–9.0)	7.38±0.36; (7.1–7.9)
Shell width (SW), mm	7.30±1.17; (5.7–9.9)	5.84±0.50; (5.1–6.6)	5.40±0.52; (4.8–6.0)
Spire height (SpH), mm	4.73±0.88; (3.2–5.9)	3.88±0.47; (3.0–4.5)	3.43±0.15; (3.3–3.6)
Body whorl height (BWH), mm	7.48±1.01; (5.7–9.0)	6.04±0.56; (5.0–6.7)	5.80±0.22; (5.6–6.1)
Aperture height (AH), mm	4.93±0.62; (3.9–6.0)	3.96±0.38; (3.3–4.4)	3.85±0.19; (3.7–4.1)
Aperture width (AW), mm	3.86±0.47; (3.1–4.6)	3.24±0.27; (2.9–3.7)	3.05±0.17; (2.9–3.3)
Whorl number	5.09±0.42; (4.45–5.50)	4.53±0.21; (4.20–4.75)	4.36±0.16; (4.20–4.50)
SW/SH	0.75±0.06; (0.70–0.89)	0.74±0.06; (0.69–0.88)	0.73±0.04; (0.68–0.77)
SpH/SH	0.48±0.03; (0.43–0.52)	0.49±0.02; (0.46–0.54)	0.46±0.01; (0.46–0.48)
BWH/SH	0.77±0.02; (0.74–0.79)	0.76±0.03; (0.73–0.81)	0.79±0.02; (0.77–0.82)
AH/SH	0.51±0.03; (0.47–0.55)	0.50±0.02; (0.48–0.53)	0.52±0.03; (0.51–0.53)
AW/SH	0.79±0.05; (0.71–0.88)	0.82±0.03; (0.77–0.88)	0.79±0.03; (0.77–0.81)

* A sample of the new species from this river included 49 specimens (see Supplementary Table 1). However, most of them had severely corroded apices and therefore were not measured.

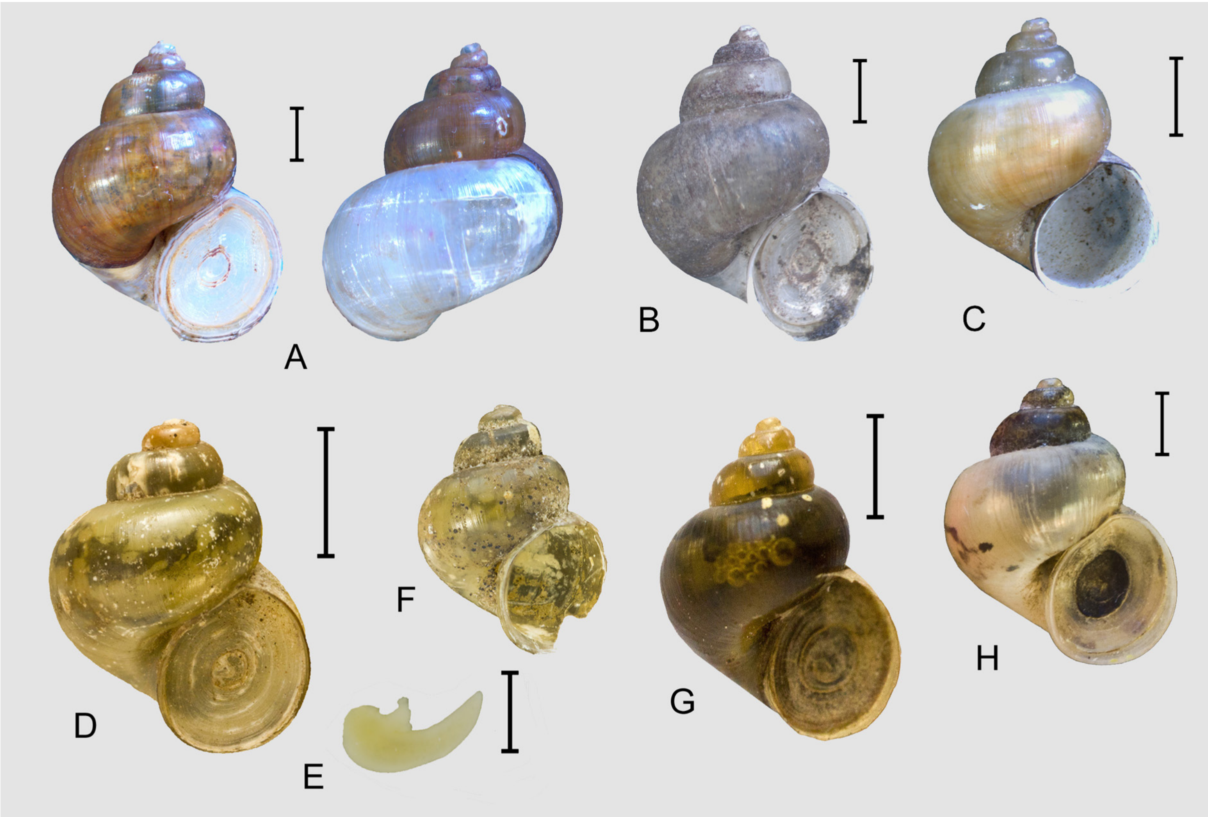

FIG. 2. Shells (**A**–**D**, **F**–**H**) and copulatory organs (**E**) of *Opisthorchophorus* ***confusus*** sp. nov. **A.** Holotype. **B, C.** Paratypes. **D, E, F.** Tyumen Region, the Bolshoy Balyk River floodplain. **G.** Moscow Region, a pond in Sharapova Okhota settlement. **H**. Chelyabinsk Region, Yuzhnouralskoye Reservoir. Scale bars 2 mm (except E – 1 mm).

РИС. 2. Раковины (**A**–**D**, **F**–**H**) и копулятивные органы (**E**) *Opisthorchophorus* ***confusus*** sp. nov. **A**. Голотип. **B, C**. Паратипы. **D, E, F**. Тюменская область, пойма р. Большой Балык. **G**. Московская область, пруд в пос. Шарапова Охота. **H**. Челябинская область, Южноуральское водохранилище. Масштабные линейки 2 мм (кроме E – 1 мм).

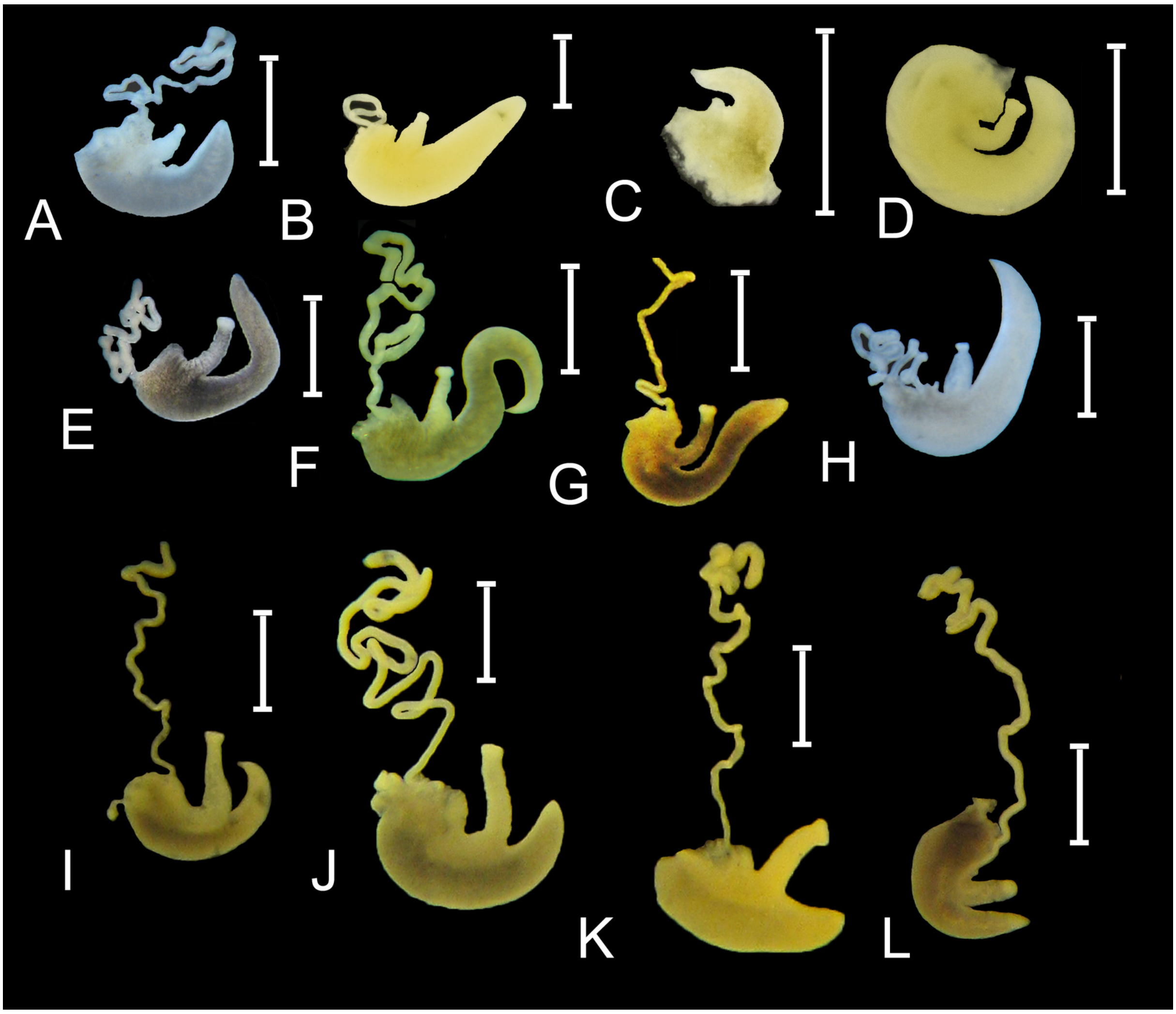

FIG. 3. Copulatory organs of various bithyniid snails collected in Western Siberia. **A–D**. *Opisthorchophorus* ***confusus*** sp. nov. **E**. *O. troschelii*. F. *O. abakumovae*. **G**. *"O. baudonianus"*. **H**. *Boreoelona sibirica*. **I–K**. *Bithynia tentaculata*. **L**. *B. tentaculata* f. *producta*. Scale bars 1 mm.

РИС. 3. Копулятивные органы различных видов битинид, собранных в Западной Сибири. **A–D**. *Opisthorchophorus* ***confusus*** sp. nov. **E**. *O. troschelii*. **F**. *O. abakumovae*. **G**. "*O. baudonianus*". **H**. *Boreoelona sibirica*. **I–K**. *Bithynia tentaculata*. **L**. *B. tentaculata* f. *producta*. Масштабные линейки 1 мм.

M.P. Miroshnichenko, 06.06.1953. Approximate coordinates: 56°29'5"N, 84°57'E.

Type series. The holotype (accession No. 1/503-2023) and ten paratypes (accession No. 2/503-2023) are kept in ZIN. 5 paratypes are deposited in RMBH. Their accession numbers are: MByt-40.1 (Omsk Region, Atachka River, 1 spec.), Mbyt-42.1 (Omsk Region, Tyukalka River, 1 spec.), Mbyt-44-1, 44-2, 44-3 (Tyumen Region, Bolshoy Balyk River, 3 spec.).

Additional material. See Supplementary Table S1 for details.

Etymology. After Latin *confusus* – 'confounded, confused'. The etymology reflects the fact that this species has been confused with other species of the Bithyniidae and has remained unrecognized until now.

Holotype dimensions at 5.5 whorls (mm). Shell height 11.7; shell width 8.3; spire height 5.7; body whorl height 9.0; body whorl height above the aperture 3.0; aperture height 6.0; aperture width – 4.6.

Description. Shell massive, low-conical or broadly conical (Fig. 2), yellow-brown, light brown or vitreous-transparent, shiny, thin-walled. Shell sculpture is represented by longitudinal densely arranged longitudinal ribs and spiral lines. Spiral lines may consist only of conchiolin and are easily erased when washing samples or cleaning shells from fouling. Adult shells are up to 11.7 mm high and 8.3 mm wide (Table 2). The last whorl massive, its height is 0.73-0.82 of shell height; elevation of the body whorl above the aperture is 0.23-0.28 shell height. Rapidly increasing whorls (up to 5.5 in number) are uniformly convex, almost stepped, separated by a deep suture. The umbilicus is open. The spire height is 0.43-0.54.

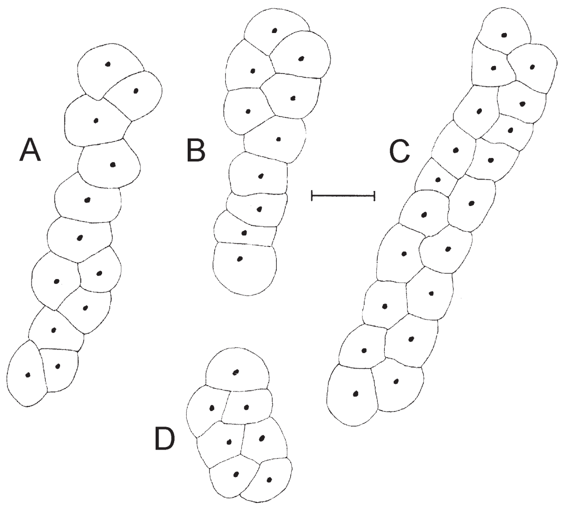

FIG. 4. Egg-clusters of *Opisthorchophorus* ***confusus*** sp. nov. **A, B**. Malyi Uchug River. **C**, **D**. Atachka River. Scale bars 2 mm.

РИС. 4. Кладки яиц *Opisthorchophorus* ***confusus*** sp. nov. **A**, **B**. Запруда на р. Малый Учуг. **C**, **D**. Р. Атачка. Масштабные линейки 2 мм.

The tangent line of the whole shell is not straight but with two breaks, the tangent line of the spire is slightly concave. The apical angle of shells with 5 whorls and more is 61–65°, in those with less than 5 turns – 63–79°. The aperture is round-oval with a pronounced angle in its upper part and thin and fragile margins. The aperture height is 0.47–0.55 of the shell height, the aperture width is 0.71-0.88 of its height. The operculum is oval with an obtuse angle in the upper part and a large nucleus located almost in its centre. The growth lines on the operculum are weakly developed. Shells of males and females do not differ externally, and no significant differences were found in their morphometric indices.

The soft body, as a rule, is lightly coloured, with a well-defined spotted pattern.

The penis is massive, curved, with a short outgrowth, the length of which is much shorter than the length of the penis. The distal end of the penis varies in length and shape: it may be uniformly or irregularly thickened along its entire length and pointed at the end to varying degrees.

Variability. The variability in shell shape and proportions is moderate; at 4.0-4.5 whorls it is close to trochoid, and at higher whorl numbers it becomes low-conical or broadly conical. The rate of whorl increase alters with age; it is highest in juvenile specimens. The most variable are such plastic characters as the shell height and width and the body whorl height (Table 2). Shells larger than 8 mm in height are rarely found in the collections; the typical shell height is 4-7 mm. Shell apexes are often corroded, which causes problems with measurements and calculation of morphometric indices. Shell coloration varies considerably; yellow-brown and colourless shells are predominantly found in the samples, but light brown and white shells also occur, as well as shells with non-uniform coloration. Shells may be covered with fouling which hides both the coloring and the suture depth. The shape and proportions of the penis of males in the samples examined are quite variable (Fig. 3).

Differential diagnosis. *Opisthorchophorus* ***confusus*** sp. nov. differs from representatives of the *Bithynia tentaculata* complex by convex whorls, which are separated by deep suture (in *Bithynia* snails, whorls are flattened or weakly convex). From species *O. abakumovae* and *O. troschelii* the new species can be distinguished by lower spire and broadly conical shell with relatively large body whorl. Shell of *O. abakumovae* is narrowly conical, almost turreted, tall, whorls increase very fast, the spire height is about half of the shell height. In *O. troschelii*, the shell is conical, massive, whorls increase fast, the spire height is not less than one third of the shell height. The presence of a distinctive sculpture on shell surface differs *O.* ***confusus*** sp. nov. from all other species previously assigned to the genus *Opisthorchophorus*, including *O. valvatoides*. In other species of *Opisthorchophorus*, the shells are smooth or slightly striated, only with thin growth lines. In *O.* ***confusus*** sp. nov., longitudinal ribs and sometimes spiral lines are clearly visible (if shells are not heavily worn). The new species is well distinguished from representatives of *Boreoelona* by shell shape and proportions; shell of *O.* ***confusus*** sp. nov. is broadly conical, while *Boreoelona sibirica* has a turriculate shell, with high spire; the whorls in *O.* ***confusus*** sp. nov. shell increase slowly compared to *B. sibirica*. *O.* ***confusus*** sp. nov. is also well distinguished from the co-occuring *Boreoelona contortrix* by shell shape. Shell of *O.* ***confusus*** sp. nov. has slowly increasing whorls and a relatively large, strongly inflated body whorl, whereas in *B. contortrix* shell is conical with rapidly increasing whorls turns and a low, less inflated body whorl.

The penis of *O.* ***confusus*** sp. nov. is rather massive with a shortened distal end compared to the penises of other species of the genus *Opisthorchophorus* and is similar in shape and proportions to the penis of *B. sibirica*, which has a more elongated distal end.

Egg-clusters. These are aggregates of unbranched yellowish transparent strands with even margins and slightly bumpy surface, consisting of densely packed large polygonal egg capsules separated from each other (Fig. 4). The egg-clusters laid by females from the Atachka River were single-rowed, supplemented at the ends by a second row of egg capsules; those from the Maly Uchug River were regular double-rowed (Fig. 4). The egg-masses are deposited on the substrate at a small distance from each other. There were from 4 to 6 egg capsules in the clutch of one female; the total number of egg capsules laid by one individual depended on the size of the animal: for example, 22 egg capsules were laid by individual with 7.5 mm shell height, and 50 egg capsules were laid by a snail of 9.0 mm shell height. The number of egg capsules in a clutch varied from 2 to 43. The size (length) of egg capsules from the Atachka River ranged from 1.3 to 1.6 mm; from the Maly Uchug River – 1.2 to 1.7 mm. The egg capsule width varied from 1.3 to 1.7 mm in the Atachka River; and from 1.3 to 2.1 mm in the Malyi Uchug River. The main index of egg capsules from the Atachka River ranged from 0.87 to 1.23; from the dam on the Malyi Uchug River from 0.88 to 1.75. It should be noted that egg capsules are flattened due to their dense packing, even if they were arranged in one row. The regularly ellipsoid or spherical shape was preserved only in egg capsules laid two or three at a time.

The double-row egg-clusters of *Opisthorchophorus* ***confusus*** sp. nov. are morphologically similar in arrangement of egg-capsules and their packing to clutches of "*Opisthorchophorus baudonianus*" from waterbodies of Western Siberia [Andreeva, Lazutkina, 2004] and species of the genus *Boreoelona* from waterbodies of the Russian Far East [Prozorova, 1992].

Distribution. The species was found in samples from waterbodies of the central regions of European Russia, the Urals, Western Siberia and central Kazakhstan. Probably, its range also covers northern areas of European Russia, northern areas of Kazakhstan and the Baikal Region (see Discussion). The sequenced specimens were collected in the southern part of Western Siberia (Omsk Region) and in the southern part of European Russia (Krasnodar Krai).

Ecology. Typical habitats of *Opisthorchophorus* ***confusus*** sp. nov. are floodplain waterbodies, as well as shallow zones of small rivers with slow current. The species is found in thickets of macrophytes, on snags and submerged artificial objects at depths up to 1.5 m, together with bithyniids of the genera *Bithynia*, *Opisthorchophorus*, and (only in Siberia) *Boreoelona*. More detailed data on the coexistence of *O.* ***confusus*** sp. nov. are presented in Supplementary Info, Table S3.

The snails of this species serve as the first intermediate hosts of the *Opisthorchis felineus* trematodes in Western Siberia. Using PCR method, Andreeva *et al*. [2024] have detected the presence of the opisthorchid parthenitae in three specimens of *O.* ***confusus*** sp. nov. collected from the Bolshoy Balyk River (Tyumen Region).

Discussion

The species *Opisthorchophorus* ***confusus*** sp. nov., which is formally described here, is, in fact, not new. Having examined many lots of bithyniids collected from many regions of Russia and Kazakhstan and kept in several depositories, we suggest that previous authors already recognized this species as a distinct one but applied wrong names for its designation. In our opinion, some (if not most) recordings of *Opisthorchophorus baudonianus* and *O. hispanicus* available from Russian literature, actually belong to *O.* ***confusus*** sp. nov. As it was stated above, both the names cannot be applied to a bithyniid species distributed in East Europa (within Russian borders), Siberia, and Northern Kazakhstan. In this respect, it is worthy to discuss the history of the application of the name *O. hispanicus* in Russian literature. Beriozkina *et al*. [1995] suggested that "their" *O. hispanicus* has repeatedly been registered from Russia's waterbodies under the name *Bithynia inflata* or *B. leachi* var. *inflata* [e.g., Westerlund, 1877; Be'er, Makeeva, 1973; Starobogatov, 1977].

However, as Beriozkina *et al*. [1995] correctly noted, *Paludina inflata* Hansén, 1846 (the basionym of *B. inflata*) is a junior homonym of *Paludina inflata* A. Villa et G.B. Villa, 1841 (and of a fossil species *Paludina inflata* Pusch, 1837) and, as such, becomes invalid. Beriozkina *et al*. [1995], without any reasoning, claimed *Bithinia hispanica* Servain, 1888 is the oldest available name to replace *Paludina inflata* Hansén, 1846, although the latter was described from Sweden, whereas the type locality of Servain's species is situated in Spain. After 1995, a series of publications reporting *O. hispanicus* from Western Siberia have appeared [Starobogatov *et al*., 2004; Andreeva *et al*., 2005].

Later on, Rusinek *et al*. [2012], giving a detailed differential diagnosis of the snails, which were supposed to serve as a vector of opisthorchiasis in Irkutsk Region (Eastern Siberia), pointed out they cannot be attributed either to *Opisthorchophorus troschelii* or to *Bithynia leachii* (Sheppard 1823), and that they do not fully correspond morphologically to *Boreoelona sibirica* (Westerlund 1886). Following the identification key by Starobogatov *et al.* [2004], Rusinek *et al*. [2012] identified the studied snails as *O. hispanicus*, despite the presence of the characteristic surface sculpture, which is clearly distinguishable on the shell photograph published by the authors. After Rusinek *et al*. [2012], other authors working in Siberia started to use the name *O. hispanicus* for designation of local bithyniid snails with low-conical shells and stepped whorls [Andreeva *et al*., 2018, 2020]. However, both shell pictures and the description of the reproductive organs of the East Siberian "*Opisthorchophorus hispanicus*" provided by Rusinek *et al*. [2012] are corresponding to the morphology of *O.* ***confusus*** sp. nov. (Fig. 5).

A similar situation is, in our opinion, with the use of the name *Opisthorchophorus baudonianus* sensu Beriozkina et al., 1995 (non Gassies). This species is

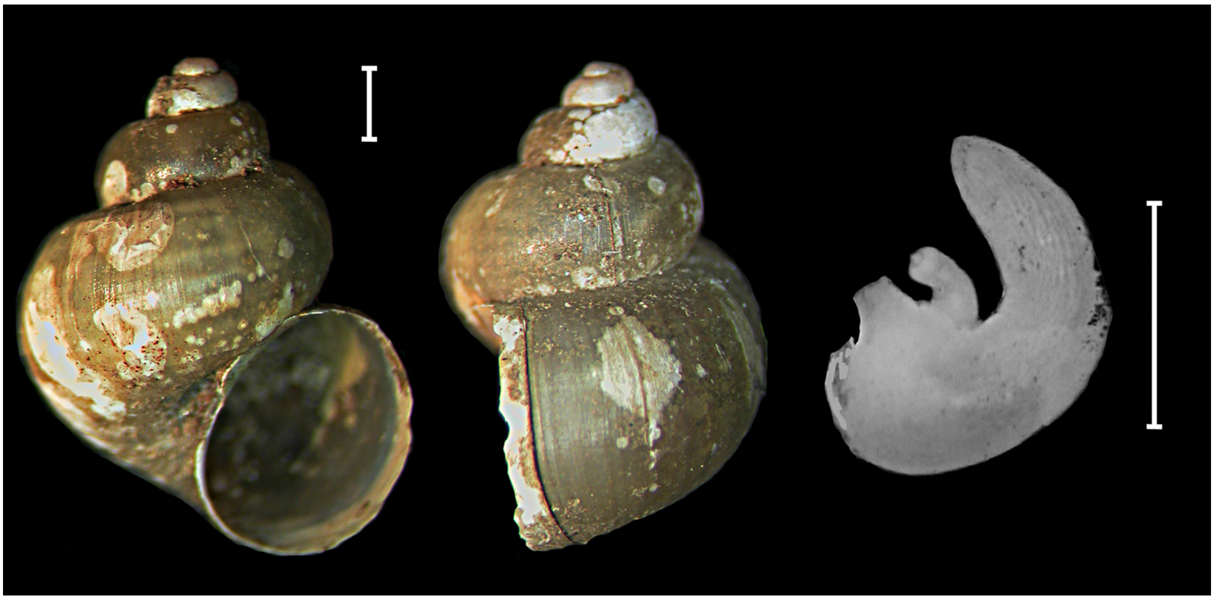

FIG. 5. Shell and copulatory organ of "*Opisthorchophorus hispanicus*" from Irkutsk Region described by Rusinek *et al*. [2012]. Scale bars 1 mm (copulatory organ), 2 mm (shell). Photo: T.Ya. Sitnikova.

РИС. 5. Раковина и копулятивный орган «*Opisthorchophorus hispanicus*» из Иркутской области, описанного Русинек с соавторами [2012]. Масштабные линейки 1 мм (копулятивный орган), 2 мм (раковина). Фото: Т.Я. Ситникова.

characterized by having a peg-top shaped shell with relatively low spire [Anistratenko, Stadnichenko, 1995; Beriozkina *et al*., 1995; Starobogatov *et al*., 2004; Andreeva *et al*., 2005]. According to our observations, made in various museum collections, at least some shells identified as *O. baudonianus* may actually belong to *O.* ***confusus*** sp. nov.

The results obtained during this study shed light on some other issues in the bithyniid taxonomy. First, our results provide additional support in favour of the multi-generic system of the family Bithyniidae (Table 3) advocated by Starobogatov and his collaborators [Starobogatov, Zatravkin, 1987; Zatravkin *et al*., 1989; Beriozkina *et al*., 1995; Starobogatov *et al*., 2004]. The genus *Bithynia* s. str. has relatively small volume and embraces the species complex *Bithynia tentaculata* s. lato alongside with a few narrowly distributed species like *B. cettinensis* Clessin, 1887. The species *Bithynia leachii* and *B. troschelii* (or *B. transsilvanica*) of West European authors must be, most probably, assigned to two distinct genera, *Codiella* Monterosato, 1894 and *Opisthorchophorus* (as it was proposed by Beriozkina *et al*. [1995]). This opinion is rather provisional, since a multi-locus study is needed to reveal the true phylogenetic relationships between the two groups (as well as the status of the genus *Boreoelona*). On the other hand, the distinctness of two other bithyniid genera, delineated by these authors, *Digyrcidum* Locard, 1882 and *Paraelona* Beriozkina & Starobogatov in Anistratenko et Stadnichenko, 1995, becomes very doubtful. These two genera do not correspond to any of the individual clades of genus rank in our cladogram (Fig. 1), which, however, may be due to insufficient taxon sampling. It should be noted, in addition, that the type species of *Paraelona*, *Bithynia majewsky* Frauenfeld, 1862, has been revised by Glöer and Maassen [2009], who identified it as a junior synonym of *Bithynia tentaculata* (Linnaeus, 1758) and concluded that "the genus *Paraelona* has no type species and is not a valid genus name".

The status of East Asian *Digoniostoma, Gabbia* and *Wattebledia* as three taxa of the genus rank within the family Bithyniidae (Fig. 1) correspond to the previous results of Ng and Tan [2024] and Zhang *et al*. [2025]. The generic status of *Parafossarulus* has been approved by Wilke *et al*. [2023]. However, our results do not support their decision to separate it out as a subfamily Parafossarulinae Starobogatov, 1983. According to our data, this genus must belong to Bithyniinae. However, a single-locus phylogeny obtained by us gives no serious reasons to consider this question solved. We believe that the true phylogenetic position and taxonomic status of *Parafossarulus* (and Parafossarulinae) will be understood in the future, when a more comprehensive phylogeny of living bithyniid snails becomes available.

At last, the status of the genus *Pseudobithynia* becomes more problematic as a result of our research. Our phylogeny reveals *Pseudobithynia* paraphyletic, with some nominal species of this genus assigned to *Opisthorchophorus* and others – to *Codiella* (Fig. 1). A similar result has recently been reported by Zhang *et al*. [2025]. To date, more than 20 nominal species have been described in this genus [Glöer, 2019]. Unfortunately, genetic data is only available for a

Table 3. A synopsis of generic classifications of the living Bithyniidae of Europe and Western Siberia proposed in the 20-21 centuries.

Табл. 3. Обзор систем рецентных Bithyniidae Европы и Западной Сибири на родовом уровне, предложенных в 20-21 вв.

Geyer [1927]*	Starobogatov, Zatravkin [1987]	Falkner *et al.* [2001]; Glöer [2002a]	Beriozkina *et al.* [1995]; Starobogatov *et al.* [2004]	Vinarski, Kantor [2016]	Glöer [2019]	This study
Bithynia s. lato	*Bithynia* s. str.	*Bithynia* (*Bithynia* s. str.)	*Bithynia* (*Bithynia* s. str.)	*Bithynia* (*Bithynia* s. str.)	*Bithynia* s. lato	*Bithynia* s. str.
			Bithynia (*Milletelona*) Beriozkina et Starobogatov, 1995			
			Digyrcidum	*Bithynia* (*Digyrcidum*)		
			Paraelona	*Bithynia* (*Paraelona*)		
	Codiella	*Bithynia* (*Codiella*)	*Codiella*	*Bithynia* (*Codiella*)		*Codiella*
			Opisthorchophorus	*Bithynia* (*Opisthorchophorus*)		*Opisthorchophorus*
					Pseudobithynia	? *Pseudobithynia*

*The same classification is used by Ehrmann [1933], Zhadin [1952], Starobogatov [1977], Falniowski [1989], and many other authors

few of them. The type species of *Pseudobithynia*, *P. irana* Glöer & Pešić, 2006, inhabits Iran. It has never been studied molecularly. In the absence of such data, it is impossible to judge on the status of the genus – whether it is a synonym of *Codiella* (or *Opisthorchophorus*) or represents a distinct taxon.

Thus, contrary to opinion of Welter-Schultes [2012], Sitnikova *et al.* [2017], and Glöer [2019], *Opisthorchophorus* is recognized here as a full genus, distinct from the genus *Bithynia* s. str. It also cannot be ranked as a subgenus of the latter, as it was proposed by Vinarski and Kantor [2016]. The morphology of the copulatory apparatus provides a morphological support to this decision. In all species of *Bithynia* studied by us, the penial outgrowth is relatively long, its length constitutes around 1/3 of the whole penis length (Fig. 3, I-L). In contrast, in *Opisthorchophorus* this appendage is much shorter, as compared with the total penis length, and is equal to ¼–1/5 length of the latter (Fig. 3 A-G). The same pattern is characteristic also of the genus *Boreoelona* (Fig. 3, H).

The final issue which can be addressed here is the applicability of the name *Bithynia troschelii*. Having been in wide use in Western European and Russian literature [Starobogatov, 1977; Glöer, 2002a, b, 2004; Falniowski *et al.*, 2004; Starobogatov *et al.*, 2004; Kołodziejczyk, Lewandowski, 2016; and others], in recent decades it was practically replaced by the name *Bithynia transsilvanica*. The reasons for that were explained by Welter-Schultes [2012, p. 38], who summarized a discussion between Falkner [2003] and Glöer [2002a, b, 2004] in such words: "The lectotype designation by Glöer 2002 <…> is invalid under Art. 74.2 because Falkner 2003 demonstrated that reasonable arguments that this was not a syntype under Art. 72.4.1.1. Glöer 2004's additional arguments were based on speculations and not on evidence as required by Art. 72.4.1.1 <…> Lectotype was fixed by Falkner 2003: 32, specimen no longer exists, but correctly designated under Art. 74.4, synonym of *B. leachii*". Although Falkner [2003] did correctly designate the lectotype of Paasch's *Paludina troschelii*, we remain unconvinced that the true identity of this name can be surely understood from the original picture (being the lectotype) provided by Paasch [1842] (reproduced in Falkner [2003]). It is of rather poor quality and depicts a contour of a small shell with convex whorls, which can belong either to *Codiella leachii* or to *Opisthorchophorus troschelii*. Low-spired individuals of the latter species are known. For example, such specimens were found in Hungary and illustrated by Glöer and Féher [2004; figs. 5, 14-17] and Welter-Schultes [2012, p. 38]. In our opinion, these forms may correspond to the original Paasch's material. In other words, the synonymy between *Bithynia troschelii* Paasch, 1842 and *Turbo leachii* Sheppard, 1823 has not been proven by Falkner

[2003] and Welter-Schultes [2012], and it can hardly be proven at all, given that Paasch's type material has been lost. Thus, there is no compelling reason to reject the use of the name *Bithynia troschelii* in favour of *B. transsilvanica* as it was proposed by Falkner [2003] and many subsequent malacologists of Western Europe.

Acknowledgements

The authors are grateful to many colleagues, who collected the samples used in this study: Dmitry M. Palatov (Moscow), the late Nikolay I. Andreev, Alfried V. Karimov and Alina V. Sverdlova (Omsk), Nikolay G. Erokhin and Maxim E. Grebennikov (Yekaterinburg), Elena A. Serbina (Novosibirsk), Rail' G. Fattakhov (Tyumen), and Svetlana N. Perova (Borok). A special thank is due to Dr. T.Ya. Sitnikova (Irkutsk), who shared with us the photos of shell and copulatory organ of "*Opisthorchophorus hispanicus*" from Irkutsk Region. The critical evaluation of the manuscript by two reviewers and their comments served to improve the original version of this text. This research was partially funded by the Foundation for Scientific and Technological Development of Yugra (project No. 2024-522-04).

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