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Enigmatic corkscrew-shaped *Liobaicalia* (Caenogastropoda: Truncatelloidea: Baicaliidae): description of three new species and their relations with regular shell species

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ABSTRACT. Three new species have been added to the formerly monotypic genus *Liobaicalia* Martens, 1876. We employed a combination of morphological, anatomical, and molecular approaches using mitochondrial *COI* gene, nuclear intron of the *ATP* synthase subunit alpha gene (*ATPsα*), and *ITS1* spacer to delineate species boundaries between *Liobaicalia stiedae* (W. Dybowski, 1875), *L.* ***sidelevae*** sp. nov., *L.* ***karabanovi*** sp. nov., and *L.* ***riedeli*** sp. nov. The *Liobaicalia* species inhabit burrowing into sandy substrates in disparate regions of the ancient and/or recent deltas of the inflows to the south and central Baikal basins near tectonic faults where gases discharge happens. The genus *Liobaicalia* was not recovered as monophyletic based on current molecular-phylogenetic analyses based on mitochondrial *COI* data. We discussed discordance between morpho-anatomical and genetic traits, the possible origin of the *Liobaicalia* species, and the occurrence of scalariform shells in Baikal and non-Baikal gastropods belonging to different families.

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Загадочный род *Liobaicalia* (Caenogastropoda: Truncatelloidea: Baicaliidae) со штопоровидной раковиной: описание трех новых видов с заметками о родственных видах с нормальной раковиной

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РЕЗЮМЕ. К ранее существовавшему монотипическому роду *Liobaicalia* Martens, 1876, добавлены три новых вида. Мы использовали комбинацию морфологических, анатомических и молекулярных подходов с применением митохондриального (*COI*) и ядерных (*интрон гена альфа-субъединицы АТФазы* и *ITS1*) маркеров для определения границ видов *Liobaicalia stiedae* (W. Dybowski, 1875), *L.* ***sidelevae*** sp. nov., *L.* ***karabanovi*** sp. nov. и *L.* ***riedeli*** sp. nov. Виды *Liobaicalia* обитают на песчаных субстратах в разрозненных регионах древних и/или современных дельт притоков южной и центральной котловин оз. Байкал, близи тектонических разломов и мест разгрузки газов. Род *Liobaicalia* оказался не монофилетичным по нуклеотидным последовательностям гена *COI* мтДНК. Обсуждается несоответствие между морфо-анатомическими и генетическими признаками, предполагаемое происхождение видов *Liobaicalia,* а также встречаемость скаляриевидных раковин у байкальских и внебайкальских гастропод разных семейств.

Introduction

The gastropod family Baicaliidae P. Fischer, 1885, is widely distributed in Lake Baikal and includes more than 40 endemic species combined into eight genera [Sitnikova, 1991]. The monotypic genus *Pyrgobaicalia* Starobogatov, 1972, described from Dunkulduk (Dunkeldyk?) Lake, Tajik Republic, Pamir was preliminarily assigned to Baicaliidae or Amnicolidae [Sitnikova *et al*., 2017], and its position in Truncatelloidea is still unclear due to the complete lack of data.

A detailed revision of the Baicaliidae has not been carried out since the beginning of the last century [Kozhov, 1936], although the female reproductive system has been studied in representatives of the genera [Sitnikova, 1991] and several new species have been described [Beckman, Starobogatov, 1975; Sitnikova *et al*., 2016].

The first study of *COI* mtDNA sequences from 14 species in the family showed discordance between morphological traits and genetic differentiation [Zubakov *et al*., 1997]. Subsequent molecular phylogenetic studies (*COI* mtDNA and *ITS1* nDNA) were devoted to the genus *Baicalia* Martens, 1876. It was shown that the intraspecific differentiation of *B. carinata* (W. Dybowski, 1875) is higher than between 5 species of this genus, thus some of the subspecies have been considered as separate species [Peretolchina *et al*., 2007; 2008]. The full mitochondrial introgressions from *B. carinata* to *B. turriformis* (W. Dybowski, 1875) and to *B. dybowskiana* (Lindholm, 1909) had been suggested; these two introgressions were not simultaneous and occurred with a time gap [Poroshina *et al*., 2020]. The complete mitochondrial genomes were obtained for four Baicaliidae species [Peretolchina *et al*., 2020]; the sets of nuclear DNA repeats of the nuclear genomes of these species have been compared to each other, and an intriguing assumption was made that some of the repeats were involved in horizontal transfer between sympatrically occurring species [Yuxiang *et al*., 2023]. The molecular phylogenetic research of other baicaliids involved an additional nuclear marker, an intron of the ATP synthase α-subunit gene [Kovalenkova *et al*., 2013]. The use of 22 species in the analysis allowed us to show the divisions of the Baicaliidae into two clades, which partially coincide with the two clades revealed by the mitochondrial *COI* gene and do not fully coincide with the morphological traits and modern taxonomy of the family. At least two genera, *Parabaikalia* Lindholm, 1909 and *Pseudobaikalia* Lindholm, 1909 appeared to be polyphyletic [Kovalenkova *et al*., 2020a].

The analysis of the nucleotide sequences of *COI* mtDNA of *Liobaicalia* representatives inhabiting three regions (Bolshie Koty, Posolskaya Bank, and Babushkin) revealed the high genetic differentiation between them [Kovalenkova *et al*., 2020b]. Initial investigation of the morphological and anatomical traits testified that the snails of these regions differ from *L. stiedae* (W. Dybowski, 1875), the type locality of which is Kultuk Bay (southern part of the Lake).

Before describing and naming new species, we tested the possibility of using the names of the intraspecific forms of *Liobaicalia stiedae* delineated without mentioning their locality by B. Dybowski and J. Grochmalicki [1920]. There are four intraspecific forms: *L. s.* f. *parva* has the smallest shell, 5–6 mm in height with 5–6 whorls; the shell height of the three other forms reaches up to ~10 mm; one of them, *L. s.* f. *polita*, has a smooth shell; the second, *L. s.* f. *rugosa,* is characterized by a wrinkled shell surface with transverse (or axial) microsculpture; and the third, *L. s.* f. *hispida,* has a spiral and transverse microsculpture with 'cilia' (periostracal outgrowths). Our investigations revealed substantial variability in shell microsculpture among and within *Liobaicalia* populations, complicating the use of these listed external features for reliable species delimitation. The names of the intraspecific forms proposed by B. Dybowsky and J. Grochmalicki [1920] cannot be used for the newly delineated species; thus, we named three new species *L.* ***sidelevae*** sp. nov., *L.* ***karabanovi*** sp. nov., and *L.* ***riedeli*** sp. nov. in honor of the scientists who study or studied the Baikal fauna.

Snails were collected in the south and central basins of the lake in various years from 1990 to 2024 by scuba divers or using box-core and dredge. The snails were found multiple times on sandy sediments with plant detritus and filaments of the sulfur bacteria *Thioploca* in some places at the depths from 12 to ~100 m in the regions of underwater river deltas, including underwater uplands (or Banks) that are remnants of the ancient delta surface [Voropinov, 1965; Naudts *et al*., 2012; Khlystov *et al*., 2016a, b; 2018; Kononov *et al*., 2019; 2023]. In some locations (Babushkin, Posolskaya Bank, Solsan, Goloustnoe, and Malye Koty) the gas emission (bubbles or diffusion) was registered nearby the focal snail habitations [Kalmychkov *et al*., 2006; 2017; Naudts *et al*., 2012; Hachikubo *et al*., 2023; V.G. Ivanov, personal communication, own observations].

The main goal of our investigations is the species delimitation and description. We employed a combination of morphological, anatomical, and molecular approaches to delineate boundaries between corkscrew-shell species inhabiting south and central basins of Lake Baikal.

Material and methods

Material

We studied the snails, including types of *Liobaicalia stiedae*, hosted in the collections of the Zoological Institute RAS (ZIN RAS, Saint Petersburg, Russia) and the Limnological Institute SB RAS (Irkutsk, Russia), and our material collected in various years. Literature data was also used to investigate the *Liobaicalia* distribution (Fig. 1). More than 190 individuals in total (dry shells and alcohol-fixed specimens) were studied; the detailed information about used material is presented in Supplementary Table S1, S2, S3 and in the section "Type material" of each species.

Morpho-anatomical investigation

The specimen identification was carried out by the same person in the present and previous studies [Zubakov *et al*., 1997; Kovalenkova *et al*., 2020a, b] using the comparison with type specimens of the Baicaliidae' species hosted in ZIN RAS collection. Teleoconch characters were studied in all specimens. Shell morphology, including protoconchs, and anatomy were studied in more detail in up to 12 individuals fixed in 80% alcohol from every locality; the foot of 3–9 of these snails was used for molecular-phylogenetic investigations. Every shell was firstly photographed with a scale bar using a

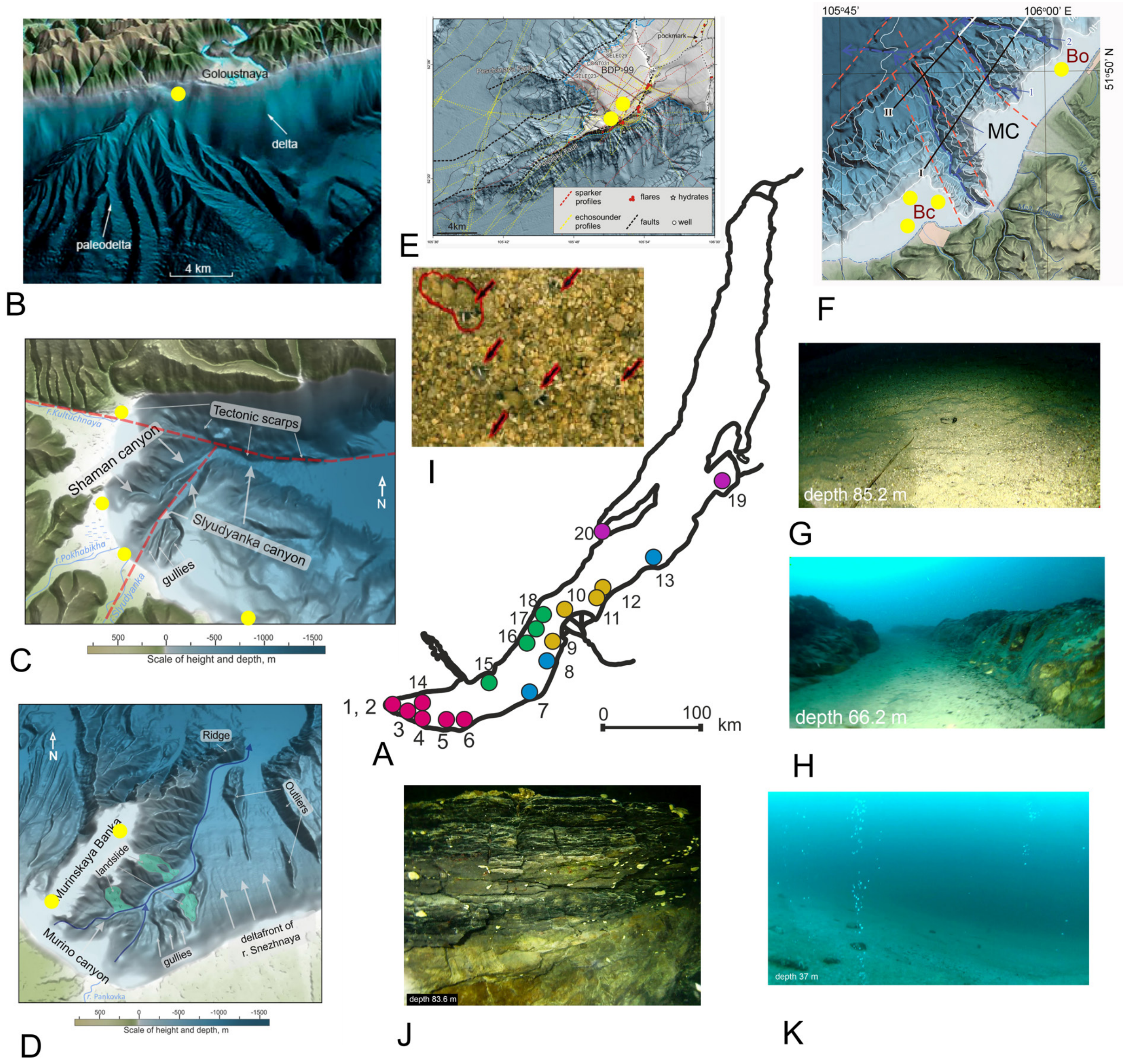

FIG. 1. The maps of the *Liobaicalia* spp. records, under water landscapes, and photographs of the habitats. **A.** A map: red circles – *L. stiedae*; green circles – *L.* ***karabanovi*** sp. nov., blue circles – ***L. sidelevae*** sp. nov., yellow circles – *L.* ***riedeli*** sp. nov., violet circles – records of other studied baicaliids. **1.** Kultuk Bay, Shaman Cape, Slyudyanka. **2.** Sukhoy Creek. **3.** Utulik. **4.** Baikalsk city, Solsan River. **5.** Murinskaya Bank. **6.** Snezhnaya River mouth. **7.** Babushkin city. **8.** Boyarskaya. **9.** Posolskaya Bank. **10**. delta Selenga River. **11.** Enckaluk. **12.** Sukhaya River. **13.** Talanka. **14.** Maritui. **15.** Bolshie Koty. **16.** Goloutsnoe. **17.** Nizhnie Khomuty. **18.** Peschanaya Bay. **19.** Barguzin Bay. **20.** Maloe More strait. **B–F.** Geomorphological maps from publications with the snail samplings indicated by yellow circles. **G–K.** Photographs of the bottom taken by (ROV) Rovbuilder RB-300. **B.** Goloustnaya River mouth and its paleodelta [Kononov *et al*., 2019]. **C.** Kultuk Bay, deltas of inflows [Kononov *et al*., 2023]. **D.** Murinskaya Bank [Kononov *et al*., 2023]. **E.** Posolskaya Bank [Naudts *et al*., 2012]. **F.** Babushkin (Bc) and Boyarskaya (Bo) regions [Khlystov *et al*., 2018, 2021]. **G.** Bolshie Koty Bay, sandy sediments of the modern delta area. **H.** Bolshie Koty River canyon. **I.** Snails *Liobaicalia stiedae* burrowing into sand [photo by P. Röpstorf]. **J.** Coal-bearing layers of the Tankhoi formation. **K.** Gas methane bubbles in the area near Babushkin city; red lines on the **C, E, F** – active tectonic faults.

РИС. 1. Карта-схема находок видов *Liobaicalia* spp., карты подводных ландшафтов с разломами и фотографии мест обитания. **A.** Карта находок: красные круги – *L. stiedae*; зеленые круги – *L.* ***karabanovi*** sp. nov., голубые круги – ***L. sidelevae*** sp. nov., желтые круги –*L.* ***riedeli*** sp. nov., фиолетовые круги – места сборов байкалиид, использованных в анализе. **1.** Залив Култук: пос. Слюдянка, Шаманский Мыс. **2.** Залив Култук: пос. Култук, Сухой ручей. **3**. Залив Култук: Утулик. **4.** г. Байкальск, р. Солзан. **5.** Муринская банка. **6.** р. Снежная. **7**. Бабушкин. **8**. Боярская. **9.** Посольская банка. **10.** Дельта р. Селенга. **11** Энкалук. **12** р. Сухая. **13.** Таланка. **14.** Маритуй. **15.** Большие Коты. **16.** Голоустное. **17**. Нижние Хомуты. **18.** Песчаная. **19.** Баргузинский залив. **20.** Малое море. **B – F.** Геоморфологические карты, места сбора улиток обозначены желтыми кружками. **G – K.** Фотографии дна, полученные подводным роботом Rovbuilder RB-300. **B.** Устье реки Голоустная и ее палеодельта [Kononov *et al.*, 2019]. **C**. Култук, дельты притоков [Kononov et al., 2023]. **D**. Муринская банка [Kononov *et al*., 2023]. **E**. Посольская банка [Naudts *et al*., 2012]. **F**. Бабушкин (Bc) и Боярская (Bo) [Khlystov *et al*., 2018, 2021]. **G.** Бухта Большие Коты, песчаные отложения современной дельты. **H**. каньон реки Большие Коты. **I**. Улитки *Liobaicalia stiedae*, зарывшиеся в песок [фото П. Репсторфа)]. **J**. Угленосные слои Танхойской свиты. **K.** Пузырьки метана в районе типового местонахождения *L. sidelevae* **sp. nov**. Красные линии на **C, E, F** – активные тектонические разломы.

Canon EOS 60D with a Canon MP-E 65 mm f/2.8 1–5x macro lens, a Nikon SMZ 25 stereomicroscope with a mounted Nikon DS-Ri2 digital camera (Japan) and using the stereomicroscope BiOptic CS-100 (Russia) with a mounted digital camera BUC5F-830DC (China).

Most live individuals, collected in 2020–2025 were treated with boiling water according to the Niku-Nuki method (Fukuda et al., 2008) and then fixed in 80% alcohol. The snails collected in earlier years were fixed in 80% alcohol or 4% formaldehyde without being treated with boiling water and partly dried.

Then the foot was cut off and used for DNA sequence analysis, and the other parts of the soft body were anatomically investigated using Nikon SMZ 25 and BiOptic CS-100 stereomicroscopes. Some organs of the female reproductive system have been stained with an alcohol solution of the orcein, and then they have been transparentized with clove oil. The protoconchs and radulae of the snails have been examined using a scanning electron microscope, Quanta 200 (USA). Prior to the investigation, the radulae and protoconchs were rinsed in chlorine bleach, washed with distilled water and alcohol, dried, and gold-plated. To describe the radular teeth and protoconch morphology, and anatomy, we followed the terminology of Radoman [1983], and Hershler and Ponder [1998].

Shells of *Liobaicalia* were measured using ImagePro-Plus v. IPWIN60. We measured five shell characters: shell height—SH, shell width—SW, aperture height—AH, aperture width—AW, and whorl number—WN.

DNA extraction, amplification, and sequencing

Total DNA was extracted using the CTAB method [Doyle, Doyle, 1987] from part of the foot. We used universal primers for amplification and sequencing fragments of the mitochondrial cytochrome c oxidase subunit I gene (*COI*), the nuclear intron of ATP synthase α-subunit gene (*ATPsα*), and the internal transcribed spacer (*ITS1*) [Folmer *et al*., 1994; Jarman *et al*., 2002; White *et al*., 1990, respectively].

Thermocycling conditions were as follows: 94°C – 2 min, 35 cycles: 94°C – 20 s, 50°C – 1 min, 72°C – 1-2 min (with a final elongation step of 3 min) for all markers. PCR products were separated on 1% agarose gel and purified using the freeze-squeeze method [Tautz, Renz, 1983]. The amplification products were sequenced at JSC Sintol (Moscow) and CCU "Ultramicroanalysis" (LIN SB RAS, Irkutsk). All nucleotide sequences are deposited in GenBank (see Supplementary Table S1). *ITS1* sequences from four *Liobaicalia* species have been deposited in GenBank NCBI under accession numbers PP786386–PP786394 with the same sample codes. Double peaks in intron chromatograms were labelled according to IUPAC nomenclature with the Heterozygotes plugin (Geneious) using a threshold of 50% peak height. Intron alleles for heterozygous specimens were twice identified using the PHASE algorithm in DnaSP v. 5.10.01 [Librado, Rozas, 2009]. Both-end Sanger sequencing was used for heterozygotes with length polymorphism.

Phylogenetic analysis

For the phylogenetic inferences, additional sequences of four other Baicaliidae species were downloaded from GenBank (Table S1). The *COI* haplotype of *Maackia herderiana* (Lindholm, 1909) (HM543406, HM559316), was used as the outgroup, because this snail belongs to the other Baicaliidae clade than *Liobaicalia* and related psammophilic species [Zubakov *et al*., 1997; Kovalenkova *et al*., 2020a]. The *COI* and *ATPsα* sequences of *Korotnewia korotnevi* (Lindholm, 1909), *K. angygira* (Lindholm, 1909), and *Pseudobaikalia zachwatkini* (Kozhov, 1936) as closely related species [Zubakov *et al*., 1997; Kovalenkova *et al*., 2020a, b] have been included as well in the dataset.

Variations in the size of orthologous introns are well documented at the intraspecific level [Moriyama *et al*., 1998], as well as on an evolutionary timescale [Vinogradov, 1999]. Single nucleotide substitution carries sufficient information for phylogenetic inference, thus the *ATPsα* sequences were included in the analysis.

The sequences were aligned and trimmed to the shortest length for each fragment using the MAFFT E-INS-i algorithm [Katoh, Standley, 2013], yielding final alignments lengths of 618 bp (*COI*), 525 bp (*ATPsα*), and 348 bp (*ITS1*). The genetic uncorrected *p*-distances with pairwise deletion between species for direct comparison were calculated using the "ape" package in R [Paradis *et al*., 2004]. The *COI* uncorrected *p*-distances greater than 1.5% have been considered as species level, adopting the similar value reported for North American *Taylorconcha* (Amnicolidae) according to Hershler *et al.* [2006] and Sitnikova *et al*. [2023].

Species delimitation was performed automatically for *COI* alignment using the distance-based ASAP method (Assemble Species by Automatic Partitioning) with raw distances [https://itaxotools.org/download.html#hyperlinkDelimit, Puillandre *et al*., 2020].

The best-fit model of sequence evolution (HKY+I+G) for *COI* was inferred based on the Bayesian information criterion in ModelFinder [Kalyaanamoorthy *et al*., 2017]. Maximum likelihood phylogenetic analysis with ultrafast bootstrap, SH-aLRT, and aBayes [Anisimova *et al*., 2011] supports in 10000 replicates was subsequently per-

Table 1. Intra- and interspecific uncorrected *p*-distances (%) based on the *COI*/*ATPsα*/*ITS1* for *Liobaicalia* spp. and their close-related species:1 – *L.* ***sidelevae*** sp. nov., 2 – *L.* ***karabanovi*** sp. nov, 3 – *L.* ***riedeli*** sp. nov. 4 – *L. stiedae*, 5 –*K. angigyra*, 6 – *K. korotnevi*, 7 – *P. zachwatkini*.

Таблица 1. Внутри- и межвидовые некорректированные попарные дистанции (в %) для *Liobaicalia* spp. и ближайших к ним родственников, рассчитанные по генам *COI*/*ATPsα*/*ITS1*.

Species	1	2	3	4	5	6	7
1	0.81/0.19/0						
2	4.09/0.27/1.43	0.65/0.38/0					
3	3.48/-/2.02	1.98/-/2.88	0/-/0				
4	3.95/0.24/0.29	2.94/0.19/1.15	2.57/-/1.73	0.16/0.38/0			
5	3.96/1.03/-	1.82/1.15/-	1.46/-/-	2.45/1.12/-	-/0/-		
6	3.64/1.11/-	0.65/1.23/-	1.78/-/-	2.73/1.2/-	1.62/0.08/-	-/0.19/-	
7	3.96/0.41/-	4.09/0.43/-	3.72/-/-	5/0.41/-	3.56/1.29/-	3.88/1.37/-	-/0.19/-

formed with IQ-tree 2.3.2 [Minh *et al*., 2020] without specific starting tree.

The phylogenetic tree was inferred based on all haplotypes of the *COI* gene using BEAST v. 1.8.4 [Drummond, Rambaunt, 2007] with HKY+I+G model. The molecular clock test was performed using the coefficient of variation criterion with log-normal distribution in the relaxed clock model. The 95% highest posterior density (HPD) interval for the coefficient of variation of branch rates includes zero, supporting the plausibility of a strict-clock model. Marginal likelihoods were estimated using path sampling and stepping-stone sampling to compare the strict-clock models with either a birth-death process or a Yule process.

To estimate divergence times of *L. stiedae* haplotypes and related baicaliids, we used the earlier suggested normal distributed divergence rate for HKY+I+G model of the "Folmer region" *COI* with 1.57 % ± 0.45% Myr^{-1} of Protostomia consistent with the hydrobioid gastropod rates [Wilke *et al*., 2009]. Two Markov chain Monte Carlo (MCMC) chains were run for 10^7 generations with strict-clock birth-death model, sampling every 1000 steps. The resulting posterior trees were combined using LogCombiner v1.10.4 [Rambaut *et al*., 2018]. The parameters after convergence (ESS > 200) were compared in TRACER v.1.7.2 [Rambaut *et al*., 2018], first 10% of trees were discarded as burn-in. TreeAnnotator was used to summarize posterior trees as maximum clade credibility (MCC) tree. The midpoint-rooted consensus tree was visualized using FigTree v1.4.1 [http://tree.bio.ed.ac.uk/software/figtree/].

Median-joining networks of *ATPsα* and *ITS1* alleles were inferred using the "Pegas v. 1.2" package in R [Paradis, 2010]. Intron alleles of heterozygous specimens were shown independently.

Since some species are highly similar in teleoconch morphology and may be considered as cryptic, species-specific nucleotide substitutions (molecular diagnostic characters) were identified by comparison with others using the DeSignate web application [Hütter *et al*., 2020]. The diagnostic molecular characters (signature characters) for all species were defined as the position of a nucleotide in an alignment, which is monomorphic within each species and differ between species.

Results

Molecular-phylogenetic traits and divergence

The optimal threshold distance of *Liobaicalia* and closely related species sequences of *COI* for the ASAP delimitation method was identified as 0.73% ($p = 0.04$). This threshold successfully discriminated four clades within corkscrew-shaped molluscs. One of them consisted of sequences of the snails from Utulik and Murinskaya Bank, located in Kultuk Bay, near the type locality of *Liobaicalia stiedae*. The second clade included the sequences of the snails collected in the water area of Babushkin city (Mysovaya railway station), and they were named *L.* ***sidelevae*** sp. nov. The sequences of the third clade belonged to habitats of the underwater upland Posolskaya Bank, and they were named ***L. riedeli*** sp. nov. The sequences of the individuals collected in Bolshie Koty Bay with a corkscrew-shaped shells perfectly fit into a joined clade with *Korotnewia korotnevi* having the normal, regularly coiled shell having been the exception. The snails *K. korotnevi* were sampled in the Maloe More Strait, which is far distant from Bolshie Koty (Fig. 1A), where it has never been found.

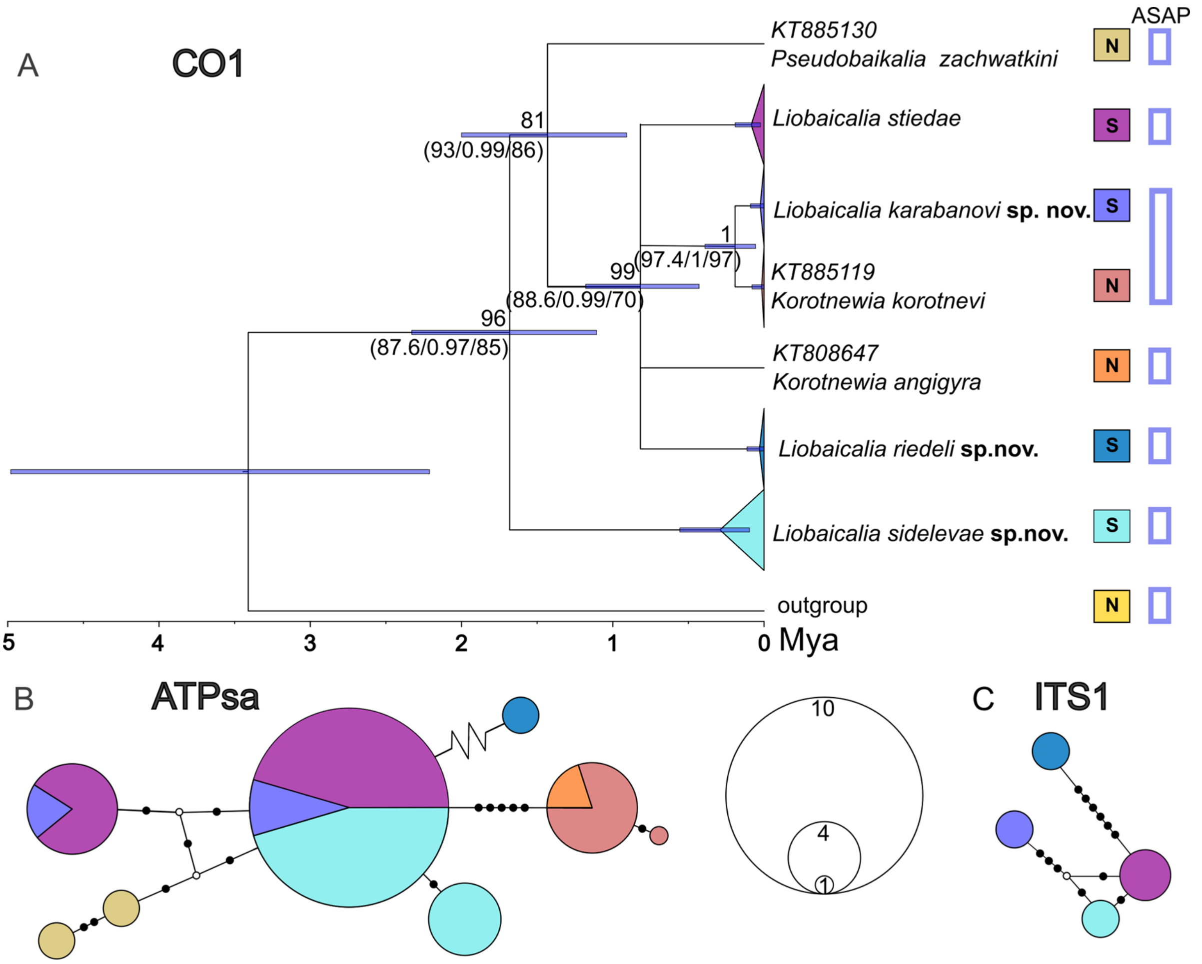

FIG. 2. Visualization of the results of the molecular-phylogenetic analyses. **A.** Time-calibrated Bayesian phylogeny for the *COI* gene fragment. Bayesian posterior probabilities (BPP) are shown at nodes without brackets, while SH-aLRT support, aBayes support, and ultrafast bootstrap values are given in brackets. Poorly supported nodes (BPP < 75) are collapsed to polytomy. Bars around nodes represent the 95% HPD interval; **B.** Median-joining network of *ATPsα* variants of *Liobaicalia* spp. and close (sister) species; **C.** *ITS1* alleles of *Liobaicalia* spp. The colors indicate every species of *Liobaicalia* spp. (S) and sister species (N); the dots indicate mutation steps. Empty dots represent median vectors. The zigzag indicates a large intron insertion in *L.* ***riedeli*** sp. nov.

РИС. 2. Визуализация результатов молекулярно-филогенетического анализа. **A.** Байесовское датированное дерево на основании гена *COI*. Байесовские апостериорные вероятности (BPP) показаны над узлами без скобок, тогда как поддержки SH-aLRT, aBayes и значения ультрабыстрого бутстрепа приведены в скобках соответственно. Слабо поддерживаемые узлы (BPP<75) свернуты в политомию. Полосы в узлах представляют 95% интервалы апостериорной вероятности датировок (HPD); **B.** Медианная сеть аллелей гена *ATPsα*; **C.** Медианная сеть аллелей *ITS1* видов *Liobaicalia* spp. и сестринских видов. Цвета обозначают каждый вид *Liobaicalia* spp. (S) и сестринские виды с нормальной раковиной (N); точки обозначают количество мутационных шагов. Пустые точки представляют медианные векторы. Зигзаг обозначает вставку (инсерцию) в интроне *L.* ***riedeli*** sp. nov.

Meanwhile, a pairwise comparison of the *COI* sequences of corkscrew-shell snails revealed the significant uncorrected *p*-distances between snails from Bolshie Koty and other localities (from 1.98 to 4.09%) (Table 1). Thus, these snails were named *L.* ***karabanovi*** sp. nov. (Fig. 2A).

Despite the *COI* similarities of *L.* ***karabanovi*** sp. nov. and *L.* ***riedeli*** sp. nov. the distance between their *ITS1* alleles is the largest (2.9% uncorrected *p*-distance) within *Liobaicalia* (Fig. 2C).

More distant in *COI* sequences, *L.* ***sidelevae*** sp. nov. and *L. stiedae* differ in one substitution only of the *ITS1* spacer. Each of the *Liobaicalia* species possesses, along with the unique ones, a single shared allele of *ITS1*. The number of binary and asymmetric molecular unique characters based on *COI* and *ITS1* sequences to distinguish *Liobaicalia* species, are presented in Supplementary Table S4.

Another genetic relationship was obtained for *Liobaicalia* spp. in *ATPsα* intron sequences (Fig. 2B). A shared allele of *ATPsα* intron was found in all *Liobaicalia* spp. except *L.* ***riedeli*** sp. nov. Agarose gel electrophoresis revealed a large insertion (~5 kb) of unknown origin within the *ATPsα* intron of *L.*

riedeli sp. nov. that obstructed its full-length sequencing. However, the 5′ (1–85 bp) and 3′ (255–523 bp, corresponding to positions 1–265 bp downstream of the insertion) regions were identical to the shared *Liobaicalia* spp. allele. Another allele was shared exclusively by *L. stiedae* and *L.* ***karabanovi*** sp. nov., while ***L. sidelevae*** sp. nov. possessed a unique allele detected only in heterozygous specimens alongside the shared *Liobaicalia* allele. The difference between *L.* ***karabanovi*** sp. nov. and *K. korotnevi* is larger in *ATPsα* intron (1.23% *p*-distance or 6 substitutions) than in *COI p*-distance (0.65%), and within *Liobaicalia* spp.

Bayesian and maximum likelihood (ML) phylogenetic trees based on *COI* sequences exhibited highly similar topologies showing the polytomy node group of *Liobaicalia* and *Korotnewia*; the genus *Liobaicalia* not recovered as monophyletic (Fig. 2A). We did not combine here the genera *Liobaicalia* Martens, 1876, *Korotnewia* Kozhov, 1936, and *Pseudobaikalia* Lindholm, 1909, into a single genus for the lack of sequences of nuclear genes, especially for species inhabiting sympatrically with *Liobaicalia* species. To achieve this, we require significantly longer and more variable sequences. Thus, we consider here four corkscrew-shaped species only in the frame of the *Liobaicalia* genus.

Our analysis indicates that the *COI* haplotypes of *L.* ***sidelevae*** sp. nov. diverged from the common ancestor of *Liobaicalia* spp. and *P. zachwatkini* approximately 1.68 Mya (95% HPD: 1.1–2.3 Mya) (Fig. 2A). The other *Liobaicalia* species, along with two *Korotnewia* species (*K. angigyra* and *K. korotnevi*), form a polytomy dating to ~0.8 Mya (95% HPD: 0.5–1.12 Mya). Notably, the haplotypes of *L.* ***karabanovi*** sp. nov. and *K. korotnevi* diverged even later than those of *L.* ***sidelevae*** sp. nov., around 200 ka (95% HPD: 80–400 ka).

Taxonomy

Class GASTROPODA Cuvier, 1795
Subclass CAENOGASTROPODA
Superfamily TRUNCATELLOIDEA Gray, 1840
Family BAICALIIDAE P. Fisher, 1885

(=Subfamily Liobaicaliinae B. Dybowski, Grochmalicki, 1913)

Genus *Liobaicalia* Martens, 1876
(Fig. 3)

(=*Leucosia* W. Dybowski, 1875)

Type species *Liobaicalia stiedae* (W. Dybowski, 1875), by subsequent designation Dall, 1877.

Diagnosis. Protoconch planospiral shape, significantly turned to the teleoconch axis; the teleoconch corkscrew-shaped (scalariform).

The genus includes *L. stiedae, L.* ***sidelevae*** sp. nov., *L.* ***riedeli*** sp. nov., and ***L. karabanovi*** sp. nov.

Description. Teleoconch corkscrew-shaped with coiled open (scalariform) 4.5–5.5 whorls, slightly brown or green-brown, smooth or finely net-sculptured with periostracum outgrowths (Fig. 4 Aa, b), especially visible on the last whorls; aperture oval-rounded, basal lip rounded or slightly angular, outer lip straight, inclined, columellar lip thin, rounded (Fig. 3Aa, Ba, Ca, Da, Ea). Protoconch planispiral (Fig. 5Aa, Ba, Ca, Da), about 1.5 rounded whorls with variously expressed spiral microsculpture (Fig. 7); protoconch axis turned to the teleoconch axis 40° or more. Operculum a little smaller than the aperture size, very thin, transparent, oval, paucispiral with about 20 axial growth lines and submarginal nucleus (Fig. 6A). Radula taenioglossate, the central (rachidian) tooth trapezoidal of various widths (from narrow to wide) in a ribbon, basal cusps of the central tooth are absent, the central cusp does not stand out strictly from other (up to 24) cusps on the cutting edge, and the cusps are small and sharp. The shape of the lateral tooth varies within the same radula (Fig. 6B, C). The working parts of the cutting edge of lateral teeth with short and mainly destroyed cusps of varied length and width, the central cusp is visible in some teeth, and there are about 16 cusps on each side of it. The wide outer wing of the lateral tooth straight, and a little longer or equal in length to the squarish face. The marginal teeth with thin and short cusps, numbering about 16–20. Mantle edge and snout slightly grey or black pigmented. 'The pocket" for trapping food particles from mantle cavity on the right side of the snout (Fig. 5Db). Prostate lobular, like a short fan, its central part thin with a passing vas deferens (Fig. 8Cc). The penis lancet shaped its tip with short, pointed papillae (Fig. 8), a glandular cap- or ellipsoid-shaped part on the dorsal-base side of the penis. Ventral groove of the female gonoduct of different widths. The renal loop of the oviduct varies in length and width; 3–6 narrow tube-like evaginations ("clusters") playing the role of seminal receptacles (Fig. 8) dilated the terminal part of the loop. One or two seminal receptacles visible in the dorsal side of the albumen gland (Fig. 8Ad, Be, Dd).

Liobaicalia stiedae (W. Dybowski, 1875)
(Figs 3A; 5A; 6C; 7A, B; 8A)

Leucosia stiedae Dybowski W., 1875: 38, Taf. III, Fig. 20–23; Taf. VI, Fig. 1, Taf. VII, Fig. 9–10;

Baicalia (*Liobaicalia*) *stiedae* – Martens, 1876: 182; Westerlund, 1877: 96;

Liobaikalia stiedae – Crosse, Fischer, 1879: 155, Pl. 4, Fig. 5;

Baikalia (Liobaikalia) stiedae – Westerlund, 1886: 24; Lindholm, 1909: 43;

Liobaikalia stiedae – Kobelt, 1910: 40, Fig. 2361; Dybowski B., Grochmalicki, 1920: 89, Fig. 1 – 7, 9, 14–15; Thiele, 1931: 158, Fig. 133; Shadin, 1933: 160, fig. 144; Kozhov, 1936 (partm): 125, Tabl. IV, Fig. 23 – 24; Tabl. XI, Fig.

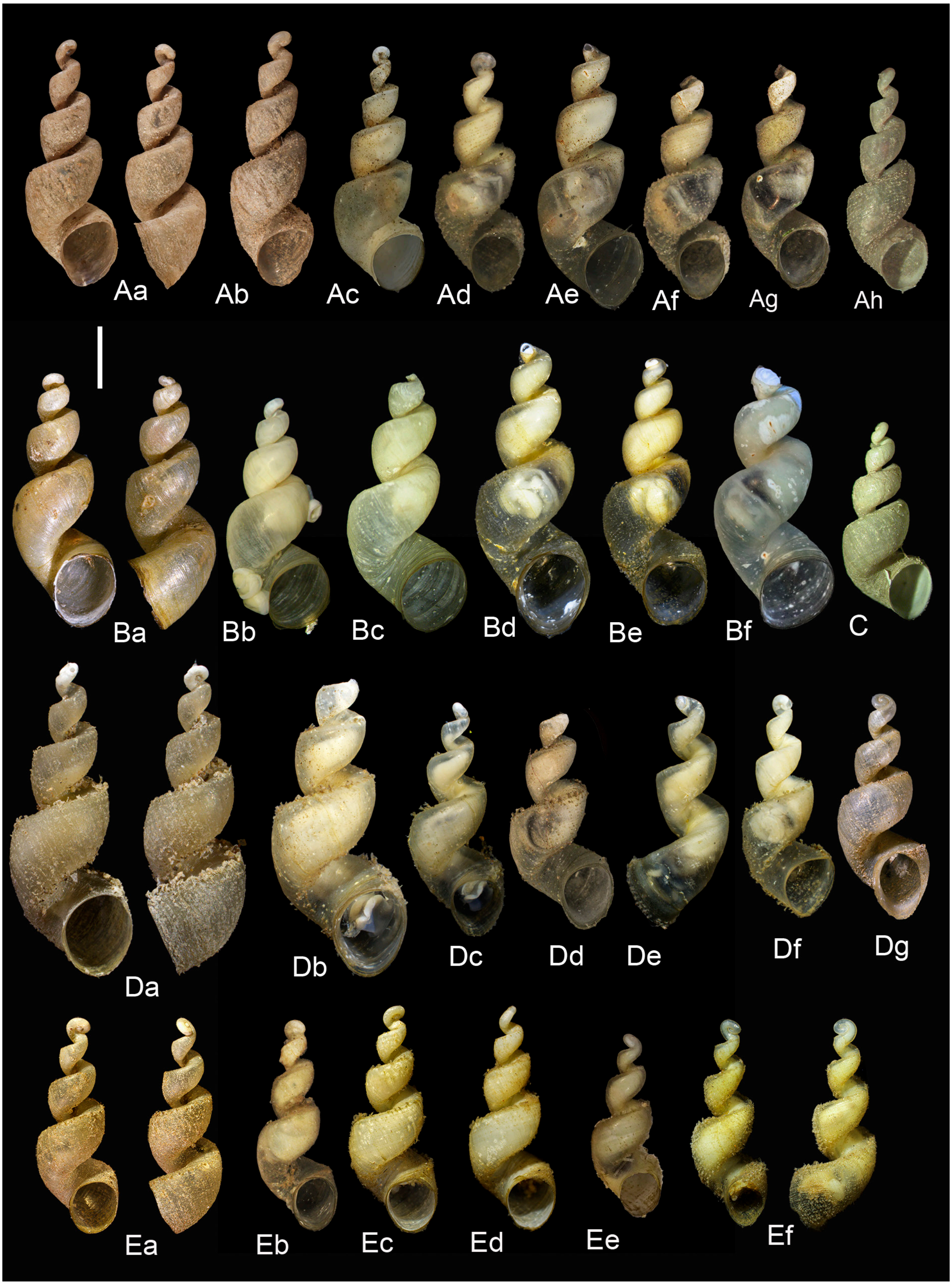

FIG. 3. Shells of the *Liobaicalia* species. **A.** *L. stiedae* (**Aa**) the lectotype, both views, (**Ab**) *L. s. hirsuta* (ZIN No. 1, det. Lindholm), (**Ac**) the topotype, leg. & det. P. Röpstorf, (**Ad, Ae**) the individuals from Utulik, (**Af, Ag**) from Murinskaya Bank, (**Ah**) from Solsan. **B.** *L.* ***sidelevae*** sp. nov., (**Ba**) the holotype., both views, (**Bb–Bf**) the paratypes. **C.** *L.* cf. ***sidelevae*** sp. nov. from Talanka Bay. **D.** *L.* ***karabanovi*** sp. nov., (**Da**) the holotype, both views, (**Db–De**) the paratypes, (**Df**) from Goloustoe, (**Dg**) from Peschanaya Bay. **E.** *L.* ***riedeli*** sp. nov., (**Ea**) the holotype, both views, (**Eb–Ef**) the paratypes. Scale bar: 2 mm.

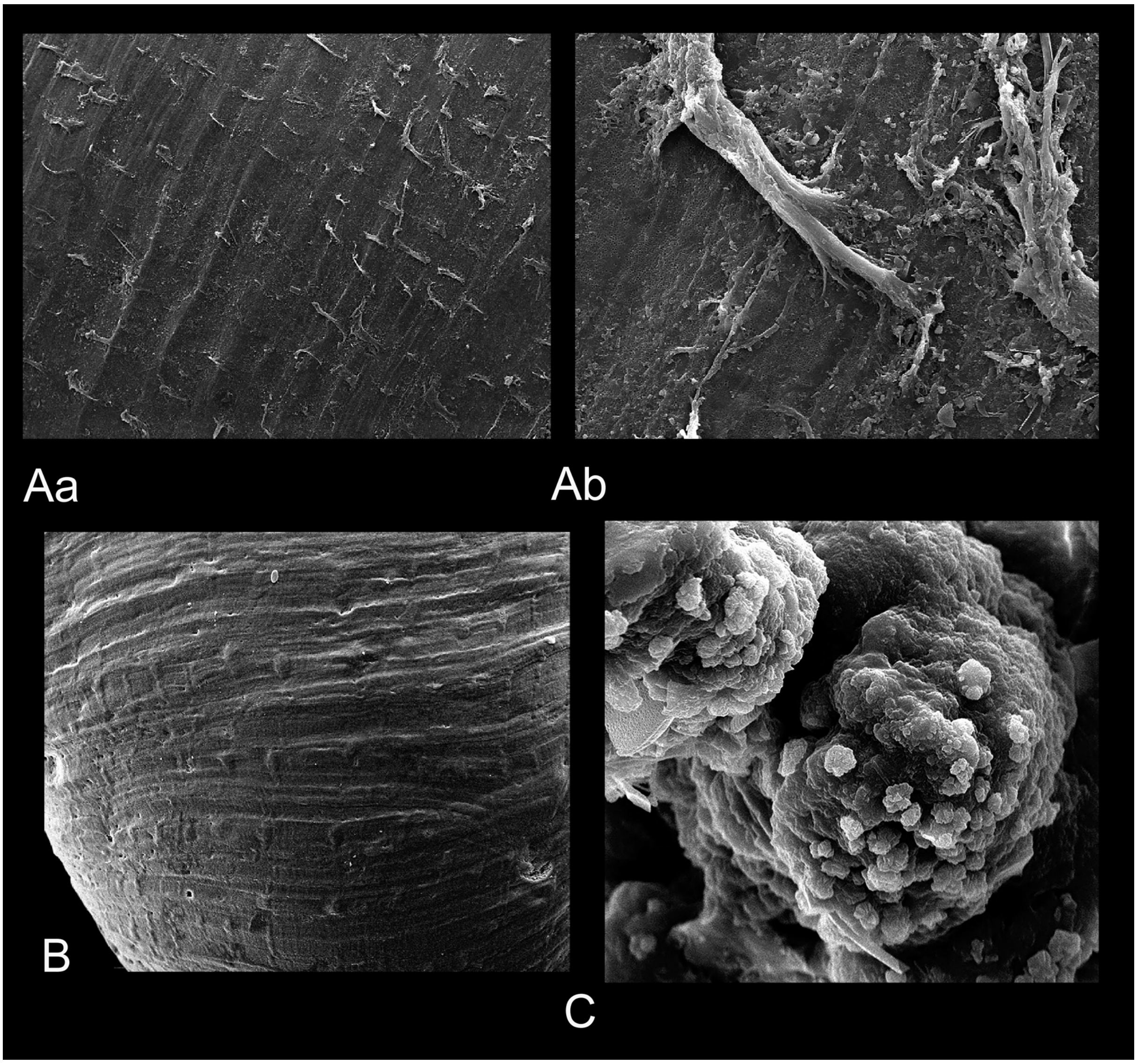

FIG. 4. SEM photographs of *Liobaicalia*. **A.** *L.* ***sidelevae*** sp. nov. teleoconch (without bleaching), (**Aa)** microsculpture with periostracal outgrowths. (**Ab)** the same, increasing part. **B.** The teleoconch microsculpture of *L.* ***riedeli*** sp. nov. (after bleaching). **C.** *L.* ***riedeli*** sp. nov., upper parts of the gill leaflets with granules, possible bacteria-ectosymbionts. Scale bars: Aa = 0.5 mm; Ab = 0.05 mm; B = 0.2 mm; C = 0.02 mm.

РИС. 4. Фотографии сканирующего электронного микроскопа *Liobaicalia*. **A.** *L.* ***sidelevae*** sp. nov., телеоконх (без чистки), **Aa.** Микроскульптура с периостракальными выростами, (**Ab)** увеличенная часть. **B.** Микроскульптура телеоконха *L.* ***riedeli*** sp. nov. (после чистки). **C.** *L.* ***riedeli*** sp. nov., верхние части жаберных лепестков с гранулами, возможными эктосимбионтами-бактериями. Масштабные линейки: Aa = 0.5 мм; Ab = 0.05 мм; B = 0.2 мм; C = 0.02 мм.

24; Shadin, 1952: 279, Fig. 242; Slugina, 1983: 144; Sitnikova, 1991: 283, Fig. 1, 1; Sitnikova *et al*., 2001: 65, 68, 77, Fig. 4B, 6A; Röpstorf *et al*., 2003: 165; Röpstorf, Sitnikova, 2006: 123; Sitnikova *et al*., 2004 (partim): 946; Kantor, Sysoev, 2005: 69; Vinarski, Kantor, 2016: 189; Kovalenkova *et al*., 2020a (partim): 724.

Type material. We designate the lectotype (with the preserved protoconch) and 11 paralectotypes from 12 syntypes of the ZIN No. 1; other 23 syntypes under ZIN No. 2 have been designated as the paralectotypes; both lots have the identical labels: “Baikal, collection of W. Dybowski, 1875.”

Material studied. See Supplementary Table S2.

Type locality. Lake Baikal**,** Kultuk Bay (southern part of Lake Baikal), between the river mouths of the Medlyanka and Slyudyanka [Dybowski B., Groch-

РИС. 3 (на предыдущей странице). Раковины видов *Liobaicalia*. **A.** *L. stiedae*, (**Aa**) лектотип, с двух сторон, (**Ab**) *L. s. hirsuta* (ZIN No. 1, опр. Lindholm), (**Ac**) топотип, сбор и определение П. Репсторф, (**Ad, Ae**) особи из Утулика, (**Af, Ag**) с Муринской банки, (**Ah**) из Солзана. **B.** *L.* ***sidelevae*** sp. nov., (**Ba**) голотип с двух сторон, (**Bb–Bf**) паратипы. **C.** *L.* cf. ***sidelevae*** sp. nov. из бухты Таланка. **D.** *L.* ***karabanovi*** sp. nov., (**Da**) голотип с двух сторон, (**Db–De**) паратипы, (**Df**) из Голоустного, (**Dg**) из бухты Песчаная. **E.** *L.* ***riedeli*** sp. nov., (**Ea**) голотип с двух сторон, (**Eb–Ef**) паратипы. Scale bar: 2 mm.

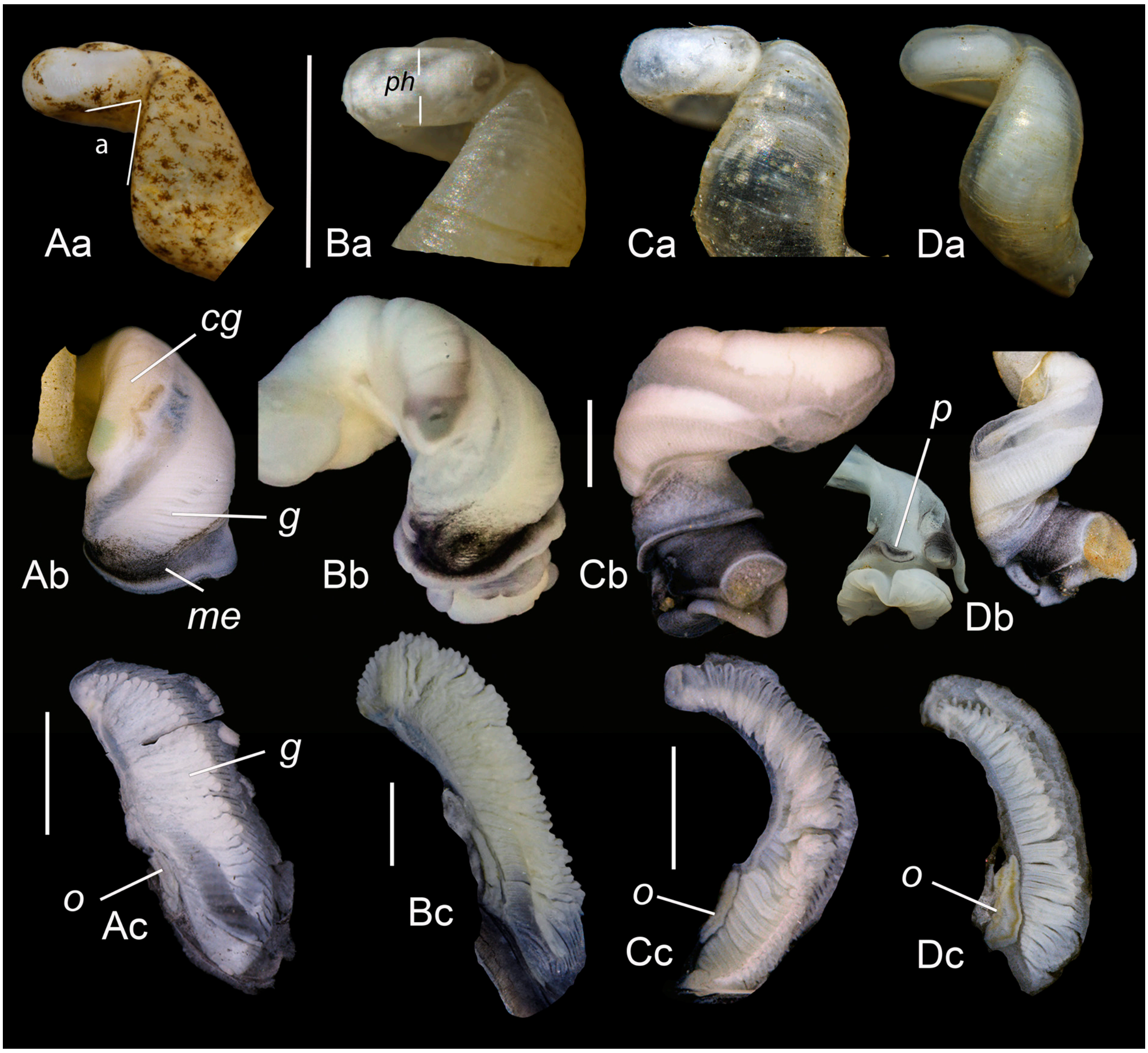

FIG. 5. The *Liobaicalia* spp. some morpho-anatomical characters. **A.** *L. stiedae*. **B.** *L.* ***sidelevae*** sp. nov. **C.** *L.* ***karabanovi*** sp. nov. **D.** *L.* ***riedeli*** sp. nov. (**Aa, Ba, Ca, Da)** the transition from protoconch to teleoconch**,** (**Ab, Bb, Cb, Db**) the last body whorl, (**Ac, Bc, Cc, Dc**) the gill and osphradium. Abbreviations: a – angle between protoconch and 1-th teleoconch whorl; cg – capsulae gland, g – gill, me –edge of the mantle, o – osphradium, p – "food pocket" on the right side, ph – height of the protoconch last whorl. Scale bars: 1 mm.

РИС. 5. Некоторые морфо-анатомические признаки *Liobaicalia* spp. **A.** *L. stiedae*. **B.** *L.* ***sidelevae*** sp. nov. **C.** *L.* ***karabanovi*** sp. nov. **D.** *L.* ***riedeli*** sp. nov. (**Aa, Ba, Ca, Da)** переход протоконха к телеокоху, (**Ab, Bb, Cb, Db**) последний оборот тела, (**Ac, Bc, Cc, Dc)** жабра и осфрадиум. Обозначения: a – угол между протоконхом и первым оборотом телеоконха; cg – капсульная железа, g – жабра, me – край мантии, o – осфрадий, p – «карман для пищи» справой стороны, ph – высота последнего оборота протоконха. Масштабные линейки: 1 mm.

malicki, 1920], so between Kultuk and Slyudyanka settlements, possible, near Shaman Cape, 51°40′N, 103°42′E (Fig. 1A, C) where the snails of this species have been found many times by different researchers (see Supplementary Table S2).

Description. The shell of medium size for the genus, shell height up to 12 mm with 5.5–6 whorls, the teleoconch whorls shouldered and strongly flattened in shape, the upper lip of aperture triangular (Fig. 3Aa–h). Protoconch diameter 0.78–0.89 mm, last whorl height 0.37–0.42 mm, and whorl number 1.75–1.85; the spiral sculpture of the 1-st whorl consists of by 4–5 spiral grooves with pits of various sizes, and the spiral threads of the last whorl continue on the teleoconch, where they form about 11–15 spiral rows of hair-like outgrowths. Osphradium thin, gill leaflets wide-triangular, in number of 72–74 (Fig. 5Ac). Penis unpigmented or slightly grey-pigmented with cap-shaped glandular part (Fig. 8Aa, Ab). The length of the capsular gland shorter than the albumen gland on the dorsal side (Fig. 8Ad), the ventral part of the capsule gland subdivided into diverticula (Fig. 8Ac); the top of the renal loop (Fig. 8Ad) visible on the dorsal part of the albumen gland; and the

Table 2. Shell dimension of *Liobaicalia stiedae*, including the published data; average ± standard deviation (minimal–maximal).

Таблица 2. Размеры раковины *Liobaicalia stiedae*, включая литературные данные; среднее значение ± стандартное отклонение (минимум–максимум).

Locality/ shell characters	SH (mm)	SW (mm)	AH (mm)	AW (mm)	WN
The lectotype	7.8	2.9	2.1	1.8	5.5
Syntypes [Dybowski, Grochmalicki, 1920] (n = 6)	7.9 ±0.5 (7.25–10.5)	2.92±0.30 (2.5–3.4)	2.23±0.29 (1.87–2.62)	1.75±0.13 (1.5–1.87)	4.3±0.4 (4.0 –5.0)
Slyudyanka [Kozhov, 1936] (n=3)	10.0–11.0	4.5–5.0	2.75–3.0	2.0	5+
Sluydyanka, Shaman Cape (n = 17) leg. P. Röpstorf	8.1±0.89 (8.7–11.7)	3.62 ±0.29 (3.05–3.9)	2.32±0.20 (2.05–2.6)	2.1±0.16 (1.86–2.3)	4.25–6.0
Solzan (LIN No. 528) (n = 7)	7.7 ±0.6 (6.8–8.7)	2.9±0.2 (2.5–3.2)	1.9±0.1 (1.8–2.0)	1.68±0.14 (1.4–1.8)	4.5±5.0 (4.5–4.0)
Murino [Kozhov, 1936] (n=2)	8.75–10.75	3.0–4.75	2.6–3.0	2.0–2.5	5+
Murinskaya Bank (n = 3) leg. M. Kovalenkova	7.4–7.89	2.67–2.85	1.94–3.0	1.61–1.78	>3.25–3.5
Utulik (n = 7) leg. M. Kovalenkova	8.1±0.8 (7.1–9.2)	2.9±0.3 (2.7–3.4)	2.3±0.3 (1.7–2.7)	1.7±0.1 (1.5–2.0)	4.25–5.5

left part of an oviduct thin and coiled. The seminal receptacles thin, numbering 4–6 (Fig. 8Af, Ag). The ventral groove width about ½ of the capsulae gland width (Fig. 8Ae).

The shell dimensions see in Table 2. Intraspecific variation of the teleoconch includes mainly the variability of the basal lip shape, which is triangular-rounded in some shells.

Molecular diagnostic characters. *COI*: 159, 288, 300 – A; 267 – T; 294 – G; 93, 186 – C.

Distribution. The shells identified as *L. stiedae* were found in some localities along the western and eastern shores of the Kultuk Bay (Maritui – Kultuk – Slyudyanka – Sukhoi Stream), Solsan and in the Vydrino water area along the eastern shore of the south Baikal basin (Fig. 1A; C, D) at the depth zone of 9–100 m in sand sediments with detritus; in Murinskaya Bank the sandy sediments included iron-magnesium nodules, which are evidence of past hydrothermal venting, usually accompanied by the release of the gas-methane [Zemskaya *et al*., 2012].

Liobaicalia ***sidelevae*** Sitnikova et Kovalenkova sp. nov.

(Figs 3B, C; 4A; 5B; 6A, B; 7C; 8B)

Zoobank registration: urn:lsid:zoobank.org:act:EA9C945E-387C-4BA7-92EA-2EEC1EEDAB19

L. stiedae –Dybowski B., Grochmalicki, 1920 (partim): 106, Fig. 8, 10–13; Kozhov, 1936 (partim): 125, T. IV, Fig. 22.

Type material. Holotype (dry shell): ZIN No. 1/509-2022 and 18 paratypes (dry shells, ZIN No. 2/509-2022), Lake Baikal, near Babushkin city, 51°44′05″N 105°49′05″E, 18 m, yellow sand, leg. Sitnikova T., dredge, 07. 10.1993. Paratypes: ZIN No. 2/509-2022 (18 dry, 6 dissected), ZIN No. 3/509-2022 (17 in alcohol), LIN No. B1234 (39 in alcohol), near Babushkin city, 51°44′N 105°49′E , 18–20 m, yellow sand, 06.06 2020, leg. Zhuikova N., dredge; LIN No. B1233 (6 in alcohol and 3 dissected) near Babushkin city, 51°45′3.9″N 105°50′16″E, 33–45 m, coarse sand, pebbles, 18.07.2018, dredge, leg. Sitnikova T.

Additional studied material. See Supplementary Table S3.

Description. The shell height up to 14 mm with 5.5–6 whorls. The teleoconch whorls slightly convex and round-shouldered (Fig. 3B, C); the protoconch diameter 1.0–1.2 mm, the height of its last whorl 0.4–0.6 mm, in total 1.5–1.85 whorls, the protoconch spiral threads of varying prominence without pits and pigtails or braids, and with axial intersecting lines (Fig. 7C). Osphradium thin, gill leaflets wide-triangular, 70–76 in number (Fig. 5Bc), without round granules. Penis slightly grey-pigmented with cap-shaped glandular part (Fig. 8Ba, Bb). The length of the capsular gland shorter than the albumen gland on the dorsal side (Fig. 8Be); the ventral part of the capsule gland subdivided into diverticula (Fig. 8Bd); the top of the renal loop visible on the dorsal part of the albumen gland; and the left branch of the oval renal loop straight, with 4–6 elongated seminal receptacles that significantly vary in width (Fig. 8Bf, Bg, Bi). The width of ventral groove about ½ of the capsule gland in transverse section (Fig. 8Bh).

The shell dimensions see in Table 3. The intraspecific variability of the shell is expressed in the degree of opening of the whorls from weak (Fig. 3C) to stronger (Fig. 3Bf), and in the aperture shape – from rounded (Fig. 3Be) to oval (Fig. Bb).

Remarks. It differs from other species of *Liobaicalia* in the unevenly increasing whorls of the protoconch; its last whorl is more heightened, and in the weak manifestation of the microsculpture. The teleoconch of *L.* ***sidelevae*** sp. nov. strongly differs in the rounded whorls, sometimes weakly opening

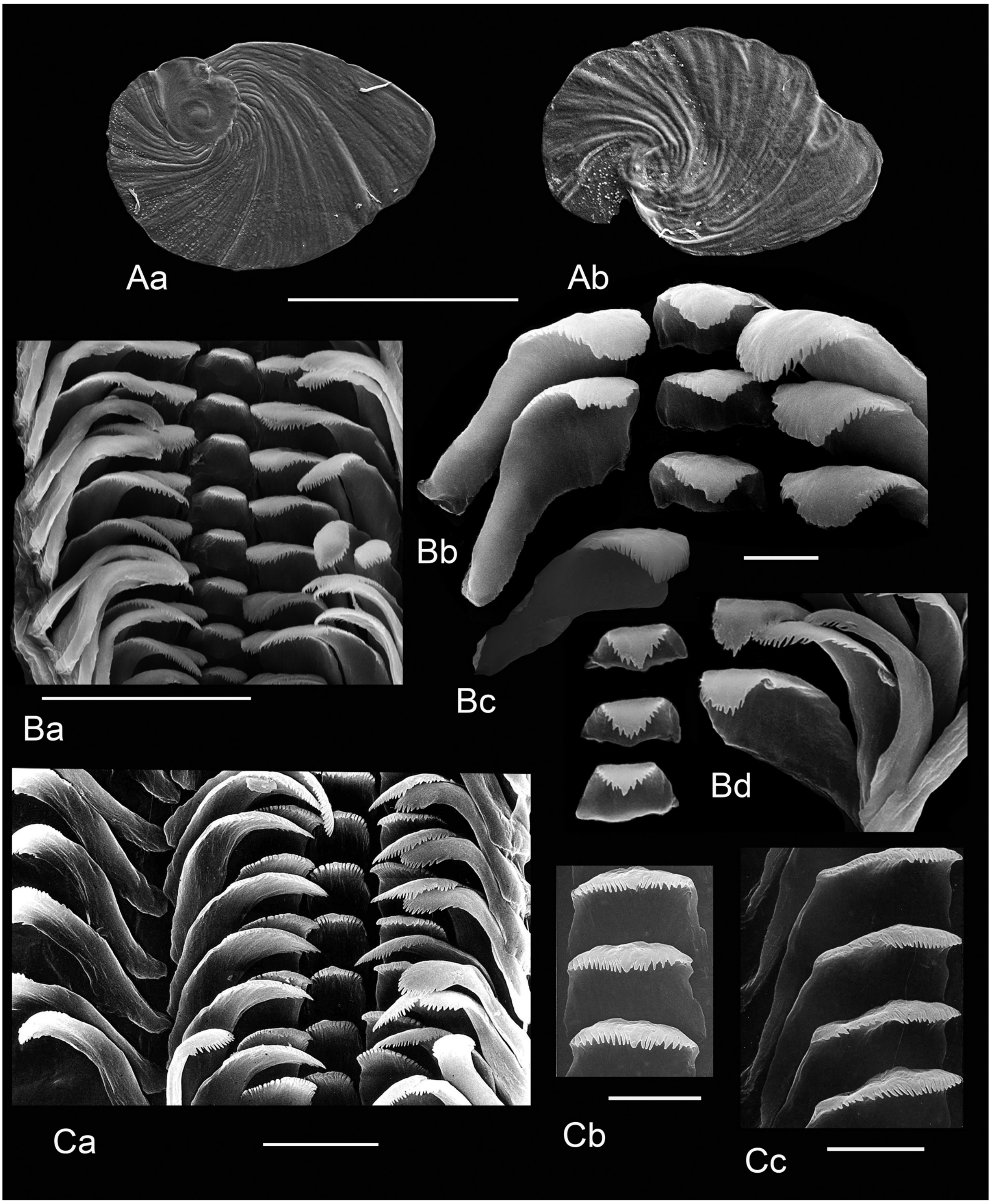

FIG. 6. SEM photographs of the operculum and radular teeth of *Liobaicalia* spp. **A, B.** *L.* ***sidelevae*** sp. nov. **C.** *L. stiedae*. (**Aa)** the outer side of the operculum, (**Ab)** the inner side of the operculum, (**Ba, Ca)** the part of the radular ribbon, (**Bb, Bc, Bd)** the radular teeth of three individuals, (**Cb)** the central teeth, (**Cc)** the lateral teeth. Scale bars: A = 1 mm; Ba = 0.05 mm; Bb, Bc, Bd, Cb, Cc = 0.01 mm; Ca = 0.02 mm. Photo P. Röpstorf (C).

РИС. 6. Фотографии крышечки и радулы *Liobaicalia* spp. **A, B.** *L.* ***sidelevae*** sp. nov. **C.** *L. stiedae*. (**Aa)** наружнаясторона крышечки, (**Ab)** внутренняя сторона крышечки, (**Ba, Ca)** часть радулы, (**Bb, Bc, Bd)** зубы радулы 3-х особей, (**Cb)** центральные зубы, (**Cc)** латеральный зуб. Масштабные линейки: A = 1 мм; Ba = 0.05 мм; Bb, Bc, Bd, Cb, Cc = 0.01 мм; Ca = 0.02 мм. Фото П. Репсторф (C).

Table 3. Shell dimension of the *L.* ***sidelevae*** sp. nov., average ± standard deviation (minimal–maximal). Abbreviations see in Table 2.

Таблица 3. Размеры раковины *L.* ***sidelevae*** sp. nov., среднее значение ± стандартное отклонение (минимум – максимум).

Locality/ shell characters	SH (mm)	SW (mm)	AH (mm)	AW (mm)	WN
The holotype	8.12	3.26	2.34	2.0	5.25
The paratypes (n=31)	9.9 ± 1.16 (11.4–6.5)	4.18 ± 0.53 (3.1–5.8)	2.58 ± 0.39 (2.05–3.1)	2.50 ± 0.32 (1.7–3.1)	4.8 ± 0.5 4.25–5.5
Talanka Bay (n=1)	6.3	2.9	1.8	1.3	4.5

Table 4. Comparison of the morpho-anatomical characters of the *Liobaicalia* spp.

Таблица 4. Сравнительная характеристика морфо-анатомических признаков *Liobaicalia* spp.

Characters/species	*L. stiedae*	*L.* ***sidelevae*** sp. nov.	*L.* ***karabanovi*** sp. nov.	*L.* ***riedeli*** sp. nov.
Teleoconch whorls shape	Strongly flattened, shouldered	Rounded	Slightly convex, shouldered	Flattened, slightly convex, shouldered
Protoconch diameter, mm	0.78–0.89 (n=3)	1.2±0.1 (1.02–1.22) (n=5)	0.9–1.0 (n=3)	0.65–0.71 (n=4)
Protoconch last whorl height, mm	0.25–0.4	0.41±0.1 (0.34–0.6)	0.28–0.4	0.2–0.28
Protoconch microsculpture	Spiral regular grooves with pits	Irregular weak spiral lines and transversal lines	Spiral irregular threads with transversal discontinuous lines in some parts	Strong spiral irregular threads, some of them like braids
Angle between the protoconch and first teleoconch whorl	56–70°	27–63°	57–70°	65–67°
Osphradium	Slender	Slender	Slender	Widened
Gill leaflets number	72–74 (n=2)	72–76 (n=2)	70–72 (n=2)	52–58 (n=2)
Capsule gland length to albumen gland	Shorter	Shorter	Equal	Equal
Capsule gland surface	With diverticula	With diverticula	Without diverticula	Without diverticula
Albumen gland surface	Strong-grained	Strong-grained	Slight-grained	Fine-grained
Renal loop shape	Oval, long, twisted left branch	Oval, long, straight left branch	Rounded, short, straight left branch	Rounded, short, straight left branch
Ventral groove	Broaden	Broaden	Thin	Thin

(Table 4). This new species is closer to *L. stiedae* in shape and size of the osphradium, in the number of gill leaflets and in structure of the female reproductive system, but its left branch of the renal oviduct is straight versus twisted in *L. stiedae.*

Molecular Diagnostic Characters. *COI* binary: 54, 210, 264, 297, 384 – A; 39, 507 – T; 150 – G; 72, 99, 126 – C; *ITS1* asymmetric: 210 – G.

Etymology. The species name '***sidelevae***' is in honor of the Russian scientist Prof. Valentina Sideleva (Zoological Institute RAS, Saint Petersburg). She lived on the shores of Lake Baikal and studied its fauna for more than 15 years, and now she still continues to be interested in the animals inhabiting gas-methane and oil seepage areas of the Lake.

Distribution. This species was many times found in some localities on flattened sandy bottoms near Babushkin city (Mysovaya railway station) near gas bubble seepages (Fig. 1A, I, K) and coal-bearing layers of the sediments (Fig. 1J). Possibly, this species also lives near Boyarskaya Bay (not far from Babushkin), where snails were recorded as *L. stiedae* by Kozhov [1936]. Shells (Fig. 3C) similar to this new species were found twice in Talanka Bay (east of the central basin) (Fig. 1A, 13) on sandy sediments at the depth of 7–10 m. The methane emission was detected in the deep zone of the Talanka Bay [Hachikubo *et al*., 2023].

Liobaicalia ***riedeli*** Sitnikova et Kovalenkova sp. nov.

(Fig. 3E; 4 B–C; 5D; 7D; 8C)

Zoobank registration: urn:lsid:zoobank.org:act:18347763-CBAA-4047-B33C-191E4819AFF3

Liobaicalia stiedae– Kozhov, 1936(partium): 125; Bazikalova, 1977: 102

Type material. Holotype: ZIN No. 1/508-2025, Posolskaya Bank, 52°03′24.8″N, 105°52′12.8″E, 35–50 m, sand, silt, iron-manganese nodules, leg. M. Kovalenkova, 16.06.2024, dredge. Paratypes: ZIN No. 2/509-2025 (4 dry); LIN B1225/a (2 in alcohol, 5 dissected), the same label; LIN

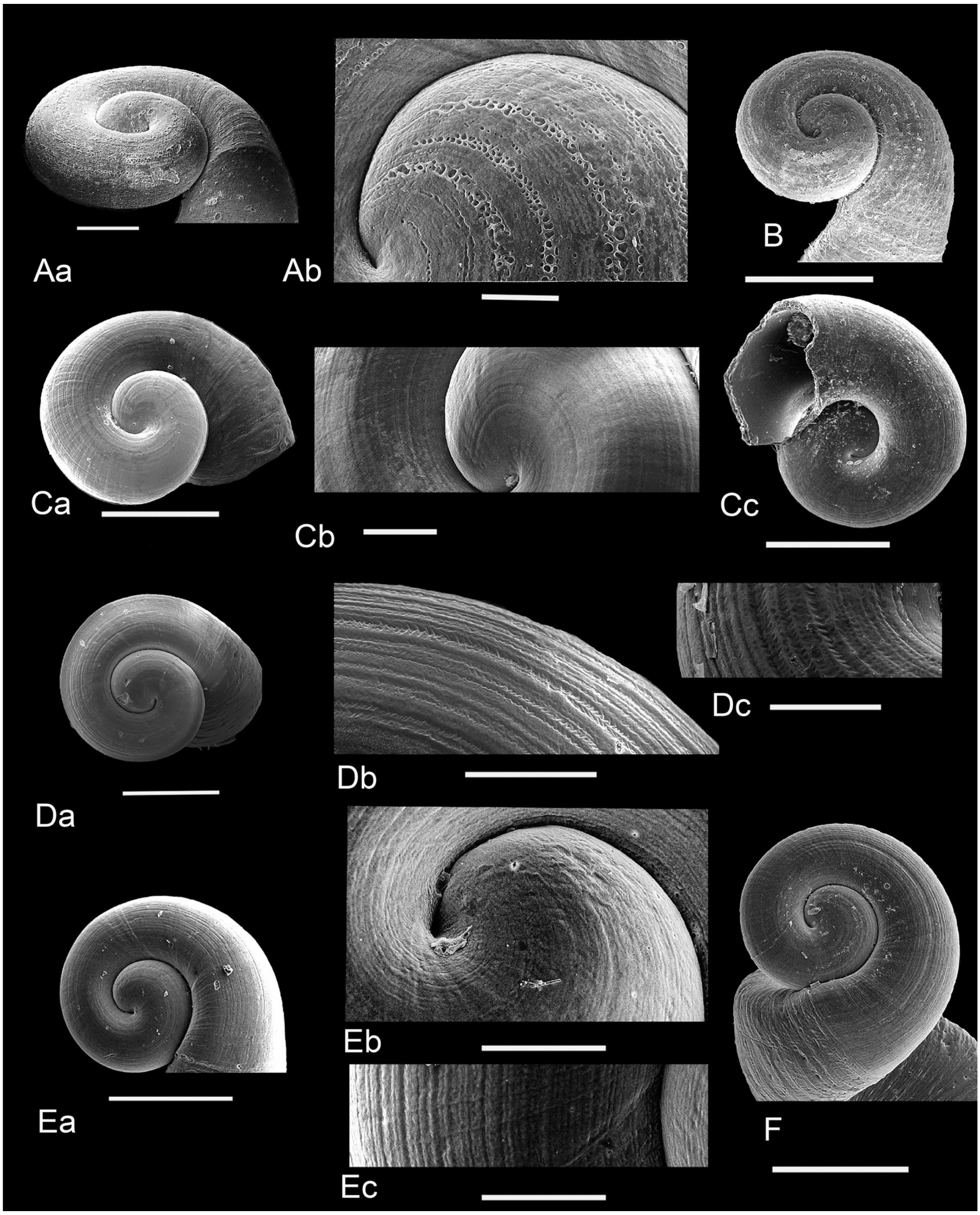

FIG. 7. SEM photographs of the protoconchs of the *Liobaicalia* spp. **A.** *L. stiedae*, the topotypes (**Aa**). the protoconch and visible boundary with teleoconch (**Ab**) the initial whorl. **B.** *L. stiedae* from Utulik. **C.** *L.* ***sidelevae*** sp. nov. the paratype. (**Ca**) the apex view, (**Cb**) the initial whorl of the apex, (**Cc**) the umbilicus side. **D.** *L.* ***riedeli*** sp. nov. paratype, (**Da**) the apex view, (**Db**) the microsculpture of the first whorl (**Dc**) the microsculpture of the umbilicus side. **E.** *L.* ***karabanovi*** sp. nov., the paratype, (**Ea**) the apex view, (**Eb**) the initial whorl, (**Ec**) the first whorl end. **F.** *L.* cf. ***karabanovi*** sp. nov. from Goloustnoe. Scale bars: Ca, Cc, B, Ea, F = 0.5 mm; Da = 0.4 mm; Aa = 0.2 mm; Cb, Db, Dc, Eb, Ec = 0.1 mm; Ab = 0.05 mm. Photo P. Röpstorf (Aa, Ab).

РИС. 7. Фотографии протоконхов *Liobaicalia* spp., полученные с помощью электронного сканирующего микроскопа. **A.** *L. stiedae*, топотип (**Aa**). Протоконх с видимой границей у телеоконха (**Ab**) начальный оборот, **B.** *L. stiedae* из Утулика. **C.** *L.* ***sidelevae*** sp. nov., паратип, (**Ca**) апикальная сторона, (**Cb**) начальный оборот с апикальной стороны, (**Cc**) со стороны пупка. **D.** *L.* ***riedeli*** sp. nov., паратип, (**Da**) апикальная сторона, (**Db**) микроскульптура первого оборота с апикальной стороны, (**Dc**) со стороны пупка. **E.** *L.* ***karabanovi*** sp. nov., паратип, (**Ea**) апикальная сторона, (**Eb**) начальный оборот сверху, (**Ec**) конец первого оборота сверху. **F.** *L.* cf. ***karabanovi*** sp. nov. из Голоустного. Масштабные линейки: Ca, Cc, B, Ea, F = 0.5 мм; Da = 0.4 мм; Aa = 0.2 мм; Cb, Db, Dc, Eb, Ec = 0.1 мм; Ab = 0.05 мм. Фото П. Репрсторф (Aa, Ab).

Table 5. Shell dimension of *L.* ***riedeli*** sp. nov., average ± standard deviation (minimal – maximal).

Таблица 5. Размеры раковины *L.* ***riedeli*** sp. nov., среднее значение ± стандартное отклонение (минимум – максимум).

Locality/ shell characters	SH (mm)	SW (mm)	AH (mm)	AW (mm)	WN
The holotype	6.9	2.6	1.6	1.5	5.0
The paratypes (n=10)	6.4 ± 0.8 (6.5 – 7.2)	2.5 ± 0.3 (2.4 – 2.8)	1.5 ±0.15 (1.4 – 1.75)	1.4 ± 0.13 (1.3 – 1.6)	5.0 ±0.45 (4.0 –5.5)

B1225/b (15 juvenile in alcohol, 4 dissected), Posolskaya Bank, 52°03′10″N, 105°51′49″E, 37.3–39 m, coarse and fine sand, iron-manganese nodules, leg. M. Kovalenkova, 27.07.2018, dredge.

Additional studied material. See Supplementary Table S3.

Description. Shell (Fig. 3E) height up to 8 mm with 5.5 whorls (Table 5); teleoconch whorls strongly shouldered, flattened or slightly convex. Protoconch diameter 0.7–1.0 mm with 1.5–1.75 whorls number (n=3), height of the last whorl of the protoconch 0.2–0.28 mm, its angle with the first teleoconch whorl about 65–67° (Fig. 5Da). Protoconch with strong spiral sculpture, braids visible between some spiral striae (Fig. 7D). Foot, head and mantle edger slightly pigmented, gill leaflets 52–58, osphradium wide, with orange border (Fig. 5Dc). Gill leaflets with spherical granules, which look like bacteria (Fig. 4C). Albumen gland fine-grained, equal length to not diverticular capsule gland (Fig. 8Dc, Dd), the renal loop straight, wide, and short; includes 2–5 seminal receptacles (Fig. 8De, Df). Ventral groove narrow (Fig. 8Dc). Penis coiled to left side; its glandular part cap-shaped (Fig. 8Da, Db).

The shell dimensions provided in Table 5. The intraspecific shell variation low in the type locality is mainly expressed in the shape of the whorl shoulder, which varies from rounded to sharp-angled. The variability of the shells found in other localities was similar.

Remarks. This species differs from other *Liobaicalia* spp. in smaller shell size (up to 8 mm with 5.5 whorls), in the smaller height of the protoconch last whorl, and in the presence of the spiral braids in protoconch microsculpture. *L.* ***riedeli*** sp. nov. is closer to *L.* ***karabanovi*** sp. nov. in female reproductive organs and differs from it in wider osphradium and in the smaller number of the gill leaflets (Table 4), which are covered by spherical granules not found on the leaflets of other *Liobaicalia* spp.

Molecular Diagnostic Characters. *COI* binary: 166 – T; 435, 576 – G; 127 – C; *ITS1* binary: 123, 134, 284 – T; 20, 81, 307 – G; 274 – C.

Distribution. It was collected multiple times on the Posolskaya Bank (Fig. 1A, H) near the water area of gas methane bubbles [Kalmychkov *et al*., 2017] on sandy sediments with iron-manganese nodules at the depth zone of 35–45 m. Perhaps, this species inhabits regions of the Kukui mud volcanoes of the Selenga River delta. According to Bazikalova [1977], snails of *Liobaicalia* have been found in “open” regions of the Selenga River delta at the depth zone of 14–280 m on silt-sand and silt sediments. The shells from the Selenga area, near Enkhaluk and the Sulkhaya River (Fig. 1A, *11–12*, Table S3) have been identified as *L. stiedae* by Kozhov [1936], but they are more similar to *L.* ***riedeli*** sp. nov. than to ***L. sidelevae*** sp. nov. and *L. stiedae,* from which they differ in a small shell height (up to 5 mm) and a sharp angle of the whorl shoulders. Two dry shells were collected by a trawl at 460 m depth on a transect between Krestovy Cape and Kukui (Table S3). The gas discharge was registered in the deep water area of the Selenga River delta, including Kukui mud volcanoes, and near Enkhaluk [Hachikubo *et al*., 2023].

Etymology. The species name ‘***riedeli***’ is in honor of the German malacologist and paleontologist Prof. Frank Riedel (Free University of Berlin), who studies the fauna of the ancient lakes of the world, including Baikal. He participated in some Baikal expeditions and initiated the investigations of the Baicaliidae and *Choanomphalus* (Planorbidae), using methods of scanning electron microscopy.

Liobaicalia ***karabanovi*** Sitnikova et Kovalenkova sp. nov.
(Figs. 3D; 5C; 7E, F; 8D)

Zoobank registration: urn:lsid:zoobank.org:act:86C53BF6-8358-4DAD-9148-F2A74A9E7CCE

Liobaicalia stiedae– Kozhov, 1936 (partim): 125; Sitnikova et al., 2010: 7.

Type material. Holotype. ZIN No. 1/510-2025, Bolshie Koty Bay, 51°54′ N 105°04′ E, 20–25 m, sand, leg. I. Khanaev, scuba diver, 28.08. 2020. Paratypes: ZIN No. 2/511-2025 (10 in alcohol) the same sample; LIN B1232 (8 in alcohol, 5 dissected), the same sample.

Additional studied material. See Supplementary Table S3.

Diagnosis. Shell (Fig. 3D) height up to 11 mm with 5.5 whorls; teleoconch whorls shouldered, flattened, slightly convex in the middle or lower part. Protoconch diameter 0.9–1.04 mm with whorls number 1.5–1.75. The height of the last protoconch whorl 0.28–0.40 mm, with the angle between the first whorl of a teleoconch varying from 57 to 70° (Fig. 5Ca). Protoconch microsculpture with irregular spiral

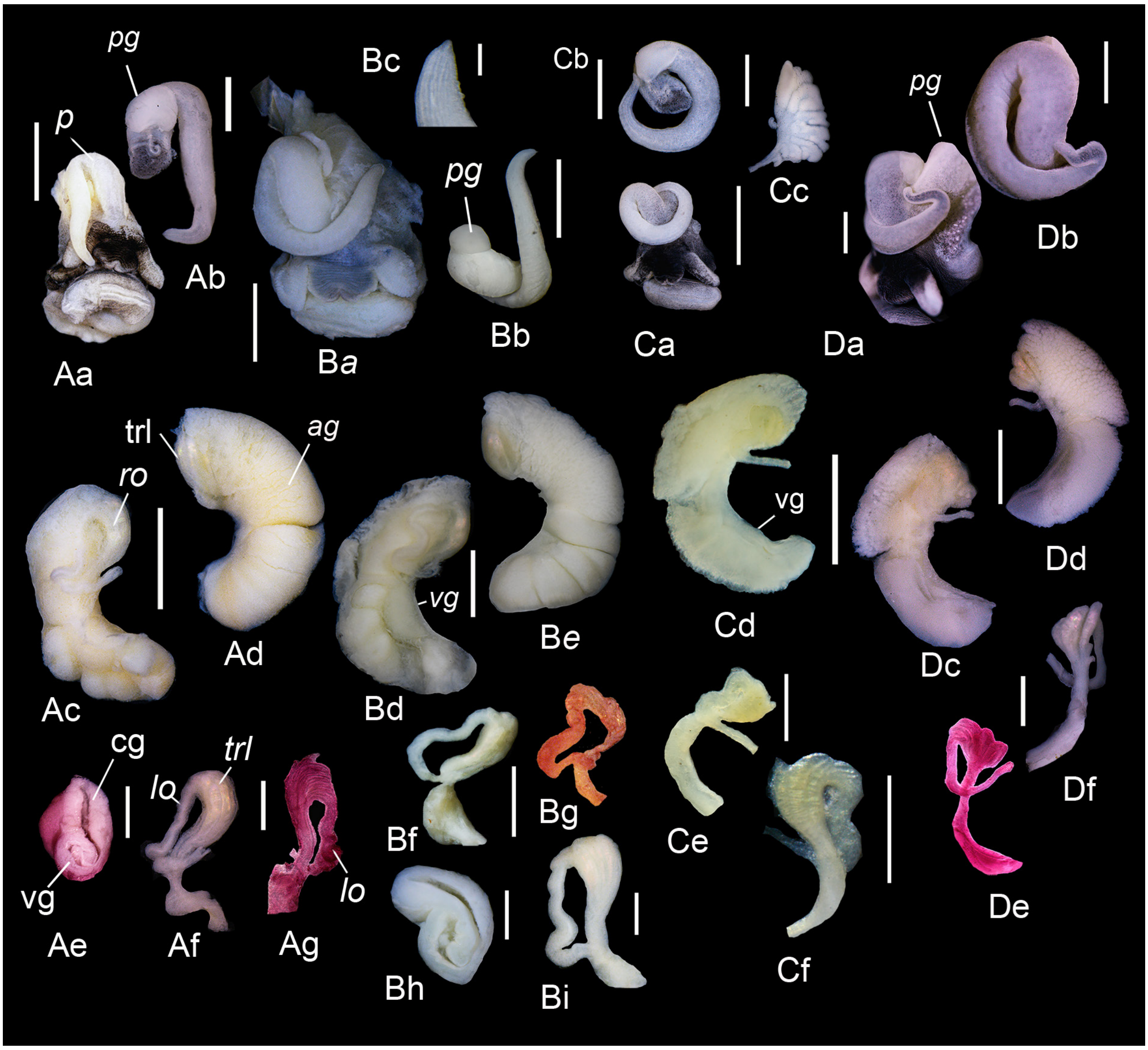

FIG. 8. The photographs of *Liobaicalia* spp. reproductive organs. **A.** *L. stiedae*. **B.** *L.* ***sidelevae*** sp. nov. **C.** *L.* ***riedeli*** sp. nov. **D.** *L.* ***karabanovi*** sp. nov. (**Aa, Ba, Ca, Da)** the front of male body with a penis, (**Ab, Bd, Cb)** the penis ventral view, (**Db)** the penis dorsal view, (**Bc)** the penis tip, (**Ad, Bc, Cc, Bc)** female organs, ventral view, (**Ae, Bd, Cd, Dd)** the dorsal view, (**Af, Bf, Bg, De)** the renal loop, ventral view, (**Ag, Cf, Df)**, the renal loop, dorsal view, (**Be, Bh)** the cross-section through the capsular gland and ventral groove, (**Cc)** the prostate. Abbreviations: ag – albumen gland, cg – capsulae gland, lo – left part of the renal loop, p – penis, ro – right part of the renal loop, pg – penial gland, trl – top of the renal loop; vg – ventral groove. Scale bars: Aa, Ab, Ad, Ae, Af, Ag, Ba, Bd, Be, Ca, Cc, Cd, Dc, Dd = 1 mm; Bb, Bf, Bg, Bh, Bi, Ce, Cf, Da, De, Df = 0.5 mm; Bc = 0.1 mm. Ae, Ae, Ag, Bg, De – stained with an alcohol solution of the orcein and transparent with clove oil; Cd, Ce, Cf – without staining in clove oil.

РИС. 8. Фотографии органов репродуктивной системы *Liobaicalia* spp. **A.** *L. stiedae*. **B.** *L.* ***sidelevae*** sp. nov. **C.** *L.* ***riedeli*** sp. nov. **D.** *L.* ***karabanovi*** sp. nov. (**Aa, Ba, Ca, Da)** передняя часть тела самца с пенисом, (**Ab, Bd, Cb)** пенис, вентральная сторона, (**Db)** пенис, дорсальная сторона, (**Bc)** конец пениса, (**Ad, Bc, Cc, Bc)** женские органы с вентральной стороны, (**Ae, Bd, Cd, Dd)** тоже с дорсальной стороны, (**Af, Bf, Bg, De)** ренальная петля с вентральной стороны (**Ag, Cf, Df)**, ренальная петля с дорсальной стороны, (**Be, Bh)** поперечный срез через капсульную железу и вентральный желобок, (**Cc)** простата. Обозначения: ag – белковая железа, cg – капсульная железа, lo – левая часть ренальной петли, p – пенис, ro – правая часть ренальной петли, pg – пениальная железа, trl – верхушка ренальной петли; vg – вентральный желобок. Масштабные линейки: Aa, Ab, Ad, Ae, Af, Ag, Ba, Bd, Be, Ca, Cc, Cd, Dc, Dd = 1 мм; Bb, Bf, Bg, Bh, Bi, Ce, Cf, Da, De, Df = 0.5 мм, Bc = 0.1 мм. Ae, Ae, Ag, Bg, De – окрашены спиртовым раствором орсеина и просветлены гвоздичным маслом, Cd, Ce, Cf – в гвоздичном масле без окрашивания.

threads of different widths, with axial discontinuous lines in some parts (Fig. 7E, F). Front of body, foot, head and mantle edge pigmented black with a violet tint, the body light grey-violet; gill leaflets 70–72, osphradium slender (Fig. 5Cc). Albumen gland, slightly grained, equal in length to not diverticular capsule gland (Fig. 8Dc, Dd), the renal loop rounded and short, with a straight left branch; the right branch with 2–5 seminal receptacles (Fig. 8De, Df). Ventral groove narrow (Fig. 8Dd). Penis coiled; its glandular part cap-shaped (Fig. 8Da, Db).

The shell dimensions provided in Table 6. The

Table 6. Shell dimension of the *L.* ***karabanovi*** sp. nov., average ± standard deviation (minimal – maximal).

Таблица 6. Размеры раковин *L.* ***karabanovi*** sp. nov., среднее ± стандартное отклонение (минимум–максимум).

Locality/ shell characters	SH	SW	AH	AW	WN
The holotype	9.9	3.8	1.3	1.1	5.0
The paratypes (n=6)	8.0±1.3 (6.8–10.0)	3.4±0.5 (2.9–4.2)	2.16±0.5 (1.9–2.8)	1.98±0.4 (1.5–2.6)	5.0±0.5 (3.0–5.25)
B. Koty (n=5) (Kozhov, 1936)	10.0±0.73 (9.0–10.5)	4.85 ±0.5 (4.0–5.5)	3.2±0.2 (3.0–3.5)	2.3±0.3 (2.0–2.75)	5.0±0.4 (4.0–5.5)
N. Khomuty (n=2) (Kozhov, 1936)	10.0–10.6	4.0–4.25	3.0	2.25–2.3	4.5–5.0+
Goloustnoe (n=1)	7.1	2.9	1.2	1.5	5.15

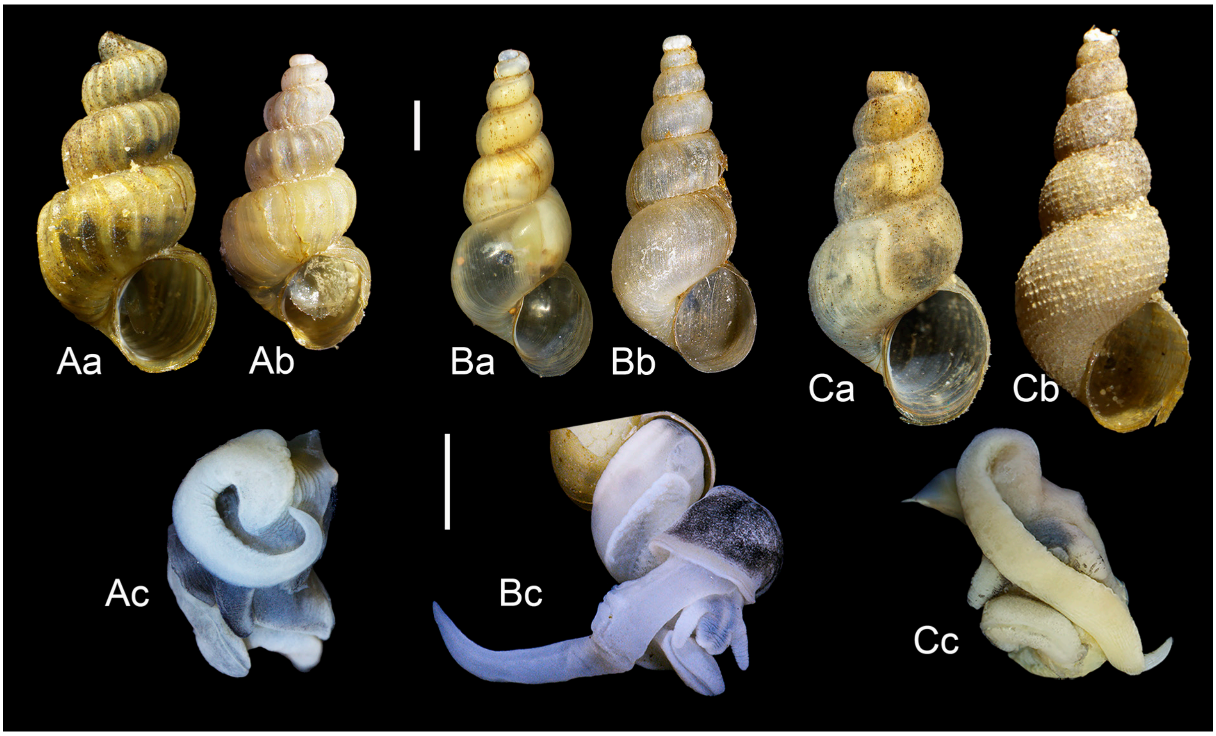

FIG. 9. Shells and penises of the close relatives of the *Liobaicalia* species. **A**. *Pseudobaikalia zachwatkini* from Maloe More. **B**. *Korotnewia angigyra* from Barguzin Bay. **C.** *K. korotnevi*, (**Ca**) from Maloe More and (**Cb**) near Posolskaya Bank. (**Ac**, **Cc**) usual penis positions, (**Bc**) penis during copulation. Scale bars: 1 mm (a short bar for shells and a long bar for penises).

РИС. 9. Раковины и пенисы близкородственных видов *Liobaicalia* **A**. *Pseudobaikalia zachwatkini* из Малого моря. **B**. *Korotnewia angigyra* из Баргузинского залива. **C.** *K. korotnevi*, (**Ca**) из Малого моря, (**Cb**) из Посольской банки. (**Ac**, **Cc**) обычная позиция пениса, (**Bc**) пенис во время копуляции. Масштабные линейки: 1 мм (короткая линейка – для раковин, длинная линейка – для пенисов).

intraspecific shell variation is high level and is expressed in the shape of the whorls and in level of opening whorls.

Molecular Diagnostic Characters. *COI* binary: 43, 309, 519 – T; 240, 387 – G; *ITSI* binary: 204, 302 – G. ITSI asymmetric: 210 – A; 215 – T; 291 – C.

Remarks. The teleoconch of this species is similar to that of *L. stiedae*, from which it differs in the structure of the female reproductive organs, which are similar to *L.* ***riedeli*** sp. nov. The other differences between species are presented in Table 4.

Etymology. The species name '*karabanovi*' is in honor of the Russian scientist of broad knowledge Prof. Evgeniy Karabanov (Limnological Institute SB RAS), who studied the geological, geomorphological, ecological, and biological aspects of Baikal Lake. He was a diver-scientist, and he was the first who studied the biological traits of the underwater Baikal landscapes.

Distribution. The species was found at the depth of 12–130 m on sandy sediments along the western shore of the south Baikal basin: Bolshie Koty Bay, near the Goloustnoe settlement, Peschanaya Bay (Fig. 1A, *15, 16, 18*), and near the Nizhnie Khomuty settlement (Fig. 1A, *17*). According to E. Karabanov [personal communication], the type locality of *L.* ***karabanovi*** sp. nov. belonged to the landscapes of the ancient delta of the river Bolshaya Kotinka (Fig. 1, E, F). The Goloustnoe is also located near the paleodelta of the Goloustnoe River (Fig. 1B) [Kononov

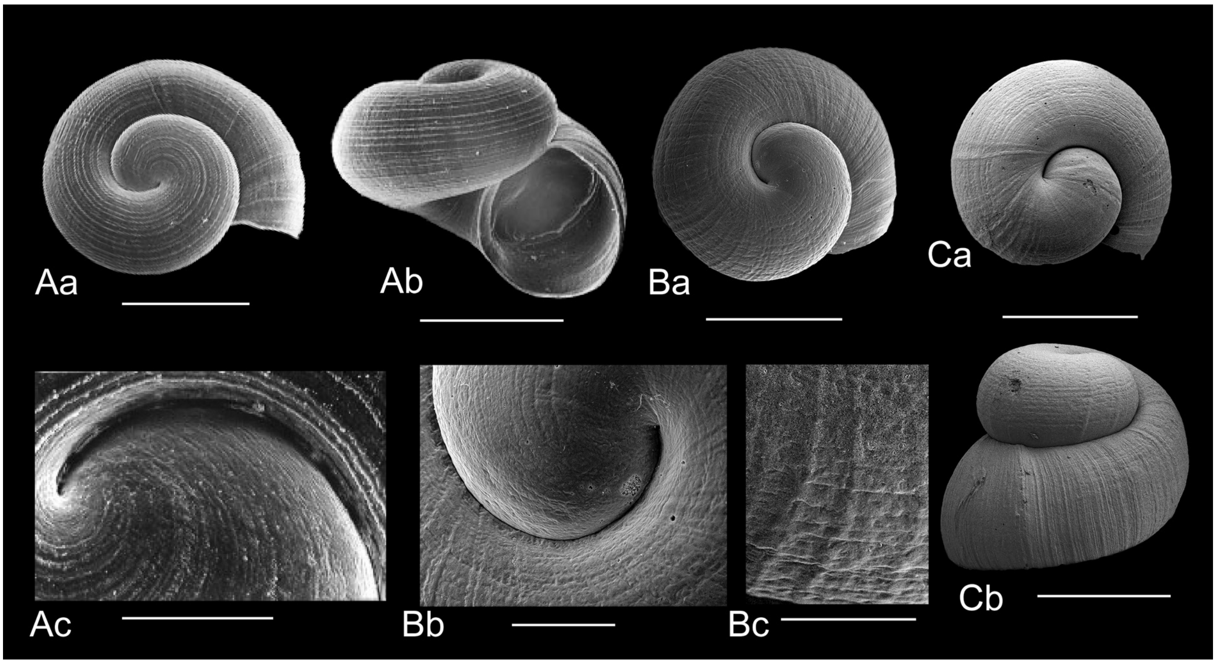

FIG. 10. Protoconchs of the close related species to *Liobaicalia* spp. **A.** *Pseudobaikalia zachwatkini*. **B.** *Korotnewia angigyra*. **C**, *Korotnewia korotnevi*. (**Aa**), apex view, (**Ab**) hatching in apertural view, (**Ba, Ca**) apex view, slightly turned, (**Ac, Bb**) the initial part, (**Bc**) increased microsculpture, (**Cb**) back view. Scale bars: Aa, Ab, Ba, Ca, Cb = 0.4 mm, Ac, Bb, Bc = 0.1 mm. **A** – from Sitnikova et al. 2001.

РИС. 10. **A**. *Pseudobaikalia zachwatkini*. **B**. *Korotnewia angigyra*. **C.** *Korotnewia korotnevi*. (**Aa**), вид сверху, (**Ab**) вид со стороны устья, (**Ba, Ca**) вид сверху, слегка повернут, (**Ac, Bb**) начальная часть, (**Bc**) увеличенная скульптура, (**Cb**) вид сзади. Масштабные линейки: Aa, Ab, Ba, Ca, Cb = 0.4 mm, Ac, Bb, Bc = 0.1 mm. **A** – from Sitnikova et al. 2001.

et al., 2019]; the sediments at the depth of 100 m of the Goloustnoe area included the filaments of sulfur bacteria *Thioploca*, and the gas emission has been observed in this region.

Discussion

Comparison of *Liobaicalia* spp. and their close related species

The snails with open coiled whorls never have been found within *P. zachwatkini* (Fig. 9A), *K. angigyra* (Fig. 9B) and *K. korotnevi* (Fig. 9C). The teleoconch of *P. zachwatkini* (Fig. 9A) has the shouldered whorls and the ribbed sculpture. Similarly, to *Liobaicalia* spp., the teleoconch of both *K. korotnevi* (Fig. 9Cb) and *K. angigyra* (Fig. 9Bb) has the periostracal outgrowths, but their shell closed whorls are rounded and increase more rapidly in width than in *Liobaicalia*.

At present, a planispiral protoconch turned is a characteristic for *Liobaicalia* only [Sitnikova *et al*., 2001]; the protoconch of *P. zachwatkini* is a discoid shape (Fig. 10Ab), and that is close to *L. **sidelevae*** sp. nov., but the spiral microsculpture of *P. zachwatkini* protoconch is stronger than the weakly visible one in *L. **sidelevae*** sp. nov.

The protoconchs of *K. korotnevi* and *K. angigyra* are rather spherical or wide-conical in shape (Fig. 10Ca, Cb). The protoconch microsculpture of both consists of numerous spiral threads and axial lines (Fig. 10 10 Ba, Ca), similar to *L. **sidelevae*** sp. nov. and *L. **karabanovi*** sp. nov., and in contrast to *L. stiedae* and *L. **riedeli*** sp. nov. has not pits and braids, The protoconch microsculpture of *K. angigyra* has reticulate patches in some parts (Fig. 10Bc).

The significant differences in penis structure between *Liobaicalia* spp. and three discussed species belonging to other genera (Fig. 9Ac, Bc, Cc) were not found. The observed variability in the penis position (curved, looped, or circular) should be studied in more detail. The differences in the characters of the female reproductive organs between *Liobaicalia* and their closely related species of other genera are more significant. The elongated oval renal loop, diverticular capsule gland, and wide ventral groove of the female reproductive system of *P. zachwatkini* (Sitnikova, 1991) make it close to *L. **sidelevae*** sp. nov. and *L. stiedae*. But the extended part of the renal loop of *P. zachwatkini* is larger than in *Liobaicalia.*

The female reproductive system of *K. korotnevi* and *K. angigyra* (Sitnikova, 1991) is similar to *L. **karabanovi*** sp. nov. and *L. **riedeli*** sp. nov.; all of them have a rounded short renal loop and a thin ventral groove, but the capsule gland of both *Korotnewia* species is subdivided into diverticula, which is not a characteristic of the two listed *Liobaicalia* species.

The combination of differences in the shape of the protoconch and its position relative to the teleoconch, as well as the differences in the female reproductive organs between *Liobaicalia* and *Korotnewia*, prevents combining these genera.

Discordance between morpo-anatomical and molecular traits

The genus *Liobaicalia* was not shown to be monophyletic based on mitochondrial *COI* data. This is not unique for the Baikal endemic gastropods. For instance, the mitochondrially defined clades are in conflict with taxonomy of rock-dwelling cichlid fishes in Lake Tanganyika [Verheyen *et al*., 1996]. The genetic and morphological discordance occurred within gastropods in other ancient lakes, for instance in Biwa [Köhler, 2016] and Titikaka [Kroll *et al*., 2012]. There are some evidences indicating that mitochondrial markers alone can lead to misleading estimates due to mito-nuclear discordance within different groups of organisms, and using additional genetic markers play down this inconsistency [Toews, Brelsford 2012; Hupało *et al*., 2023; Gusmao *et al*., 2025, etc.]. The mito-nuclear discordance was illustrated for *Baicalia* genus [Poroshina *et al*., 2020]. Unlike *Liobaicalia* and *Baicalia*, the genus *Kobeltocochlea* Lindholm, 1909 (Truncatelloidea: Benedictiidae) is paraphyletic based on nuclear *ITS1* sequences and monophyletic in *COI* dataset [Sitnikova *et al*., 2021].

Our analysis revealed that the distinction in *ATPsα* sequences between *L.* ***karabanovi*** sp. nov. and *Korotnewia* is larger than in *COI* (6 substitutions versus 3). We studied only two (*K. korotnevi* and *K. angigyra*) of three *Korotnewia* species and one of the three subspecies of *K. korotnevi*. The third species, *K. semenkewitschi* (Lindholm, 1909), includes two subspecies, one of which co-occurs with four *Liobaicalia* species. Genus *Pseudobaikalia* includes eight species; most of them are needed to study.

According to Blasco-Aróstegui *et al.* [2025], the evolutionary incongruence between the mitochondrial and nuclear genomes may obscure signals of introgression and hybridization important for understanding evolutionary trajectories and species boundaries. The mito-nuclear discordance is explained by hybridization, for instance, between river and lacustrine species of Biwa Lake *Semisulcospira* Boettger, 1886 [Morita *et al*., 2024], between African cichlid fishes differentiated in morphology, trophic and reproductive behavior, and other biological traits, and environment patterns [Verheyen *et al*., 1996; Loh *et al*., 2013; Svardal *et al*., 2020; etc.]. Biogeographical patterns and vicariance may result in the discordance between mtDNA and nDNA, which was found in some animals [Toews, Brelsford, 2012; Blasco-Aróstegui *et al*., 2025; etc.] We agree with Santos *et al*. [2023], who wrote that the evolutionary histories of rapid radiations are challenging to reconstruct due to the prevalence of incomplete lineage sorting in combination with introgression and hybridization, which are so complex that they cannot be fully described, especially in young lineages. The revealed discordance between mito- and nuclear differences within *Liobaicalia* spp. is to indicate the complicated process of these species' diversification during the Quaternary. The calculated age for the recent Baikal endemic gastropods, including Baicaliidae, is 3.5–2.5 My, which is evidence of their rapid speciation [Zubakov *et al*., 1997; Sherbakov, 1999] after mass extinction during global climate cooling on the boundary of the Pliocene–Pleistocene.

Origin of the scalariform species

Three species, *L. stiedae*, ***L. sidelevae*** **sp.** nov**.** and ***L. karabanovi*** sp. nov. characterized by the same intron allele in *ATPsα* that can be indicated their share a common ancestor. The fourth, ***L. riedeli*** sp. nov., has a similar allele but with a large insertion, which is likely the result of a single mutation. Common ancestor of corkscrew-shell baicaliids, possibly, was adapted to life inside the soft sediment (Fig. 1I). The available information on the species distribution indirectly indicates a vicariate way of subdivision of *Liobaicalia*.

Species with similar morphology of the female reproductive organs, *L. stiedae* and *L.* ***sidelevae*** sp. nov. (3.95% uncorrected *p*-distance of *COI*), live nearby along the eastern shoreline (Fig. 1), but were not found syntopically. Another pair of species with similar genital morphology, *L.* ***karabanovi*** sp. nov. and *L.* ***riedeli*** sp. nov. (1.98% uncorrected *p*-distances) are geographically isolated from each other. The first of them inhabits the western part of the lake, while the second was found on an underwater upland not far from the east shore, and in Selenga River region, wedging to the range of *L.****sidelevae*** sp. nov. The differences in morphology of the female genitals and in *COI p*-distance (3.48%) are significant between *L.* ***riedeli*** sp. nov. and *L.* ***sidelevae*** sp. nov. The distribution of *L.* ***karabanovi*** sp. nov. and *L. stiedae* (*COI* 2.94% uncorrected *p*-distance) is interrupted by the Angara outlet.

The time divergence of *L.* ***sidelevae*** sp. nov. according to our calculation, was about 1.7 Mya, which coincided, according to Karabanov *et al*. [2000] with the beginning of warming after the II cold period of 1.75–1.45 Mya in the Pleistocene. Similarly, the calculated age of *L.* ***riedeli*** sp. nov. and *L. stiedae* (about 0.8 My, MIS 19) and *L.* ***karabanovi*** sp. nov. (about 0.2 My, MIS 6) coincided with the different registered interglacial stages (Karabanov *et al*., 2001). Cold periods were accompanied by a significant reduction in photosynthetic food [Karabanov *et al*., 2000, 2001, etc.], and animals including gastropods, capable of assimilating the chemosynthetic organic matter (free-living methanotrophic microorganisms), survived in regions similar to recent of the methane discharge area in Baikal (Fig. 1E, F, K) [Zemskaya *et al*., 2012; Sideleva, Sitnikova, 2021, etc.]. So, we speculate that climate changes and geo-hydrological processes in zones of active tectonic faults (including earthquakes and gas emissions) [Khlystov *et al*., 2016a, 2018] likely triggered habitat fragmentation and population decline among low-mobility burrowing gastropods, thereby possibly hybridizing different species with similar genitalia. In this context, especially two pairs of species deserve attention: corkscrew-shaped *L.* ***karabanovi*** sp. nov. – normal-shaped *K. korotnevi* (0.65% uncorrected *p*-distance of *COI*), and corkscrew-shaped *L.* ***riedeli*** sp. nov. – normal-shaped *K. angigyra* (1.46% uncorrected *p*-distance of *COI*), which are characterized by similar (not identical) morphology of the female genitalia. These small genetic distances were revealed between individuals of the normal- and corkscrew-shaped shells that lived far from each other (Fig. 1A), and they are deprived of the possibility meeting and interbreeding. It should be noted that due to the young age of the species, *L.* ***karabanovi*** sp. nov. and *K. korotnevi*, even in the absence of gene flow, the expected genetic distances can be quite small.

The data on the radular teeth morphology of the listed above species [Dybowski, 1875; Kozhov, 1936; own data] allow us to assume the trophic differentiation between close related species of *Liobaicalia* and *Korotnewia* inhabiting sandy substrate. Divergent adaptation to different trophic resources recorded among sympatric gastropod taxa in ancient lakes, for example in Tanganyika [Michel, 2000] and Sulawesi, Indonesia [von Rintelen *et al*., 2004].

Occurrence of scalariform shells

The scalariform shells were recorded among fossil baicaliids (Fig. 11) in Low-Middle Miocene deposits and named *Liobaicalia substiedae* by Martinson [1961]. The affiliation of this fossil to the genus *Liobaicalia* is conditional, since the shell apex is not similar to recent representatives of the genus; however, this circumstance is possible evidence of the multiple and independent occurrences of the scalariform shells during Baikal history.

At present, scalariform shells sometimes appear as aberrant variants within Baikal endemics, for instance, among *Choanomphalus patulaeformis* Lindholm, 1909 (Planorbidae), *Megalovalvata baicalensis* (Gerstfeldt, 1859), and *M. demersa* (Lindholm, 1909) (Valvatidae). The scalariform shells were often found in the eastern littoral of the central Baikal basin but not in abundance. In contrast to *Liobaicalia* spp., these snails with open coiled whorls do not form the stable populations, shells of which would be characterized by equally opening whorls.

FIG. 11. Fossil holotype of *L. substiedae* Martinson, 1961, Miocene deposits of the Tankhoi formation, southeastern shore of Baikal Lake, No. 96/177 of the collection of the Karpinsky Russian Geological Institute (VSEGEI, St. Petersburg, Russia). Scale bar: 1 mm.

РИС. 11. Голотип ископамого *L. substiedae* Martinson, 1961, миоценовые отложения Танхойской свиты, юго-восточное побережье оз. Байкал. Коллекция Всероссийского научно-исследовательского геологического института им. А.П. Карпинского, № 96.177. Масштабная линейка = 1 мм.

Similarly, scalariform shells were registered among *Gyraulus* spp. (Planorbidae) in Lake Bangong, Tibetan Plateau [Clewing *et al*., 2015], and *Bulinus* sp. (Bulinidae) from Lake Malawi [Clewing *et al*., 2020] or were described like the species, for example, *Heleobia mirum* (Haas, 1957) (Hydrobiidae) from Lake Titicaca [Kroll *et al*., 2012] and stygobiotic *Caucasopsis* sp. 3 (Hydrobiidae) from Caucasus [Chertoprud *et al*., 2025]. The corkscrew morpho-ecotype of *Bulinus* sp., lives together with snails of normal, regularly shaped shells, from which it is low genetically differentiated [Clewing *et al*., 2020]. The corkscrew *Caucasopsis* sp. 3 inhabits a separate cave from a sister, normal-shaped species [Chertoprud *et al*., 2025].

Thus, the description of the three-new species raised new questions in the taxonomy of Baicaliidae and gastropod endemic diversification. Further studies of the morphology and ecology of a larger number of representatives of Baicaliidae, as well as the use of specific genetic markers and analysis of the stable carbon and nitrogen isotopes in tissues, are necessary to study the origin of closely related species. We have not yet studied all species of baicaliids living on sand, the shell of which has hair-like short outgrowths and planispiral protoconch similar to *Liobaicalia*. According to Riedel [1993], the knowledge of the protoconchs of freshwater gastropods is essential to taxonomic decisions and to trace back evolution.

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