




# New data on *Buldowskia* Moskvicheva, 1973 (Bivalvia: Unionidae) from southern Primorsky Krai, Russian Far East

ELENA M. SAYENKO<sup>1,2</sup>, NIKITA A. SELIVERSTOV<sup>3,4</sup> & ALEXANDER A. SEMENCHENKO<sup>1,5</sup>

**1** Federal Scientific Center of the East Asia Terrestrial Biodiversity, Far Eastern Branch of Russian Academy of Sciences, Vladivostok 690022, Russia **2**  <http://orcid.org/0000-0002-5459-2692> **3** Far Eastern Federal University, Vladivostok 690922, Russia **4**  <http://orcid.org/0009-0000-6500-3796> **5**  <http://orcid.org/0000-0001-7207-9529> • Corresponding author: E.M. Sayenko (sayenko@biosoil.ru)

**Abstract.** Based on *COI* DNA barcoding data, the distribution of 2 species of *Buldowskia*, namely *B. shadini* (Moskvicheva, 1973) and *B. suifunica* (Lindholm, 1925) is clarified in southern Primorsky Krai in the Russian Far East. *Buldowskia suifunica* is confirmed from freshwater basins in the Khasansky District (the southernmost part of the Primorye). The presence of *B. shadini* in the coastal drainages, not part of the basin of Lake Khanka, and in the Razdolnaya river basin is noted for the first time. Both species are shown to occur in the Razdolnaya river basin, although they do not occur together at the same localities. Distinct distribution and low intraspecific divergence of *B. shadini* suggest that it was unintentionally introduced into the rivers of southern Primorsky Krai. *B. suifunica* is native to the Razdolnaya River basin, its distribution is apparently associated with the regression of the Sea of Japan in the Pleistocene. The outer shell microsculpture of *B. suifunica* glochidia consists of a multilayered loosely looped network in the centre of the valves, which differs from the other studied anodontines with loop-like microsculpture of the exterior of glochidial valves.

**Key words.** Anodontinae, freshwater Bivalvia, DNA barcoding, *COI*, glochidia

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## Introduction

Before the use of molecular phylogenetic methods, the generic taxonomy of the Unionidae from the Russian Far East varied greatly. Based almost exclusively on conchological characters, the taxonomy of Far Eastern anodontines (Unionidae: Anodontinae), including the validity and composition of the genus *Buldowskia* Moskvicheva, 1973, has been questioned (e.g. MARTYNOV & CHERNYSHEV 1992, BOGATOV & STAROBOGATOV 1996, STAROBOGATOV et al. 2004, GRAF 2007, RIZHINASHVILI 2011, BOGATOV 2015).

LINDHOLM (1925) described *Anodonta arcaeformis* var. *suifunica* from the Suifun River (now the Razdolnaya River, Primorsky Krai, Russian Far East; Fig. 1). MOSKVICHEVA (1973) later described the genus *Buldowskia* with *B. suifunica* as the type species. BOGATOV & STAROBOGATOV (1996) recognized this genus as valid and noted that it occurs only in southern Primorsky Krai. CHERNYSHEV (1998) considered *Buldowskia* to be a subgenus of *Anemina* Haas, 1969. Because of the highly variable shell shape, convexity, and anatomy in freshwater anodontines, the status and composition of *Buldowskia* has repeatedly changed prior to the introduction

of an integrative approach by BOLOTOV et al. (2020) and LOPES-LIMA et al. (2020), who considered both morphological and genetic data.

Preliminary data on the morphology of glochidial shells did not provide reliable characters for distinguishing the genera *Anemina*, *Buldowskia*, and *Amuranodonta* Moskvicheva, 1973 (SAYENKO 2006). Glochidia of *Buldowskia*, including species first described as members of *Anemina* and later transferred to *Buldowskia*, have been studied under both light and scanning electron microscopes. SHADIN (1938) and INABA (1941) provided the first brief descriptions of the glochidium of *Buldowskia shadini* (Moskvicheva, 1973), as *Anemina shadini*. Several other authors later continued the study the glochidial morphology and reproductive cycles in this group of mussels (ANTONOVA & STAROBOGATOV 1988, JEONG et al. 1992, KWON et al. 1993, PARK & KWON 1993, SAYENKO & SHEDKO 2005, SAYENKO 2006, ITOH et al. 2022, SAYENKO et al. 2023), although a detailed study of glochidial shell morphology including the outer shell microsculpture has not been undertaken.

Using *COI* DNA barcoding data, BOLOTOV et al. (2020) and LOPES-LIMA et al. (2020) found *Anemina*, *Buldowskia*, and *Amuranodonta* to be valid, and *Buldowskia*

was shown to contain 5 species, with 2 species in Russia. Among these species, *B. iwakawai* (Suzuki, 1939) and *B. kamiyai* Sano, Hattori & Kondo, 2020 have a disjunct distribution; *B. iwakawai* occurs in a single river basin in South Korea, several basins in western Honshu and Hokkaido, Japan, and southern Sakhalin, Russia; and *B. kamiyai* is endemic to river basins in northeastern Honshu, Japan. The other 3 *Buldowskia* species occur only in mainland East Asia. *Buldowskia flavotincta* (Martens, 1905) is endemic to the Hangang, Geumgang, and Nakdong river basins in South Korea; *B. suifunica* inhabits the Razdolnaya River and other coastal basins in North Korea and southern Primorsky Krai in Russia; and *B. shadini* has a wider, although disjunct, distribution throughout the Amur river basin (including the basin of Lake Khanka) and in 4 major river basins (Hangang, Nakdong, Gokgang, and Hyeongsang rivers) of South Korea (LOPES-LIMA et al. 2020).

The revisions by BOLOTOV et al. (2020) and LOPES-LIMA et al. (2020) highlight future possibilities for research. One area of investigation is determining the exact geographic boundary between *B. suifunica* and *B. shadini* in southern Primorsky Krai. LOPES-LIMA et al. (2020) thought that *B. suifunica* occurs in areas of Primorsky Krai other than the basin of Lake Khanka; however, they had samples only from Khasansky District, the southernmost area of the krai, and not from the coastal drainages in the north outside of the Razdolnaya basin. A human-caused introduction of fish into some water basins of Primorsky Krai (BARABANSHCHIKOV & MAGOMEDOV 2002) has not been considered as one of the possible causes of the dispersal of *B. shadini*.

To clarify the boundaries between the distributions of *B. suifunica* and *B. shadini* in southern Primorsky Krai, we examined specimens from several localities, namely from the Razdolnaya river basin, from the unstudied basin of the Khasansky District, as well as from several coastal basins, not connected to the Razdolnaya River, north of the Khasansky District. In addition, we investigated in detail glochidial shell morphology, especially the exterior valves microsculpture, with the aim to check

the variability of this character. Our results contribute to a better understanding of differences between *B. suifunica* and *B. shadini*.

## Materials and Methods

Samples for investigation were collected from several localities in southern Primorsky Krai in the Russian Far East (Table 1, Fig. 1). Gravid adult mussels varied in shell size and shape (Fig. 2). The adult mussels were identified using partial mitochondrial DNA sequences of the cytochrome *c* oxidase subunit I (*COI*) gene, or they were collected from localities (Solenoye and Utinoye lakes) where the species present had been determined earlier by DNA barcoding (LOPES-LIMA et al. 2020). Glochidia were extracted from the demibranchs of adult mussels. The identity of larvae was established from the identity of the corresponding adult specimens.

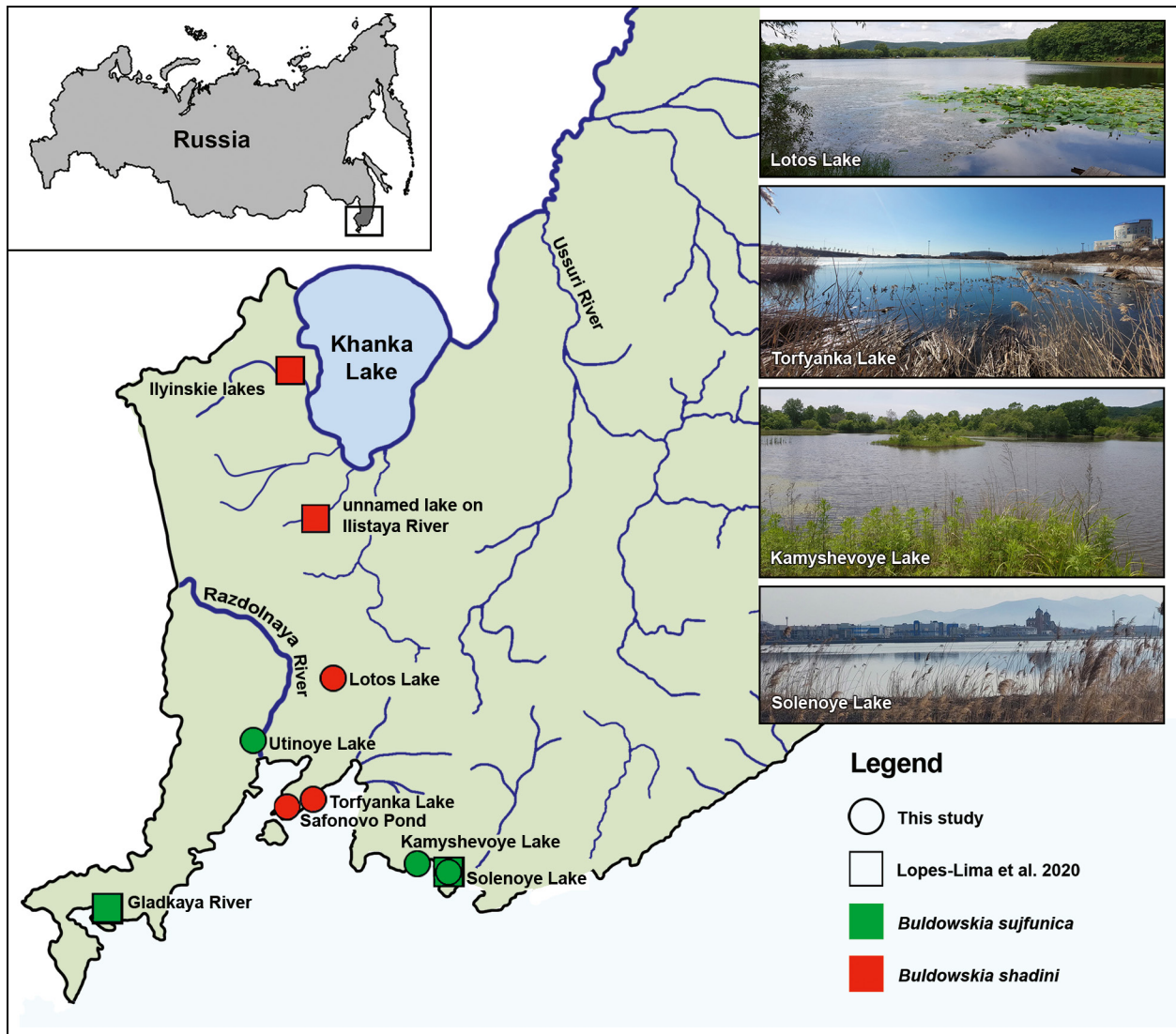
Samples of adults and glochidia were deposited at the Federal Scientific Center of the East Asia Terrestrial Biodiversity, the Far Eastern Branch of the Russian Academy of Sciences, Vladivostok, Russia (**FSCEATB FEB RAS**). Dry adult shells and localities were photographed by E.M. Sayenko, and a photograph of Torfyanka Lake was kindly taken by Rada S. Surmach (FSCEATB FEB RAS).

The DNA-barcoding analysis was carried out by N.A. Seliverstov at the Far Eastern Federal University, Vladivostok. Total genomic DNA was extracted from mussel foot tissue using a QIAamp Fast DNA Tissue Kit (Qiagen, Hilden, Germany), and the resultant DNA was eluted in 100 µl of elution buffer (10 mM Tris-Cl; 0.5 mM EDTA; pH 9.0). The barcode of the partial mitochondrial *COI* gene was amplified using the polymerase chain reaction (PCR) with the primers LCO1490 (5' – GGTCACAAATCATAAAGATATTGG – 3') and HCO2198 (5' – TAAACTTCAGGGTGACCAAAAAATCA – 3') (FOLMER et al. 1994). The PCR reactions comprised a heating step at 95 °C for 2 min 30 s, followed by 35 cycles of denaturation at 95 °C for 30 s, annealing at 48 °C for

**Table 1.** List of investigated *Buldowskia* samples and collection data; *n* = number of investigated adult specimens.

Species	Sampling sites, from N to S	Date	Collectors	<i>n</i>	
				DNA	Glochidia
<i>B. shadini</i>	Russian Far East, Ussuryisk Urban District, Razdolnaya river basin, Lotos Lake between Dubovy Kluch and Kondratenovka villages	12.VII.2023	I.A. Rodionov, E.M. Sayenko	3	—
	Russian Far East, Vladivostok, Ob'yasnieniya river basin, Safonovo Pond	19.IX.2021	T.S. Vshivkova	1	1*
	Russian Far East, Vladivostok, Patrokl Bay, Torfyanka Lake	03.VIII.2023	A.A. Semenchenko	2	1*
<i>B. suifunica</i>	Russian Far East, Nakhodka Urban District, Rifovaya Bay, Kamyshevoye Lake	16.IX.2017, 21.IX.2020, 17.IV.2022, 16.VI.2023	I.A. Rodionov, E.M. Sayenko	2	4
	Russian Far East, Nakhodka Urban District, Nakhodka Bay, Solenoye Lake	22.VI.2017	E.V. Kolpakov	—	1
	Russian Far East, Khasansky District, Troitsa Bay, Utinoye Lake	11.XI.2005	A.Yu. Semenchenko	—	1

\*Specimens with immature glochidia.



**Figure 1.** Collecting sites of *Buldowskia shadini* and *B. suifunica* in southern Primorsky Krai, Russian Far East.

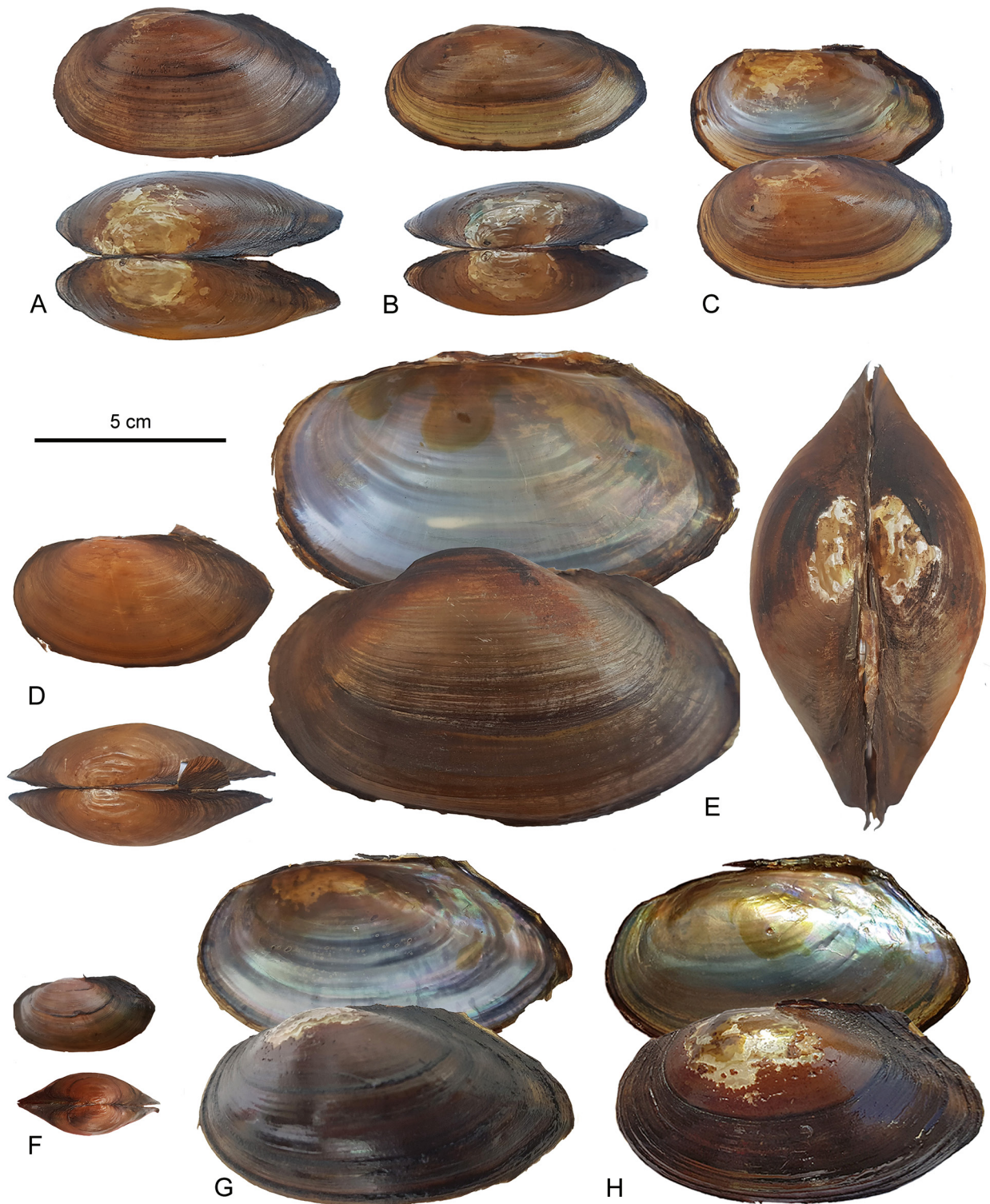
30 s, and elongation at 72 °C for 1 min, with a final extension phase of 72 °C for 10 min. The PCR was performed in a reaction volume of 10 µl using 5 µl Go Taq Green Master Mix (Promega Corp., Madison, WI, USA), 0.5 µM of each primer, 3 µl nuclease-free water, and 1 µl of genomic DNA. The PCR products were confirmed by electrophoresis in 1.5% agarose gels and then sequenced bidirectionally. Each amplicon was purified using Exonuclease I (ExoI) and Thermosensitive Alkaline Phosphatase (FastAP) (Thermo Fisher Scientific Inc., Waltham, MA, USA). Sequencing reactions had a total volume of 10 µl and included 10 pmol of each primer and reagents of BigDye terminator v. 3.1 cycle kit. The PCR products were bidirectional sequenced on an ABI 3500 sequencer (Applied Biosystems) and were aligned in MEGA7 (KUMAR et al. 2016).

The inter- and intraspecific genetic distances were calculated using *p*-distances in MEGA7. An Assemble Species by Automatic Partitioning (ASAP) analysis using *p*-distances was implemented on the website ([https://](https://bioinfo.mnhn.fr/abi/public/asap/asapweb.html)

[bioinfo.mnhn.fr/abi/public/asap/asapweb.html](https://bioinfo.mnhn.fr/abi/public/asap/asapweb.html); PUILLANDRE et al. 2021).

The phylogenetic analysis was carried out by A.A. Semenchenko and N.A. Seliverstov using partial-*COI* sequence data from newly collected specimens and from GenBank (Tables 1, 2) and the Barcode of Life Data System (BOLD, <http://www.boldsystems.org/>, accessed 2024. ii.2). As a result, 2 different datasets, the first aimed at constructing a phylogenetic tree and computing an ASAP analysis, the second at calculating inter- and intraspecific distances, were prepared. To obtain the first dataset, 3 specimens from each barcoding index number (BIN) from BOLD were used while the second dataset includes all available sequences of *Buldowskia shadini* ( $n = 22$ ) and *Buldowskia suifunica* ( $n = 10$ ). For the first data set, separately for each codon position of protein-coding genes, PartitionFinder v. 2.1.1 (LANFEAR et al. 2012) was used to select the best-fit partitioning scheme and models, using a greedy algorithm with linked branch lengths for the corrected Bayesian Information Criterion as an optimality criterion for model selection. The best models for the first,





**Figure 2.** Shells of *Buldowskia* species. **A–F.** *B. shadini*, from (**A–C**) Lotos Lake, (**D, E**) Torfyanka Lake, (**F**) Safonovo Pond. **G, H.** *Buldowskia sujfunica*, from Kamyshevoye Lake.

second and third codon position of *COI* were SYM+G (ZHARKIKH 1994), F81+I (FELSENSTEIN 1981), and HKY (HASEGAWA et al. 1985), respectively. Bayesian phylogenetic analyses were carried out using Markov Chain Monte Carlo (MCMC) randomization in MrBayes v. 3.2.7

(RONQUIST et al. 2012). Four Markov chains (1 cold and 3 heated chains) were run for 5 million generations, with the first 25% of sampled trees discarded as burn-in. The strict clock model was used to obtain an ultrametric tree. Moreover, trace files of BI analysis were visually inspected in

Tracer v. 1.7 (RAMBAUT et al. 2018), and the tree was visualized in FigTree v. 1.4.4.

The fine structure morphology of the outer valve surface of glochidia of *B. suifunica* was investigated using scanning electron microscopy (SEM). The procedure for preparing larval shells was carried out in accordance with standard methods (SAYENKO & KAZARIN 2023). For our investigation we used samples with glochidia initially preserved in 75% alcohol. To prevent deformation or destruction of the hooks, only chemical cleaning with 5% KOH solution was used. To prevent destruction of the thin outer layer of the shells during the chemical cleaning, the glochidia were occasionally examined by light microscopy (LM). The cleaned shells were washed several times in distilled water and in an alcohol series (80, 90, and 96%), after which they were mounted as permanent slides for LM or on stubs for SEM.

To avoid crushing the glochidia under the coverslip during mounting on permanent slides, each group of larvae was surrounded by a hair. To prevent the deformation of the hooks and outer shell layer, glochidia were sputter-coated with gold immediately after drying the samples and mounting on a stub for SEM.

The description of the microsculpture on the valve exteriors follows HOGGARTH (1999), SAYENKO (2016), and SAYENKO & AKIYAMA (2020). Glochidial microsculpture was examined at least at 3 points: close to the ventral terminus near the hook, at the centre in the adductor muscle region, and at the valve rim near the ligament. Glochidia were photographed by E.M. Sayenko, with the help of Vitalyi M. Kazarin, on a Zeiss MERLIN scanning electron microscope at the Biology and Genetic Engineering Center for Collective Use of the FSCEATB FEB RAS.

## Results

The 8 new barcode sequences obtained from *Buldowskia shadini* and *B. suifunica* ranged in size from 582–685 base pairs. After assembly and alignment, nucleotide frequencies in these sequences were as follows: A = 20.9%, T = 37.2%, G = 23.1%, and C = 18.7%.

Using the second dataset, we calculated that the average interspecific pairwise distances between these 2 species were 13.4%, which is similar to data obtained by LOPES-LIMA et al. (2020). Sequence divergences in *B. shadini* and *B. suifunica* were 0.4% and 0.27%, respectively, which corresponds to intraspecific levels of divergence.

Using the first dataset, the high divergence between *B. shadini* and *B. suifunica* were confirmed in our ASAP analysis, which yielded 9 molecular operational taxonomic units (MOTUs) within the genus *Buldowskia* (Fig. 3). These 2 species appear in different MOTUs, each corresponding to a different species.

We used the *COI* marker to reconstruct species relationships in the genus *Buldowskia*. In our Bayesian tree using posterior probability (BPP) (Fig. 3), *B. suifunica* occupied the basal node with moderate support (BPP =

0.73). The next moderately supported clade (BPP = 0.71) includes *B. shadini* and the remaining sister taxa. The results of our ASAP analysis, as well as the strongly supported clades with the 2 investigated species, confirm the identifications of *Buldowskia* species from the Russian Far East.

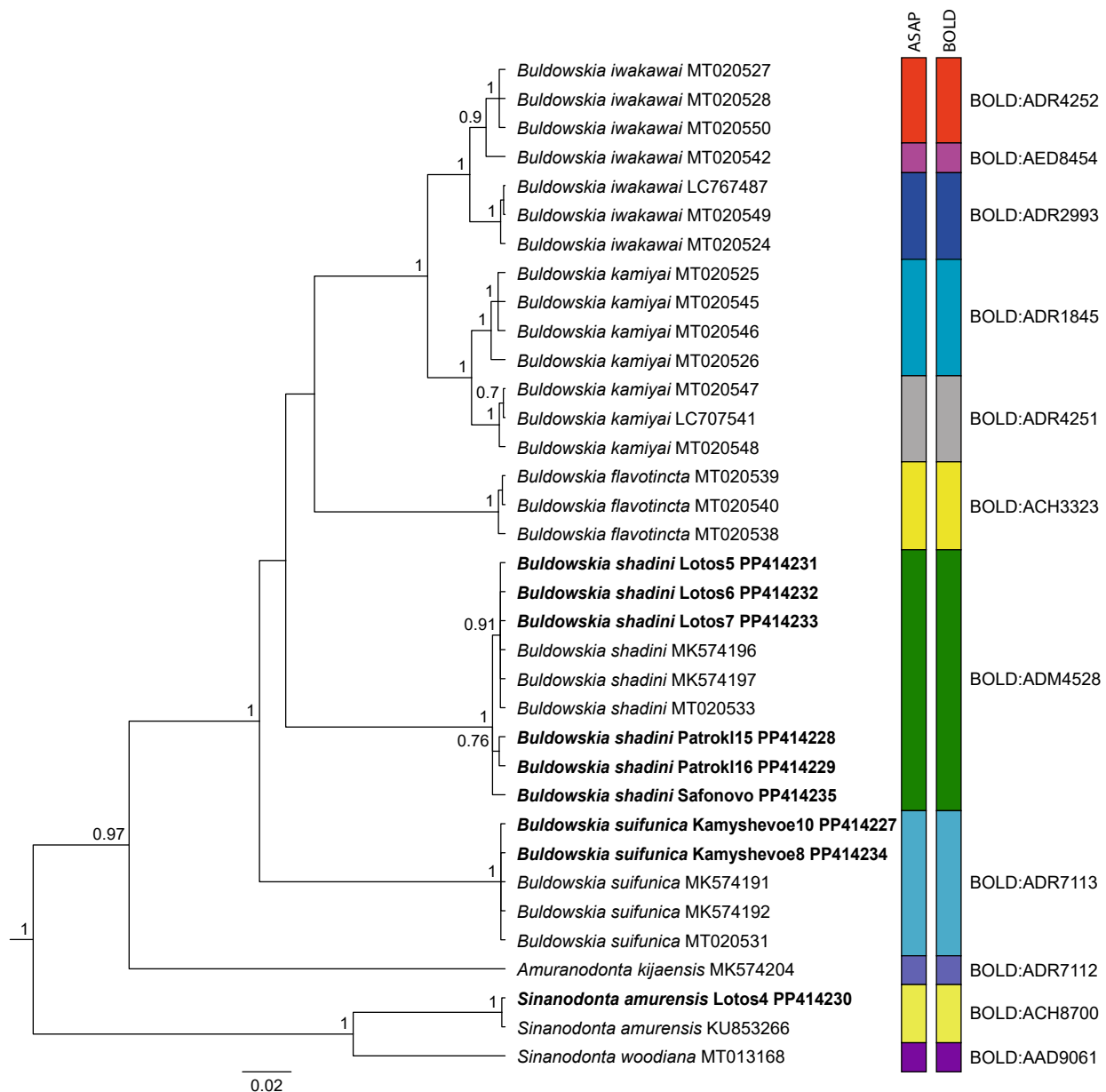
Based on the *COI* sequences, the distribution of *B. shadini* and *B. suifunica* in southern Primorsky Krai is clarified (Tables 1, 2). Our results reveal that in *B. suifunica* inhabits basins in Khasansky District, the southernmost part of Primorsky Krai, and also the coastal drainages to the northeast; the northeastern boundary is the basins in the Nakhodka urban district. *Buldowskia shadini* occurs further north, in the coastal drainages not part of the basin of Lake Khanka, namely in the ponds of the Muravyov-Amursky Peninsula. Both species were found to occur in the basin of the Razdolnaya River. However, we did not find these species together at the same localities. Conversely, *B. shadini* was found at some localities together with the other unionids, for example, with *Sinanodonta schrenkii* (Lea, 1870).

Immature glochidia of *B. shadini* were collected at 2 different stages of development: first, at the very beginning of shell formation in early August, and next at the cap-like shell formation stage in mid-September. Mature glochidia of *B. suifunica* with developed hooks were collected in the end of April, in June, September and November; gills were free of glochidia in mid-May, June, and July.

Immature glochidia of *B. shadini* at the very initial stage of shell formation were 183–185 µm in length and 116–118 µm in height. Developing *B. shadini* glochidia without hooks at the cap-like shell-formation stage were 230–260 µm long, 200–215 µm high, and the ligament was 210–230 µm long (Fig. 4).

Mature glochidia of *B. suifunica* are typical of anodontines with hooks, in being subtriangular with the protruding ventral margin (Fig. 5A–C). The 2 valves are equal in size, held together by a ligament. Mature glochidia are large, up to 395 µm in height and 407 µm in length; they are longitudinally elongate, so the length is always greater than the height. The length of the ligament is 270–285 µm. We found that glochidia shells of *B. shadini* range in length from 328 to 386 µm in the Amur river basin, 307–393 µm in the Razdolnaya river basin, and 322–385 µm in the basin of Lake Khanka. The styliform hook is in the shape of a triangular plate (Fig. 5D–F) and is of 107–178.5 µm long, which is more than 30% of the valve height. The hook is covered by more than 20 lanceolate macrospines, up to 16.8 µm long, which are arranged in 2 or 3 longitudinal rows near the ventral terminus and reduced to single row distally. Microspines and micropoints (<1 µm long) cover the entire ventral terminus and less than a third of the hook lateral lobes; these continue in narrow strips along the macrospines almost to the end of the hook stylet.

The outer glochidial shell layer is characterized by species-specific microsculpture, which in the *B. suifunica* is loose-looped (Fig. 6). The loops form a loose network, which is multilayered on the centre of the valves,



**Figure 3.** Bayesian-inference tree based on partial-COI sequence data of the genus *Buldowskia* with results of species delimitation of ASAP and BIN BOLD analysis. Bayesian posterior probabilities ( $\geq 0.7$ ) are given above tree nodes. Specimens obtained in this study are in bold.

with distinct, curved lines or an even net going over the main loop pattern (Fig. 6D, F). Closer to the ventral edge of the valves (Fig. 6A–C), to the valve rim or ligament (Fig. 6E), the exterior microsculpture ceases to be multilayered, and the loops are more tightly spaced and smaller. The thickness of the lines varies from 0.044 to 0.056  $\mu\text{m}$ , with the average of 0.05  $\mu\text{m}$ .

Pores of the inner glochidial layer vary from 0.8 to 3.4  $\mu\text{m}$  in diameter.

## Discussion

Mitochondrial DNA barcoding using the *COI* gene has become an effective tool for the identification of species of Unionidae, including in the genus *Buldowskia* (e.g.

BOLOTOV et al. 2020, LOPES-LIMA et al. 2020, KAWASE et al. 2021a, b, ITOH et al. 2022). According to our reconstructed phylogeny of *Buldowskia*, the genus has 5 main clades which correspond to 5 species: *B. iwakawai*, *B. kamiyai*, *B. flavotincta*, *B. shadini*, and *B. suifunica*. *Buldowskia iwakawai* and *B. kamiyai* from Japan and South Korea show deep intraspecific divergences in the ASAP and BOLD analyses, as shown by their delineation into 3 and 2 MOTUs, respectively, (Fig. 3). The type locality of *B. shadini* is the Mandzhurka River, part of the Lake Khanka basin. To date, DNA barcodes of *B. shadini* from Japan (KAWASE et al. 2021a, b), South Korea (LOPES-LIMA et al. 2020), and Russia (LOPES-LIMA et al. 2020, this study) show low intraspecific divergence (mean 0.25%) across this species' disjunct distribution. We believe that *B. shadini* occurs naturally in the basin

**Table 2.** List of GenBank accession numbers for *COI* gene sequences used in this study.

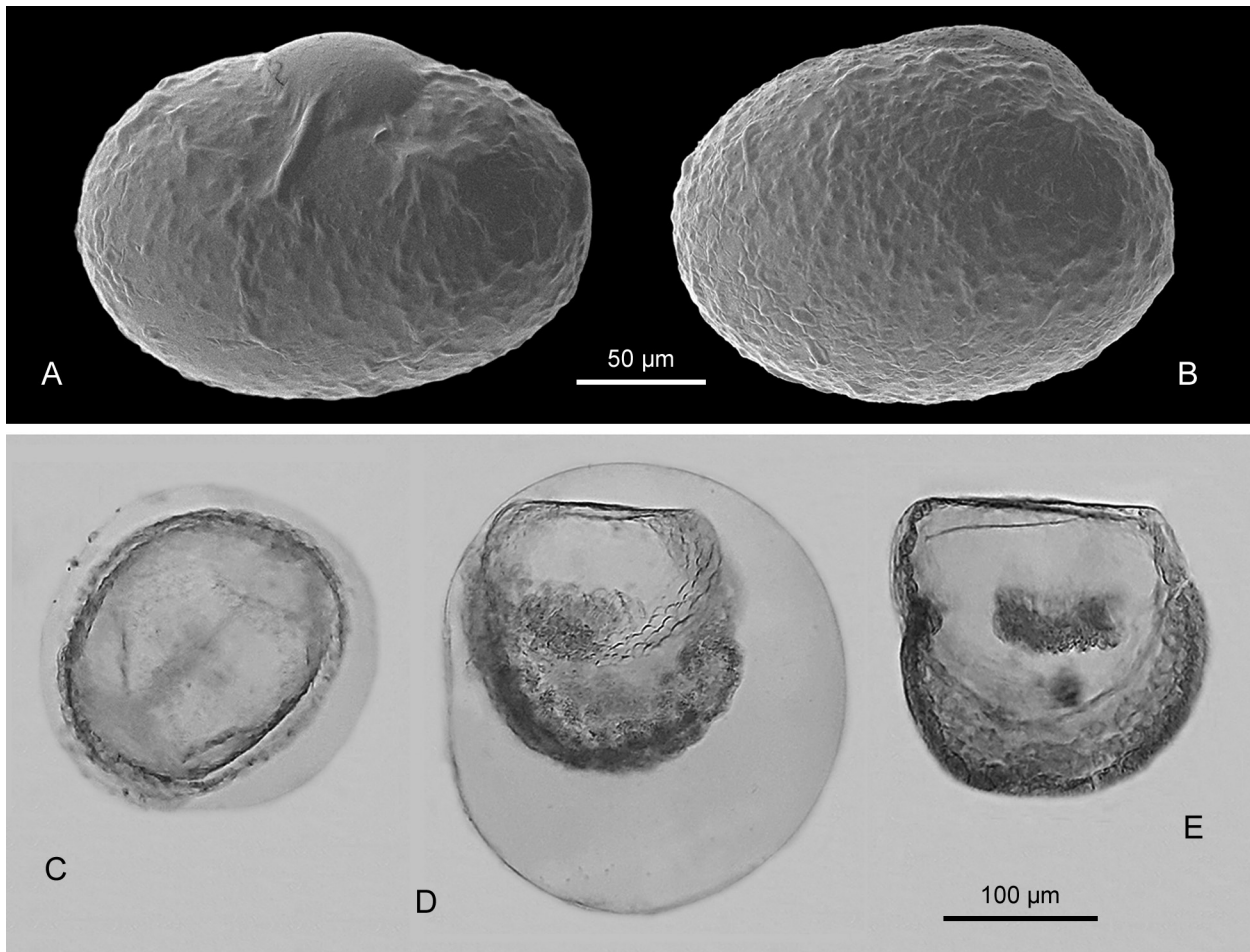
Taxa	COI	Locality, from N to S for each species	Reference
Ingroup			
<i>Buldowskia iwakawai</i>	LC767487	Japan, Hokkaido Prefecture, Teshio River	ITO et al. 2022
	MT020549	Japan, Niigata Prefecture, Kaji River	LOPES-LIMA et al. 2020
	MT020524	Japan, Niigata Prefecture, Shinano River	LOPES-LIMA et al. 2020
	MT020550	Japan, Tottori Prefecture, Gamo River	LOPES-LIMA et al. 2020
	MT020527, MT020528	Japan, Shimane Prefecture, Ohara River	LOPES-LIMA et al. 2020
	MT020542	South Korea, Imsil-gun, Seomjin River	LOPES-LIMA et al. 2020
<i>Buldowskia kamiyai</i>	MT020546, MT020547, MT020548	Japan, Iwate Prefecture, Oizumigaike Pond	LOPES-LIMA et al. 2020
	LC707541	Japan, Iwate Prefecture, Hanamaki	SANO et al. 2022
	MT020525	Japan, Miyagi Prefecture, Abukuma River	LOPES-LIMA et al. 2020
	MT020545	Japan, Fukushima Prefecture, Inawashiro Lake	LOPES-LIMA et al. 2020
	MT020526	Japan, Ibaraki Prefecture, Naka River	LOPES-LIMA et al. 2020
<i>Buldowskia flavotincta</i>	MT020539	South Korea, Yeongwol-gun, Han River	LOPES-LIMA et al. 2020
	MT020540	South Korea, Boryeong-si, Ungcheon Stream	LOPES-LIMA et al. 2020
	MT020538	South Korea, Uiseong-gun, Nakdong River	LOPES-LIMA et al. 2020
<i>Buldowskia shadini</i>	MK574196, MK574197	Russian Far East, Khorolsky District, basin of Khanka Lake, unnamed lake on Ilistaya River near Blagodatnoye village	BOLOTOV et al. 2020
	MT020533	Russian Far East, Khorolsky District, basin of Khanka Lake, Ilyinskie lakes on Komissarovka River	LOPES-LIMA et al. 2020
	PP414231, PP414232, PP414233	Russian Far East, Ussuryisk Urban District, Razdolnaya river basin, Lotos Lake	This study
	PP414235	Russian Far East, Vladivostok, Safonovo Pond	This study
	PP414228, PP414229	Russian Far East, Vladivostok, Patrokl Bay, Torfyanka Lake	This study
	PP414227, PP414234	Russian Far East, Nakhodka Urban District, Rifovaya Bay, Kamyshevoye Lake	This study
	MT020531	Russian Far East, Nakhodka Urban District, Nakhodka Bay, Solenoye Lake	LOPES-LIMA et al. 2020
	MK574191, MK574192	Russian Far East, Khasansky District, Gladkaya River	LOPES-LIMA et al. 2020
Outgroup			
<i>Amuranodonta kijaensis</i>	MK574204	Russian Far East, Zabaikalsky Region, Arey Lake	LOPES-LIMA et al. 2020
<i>Sinanodonta schrenkii</i> (= <i>S. amurensis</i> )	KU853266	Russian Far East, Ussuryisk Urban District, Razdolnaya River	SAYENKO et al. 2017
<i>Sinanodonta schrenkii</i>	PP414230	Russian Far East, Ussuryisk Urban District, Razdolnaya river basin, Lotos Lake	This study
<i>Sinanodonta woodiana</i>	MT013168	Russian Far East, Kemerovo Oblast, Belovskoe Reservoir, Ob river basin	KONDAKOV et al. 2020

of Lake Khanka, which is part of the Amur basin, but that it has been introduced by humans with fish into the Razdolnaya river basin and ponds in Vladivostok with fish (BARABANSHCHIKOV & MAGOMEDOV 2002). In contrast to the pelagic veliger larvae of marine bivalves, the temporary, parasitic attachment of glochidia to the host fish can be an effective dispersal strategy for unionids (YOUNG 1911, WÄTCHLER et al. 2001, BARNHART et al. 2008, CASTRILLO et al. 2022).

Four *COI* sequences of *B. suifunica* belong to a single haplotype, with no intraspecific divergence, despite coming from 4 unconnected bodies of water, Razdolnaya and Gladkaya rivers and Kamyshevoye and Solenoye

lakes near Nakhodka city (Fig. 1). *Buldowskia suifunica* is native to the Razdolnaya river basin, unlike *B. shadini*, which has been introduced. Expansion of *B. suifunica* in southern Primorsky Krai occurred during periods of glaciation in the Pleistocene when the Sea of Japan was as much as 120 m lower than at present (NAKAZAWA & BAE 2018, LYASHCHEVSKAYA et al. 2022), the coastal landscape of southern Primorsky Krai differed, and the paleo-Razdolnaya (= paleo-Suifun) River was united with rivers flowing into Peter the Great Bay (BELYANINA et al. 2009, PROKUDIN et al. 2018). The recentness of these events explains the lack of divergence found in the *COI* genes among *B. suifunica* samples.





**Figure 4.** Immature glochidia of *Buldowskia shadini*. **A, B.** Early larvae at the initial stage of glochidial shell formation. **C.** Early larva at the stage of rounded embryo with the vitelline membrane around. **D.** Larva at the trochophore-like stage with the vitelline membrane, the developing transparent shell and adductor muscle inside are observed. **E.** Larvae of the shell cap-like stage, the vitelline membrane is no longer present. Specimens from **(A, B)** from Torfyanka Lake and **(C–E)** from Safonovo Pond.

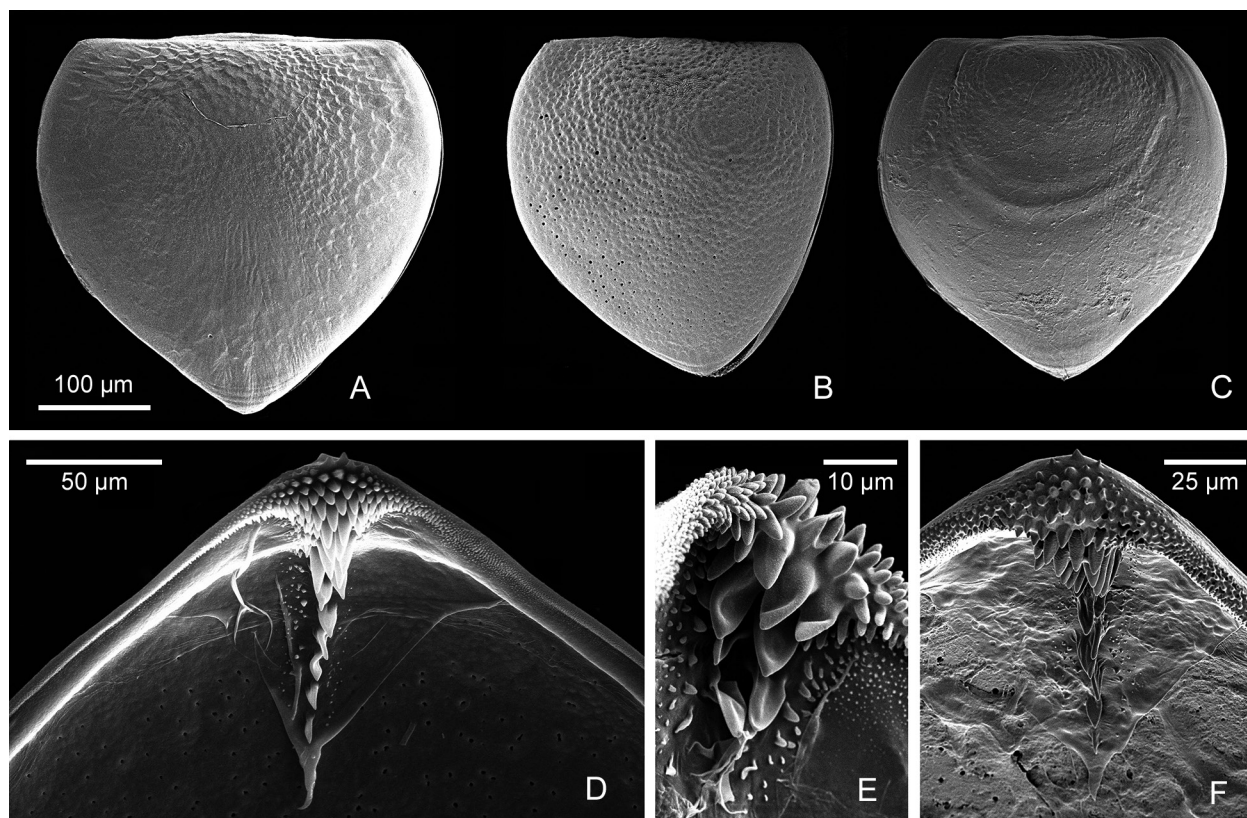
In summary, the current geographic distribution of *Buldowskia* species was affected by both natural and human-caused events. The expansion of the paleo-Razdolnaya River caused by a change in the sea level during the Pleistocene led to the presence of this genus in the basins of lowland rivers having an extended estuarine zone, while *Buldowskia* is absent from rivers in the mountains. The second event has the introduction of fish to some of the basins in Primorsky Krai in modern history.

Together with other Far Eastern anodontines, including species of *Anemina*, *Buldowskia* is characterized by having a long brooding period, which means that *Buldowskia* spawns at the end of summer, brood glochidia in their marsupia over the winter, and release glochidia in spring and early summer, depending on water temperature and seasonal host-fish activities (SAYENKO & SHEDKO 2005, SAYENKO 2006, FUKUHARA et al. 2013, KONDO et al. 2015). According to published data (MARTYNOV & CHERNYSHEV 1992, SAYENKO & SHEDKO 2005, SAYENKO 2006, RAKOV & SHAROVA 2008), females of *B. shadini* begin incubating eggs in their outer gills in late August or September; glochidia mature in September to early spring and are released in April and May; in

summer, the gills of adults are empty of glochidia. The brooding period of *Anemina arcaiformis* (Heude, 1877) in Japan is known to begin in September, mature larvae were found from late November to throughout the winter, and glochidia are released from late January to April, but mainly in March (FUKUHARA et al. 2013, KONDO et al. 2015).

Glochidial shell size in *Buldowskia* varies considerably among populations and river basins (SAYENKO & SHEDKO 2005). Among *Buldowskia* species, glochidia of *B. iwakawai* are the largest at 360–390 µm high and 360–400 µm long (ITO et al. 2022). In *B. shadini*, glochidia from the Amur river basin were largest (length 414 µm) and those from the Razdolnaya river basin smallest (length 314 µm) (SAYENKO & SHEDKO 2005, SAYENKO 2006). RAKOV & SHAROVA (2008) gave the length of glochidia in a population of *B. shadini* from Torfyanka Lake as 250–300 µm, but this may be for immature glochidia because no mention of glochidial hooks was made. Only in *B. shadini* did we measure the maximum length of macrospines on the hooks. Our new data, which range from 15.3 to 16.2 µm, are consistent with





**Figure 5.** Mature glochidia of *Buldowskia suifunica*. **A–C.** Glochidial shells. **D–F.** Glochidial hooks with spines. Specimens from (**A, D**) Kamyshevoye Lake, (**B, E**) Solenoye Lake, and (**C, F**) Utinoye Lake.

that from earlier publications (SAYENKO & SHEDKO 2005, SAYENKO 2006).

Our study confirms earlier studies that the glochidia of *Buldowskia* are longitudinally elongate, with the valve length exceeding the height (ANTONOVA & STAROBOGATOV 1988, 1989, SAYENKO & SHEDKO 2005, SAYENKO 2006, ITOH et al. 2022). Longitudinally elongate glochidia have also been noted for *Anemina* species in Korea and Japan (SUZUKI 1939, LEE et al. 1989, 2007, PARK & KWON 1993, KONDO 2008). Among anodontines from Primorsky Krai, glochidia of *Buldowskia* and *Anemina* are very close in their shape and size, while those of *Sinanodonta* Modell, 1945 are smaller in size and vertically elongate (SAYENKO 2006).

Size ranges of glochidia overlap among *Buldowskia* species and are not helpful in determining species, but exterior microsculpture of mature glochidial shells do provide taxonomically diagnostic characters for identifying species. We studied the exterior microsculpture of *Buldowskia* glochidia to identify possible differences between species. In doing this, we hope to lay the groundwork for a future investigations in *Buldowskia* and *Anemina*. Previously published data on *Buldowskia* and *Anemina* species do not include exterior microsculpture of glochidia shells. In glochidia of *Amuranodonta kijaensis* Moskvicheva, 1973, the exterior microsculpture is tight-looped, with loops which are densely packed in one plane, while the thickness of the lines does not exceed 0.057 µm (SAYENKO et al. 2024). In

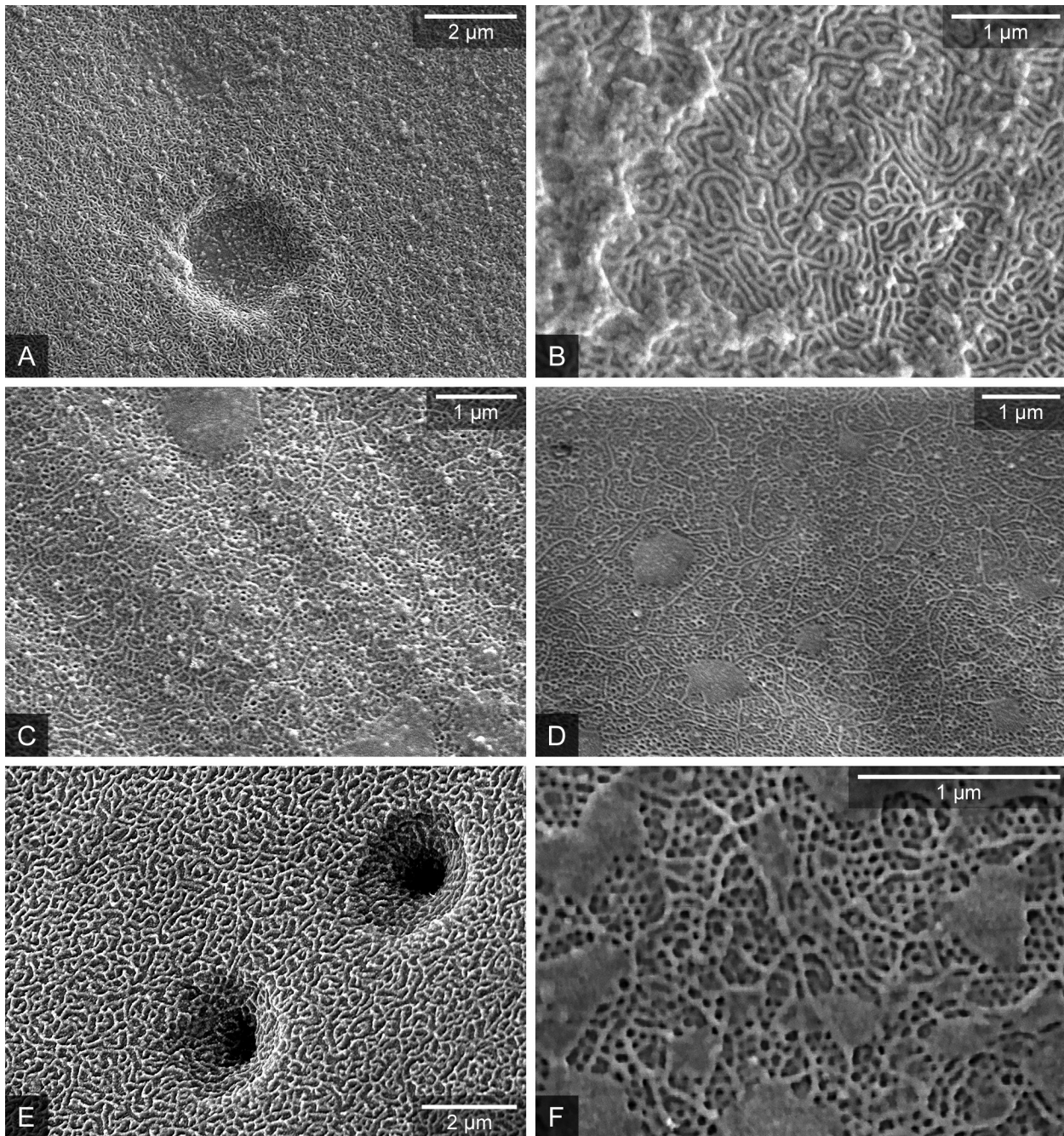
glochidia of *Sinanodonta schrenkii* (= *S. amurensis* Moskvicheva, 1973) and *S. woodiana* (I. Lea, 1834), the external microsculpture consists of convex overlapping looped lines forming a fine-meshed structure where the thickness of the lines does not exceed 0.1 µm and are 0.07 µm on average (SAYENKO & SOROKA 2013, SAYENKO 2016).

The newly identified populations of *Buldowskia*, including the threatened *B. suifunica*, significantly reduce an existing knowledge gap, help to better understand the patterns of geographic distribution, and create the basis for the conservation of these molluscs. Our results suggest new taxonomic characters and provide direction for subsequent research.

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**Figure 6.** Exterior microsculpture of mature glochidia of *Buldowskia suffunica* at various points of the valves and different magnifications. **A, C.** Sculpture near ventral corner of the valves. **B, D, F.** Sculpture at the central part of the valves. **E.** Sculpture near the valve rim. Specimens from (**A, B**) Utinoye Lake, (**C, D, F**) Kamyshevoye Lake, and (**E**) Solenoye Lake.

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