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The Pond Snails of the Genus *Radix* (Gastropoda, Lymnaeidae) in Issyk-Kul Lake (Central Asia), with a Review of *Radix* in Ancient Tectonic Lakes of the World

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Abstract: Lake Issyk-Kul, situated in the Republic of Kyrgyzstan, is one of the largest lakes in Central Asia. Though this brackish-water basin holds only a species-poor fauna of molluscs, the number of species inhabiting Issyk-Kul and their true taxonomic position remain unsatisfactorily studied. Most nominal species of Mollusca reported from Issyk-Kul are known from empty shells only and have never been studied molecularly. This study reports the results of a revision of the genus *Radix* (Gastropoda:Hygrophila:Lymnaeidae) based on the integrated approach. We revealed that only two species of this genus inhabit Issyk-Kul Lake: *Radix auricularia* (Linnaeus, 1758) and *R. obliquata* (von Martens, 1864). The former species is widespread in the Palearctic and has an enormous range, whereas the latter is considered here to be endemic to Issyk-Kul Lake. All records of *R. obliquata* from waterbodies other than Issyk-Kul Lake are, most probably, based on misidentification. To date, no molecular evidence of the presence of *R. obliquata* outside Issyk-Kyl is available. The third species of *Radix* discussed in this paper, *R. subdisjuncta* (Nevill, 1878) sensu Kruglov and Starobogatov, 1993, is identical to *R. obliquata* and represents, most probably, an ecological morph ("race") of the latter. The paper provides a review of *Radix* species recorded in other ancient tectonic lakes of the world (Baikal, Victoria, Ohrid, etc.). Though the lymnaeid snails are generally scarce in such lakes, the genus *Radix* represents an exception, with several species being endemics of various tectonic lakes (Issyk-Kul, Lugu, Skadar, Trichonis, and Biwa).

Keywords: species diversity; haplotype diversity; lacustrine endemism; pond snails; integrative taxonomy; freshwater snails

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1. Introduction

Lake Issyk-Kul (an alternative spelling—Issyk Kool) is one of the largest lakes in Central Asia (Figure 1), and the second largest (after the Aral Sea) waterbody situated in so-called "Middle Asia" (a part of Central Asia that lay within the ex-USSR's territory). Nowadays, this lake belongs to the Republic of Kyrgyzstan. It is located at an altitude of 1606 m and forms an oval-shaped basin with a surface area of 6236 km^2 [1]. The lake depression is located between two ridges of the Tien Shan Mts—Kungay-Alo-Too and Terskey-Ala-Too. The maximum depth of Issyk-Kul is 668 m (the average depth is 278 m), which makes it one of the deepest lakes in the world [2]. This is an oligotrophic basin. The water of the lake is slightly brackish; its salinity reaches 5.8–5.9‰ [2]. The lake is now drainless and has about 80 small tributaries. Issyk-Kul is of tectonic origin; initially, an isolated intermountain depression was formed by intensive tectonic movements and then it was filled with water [1,3]. The history of Issyk-Kul can be traced back to the early Miocene period, and its absolute age is about 20 myr [1]. That history was very complicated: according to some authors [3], over time, the lake has experienced strong fluctuations in its water level as well as salinity variations. In some epochs, it became a completely freshwater basin [3].

The Issyk-Kul Lake malacofauna, according to available publications, is rather poor. The first European explorer of the lake, Russian traveller Pyotr Semyonov, visited the lake twice, in 1856 and 1857, and published a pioneering account of the physical and geographical properties and natural history of Issyk-Kul [4]. He collected some shells of molluscs deposited on the lake's shores and in other places in the Tien Shan Ridge; later, these materials were sent to Eduard von Martens, a prominent German malacologist of the 19th century. Von Martens established that there were three new species of snails, two belonging to the terrestrial genus *Helix*, and the third classified by him as a lymnaeid—*Limnaeus obliquatus* Martens, 1864 [5,6]. Another German malacologist of that epoch, S. Clessin, published two articles with descriptions of continental molluscs of Issyk-Kul Lake and its surroundings [7,8]. This author compiled the first list of the Issyk-Kul snails and bivalves, containing 16 species [8]. One of the most characteristic snail species of the lake is *Caspia issykkulensis* Clessin, 1894, whose empty shells are very abundant on the northern shore of Issyk-Kul. In 1972, this snail was reclassified as a member of the genus *Pseudocaspia*, Starobogatov, 1972 [9].

Zhadin [10], in his monograph on freshwater Mollusca of the former USSR, listed only three species of molluscs living in the lake: *Caspia issykkulensis*, *Radix auricularia* var. *obliquata* (Martens), and *Radix ovata* (Draparnaud, 1805) var. (undefined by the author). Since Zhadin's work, no comprehensive survey of the Issyk-Kul malacofauna has been published. A drastic difference between species lists published by Clessin [8] and Zhadin [9] (16 species vs. 3) indicates that a revised study of the malacofauna of this waterbody is an urgent task. The taxonomic identity of several nominal species of molluscs, described by Clessin (*Ancylastrum ovatum* Clessin, 1907; *A. turkestanicum* Clessin, 1907; *Gyraulus acutus* Clessin, 1907; *Pisidium schmidti* Clessin, 1907; etc.), remains unresolved. All these species listings were established based on empty shells only and, unfortunately, living specimens of them are inaccessible. For example, nobody since Clessin has ever found a single species of freshwater limpet of the genus *Ancylastrum* Bourguignat, 1853, established by him. Hubendick [11] synonymized the four species of *Ancylastrum* of Issyk-Kul with the widespread Northern Eurasian species *Ancylus fluviatilis* O.F. Müller, 1774 (Gastropoda: Planorbidae), however, the existence of this species in Central Asia is highly problematic, and the taxonomic position of Clessin's limpets remains extremely obscure [12].

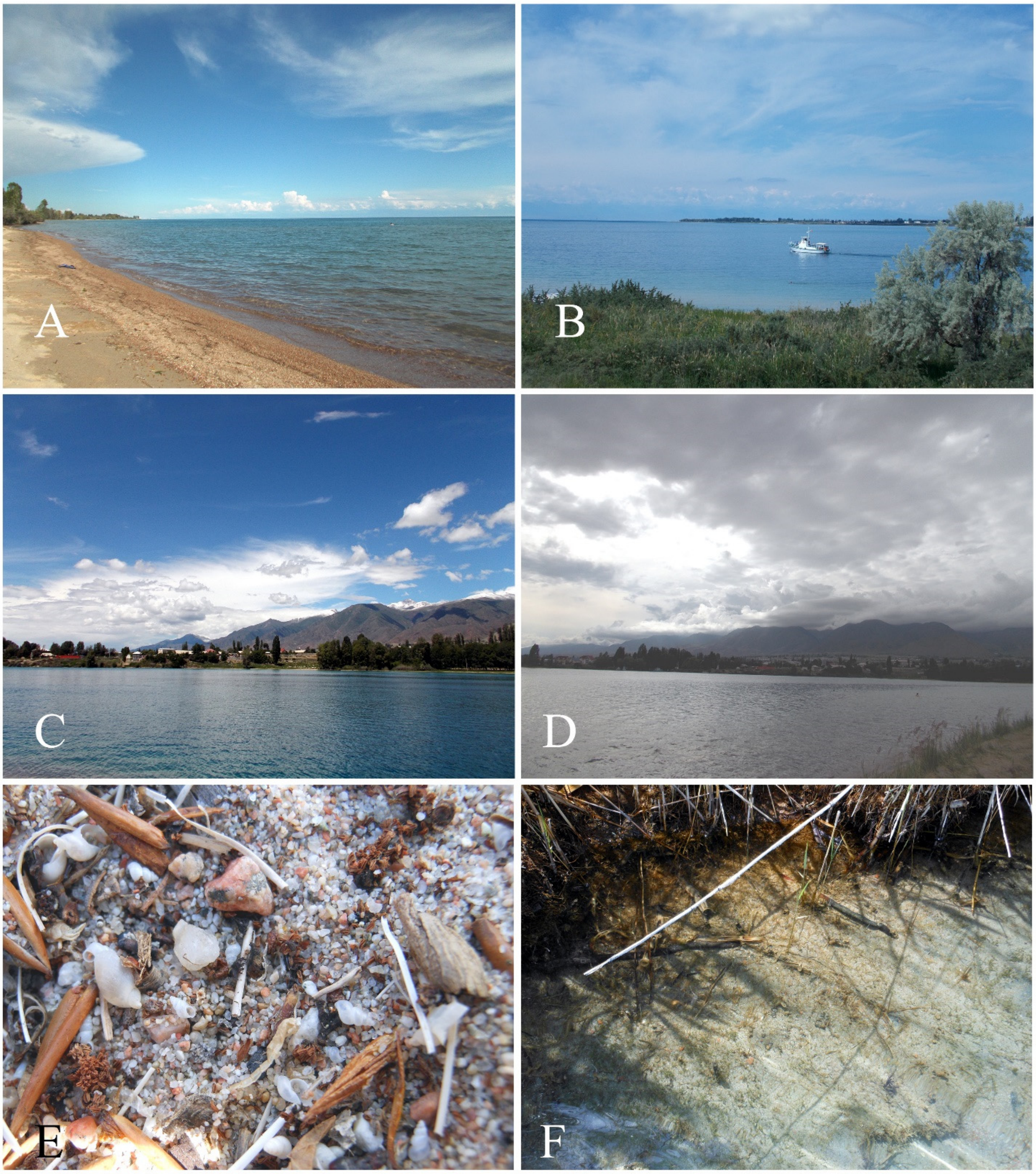

Figure 1. (**A**–**D**). Views of the northern shore of Lake Issyk-Kul and (**E**) lake deposits on a beach in Cholpon-Ata settlement. Empty shells of *Pseudocaspia issykkulensis* and juvenile *Radix* sp. are seen; (**F**) shallow zone of a bay of the Issyk-Kul Lake in Cholpon-Ata—a habitat of *Radix* sp. Photos by M. Vinarski.

Despite the low species richness of the Issyk-Kul malacofauna, Izzatullaev and Starobogatov [13] separated this lake and its drainage basin into a special malacofaunistic province. The last species of molluscs described from Lake Issyk-Kul is *Odhneripisidium issykkulense*, Izzatullaev and Starobogatov, 1986, from the family Sphaeriidae (Bivalvia) [14].

The use of molecular approaches to phylogeny and systematics is today a standard for the taxonomy of freshwater Mollusca, and the absence of fresh material on most of the nominal species mentioned by Clessin, Starobogatov, and other researchers makes it impossible to present now a full checklist of the Issyk-Kul malacofauna. In this research, we took a first step towards the full understanding of the Issyk-Kul molluscs. We report the results of a molecular revision of lymnaeid snails of the genus *Radix* Montfort, 1810, inhabiting this basin. Zhadin [10] mentioned two species of *Radix* in the lake (see above). More recently, Kruglov and Starobogatov [15] and Kruglov [16], in their comprehensive studies of the Lymnaeidae of Eurasia, also recognized two species of *Radix* [=*Lymnaea* (*Radix*) sensu Kruglov and Starobogatov, 1993]—*R. obliquata* and *R. subdisjuncta* (Nevill, 1878).

Another goal of our publication is to review all species of *Radix* reported from the ancient deep lakes of the world, with remarks on their taxonomy and ecology. We believe this provides helpful comparative material to all interested in molluscan radiations in ancient lakes.

2. Material and Methods

2.1. Primary Material and Morphological Studies

The type series of the two species of *Radix* recently reported in Issyk-Kul Lake (i.e., *Radix obliquata* and *R. subdisjuncta*), were examined by us (Figure 2). The type series of *Limnaeus obliquatus* contains two syntypes and is kept in the Natural Historical Museum of Berlin, Germany (ZMB) [6,17]. The taxonomic identity and shell variability of this species have been discussed many times in the literature [16–22]. The whereabouts of the holotype of *Limnaea lagotis* var. *subdisjuncta* is unknown to us. Probably, it is kept in the Indian Zoological Museum in Kolkata. We studied seven paratypes of this taxon deposited in the Natural History Museum of the United Kingdom, London, UK (NHMUK, see Figure 2). The type locality of *R. subdisjuncta* lies in Kashmir ("neighbourhood of Leh"; see [23]). Though Kruglov and Starobogatov [15,16,21] accepted it as a "good" species, subsequent researchers consider it a species of unclear identity [24]. Though this species was reported in Inner Mongolia (China) [15], it is absent from Yen's comprehensive account on the Chinese freshwater snails [25,26]. In a more recent work, Liu [27] also did not discuss this snail. Subba Rao [28], in his survey of Indian molluscs listed this taxon as a variety of *Lymnaea peregra* (O.F. Müller, 1774). However, this species (*Peregriana peregra* of the current system) does not inhabit India [29].

In addition, numerous samples of *Radix* collected from the Issyk-Kul Lake and its basin as well as from other regions of Central Asia were examined. These lots are kept in the abovementioned museums in Berlin and London as well as in other depositories in Europe: Zoological Institute of the Russian Academy of Sciences, Saint-Petersburg, Russia (ZIN); the Naturmuseum Senckenberg, Frankfurt am Main, Germany (SMF); Zoological Museum of Copenhagen University, Denmark (ZMUC); Zoological Museum of Moscow State University, Russia (ZMMU); and Museum of the Institute of Plant and Animal Ecology, the Ural Branch of the Russian Academy of Sciences (UB RAS), Yekaterinburg, Russia (IPAE).

We sampled molluscs in Issyk-Kul Lake thrice, in 2013, 2018, and 2023, in several habitats located along the northern shore of this waterbody. Most samples were collected in vicinities of Cholpon-Ata (approximate coordinates: 42.639 N, 77.072 E) and Ananievo (approximate coordinates: 42.706 N, 77.696 E) settlements. The collected specimens were represented by empty shells and live individuals (mostly subadult) sampled from sand beaches (see Figure 1E) and from bottom sediment and /or vegetation in shallow areas of bays protected from the strong wave action typical of open parts of the lake. These samples are kept in the Laboratory of Macroecology and Biogeography of Invertebrates at the St.-Petersburg State University, Russia (LMBI) and the Russian Museum of Biodiversity Hotspots, N. Laverov Federal Center for Integrated Arctic Research, UB RAS, Arkhangelsk, Russia (RMBH).

Figure 2. Upper row—syntypes of *R. obliquata* and their labels, ZMB (accession No. 7164). **Lower row**—three paratypes of *R. subdisjuncta* with their labels, NHMUK (accession number 1824). Scale bars—2 mm (*R. subdisjuncta*) and 5 mm (*R. obliquata*). Photos by Maxim Vinarski.

In August 2023, a series of invertebrate samples was taken from the shallow part of the lake (northern shore) by two scuba divers. Live specimens of *Radix* sp. were found in two samples: (1) Issyk-Kul Lake off Kosh-Kol settlement [coordinates: 42.4846 N 76.486 E]; depth 2.5 m; substrate—underwater vegetation (thickets of *Sparganium*, with admixture of other macrophytes) and (2) Issyk-Kul Lake off Cholpon-Ata settlement [coordinates: 42.5906 N 77.082 E]; depth 17.5 m; substrate—stones and vegetation. In addition to living *Radix* snails, the samples contained numerous empty shells of *Pseudocaspia issykkulensis*.

The initial taxonomic identification of collected individuals was carried out using Kruglov's monograph [16]. Our specimens were also compared with the type specimens of *R. obliquata* and *R. subdisjuncta*. Shell measurements were taken by means of ocular-micrometer of a binocular microscope with accuracy to 0.1 mm. The measurement scheme of Vinarski [30] was followed. Six measurements were taken: shell height and width, spire height, body whorl height, and height and width of aperture. Whorl number was counted with accuracy to 1/8. These primary variables were then subjected to statistical analysis, including descriptive statistics and PCA (principal component analysis).

We did not have fixed adult specimens of the Issyk-Kul *Radix* at our disposal. All individuals that could be found in the shallow bays of the lake were juvenile or subadult. The macrostructure of genital organs was, therefore, studied on these immature specimens. The absence of mature snails made it impossible for us to reveal if there are diagnostically significant structures in their genital system. The reproductive anatomy of the Lymnaeidae was thought to serve as a major source of taxonomic and phylogenetic signal in this family [16,31]. However, the recent studies on taxonomy and variation in *Radix* have shown that anatomy does not provide an effective tool for species delineation in this group; the reproductive anatomy of these snails appears to be almost identical among species whose taxonomic independence was supported molecularly [29,32,33]. Therefore, in this study, we report and illustrate some features of the soft body of studied snails, but do not use them in our phylogenetic and taxonomic conclusions.

For comparative purposes, samples of *Radix* collected by us in various regions of Eurasia and Africa were used. In particular, we examined, both molecularly and morphologically, samples of *Radix natalensis* (Krauss, 1848) s. lato (near Entebbe, Uganda: sampling date 07.2018) and *R. skutaris* Glöer and Pešić, 2008, from Skadar Lake, Montenegro and adjacent waterbodies (sampling date: 08.2021). In August 2018, a sample of *Radix* was also collected from Albert Lake near Butiaba (Uganda). The materials sampled from Albert and Victoria Lakes are kept in LMBI and RMBH; those from Skadar Lake—in RMBH only.

2.2. DNA Analysis, Sequence Alignment, Phylogenetic Study, and Species Delimitation

In the course of this research, 28 new sequences were generated (Table 1). Total genomic DNA was extracted from 96% ethanol-preserved tissues of collected specimens using the NucleoSpin Tissue Kit (Macherey-Nagel GmbH & Co. KG, Düren, Germany), following the manufacturer's protocol. In the present study, we used data from the mitochondrial cytochrome *c* subunit I (COI) gene, 16S ribosomal RNA (16S rRNA) gene, and the nuclear 28S ribosomal RNA (28S rRNA) gene fragment. COI primers were LCO1490 and HCO2198 [34]. For 16S, the primers 16Sar and 16Sbr [35] were used. 28S primers were D23F [36] and D2 [37]. The PCR mix contained approximately 200 ng of total cellular DNA, 10 pmol of each primer, 200 μmol of each dNTP, 2.5 μL of PCR buffer (with 10 × 2 mmol $MgCl_2$), 0.8 units of Taq DNA polymerase (SibEnzyme Ltd., Novosibirsk, Russia), and H_2O, which was added up to a final volume of 25 μL. Thermocycling was implemented with markers-specific PCR programs as follows: (I) COI and 16S: 95 °C (4 min), followed by 28–30 cycles of 95 °C (50 s), 50 °C (50 s), 72 °C (50 s), and a final extension at 72 °C (5 min) and (II) 28S: 95 °C (4 min), followed by 30–31 cycles of 95 °C (50 s), 58 °C (50 s), 72 °C (50 s), and a final extension at 72 °C (5 min). Forward and reverse sequencing was performed on an automatic sequencer (ABI PRISM3730, Applied Biosystems, Foster City, CA, USA) using the ABI PRISM BigDye Terminator v.3.1 reagent kit. The resulting sequences were checked using a sequence alignment editor, BioEdit version 7.2.5 [38]. The phylogenetic affinities of the nucleotide sequences of certain specimens were identified using the Basic Local Alignment Search Tool, BLAST [39].

Table 1. New DNA sequences generated from *Radix* specimens from Kyrgyzstan and Montenegro, with their GenBank numbers. N/A—not available.

Species	Voucher No.	Locality, Coordinates	COI Haplotype	COI acc. No.	16S rRNA acc. No.	28S rRNA acc. No.
R. auricularia	RMBH MLym985/1/1	Issyk-Kul Lake, 42.706389, 77.686389	AUR1	PQ771848	N/A	N/A
R. auricularia	RMBH MLym985/1/2	Issyk-Kul Lake, 42.706389, 77.686389	AUR1	PQ771849	N/A	N/A
R. auricularia	RMBH MLym985/2	Issyk-Kul Lake, 42.706389, 77.686389	AUR2	PQ771850	N/A	N/A
R. obliquata	RMBH MLym985/3	Issyk-Kul Lake, 42.706389, 77.686389	AUR2	PQ771851	N/A	N/A
R. obliquata	RMBH MLym984/1/1	Issyk-Kul Lake, 42.646944, 77.098056	OBL1	PQ771843	PQ772053	PQ772069
R. obliquata	RMBH MLym984/1/2	Issyk-Kul Lake, 42.646944, 77.098056	OBL1	PQ771844	PQ772054	PQ772070
R. obliquata	RMBH MLym984/2	Issyk-Kul Lake, 42.646944, 77.098056	OBL2	PQ771845	PQ772055	PQ772071
R. obliquata	RMBH MLym984/3	Issyk-Kul Lake 42.646944, 77.098056	OBL3	PQ771846	PQ772056	PQ772072

Table 1. *Cont.*

Species	Voucher No.	Locality, Coordinates	COI Haplotype	COI acc. No.	16S rRNA acc. No.	28S rRNA acc. No.
R. obliquata	RMBH MLym984/4	Issyk-Kul Lake 42.646944, 77.098056	OBL3	PQ771847	PQ772057	PQ772073
R. skutaris	RMBH MLym1220/1	Montenegro: Sitnica River, 42.46081, 19.176929	SKU1	PQ771852	PQ772058	PQ772074
R. skutaris	RMBH MLym1226/1	Montenegro: Crnojevića River, 42.355589, 19.022553	SKU2	PQ771853	PQ772059	PQ772075
R. skutaris	RMBH MLym1226/2	Montenegro: Crnojevića River, 42.355589, 19.022553	SKU3	PQ771854	PQ772060	PQ772076

The sequences were aligned using the MUSCLE algorithm of MEGAX [40]. The phylogeographic analyses of *Radix auricularia* were performed based on a median-joining network approach using Network ver. 4.6.1.3 software with default settings [41]. Two hundred and thirty COI sequences of *R. auricularia* were obtained from NCBI GenBank in addition to those freshly generated (Table S1 of Supplementary Materials).

For species delimitation procedures, we added five COI haplotype sequences of *Radix* species from Lake Issyk-Kul and three haplotypes of *R. skutaris* from Skadar Lake basin to a comprehensive dataset of Aksenova et al. [42], containing 763 COI haplotypes of various Lymnaeidae. A sequence of *Aplexa hypnorum* (Linnaeus, 1758) (Physidae) was used as an outgroup. The COI haplotype phylogeny was reconstructed using a maximum likelihood approach through an online Web server for IQ-TREE v.1.6.12 (http://iqtree.cibiv.univie.ac.at, accessed on 12 December 2024) with an automatic identification of the most appropriate substitution model (K3Pu+F+I+G4) [43–45]. The support values of the tree were identified with an ultrafast bootstrapping algorithm, UFBoot [46]. This large tree was used to calculate the multi-rate Poisson tree processes (mPTP) species delimitation model via a web server (http://mptp.h-its.org, accessed on 12 December 2024) [47]. Additionally, the Automatic Barcode Gap Discovery (ABGD; https://bioinfo.mnhn.fr/abi/public/abgd, accessed on 12 December 2024) was applied as a distance-based species delimitation approach with the JC69 measure of distance [48]. As an input dataset, we used the alignment with 768 COI haplotypes of the Lymnaeidae (see above).

The maximum likelihood multi-locus phylogeny (three codons of COI + 16S rRNA + 28S rRNA) was also based on the dataset of Aksenova et al. ([42], Table S1 of Supplementary Materials), which contains 123 ingroup haplotypes of 113 lymnaeid species. To this dataset, we added newly generated haplotype-level data for *Radix obliquata* and *R. auricularia* from Lake Issyk-Kul, as well as for *Radix skutaris*, from Lake Skadar basin in Montenegro. Haplotypes of *Physella acuta* (Draparnaud, 1805) and *Sibirenauta elongata* (Say, 1821) were used as outgroups. The maximum likelihood multi-locus phylogeny was reconstructed with an online Web server for IQ-TREE v.1.6.12 (http://iqtree.cibiv.univie.ac.at, accessed on 15 December 2024), as described above. The best evolutionary models for each partition were as follows: first codon of *COI*, HKY+F+G4; second codon of *COI*, SYM+I+G4; third codon of *COI*, TPM3u+F+I+G4; *16S rRNA*, TVM+F+I+G4; and *28S rRNA*, GTR+F+G4.

3. Revision of *Radix* Species in Lake Issyk-Kul

A multi-locus phylogeny obtained during our research has revealed that Lake Issyk-Kul is inhabited by two species of *Radix* (Figure 3). One of them is identical to the widespread Palearctic species *R. auricularia* (Linnaeus, 1758). The other one belongs to an apparently endemic clade, which can properly be named *Radix obliquata* sensu lato (using the only available taxonomic name established for a *Radix* species with the type locality situated in Issyk-Kul). The results of a COI-based species delimitation procedure (Figure S1 in Supplementary Materials) are in good agreement with the multi-locus phylogentic analysis.

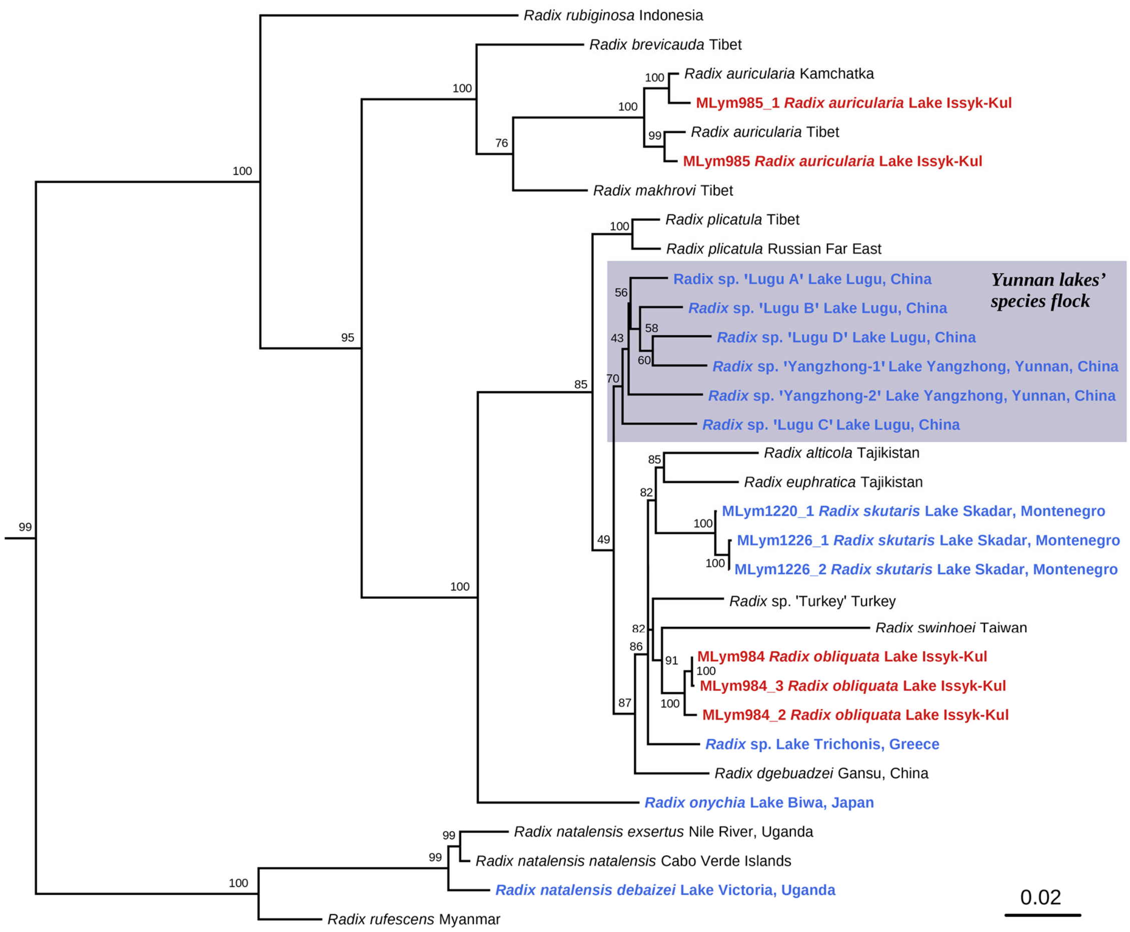

Figure 3. Maximum likelihood consensus multi-locus phylogeny of the genus *Radix* (three codons of COI + 16S rRNA + 28S rRNA) reconstructed through IQ-TREE v.1.6.12. Black numbers near nodes are ultrafast bootstrap support values. Labels of haplotypes from Lake Issyk-Kul are red. Labels of haplotypes from other ancient lakes are blue. This tree is a fragment of a global phylogeny of the family Lymnaeidae (non-target clades and outgroup are omitted). The scale bar indicates the branch lengths (substitutions per site).

The presence of *R. auricularia* in Issyk-Kul is not surprising. This snail is ecologically plastic and able to colonize very diverse waterbodies, varying from deep ancient lakes (e.g., Lake Baikal) to the smallest thermal pools and ponds [49–51]. *R. auricularia* is very common in Central Asia and could have penetrated the lake from adjacent waterbodies. It is not known how long this snail has lived in Issyk-Kul Lake, and it is not improbable that it has only recently colonized the waterbody (as is the case with *R. auricularia* in Lake Baikal [50]). However, the presence of two, rather distant, haplotypes of *R. auricularia* in the lake suggests that there could be at least two events of invasion of Issyk-Kul by this snail, and that the sources of invasion were geographically distinct. One of the haplotypes (AUR1) is identical to those found in Northern Siberia (widely distributed from the Novosibirsk Region in the west to Transbaikalia in the east) and in Northeastern Europe (Figure 4). Haplotype AUR2 forms a sister lineage to a haplotype found in Tibet (GenBank No. MH189863). In turn, there is a sample from Xinjiang (Western China) that is a sister lineage to the clade (AUR2 + MH189863). Thus, the second haplotype of *R. auricularia* from Issyk-Kul has a clear Central Asian ancestry.

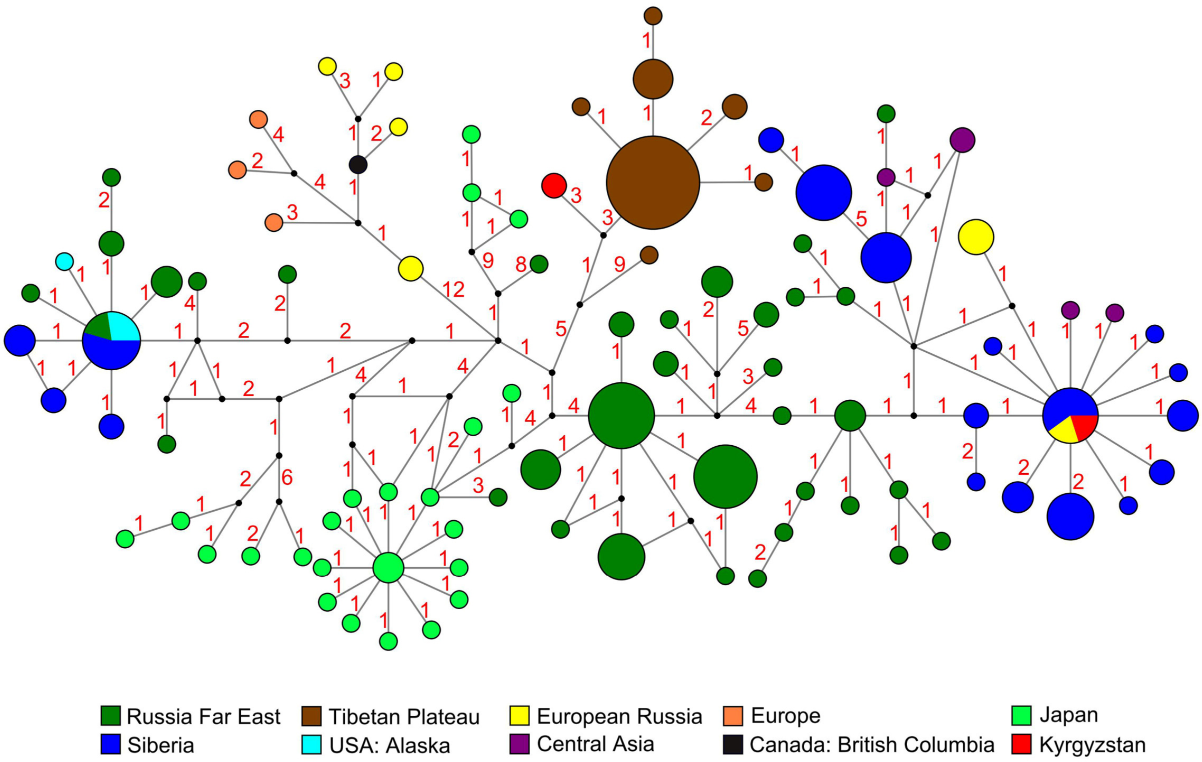

Figure 4. Median joining network of the COI sequences of *Radix auricularia*. Circle symbols represent different haplotypes, with the size reflecting their frequency (smallest = 1). Numbers near branches are numbers of nucleotide substitutions per site. The dataset contains 234 COI sequences (length = 572 bp).

The species *R. obliquata* in the studied sample was represented by three haplotypes, which, given the limited size of the sample, indicates a notable genetic diversity. One of these haplotypes (OBL2) is markedly different from the other two (distance 1.2–1.4%, according to COI). There are two explanations for this fact. First is that the haplotype divergence is a product of a more or less prominent intralacustrine radiation (comparable with that of *Radix* in the ancient Lake Lugu, Yunnan, China [52]). Alternatively, *R. obliquata* may present as not truly endemic to Issyk-Kul but, instead, as a certain Central Asian species of *Radix*, still underrepresented in GenBank. If true, this would explain the high genetic diversity by the hypothesis of its double (at least) introduction into Lake Issyk-Kul. However, the deficiency of *Radix* sequences from China, Tajikistan, Afghanistan, and other Central Asian countries located close to Issyk-Kul makes this assumption unverifiable.

The question of the taxonomic identity of the two *Radix* species reported in Issyk-Kul Lake by Kruglov and Starobogatov [15,16] needs special consideration. Specimens of *Radix* found in the samples of the Issyk-Kul molluscs examined by us belonged to three morphospecies (Figure 5A–C,H–J), corresponding to the species *Radix obliquata* and *R. subdisjuncta* sensu Kruglov and Starobogatov and *Radix auricularia* [15,16]. Unfortunately, the living specimens of *Radix* used in the molecular analysis were not full-grown (Figure 6), and, potentially, may belong to either of the two species.

Conchologically, *Radix obliquata* and *R. subdisjuncta* sensu Kruglov and Starobogatov [15] can be distinguished from each other by different shell size and shape (see Figure 5; Table S2 in Supplementary Materials for this article). A PCA analysis has revealed that these entities form two very closely situated but nonetheless distinct "clouds" in the space of the first two PCs (Figure 7). However, one can note that the separation between these clouds is chiefly along the first PC, which is the "size component", explaining 98.18% of the total variance (see Table S3 in Supplementary Materials). Most linear measurements, except for spire height, correlate with it. In simple terms, this means that the two groups are separated by their absolute size and, thus, may represent two age cohorts of a single species. Indeed, the trend lines approximating linear shell growth in these two groups are similar, albeit not identical (Figure 8), indicating a slight dissimilarity in the parameters determining linear shell growth in ontogeny. There is, nonetheless, an alternative explanation, which considers these morphospecies as ecotypes (or ecological "races") of the same species: *R. obliquata*, with its broadly auriculate shell and enlarged aperture, may inhabit deeper part of the lake (according to Pavlova [53], this mollusc occurs at depths up to 60 m), whereas *R. subdisjuncta* is a morph adapted to relatively shallow habitats. It is characterized by a slender and relatively small shell with a high spire and a moderately or weakly inflated body whorl. However, this assumption should be checked by direct observation of snails inhabiting different depth zones of the lake. Unfortunately, during diving into Issyk-Kul Lake, to depths of 2.5–17.5 m, only small-sized specimens of *Radix* were found (see Figure 6).

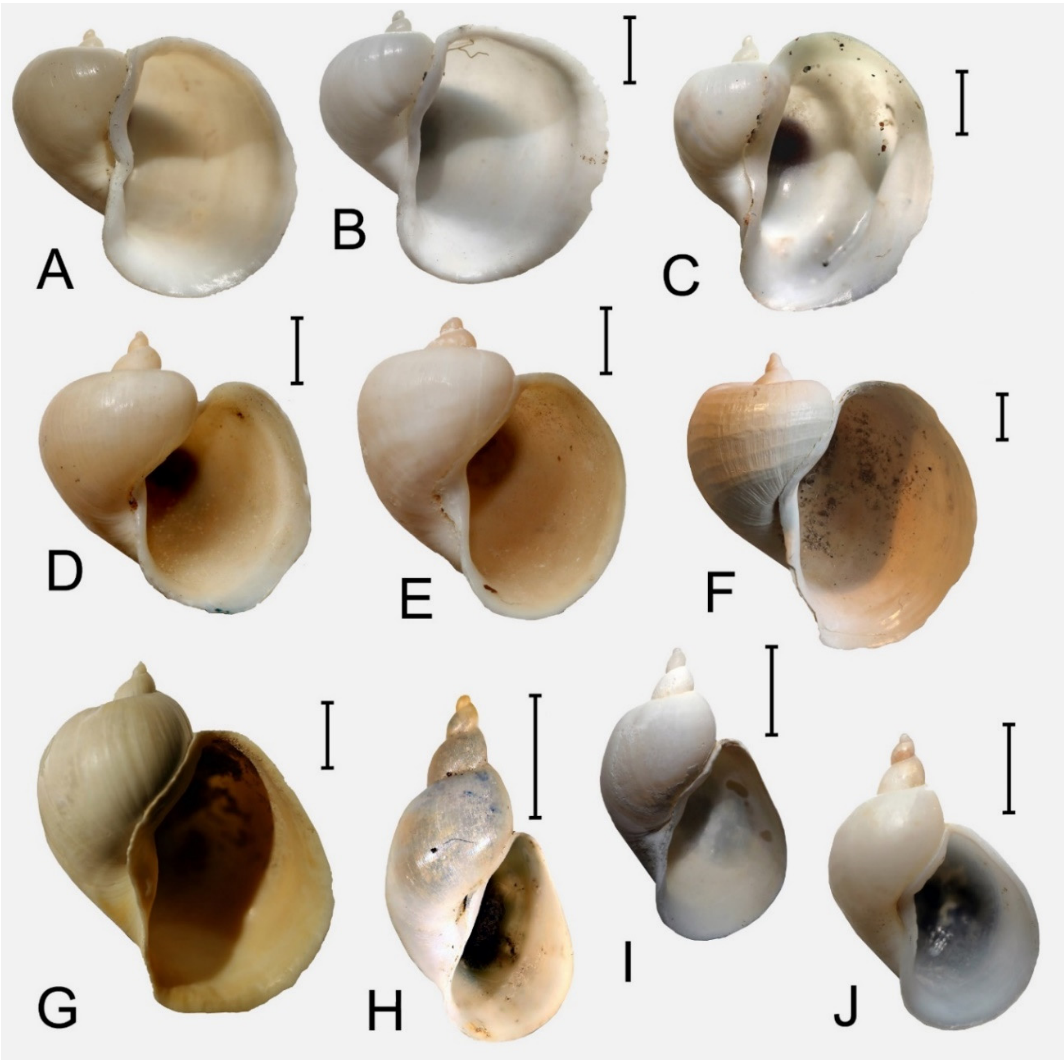

Figure 5. Shells of *Radix obliquata* (**A**–**G**) and *R. subdisjuncta* sensu Kruglov and Starobogatov (**H**–**J**) from various localities of Central Asia. (**A**–**C**) Issyk-Kul Lake, Cholpon-Ata, 07.2013 (LMBI, accession No. 15-2535); (**D**,**E**) Russia, Republic of Tuva, Terekhol Lake, 07.1980 (IPAE, accession No. 130); (**F**) Mongolia, east of Ubsunur Lake, 06.1978 (ZIN, accession No. 23); (**G**) China, Inner Mongolia, Alashan Desert, Djaratay-dabasun (ZMUC, accession No. unknown); (**H**) Issyk-Kul Lake, Kutarga settlement, 07.1979 (ZIN, uncatalogued); and (**I**,**J**) Issyk-Kul Lake, Cholpon-Ata, 07.2013 (LMBI, accession No. 15-2536). Scale bars 5 mm. Photos by Maxim Vinarski.

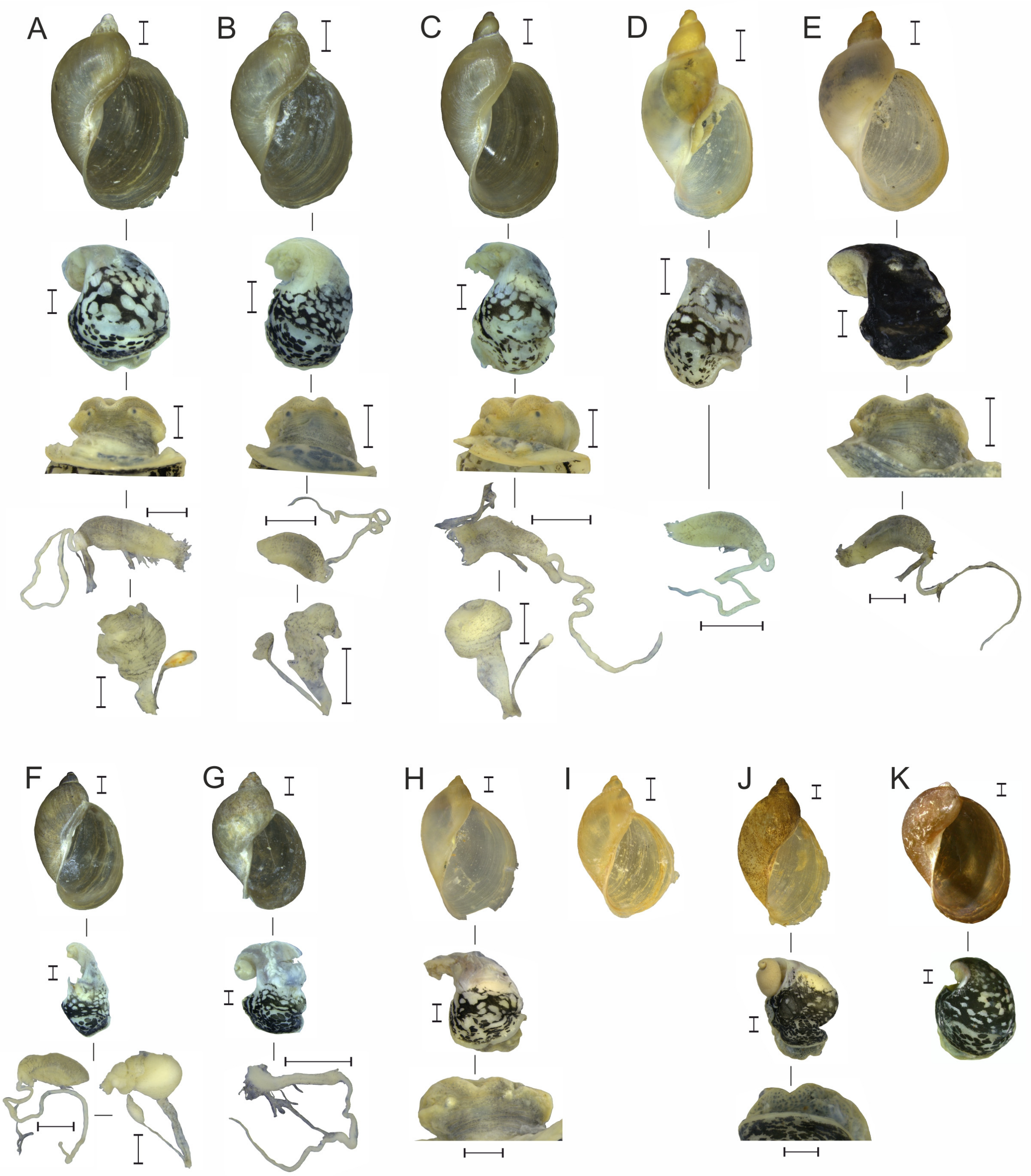

Figure 6. Shells, mantle pigmentation, and anatomy of the *Radix* species discussed in this study. (**A**) *Radix obliquata*, Issyk-Kul Lake (RMBH, accession No. MLym-984); (**B**) *R. obliquata*, Issyk-Kul Lake (RMBH, accession No. MLym-984/2); (**C**) *R. obliquata*, Issyk-Kul Lake (RMBH, accession No. MLym-984/3; (**D**) *R. obliquata*, Issyk-Kul Lake (RMBH, accession No. MLym-1336/2); (**E**) *R. obliquata*, Issyk-Kul Lake (RMBH, accession No. MLym-1348/4); (**F**) *R. auricularia*, Issyk-Kul Lake, (RMBH, accession No. MLym-985/1); (**G**) *R. auricularia*, Issyk-Kul Lake, (RMBH, accession No. MLym-985); (**H**) *R. skutaris* from Sitnica River, Skadar Lake basin, Montenegro (RMBH, accession No. MLym-1220/1); (**I**) *R. skutaris* from Crnojevića River, Skadar Lake basin, Montenegro (RMBH, accession No. MLym-1226/2); (**J**) *R. natalensis exsertus* from Albert Lake, Uganda (RMBH, accession No. MLym-743/3); and (**K**) *R. natalensis debaizei*, Lake Victoria, Uganda (RMBH, accession No. MLym-739/1). Scale bars 1 mm. Photos by Olga Aksenova.

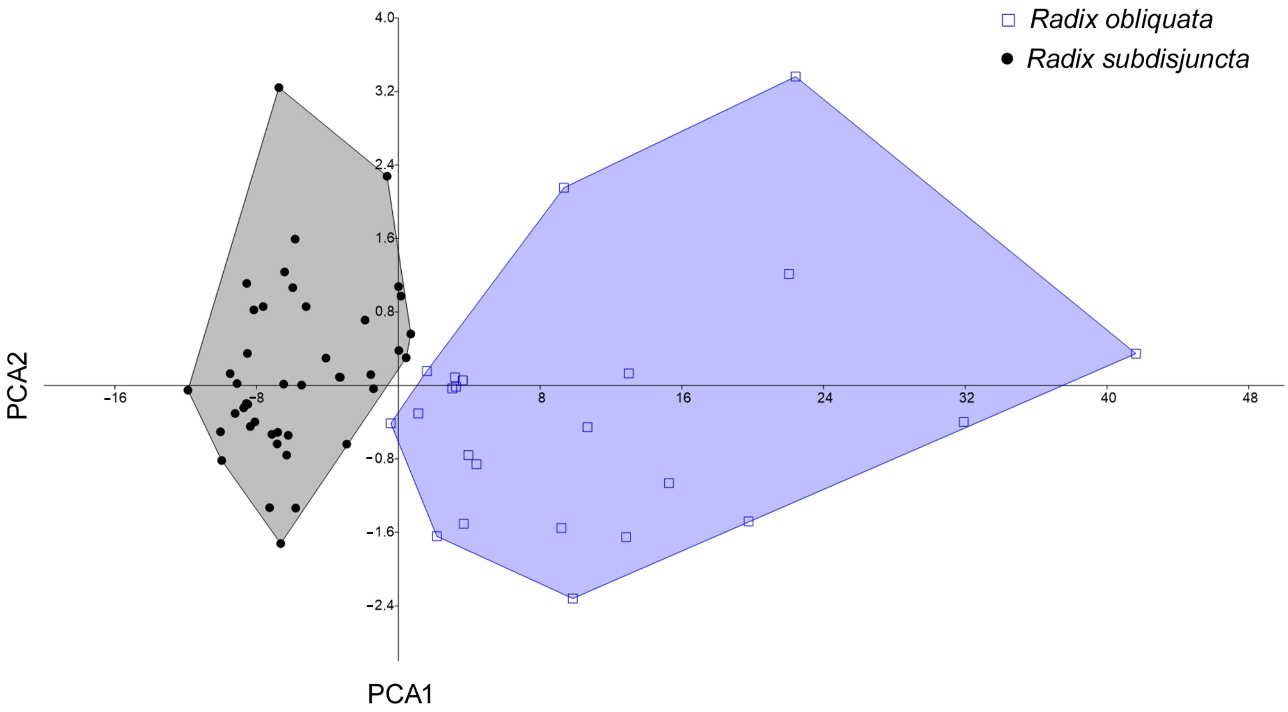

Figure 7. Principal component analysis of whorl number and shell measurements of two nominal species of *Radix* of Lake Issyk-Kul. The first three principal components (PC) combined account for 99.72% of variance (PC1 98.18%, PC2 1.06%, and PC3 0.48%).

Typical specimens of *Radix obliquata*, with greatly enlarged aperture and short spire, have never been found alive and, thus, neither anatomical nor molecular data on them are available. Though there still remains a possibility that *R. subdisjuncta* sensu Kruglov and Starobogatov is a species distinct from *R. obliquata*, the available data are not enough to support such a decision. Although the mean values of all studied shell parameters differ markedly between *R. obliquata* and *R. subdisjuncta*, we were unable to find a hiatus in the distribution of any of these quantitative variables (see Table S2 in Supplementary Materials).

Specimens of *Radix* from Issyk-Kul Lake that were analysed by us have small shells (up to 10 mm in height) with a high spire and a moderately enlarged body whorl (Figure 6A–E), are relatively thick-walled, and are light brown coloured. The shell surface sculpture has thin axial growth lines. The whorl number is 3.5–4.0. The whorls are very weakly convex and are separated by a shallow suture. The aperture is drop-shaped or ovoid, with an evenly rounded basal margin.

The mantle is light grey with black spots (see Figure 6A–D) or black with grey spots (Figure 6E) and "freckles" on the back of the head. There is a slight difference between *R. auricularia* and *R. obliquata* in the colour pattern of their soft body. Specimens of the former species from Issyk-Kul Lake have dark pigmentation with numerous small spots of white colour (see Figure 6F,G). *R. obliquata* snails demonstrate an opposite pattern—light background with black spots (see Figure 6A–D). However, we have only a limited number of specimens at our disposal and, thus, it remains unknown whether this difference is stable and can serve as a diagnostic feature.

The morphology of the copulatory apparatus of *R. obliquata* is typical of the genus *Radix* (see Figure 6A–E). The apparatus consists of tubular praeputium and a very thin and narrow penis sheath (see Figure 6E). The praeputium is oblong, light grey with black dots, and its width is almost the same along the entire length. The penis sheath is much narrower, and its distal end is somewhat swollen. The praeputium length is slightly shorter or equal to the length of the penis sheath, which is characteristic of many other species of this genus [29]. The spermathecal duct is long.

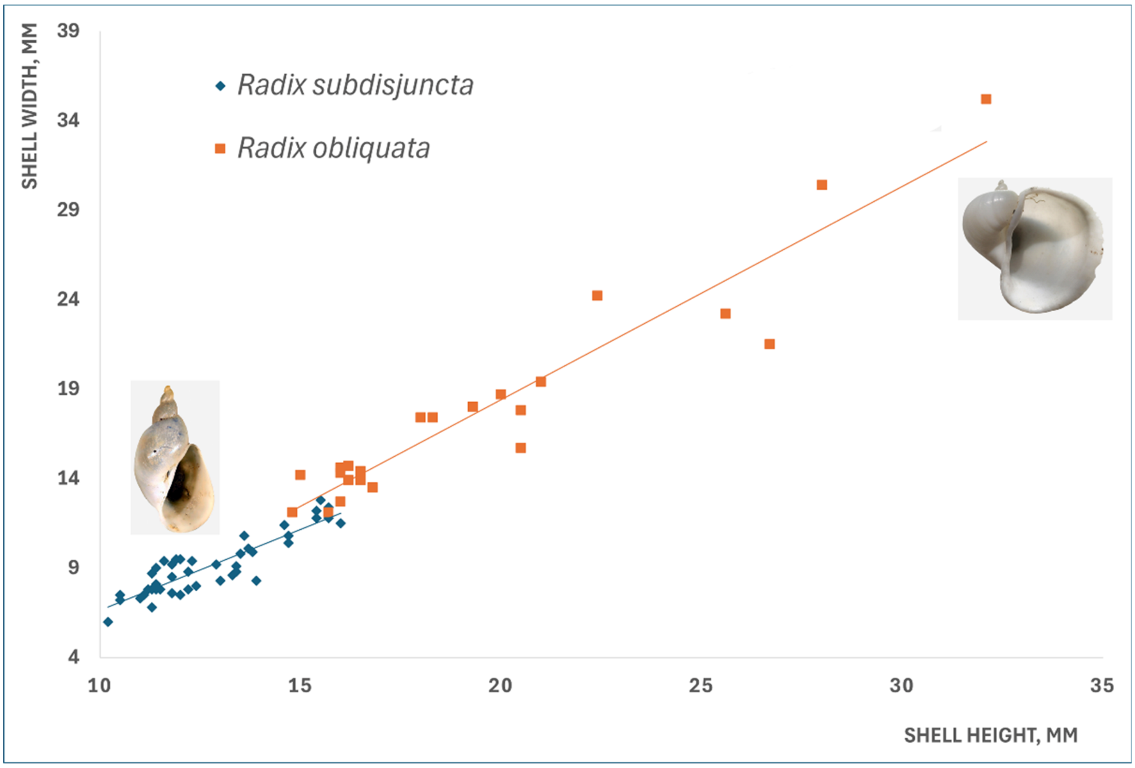

Figure 8. A scatterplot of shell width vs. shell height in two nominal species of *Radix* of Lake Issyk-Kul.

Conchologically, shells of *R. subdisjuncta* sensu Kruglov and Starobogatov [15] found in Issyk-Kul Lake are different from the paratypes of *Limnaea lagotis* var. *subdisjuncta* (compare Figure 2, lower row, and Figure 5H–J). The type locality of the latter lies far from Kyrgyzstan, and its identity is still unresolved due to the lack of molecular data on snails collected in Northern India. Most probably, it represents a junior synonym of *Ampullaceana lagotis* (Schrank, 1803), a lymnaeid species common to Central Asia [29,32]. The application of the taxonomic name *Lymnaea lagotis* var. *subdisjuncta* to a conchologically dissimilar morphospecies found in Lake Issyk-Kul is, in our opinion, untenable, especially since Kruglov and Starobogatov [15,16,22] did not have the opportunity to study the type series of this taxon. The identification of shells from former Soviet Central Asia with the species described from Kashmir was made by them on the basis of superficial similarities in the shape and proportions of the shells.

Radix obliquata, in terms of its true range and biogeographic affinities, poses a more complicated problem. Shells of lymnaeids with similar shape and proportions are known from various parts of Central Asia, which has led to a conclusion that the range of *R. obliquata* is not restricted to Lake Issyk-Kul. For example, Yen [26] reported this snail in Tibet. In different museums, we found shells of snails identified as *R. obliquata* that originated from such diverse regions as the Republic of Tuva (Eastern Siberia, Russia), Western Mongolia, Tibet, Uzbekistan (the environs of Tashkent), and the former Lob-Nor Lake in Western China. Their conchological traits overlap, and the measured shells formed a continuous "cloud" of points on the PC1–PC2 axes (Figure S3 in Supplementary Materials). However, it would be premature to follow Kruglov and Starobogatov ([15], p. 88) and to outline the range of *R. obliquata* as stretched throughout "desert and semidesert regions of Central Asia, to Inner Mongolia in the east". Previously, we molecularly studied many dozens of *Radix* spp. from different regions of Northern and Central Asia, including Tibet, Tajikistan, and Xinjiang [32,33,42,49,51,54]. No sequences identical to those found in Lake Issyk-Kul were discovered. Thus, the most cautious assumption we can make now is that *R. obliquata* is endemic to Issyk-Kul Lake. Shells of *Radix* from Tuva and other regions of Central Asia, which have external similarity to *R. obliquata* (see Figure 5D–G), are, most probably, not conspecific with the latter. This similarity could have arisen as a product of convergent processes, which are observed among lymnaeids [51] and other groups of freshwater and terrestrial pulmonates [55–57]. To claim the conspecificity between snails of Lake Issyk-Kul and Tuva (or Western Mongolia) would suggest numerous instances of their long-distance dispersal, with no living populations located between lakes separated by hundreds and thousands of kilometres. As long as we do not have genetic data on snails inhabiting Western Mongolia, Tuva, or the Lob-Nor Lake region, it would be imprudent to claim that *R. obliquata* inhabits anywhere outside Issyk-Kul. For example, the molecular data currently available [33,58,59] indicate that literary records of this species from the Tibetan Plateau should be rejected as being based on misidentifications.

Although, unlike lakes Baikal or Tanganyika, Issyk-Kul is not home to dozens or hundreds of endemic species, some groups of invertebrates have species endemic to this basin. Endemic species are known among monogeneans, nematodes, and rotifers of Lake Issyk-Kul [3,60–63] as well as among some other invertebrates. A few species of endemic fish are also known [64]. However, the degree of endemism varies greatly among groups. For example, the fauna of Rotifera, as of 1996, contained 94 species, but only one of them, *Lecane brodskii* Muraveiskiy, 1937, was considered endemic to this lake [62]. The bulk of the fauna is formed by cosmopolitan species, which can be explained by the ease of long-distance passive dispersal of these animals [65–67]. Out of 70 species of free-living Nematoda, registered in Issyk-Kul Lake by 1989, 11 (or 15.7%) were considered endemics [61]. No unique species is known among Issyk-Kul aquatic beetles (A. Prokin, pers. comm.), crustaceans [68,69], and water mites [70].

Compared to other groups of invertebrates, molluscs of Issyk-Kul Lake do not demonstrate a high level of endemism. However, as it was noted above, an integrative revision of the nominal species of snails and clams described is needed to know the true magnitude of their diversity. This is applicable to many other taxa of Issyk-Kul animals, since most presumed endemic species were described based on morphology only. DNA taxonomy has revealed that in groups, such as Rotifera [67], cryptic speciation and hidden diversity are quite common phenomena, and all biogeographical conclusions and estimates of species richness made using a morphological approach can be questioned.

It would be interesting to compare the results of our revision of the Issyk-Kul *Radix* with the data on *Radix* diversity in other ancient lakes of tectonic origin across the world.

4. *Radix* Species in Deep Ancient Lakes

There is a group of large permanent waterbodies, scattered throughout the world, which are called "ancient lakes" or "deep ancient lakes" [71]. Another, similar category, is dubbed simply "large lakes" [72,73], and several lakes included in this are also considered to be "ancient lakes". There is no commonly accepted definition for both groupings; for example, "ancient" lakes may be defined as either basins older than 1 myr [74] or, alternatively, as "those that contain sedimentary records that span timescales since at least the last interglacial (c. 128 ka before present (BP))" ([75], p. 209). Other important characteristics of the ancient lakes is that most of them are "oligotrophic and situated in active tectonic graben settings or impact craters with low sediment supply from the catchment" [74]. The low sediment supply prevents them for being filled with external matter and consequently vanish [76].

We do not aim to discuss here the question of lake classification but rather to analyse a group of lakes that were conditionally selected as having a set of features: (1) ancient age (pre-mid-Pleistocene); (2) Tectonic origin; and (3) considerable depth. The last feature was not followed very strictly, and a few relatively shallow lakes were included for consideration. This decision was based on the previous literature, where these basins were discussed from a malacologist's point of view. For instance, Lake Inle of Myanmar is rather shallow, but Boss [71] included it in his review of freshwater molluscs of ancient lakes. Also, Skadar Lake is shallow, with an average depth of 5 m and a maximum depth of 8.3 m [77]; the lake itself cannot be termed as an ancient lake, but its basin and hydrological network with a large system of karst springs are definitely ancient, originated from more than 2.5 Ma [78]. On the other hand, the Caspian Sea, which is sometimes included in the group of large lakes [74], has been omitted from our review since this is a brackish-water basin, being a remnant of the Paratethys sea-lake of the Neogene epoch. The history of the Caspian Sea malacofauna (reviewed in [79]) is very peculiar and differs from the history of malacofaunas of other ancient lakes. In total, we collected information on 26 lakes (Table 2). Our list of basins is by no means exhaustive and could be extended, for example, to include Lake El'gygytgyn in Chukotka, Russia, or Lake Tovuti in Indonesia, which are included by some authors (e.g., [74]) in their reviews of ancient lakes.

Table 2. A summary of diversity of the genus *Radix* in ancient tectonic lakes (with basic morphometric data on the lakes *).

Lake Name	Country	Surface Area, km^2	Volume, km^3	Elevation, m a.s.l.	Depth, m		Species of *Radix*	Source
					Mean	Maximum		
Albert	Congo (DRC)/Uganda	5300	280	619	25	58	*R. natalensis exsertus*	([80] this study)
Baikal	Russia	31,500	23,000	456	680	1741	*R. auricularia*	[48]
Balkhash	Kazakhstan	18,200	106	340	5.8	26.5	*R. auricularia*	[81]
Biwa	Japan	674	27.5	87	41	103	*R. onychia*	[42,82]
Edward	Congo (DRC)/Uganda	2150	78	912	34	117	*R. natalensis*	[80]
Eyre	Australia	7690	30.1	−12	?	3.1	No	This study
Hövsgöl (Khubsugul)	Mongolia	2620	480	1624	246	480	*R. auricularia* *R. mongolica*	[83]
Inlé	Myanmar	116	Fluctuating	880	2.1	3.7	*R. rufescens*	This study
Issyk-Kul	Kyrgyzstan	6236	1738	1606	278	668	*R. auricularia* *R. obliquata*	This study
Kivu	Congo (DRC)/Rwanda	2220	333	1460	240	480	*R. natalensis*	[84]
Lanao	Philippines	375	21.28	700	60.3	112	*R. rubiginosa*	This study
Lugu	China	48.5	1.953	2685	40.3	105.3	Four, still undescribed species	[52]
Malawi	Malawi/Mozambique/Tanzania	29,600	8400	475	292	706	*R. natalensis*	[85]
Mweru	Congo (DRC)/Zambia	5120	32	922	7.5	27	Unknown (no data)	
Ohrid	Albania/Macedonia	358	53.63	693	155	288	No	This study
Prespa	Albania/Greece/Macedonia	259	55.5	849	14	48	*R. auricularia*	[86]
Skadar (Shkodra)	Albania/Montenegro	372	1.93	5	5	8.3	*R. skutaris*	This study
Tahoe	USA	499	156	1899	249	501	No	This study
Tanganyika	Burundi/Congo (DRC)/Tanzania/Zambia	32,000	17,827	774	572	1471	*R. natalensis*	[71]
Titicaca	Bolivia/Peru	8030	903	3809	107	304	No	[87,88]

Table 2. *Cont.*

Lake Name	Country	Surface Area, km^2	Volume, km^3	Elevation, m a.s.l.	Depth, m		Species of *Radix*	Source
					Mean	Maximum		
Trichonida (Trichonis)	Greece	98.6	2868	15	~10	58	*Radix* sp. (still undescribed)	This study
Tule	USA	53	40	1230	1.22	?	No	This study
Turkana	Ethiopia/Kenya	6750	203.6	427	30.2	73	Unknown (no data)	This study
Victoria	Kenya/Tanzania/Uganda	62,940	2518	1134	40	85	*R. natalensis debaizei*	This study
Yangzong	China	32	0.617	1777	19.5	30	Two undescribed species	This study
Zaisan	Kazakhstan	5510	53	386	5	10	*R. auricularia* *R.* (?) *gebleri* (Middendorff, 1850)	([89]; this study])

* The morphometric data are taken mostly from Herdenford [74] and World Lake Database (https://wldb.ilec.or.jp/; accessed on 1 December 2024).

According to Boss, "distinguished by unique faunas and floras, usually with high degrees of endemism, these lakes differ from other fresh waters in their age" ([71], p. 385). The uniqueness of the biota of these lakes has attracted researchers since the mid-19th century. In the second half of the last century, some review works, especially devoted to large lakes and their malacofauna, were published [71,77,78,90]. The considerable geological age of such basins, which have numerous ecological niches and biotopes of various sorts, makes them "natural laboratories", where large-scale evolutionary processes can be observed [91,92]. Classical examples of intralacustrine radiations are the amphipods of Lake Baikal, cichlid fishes, and the so-called "thalassoid" snails of Tanganyika and some other lakes in Central Africa [85,93–95].

It is known that the lymnaeid snails, unlike some other families of freshwater gastropods (Acroloxidae, Baicaliidae, Planorbidae, Thiaridae, etc.), provide almost no examples of extensive diversification in ancient lakes [70,96–99]. However, the genus *Radix* seems to represent an exception to this pattern since its representatives are more or less common in lacustrine basins of relatively old age and tectonic origin [97].

We divided the lakes included in our analysis into four groups.

1. Those situated outside the native range of the genus *Radix*. This genus is of old-world origin [32] and is distributed almost exclusively in Africa and Eurasia (known also in Alaska [99]). Among these lakes, three lie in the Americas (Tahoe, Titicaca, and Thule), and a single one, Eyre, in Australia. Potentially, non-native species of *Radix* can penetrate them, as is the case with Palearctic *R. auricularia* in the Great Lakes of North America [100].
2. Old-world lakes with no data on their malacofauna. We were unable to find recent information about *Radix* in two large lakes in Africa, Mweru and Turkana. However, it is quite possible that the species *Radix natalensis* inhabits them (see below).
3. Lakes having no endemic species of *Radix*. This group of lakes is the largest. It includes such basin as Baikal, Tanganyika, Victoria, Lanao, and some others (see below).
4. Lakes with endemic representatives of the genus *Radix* in their fauna. In addition to Lake Issyk-Kul, such lakes as Lugu, Skadar, Yangzong, and Zaisan fall to this category.

Below, some lakes will be discussed separately (in alphabetic order).

African deep lakes (Albert, Edward, Kivu, Malawi, Tanganyika, and Victoria), which form a group of basins associated with the Central African Rift sub-system. In all the abovementioned lakes, only one species of *Radix*, *R. natalensis* sensu lato, is represented (see

Table 2). According to our observations, recorded in 2018 at lakes Albert and Victoria, these snails are restricted to the shallow zone of the lakes, being found on submerged stones, vegetation, and also in small waterbodies situated on the lakes' shores and periodically connected with them. Our results show, however, that *R. natalensis* represents a species complex, with at least three distinct subgroups, which are conditionally ranked here as subspecies. Lake Victoria is inhabited by the subspecies *R. natalensis debaizei* (Bourguignat, 1887), whereas another subspecies, *R. natalensis exsertus* (von Martens, 1866), has been identified in a sample from Albert Lake (see Figure 6J).

The taxonomic identity of *R. natalensis* from other lakes in Central Africa remains unclear. Most probably, *R. natalensis* sensu lato lives in the shallow zone of lakes Mweru and Turkana, but we lack evidence for this in the accessible literature.

Baikal Lake. Formerly, it was thought that this lake is inhabited by three species of *Radix*: *R. auricularia*, *R. intercisa* (Lindholm, 1909), and *R. psilia*, Bourguinat, 1862 [101]. A recent "integrative" revision [48] has revealed, however, that all *Radix* populations in Lake Baikal belong to *R. auricularia*, which probably penetrated the waterbody several times from different sources. *R. auricularia* still lives in Baikal, but only at shallow depths (up to 30 m), but its expansion into deeper parts of the lake is not excluded, which may have serious consequences for the aboriginal malacofauna, with there being dozens of endemic species of Gastropoda [48].

Biwa Lake. This basin has its own endemic species of *Radix*—*R. onychia* (Westerlund, 1883). According to our results, this is the most phylogenetically isolated species of *Radix* in ancient lakes (see Figure 3). Perhaps, the absolute age of this species is comparable with that of some endemic fish of Lake Biwa. According to Tabata et al. ([102], p. 2601), some of the endemic fish species "diverged from their closest relatives earlier (1.3–13.0 Ma) than the period in which the present environmental characteristics of the lake started to develop (ca. 0.4 Ma)".

Hövsgöl Lake. Sitnikova et al. [83] reported two species of *Radix* in this lake: *R. auricularia* and *R. mongolica* (Yen, 1939). The latter one is rather problematic and has never been subjected to molecular analysis. Its range covers Mongolia, northern China (Inner Mongolia), and the Russian Far East [15,16]. Though some malacologists accept it as a distinct species [15,16,103,104], it is absent from the most recent surveys of Central Asian and Far Eastern lymnaeids, based on the "integrative" approach [32,42].

Inle Lake. The data on the malacofauna of this lake are chiefly from the last century [28,105,106]. A single species of *Radix*, *R. mimetica* (Annandale, 1918), has been reported in Lake Inle. This is a synonym of *Radix* (*Exsertiana*) *rufescens* (J. E. Gray, 1822), which is common in South Asia, including Myanmar [24].

Lanao Lake. Stelbrink et al. [107] published a detailed survey of the malacofauna of this Indonesian lake. In their list, a species of *Radix*, whose species identity was not determined, has been included. Having compared sequences of these snails with those of our sequence library, we found that Lake Lanao is inhabited by *R. rubiginosa* (Michelin, 1831), a species widely distributed in Indonesia and some other countries of South-East Asia.

Lugu Lake, situated in Yunnan Province, China, represents the most intriguing case, since a small species flock of endemic *Radix* was found to have evolved in it [52]. Regrettably, the four *Radix* species identified in Lugu by means of the molecular taxonomic approach have not been formally described, and, thus, form part of the "grey names" group (sensu Minelli [108]), i.e., names non-compliant with ICZN rules. To date, this is the most intensive evolutionary radiation in a lake to be reported for *Radix* snails (the paleontological literature may provide other cases of such kind (e.g., [109]), but we are not sure that all fossil species classified in the genus *Radix* actually belong to this taxon).

Ohrid and Prespa Lakes, are two “sister lakes” in the Balkans. Albrecht et al. [86] listed two species of *Radix*: *R. relicta* (Poliński, 1929), endemic to Ohrid, and *R. pinteri*, Schütt, 1974, which is unique to Lake Prespa. *R. auricularia* was mentioned in this paper as living in Prespa. According to current taxonomy of the Lymnaeidae, both *R. relicta* and *R. pinteri* are not members of the genus *Radix.* Aksenova et al. [32] classified them as belonging to the genus *Ampullaceana*, Servain, 1882.

Skadar Lake. In 2008, an endemic species, *Radix skutaris*, was described for this lake [110]. The original description was exclusively based on morphological data, and lately Glöer ([111], p. 246) acknowledged that *R. skutaris* is “genetically conspecific with *R. auricularia* but there are morphological arguments enough for the distinction of this species”. Our results demonstrate that *Radix skutaris* is not only not genetically identical to *R. auricularia* but forms a phylogenetically distant clade close to the group of Central Asian members of the genus—*R. alticola* (Izzatullaev and Kruglov and Starobogatov, 1983) and *R. euphratica* (Mousson, 1874).

Trichonis Lake. Having analysed a large library of sequences of various species of *Radix*, Aksenova et al. [32] found that this lake maintains a separate, but still undescribed, species of the genus *Radix*. We do not have material on this snail at our disposal and, thus, are unable to describe it as a new species.

Yangzong Lake. This lake, situated in Yunnan Province, China, is inhabited by two undescribed species of *Radix* revealed by our phylogenetic and species delimitation analyses. Together with four undescribed species from Lugu Lake, they form what can be called “Yunnan lakes’ species flock” (see Figure 3). Its structure, species composition, and the relationships between its constituent species need special study.

Zaisan Lake. Vinarski [89] discussed the status of *Radix gebleri* (Middendorff, 1850), a species thought to be endemic to Zaisan Lake (East Kazakhstan). Unfortunately, in the 1960s, a dam was built on the Upper Irtysh River, which drastically transformed the ecosystem of Zaisan Lake and its hydrological regime [3]. Since 1965, no new findings of *R. gebleri* have been made. In July 2018, one of the authors (MVV) undertook a special trip to Zaisan Lake in the hope of collecting living specimens of *R. gebleri*. That attempt failed, and neither living individuals nor empty shells of the snails were found. However, the presence of *R. auricularia* in the shallow zone of Zaisan Lake was observed (M. Vinarski, unpublished data). Perhaps, *R. gebleri* has disappeared in the waterbody following the transformation of its ecosystem. Conchologically, this species is rather similar to another lymnaeid species, *Ampullaceana ampla* (Hartmann, 1821), and, probably, does not belong to the genus *Radix*.

5. Conclusions

1. Issyk-Kul Lake is inhabited by two genetically distinct species of the genus *Radix*: *R. auricularia*, which is broadly distributed throughout Palearctic, and the presumably endemic *R. obliquata*.
2. Within the Lymnaeidae, *Radix* is the only genus whose members are widely represented in malacofaunas of ancient tectonic lakes, and several endemic species have evolved within *Radix* in these lakes (in Europe, Central, and East Asia).
3. A list of endemic *Radix* of ancient tectonic lakes includes *Radix obliquata*, *R. onychia*, and *R. skutaris,* as well as four undescribed species from Lake Lugu and two species from Lake Yangzong (both lakes are in Yunnan Province, China). Both the taxonomic identity and current status of *R. gebleri* of Zaisan Lake remain obscure.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/d17020112/s1, File S1. Supplementary tables and File S2. Supplementary figures.

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References

1. World Lake Database. Lake Issyk-Kool. Available online: https://wldb.ilec.or.jp/Lake/ASI-55 (accessed on 12 December 2024).
2. Edelshtein, K.K. Issyk-Kul Lake. In *Bolshaya Rossiyskaya Encyclopedia [The Great Russian Encyclopedia]*; Osipov, Y.S., Ed.; BRE: Moscow, Russia, 2008; Volume 12, p. 95. (In Russian)
3. Sevastianov, D.V. (Ed.) *A History of Sevan, Issyk-Kul, Balkhash, Zaisan and Aral Lakes*; Nauka Publishers: St. Petersburg, Russia, 1991; pp. 1–304. (In Russian)
4. Semyonov, P.P. The first trip to T'ien-Shan, or the Sky Ridge, towards the upper courses of the Yaxart, or Syr-Daria, River, in 1857. *Vestn. Rus. Imp. Geogr. Obs.* **1858**, *23*, 1–25. (In Russian)
5. Von Martens, E. Drei centralasiatische Schnecken. *Malakozool. Blätter* **1864**, *11*, 114–119.
6. Vinarski, M.V. Eduard von Martens's contribution to the knowledge of the Russian continental malacofauna (with examination of type materials of aquatic species accepted by Russian taxonomists). *Ruthenica Russ. Malacol. J.* **2016**, *26*, 1–16.
7. Clessin, S. Beschreibung neuer Arten aus der Umgebung des Issykkul-sees. *Nachrichtsblatt Dtsch. Malakozool. Ges.* **1894**, *26*, 64–66.
8. Clessin, S. Mollusken aus dem Issykul. *Nachrichtsblatt Dtsch. Malakozool. Ges.* **1907**, *40*, 5–9.
9. Starobogatov, Y.I. New species of gastropods from springs and subterranean waters of Middle Asia. *Tr. Zool. Instituta AN SSSR* **1972**, *50*, 165–172. (In Russian)

10. Zhadin, V.I. *Molluscs of Fresh- and Brakishwaters of the USSR*; The USSR Academy of Sciences Press: Moscow-Leningrad, Russia, 1952; pp. 1–346. (In Russian)
11. Hubendick, B. Studies on Ancylidae. The palaearctic and oriental species and formgroups. *Acta Regiae Soc. Sci. Litt. Gothoburgensis. Zool.* **1970**, *5*, 1–52.
12. Vinarski, M.V.; Kantor, Y.I. *Analytical Catalogue of Fresh and Brackish Water Molluscs of Russia and Adjacent Countries*; A.N. Severtsov Institute of Ecology and Evolution of RAS: Moscow, Russia, 2016; pp. 1–544.
13. Izzatullaev, Z.I.; Starobogatov, Y.I. Zoogeographic characteristics of the freshwater molluscs in Central Asia and the problem of validity of the Mountain-Asian subregion of the Palearctic. *Zool. Zhurnal* **1985**, *54*, 506–517. (In Russian)
14. Izzatullaev, Z.I.; Starobogatov, Y.I. *Odhneripisidium* species from the fauna of the USSR (Bivalvia, Pisidiidae). *Tr. Zool. Instituta AN SSSR* **1986**, *148*, 54–70. (In Russian)
15. Kruglov, N.D.; Starobogatov, Y.I. Annotated and illustrated catalogue of species of the family Lymnaeidae (Gastropoda Pulmonata Lymnaeiformes) of Palaearctic and adjacent river drainage areas. Part I. *Ruthenica Russ. Malacol. J.* **1993**, *3*, 65–92.
16. Kruglov, N.D. *Lymnaeid Snails of Europe and Northern Asia*; Smolensk State Pedagogical University Press: Smolensk, Russia, 2005; pp. 1–508. (In Russian)
17. Vinarski, M.V. Annotated type catalogue of lymnaeid snails (Mollusca, Gastropoda) in the collection of the Natural History Museum, Berlin. *Zoosystematics Evol.* **2016**, *92*, 131–152. [CrossRef]
18. Heynemann, D.F. Einige Bemerkungen über die Veränderlichkeit der Molluskenschalen und Verwandtes. *Nachrichtsblatt Dtsch. Malakozool. Ges.* **1870**, *2*, 1–40.
19. von Martens, E. Slugs (Mollusca). In *A.P. Fedchenko's Travel to Turkestan. Volume II. Zoogeographic Studies*; The Imperial Society of Naturalists: Saint-Pétersbourg, Moscow, Russia, 1874; Volume 1, pp. 1–66. Available online: https://www.biodiversitylibrary.org/page/12906577 (accessed on 1 December 2024). (In Russian)
20. von Martens, E. Über centralasiatische Mollusken. *Mémoires L'académie Impériale Sci. St. Pétersbourg Ser. 7* **1882**, *30*, 1–65.
21. Weber, A. Wissenschaftliche Ergebnisse der Reise von Prof. Dr. G. Merzbacher im zentralen und östlichen Thian-Schan 1907/8 III. Mollusken. *Abh. Math.-Phys. Kl. Königlich Bayer. Akad. Wiss.* **1913**, *26*, 1–26.
22. Izzatullaev, Z.I.; Kruglov, N.D.; Starobogatov, Y.I. New and ill-known species of mollusks of the subgenus *Radix* of the genus *Lymnaea* of the USSR fauna from the Central Asia (Gastropoda, Pulmonata). *Izv. Akad. Nauk Tajikskoy SSR Otd. Biol. Nauk* **1983**, *4*, 53–57.
23. Nevill, G. Mollusca. In *Scientific Results of the Second Yarkand Mission; Based Upon the Collections and Notes of the Late Ferdinand Stoliczka Ph.D.*; Office of the Superintendent of Government Printing: Calcutta, India, 1878; pp. 1–21.
24. Vinarski, M.V. Nomenclator of species-group taxa of the Recent Lymnaeidae (Gastropoda: Hygrophila). *Ruthenica Russ. Malacol. J.* **2024**, *34*, 191–324. [CrossRef]
25. Yen, T.-C. Die chinesischen Land- und Süßwasser-Gastropoden des Natur-Museums Senckenberg. *Abh. Senckenberg. Naturforschenden Ges.* **1939**, *444*, 1–233.
26. Yen, T.-C. A review of Chinese gastropods in the British Museum. *Proc. Malacol. Soc. Lond.* **1942**, *24*, 170–289. [CrossRef]
27. Qi, Z.-Y.; Ma, X.-T.; Liu, Y.-Y.; Chen, D.-N.; Wang, Y.-X.; Zhang, W.-Z.; Gao, J.-Z. *Atlas of Animals of China. Volume 4. Mollusca*; Science Press: Bejing, China, 1985. (In Chinese)
28. Subba Rao, N.V. *Handbook: Freshwater Molluscs of India*; Zoological Survey of India: Calcutta, India, 1989; pp. 1–289.
29. Vinarski, M.V.; Aksenova, O.V.; Bolotov, I.N. Taxonomic assessment of genetically-delineated species of radicine snails (Mollusca, Gastropoda, Lymnaeidae). *Zoosystematics Evol.* **2020**, *96*, 577–608. [CrossRef]
30. Vinarski, M.V. On the reality of local and ecological races in lymnaeid snails (Mollusca, Gastropoda, Lymnaeidae). *Biol. Bull.* **2016**, *43*, 1003–1017. [CrossRef]
31. Jackiewicz, M. European species of the family Lymnaeidae (Gastropoda, Pulmonata, Basommatophora). *Genus* **1998**, *9*, 1–93.
32. Aksenova, O.V.; Bolotov, I.N.; Gofarov, M.Y.; Kondakov, A.V.; Vinarski, M.V.; Bespalaya, Y.V.; Kolosova, Y.S.; Palatov, D.M.; Sokolova, S.E.; Spitsyn, V.M.; et al. Species richness, molecular taxonomy and biogeography of the radicine pond snails (Gastropoda: Lymnaeidae) in the Old World. *Sci. Rep.* **2018**, *8*, 11199. [CrossRef] [PubMed]
33. Vinarski, M.V.; von Oheimb, P.V.; Aksenova, O.V.; Gofarov, M.Y.; Kondakov, A.V.; Nekhaev, I.O.; Bolotov, I.N. Trapped on the Roof of the World: Taxonomic diversity and evolutionary patterns of Tibetan Plateau endemic freshwater snails (Gastropoda: Lymnaeidae: *Tibetoradix*). *Integr. Zool.* **2022**, *17*, 825–848. [CrossRef]
34. Folmer, O.; Black, M.; Hoeh, W.; Lutz, R.; Vrijenhoek, R. DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Mol. Mar. Biol. Biotechnol.* **1994**, *3*, 294–299.
35. Palumbi, S.R. Nucleic Acids II: The Polymerase Chain Reaction. In *Molecular Systematics*; Hillis, D.M., Moritz, C., Mable, B.K., Eds.; Sinauer Associates: Sunderland, MA, USA, 1996; pp. 205–247.
36. Park, J.K.; Foighil, D.Ó. Sphaeriid and corbiculid clams represent separate heterodont bivalve radiations into freshwater environments. *Mol. Phylogenet. Evol.* **2002**, *14*, 75–88. [CrossRef]

37. Mollaret, I.; Jamieson, B.G.; Adlard, R.D.; Hugall, A.; Lecointre, G.; Chombard, C.; Justine, J.L. Phylogenetic analysis of the Monogenea and their relationships with Digenea and Eucestoda inferred from 28S rDNA sequences. *Mol. Biochem. Parasitol.* **1997**, *90*, 433–438. [CrossRef]
38. Hall, T.A. BioEdit: A user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symp. Ser.* **1999**, *41*, 95–98.
39. Johnson, M.; Zaretskaya, I.; Raytselis, Y.; Merezhuk, Y.; McGinnis, S.; Madden, T.L. NCBI BLAST: A better web interface. *Nucleic Acids Res.* **2008**, *36*, W5–W9. [CrossRef]
40. Kumar, S.; Stecher, G.; Li, M.; Knyaz, C.; Tamira, K. MEGA X: Molecular evolutionary genetics analysis across computing platforms. *Mol. Biol. Evol.* **2018**, *35*, 1547–1549. [CrossRef]
41. Bandelt, H.J.; Forster, P.; Röhl, A. Median-joining networks for inferring intraspecific phylogenies. *Mol. Biol. Evol.* **1999**, *16*, 37–48. [CrossRef]
42. Aksenova, O.V.; Vinarski, M.V.; Itagaki, T.; Ohari, Y.; Oshida, T.; Kim, S.K.; Lee, J.H.; Kondakov, A.V.; Khrebtova, I.S.; Soboleva, A.A.; et al. Taxonomy and trans-Beringian biogeography of the pond snails (Gastropoda: Lymnaeidae) of East Asia: An integrative view. *Zool. J. Linn. Soc.* **2024**, *201*, zlae083. [CrossRef]
43. Nguyen, L.-T.; Schmidt, H.A.; von Haeseler, A.; Minh, B.Q. IQ-TREE: A fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. *Mol. Biol. Evol.* **2015**, *32*, 268–274. [CrossRef] [PubMed]
44. Trifinopoulos, J.; Nguyen, L.T.; von Haeseler, A.; Manh, B.Q. W-IQ-TREE: A fast online phylogenetic tool for maximum likelihood analysis. *Nucleic Acids Res.* **2016**, *44*, W232–W235. [CrossRef] [PubMed]
45. Minh, B.-Q.; Schmidt, H.A.; Chernomor, O.; Schrempf, D.; Woodhams, M.D.; von Haeseler, A.; Lanfear, R. IQ-TREE 2: New Models and Efficient Methods for Phylogenetic Inference in the Genomic Era. *Mol. Biol. Evol.* **2020**, *37*, 1530–1534. [CrossRef] [PubMed]
46. Hoang, D.T.; Chernomor, O.; von Haeseler, A.; Mihn, B.Q.; Vihn, L.S. UFBoot2: Improving the ultrafast bootstrap approximation. *Mol. Biol. Evol.* **2017**, *35*, 518–522. [CrossRef]
47. Kapli, P.; Lutteropp, S.; Zhang, J.; Kobert, K.; Pavlidis, P.; Stamatakis, A.; Flouri, T. Multi-rate Poisson tree processes for single-locus species delimitation under maximum likelihood and Markov chain Monte Carlo. *Bioinformatics* **2017**, *33*, 1630–1638. [CrossRef]
48. Puillandre, N.; Lambert, A.; Brouillet, S.; Achaz, G. ABGD, automatic barcode gap discovery for primary species delimitation. *Mol. Ecol.* **2012**, *21*, 1864–1877. [CrossRef]
49. Aksenova, O.; Vinarski, M.; Bolotov, I.; Kondakov, A.; Bespalaya, Y.; Tomilova, A.; Paltser, I.; Gofarov, M. Two *Radix* spp. (Gastropoda: Lymnaeidae) endemic to thermal springs around Lake Baikal represent ecotypes of the widespread *Radix auricularia*. *J. Zool. Syst. Evol. Res.* **2017**, *55*, 298–309. [CrossRef]
50. Schniebs, K.; Sitnikova, T.Y.; Vinarski, M.V.; Müller, A.; Khanaev, I.V.; Hundsdoerfer, A. Morphological and genetic variability in *Radix auricularia* (Mollusca: Gastropoda: Lymnaeidae) of Lake Baikal, Siberia: The story of an unfinished invasion into the ancient deepest lake. *Diversity* **2022**, *14*, 527. [CrossRef]
51. Vinarski, M.V.; Aksenova, O.V.; Bespalaya, Y.V.; Gofarov, M.Y.; Kondakov, A.V.; Khrebtova, I.S.; Makhrov, A.A.; Bolotov, I.N. How an Ecological Race Is Forming: Morphological and Genetic Disparity among Thermal and Non-Thermal Populations of Aquatic Lymnaeid Snails (Gastropoda: Lymnaeidae). *Diversity* **2023**, *15*, 548. [CrossRef]
52. Wiese, R.; Clewing, G.; Albrecht, C.; Rabethge, C.; Zhang, H.; Riedel, F. How ancient is Lake Lugu (Yunnan, China)? The gastropods' viewpoint with focus on *Radix* (Lymnaeidae). *J. Great Lakes Res.* **2020**, *46*, 1099–1112. [CrossRef]
53. Pavlova, M.V. Biology and productivity of *Limnaea* (*Radix*) *auricularia* (L.) var. *obliquata* Martens in the Lake Issyk-Kul. In *Limnologicheskiye Issledovaniya v Kirgizii*; Konurbaev, A.O., Ed.; Ilim: Frunze, Kyrgyzstan, 1983; pp. 34–46. (In Russian)
54. Aksenova, O.V.; Vinarski, M.V.; Kondakov, A.V.; Tomilova, A.A.; Artamonova, V.S.; Makhrov, A.A.; Kononov, O.D.; Gofarov, M.Y.; Fang, Y.; Bolotov, I.N. A new *Radix* species from Qinling Mountains, China (Gastropoda: Lymnaeidae). *Ecol. Montenegrina* **2019**, *26*, 137–146. [CrossRef]
55. Albrecht, C.; Wilke, T.; Kuhn, K.; Streit, B. Convergent evolution of shell shape in freshwater limpets: The African genus *Burnupia*. *Zool. J. Linn. Soc.* **2004**, *140*, 577–588. [CrossRef]
56. Köhler, F.; Criscione, F. A molecular phylogeny of camaenid land snails from north-western Australia unravels widespread homoplasy in morphological characters (Gastropoda, Helicoidea). *Mol. Phylogenet. Evol.* **2015**, *83*, 44–55. [CrossRef]
57. Chang, Z.-Y.; Liew, T.-S. A molecular phylogeny of *Geotrochus* and *Trochomorpha* species (Gastropoda: Trochomorphidae) in Sabah, Malaysia reveals convergent evolution of shell morphology driven by environmental influences. *PeerJ* **2021**, *9*, e10526. [CrossRef]
58. von Oheimb, P.V.; Albrecht, C.; Riedel, F.; Du, L.; Jang, J.; Aldridge, D.C.; Bössneck, U.; Zhang, H.; Wilke, T. Freshwater biogeography and limnological evolution of the Tibetan Plateau—Insights from a plateau-wide distributed gastropod taxon (*Radix* spp.). *PLoS ONE* **2011**, *6*, e26307. [CrossRef]
59. Clewing, C.; Albrecht, C.; Wilke, T. A complex system of glacial sub-refugia drives endemic freshwater biodiversity on the Tibetan Plateau. *PLoS ONE* **2016**, *11*, e0160286. [CrossRef]
60. Tsalolikhin, S.Y. The origin of the fauna of Nematoda of Issyk-Kul Lake. *Zool. Zhurnal* **1979**, *58*, 629–635. (In Russian)

61. Lemzina, V.L. *Free-Living Nematoda of Issyk-Kul and Son-Kul Lakes*; Ilim: Frunze, Russia, 1989; pp. 1–143. (In Russian)
62. Kutikova, L.A.; Foliyan, L.A. The Rotifera of Issyk-Kul Lake. *Tr. Zool. Instituta RAN* **1996**, *267*, 1–164. (In Russian)
63. Karabekova, D.U. Results of studying of Issyk-Kul Lake basin's monogeneas (Monogenea). *Parazitologiya* **2007**, *41*, 145–149. (In Russian)
64. Pivnev, I.A. *Fishes of Kirgizia (Conservation and Reproduction)*; Kyrgyzstan Publishers: Frunze, Kyrgyzstan, 1990; pp. 1–128. (In Russian)
65. Dumont, H.J. Biogeography of rotifers. *Hydrobiologia* **1983**, *104*, 19–30. [CrossRef]
66. Curini-Galletti, M.; Artois, T.; Delogu, V.; De Smet, W.H.; Fontaneto, D.; Jondelius, U.; Leasi, F.; Martinez, A.; Meyer-Wachsmuth, I.; Nillson, K.S.; et al. Patterns of Diversity in Soft-Bodied Meiofauna: Dispersal Ability and Body Size Matter. *PLoS ONE* **2012**, *7*, e33801. [CrossRef] [PubMed]
67. Fontaneto, D. Long-distance passive dispersal in microscopic aquatic animals. *Mov. Ecol.* **2019**, *7*, 10. [CrossRef]
68. Rylov, V.M. Some qualitative and quantitative data on the Issyk-Kul Lake plankton. *Tr. Kirg. Kompleks. Ekspeditsii AN SSSR* **1935**, *3*, 87–96. (In Russian)
69. Akekseev, V.R.; Sukhikh, N.M.; Chaban, O.A. Expected and unexpected results of the first study of Copepoda of Issyk-Kul Lake by means of aqualung. In *Tezisy Dokladov Otchetnoy Nauchnoy Sessii Zoologicheskogo Instituta RAN po Itogam Rabot 2023 g*; ZIN RAN: St.-Petersburg, Russia, 2024; pp. 4–6. (In Russian)
70. Pešić, V.; Smit, H. A checklist of the water mites of Central Asia with description of six new species (Acari, Hydrachnidia) from Kyrgyzstan. *Acarologia* **2018**, *58*, 165–185. [CrossRef]
71. Boss, K. On the evolution of gastropods in ancient lakes. In *Pulmonates. Volume 2A. Systematics, Evolution and Ecology*; Fretter, V., Peake, J., Eds.; Academic Press: Cambridge, MA, USA, 1978; pp. 385–428.
72. Pešić, V.; Karaman, G.S.; Kostianoy, A.G. Introduction. In *The Skadar/Shkodra Lake Environment*; The Handbook of Environmental Chemistry; Pešić, V., Karaman, G., Kostianoy, A., Eds.; Springer: Cham, Switzerland, 2018; Volume 80, pp. 1–10. [CrossRef]
73. Grabowski, M.; Jabłońska, A.; Wysocka, A.; Pešić, V. The Obscure History of the Lake Skadar and Its Biota: A Perspective for Future Research. In *The Skadar/Shkodra Lake Environment*; The Handbook of Environmental Chemistry; Pešić, V., Karaman, G., Kostianoy, A., Eds.; Springer: Cham, Switzerland, 2018; Volume 80, pp. 47–61. [CrossRef]
74. Herdendorf, C.E. Large lakes of the world. *J. Great Lakes Res.* **1982**, *8*, 379–412. [CrossRef]
75. Mackay, A.W. Large Lakes. In *The Encyclopedia of Quaternary Science*; Elias, S.A., Ed.; Elsevier: Amsterdam, The Netherlands, 2013; Volume 1, pp. 546–553.
76. Wilke, T.; Wagner, B.; Van Bocxlaer, B.; Albrecht, C.; Ariztegui, D.; Delicado, D.; Francke, A.; Harzhauser, M.; Hauffen, T.; Holtveth, J.; et al. Scientific drilling projects in ancient lakes: Integrating geological and biological histories. *Glob. Planet. Chang.* **2016**, *143*, 118–151. [CrossRef]
77. Mackay, A.W.; Edlund, M.B.; Khursevich, G. Diatoms in ancient lakes. In *The Diatoms: Applications for the Environmental and Earth Sciences*, 2nd ed.; Smol, J.P., Stoermer, E.F., Eds.; Cambridge University Press: Cambridge, UK, 2010; pp. 209–228. [CrossRef]
78. Brooks, J.L. Speciation in ancient lakes. *Q. Rev. Biol.* **1950**, *25*, 30–60, 131–176. [CrossRef]
79. Vinarski, M.V.; Kijashko, P.V.; Andreeva, S.I.; Sitnikova, T.Y.; Yanina, T.A. Atlas and catalogue of the living mollusks of the Aral and Caspian Seas. *Vita Malacol.* **2024**, *23*, 1–124.
80. Van Damme, D.; Van Bocxlaer, B. Freshwater Molluscs of the Nile Basin, Past and Present. In *The Nile: Origin, Environments, Limnology and Human Use*; Dumont, H.J., Ed.; Springer: Dordrecht, The Netherlands, 2010; pp. 585–629. [CrossRef]
81. Butenko, Y.V. On the fauna of freshwater molluscs of the South and South-East Kazakhstan. *Tr. Zool. Instituta AN SSSR* **1967**, *42*, 205–212. (In Russian)
82. Habe, T. Type specimens of the Japanese land and freshwater molluscs collected during the Vega Expedition and housed in the Swedish Natural History Museum in Stockholm. *Venus Jpn. J. Malacol.* **1984**, *43*, 305–313.
83. Sitnikova, T.; Goulden, C.; Robinson, D. On gastropod mollusks from lake Hövsgöl. In *The Geology, Biodiversity and Ecology of Lake Hövsgöl (Mongolia)*; Goulden, C., Sitnikova, T.Y., Gelhaus, J., Boldgiv, B., Eds.; Backhuys Publishers: Leiden, The Netherlands, 1997; pp. 233–252.
84. Dusabe, M.C.; Kalinda, C.; Clewing, C.; Hyangya, B.L.; Van Bocxlaer, B.; Albrecht, C. Environmental perturbations and anthropogenic disturbances determine mollusc biodiversity of Africa's explosive Lake Kivu. *J. Great Lakes Res.* **2024**, *50*, 102339. [CrossRef]
85. Van Damme, D.; Gautier, A. Lacustrine mollusc radiations in the Lake Malawi Basin: Experiments in a natural laboratory for evolution. *Biogeosciences* **2013**, *10*, 5767–5778. [CrossRef]
86. Albrecht, C.; Wolff, C.; Glöer, P.; Wilke, T. Concurrent evolution of ancient sister lakes and sister species: The freshwater gastropod genus Radix in lakes Ohrid and Prespa. *Hydrobiologia* **2008**, *615*, 157–167. [CrossRef]
87. Dejoux, C. The Mollusca. In *Lake Titicaca—A Synthesis of Limnological Knowledge*; Dejoux, C., Ilties, A., Eds.; Kluwer: Dordrecht, The Nethelands, 1992; pp. 311–336.

88. Kroll, O.; Hershler, R.; Albrecht, C.; Terrazas, E.M.; Apazo, R.; Fuentealba, C.; Wolff, C.; Wilke, T. The endemic gastropod fauna of Lake Titicaca: Correlation between molecular evolution and hydrographic history. *Ecol. Evol.* **2012**, *2*, 1517–1530. [CrossRef]
89. Vinarski, M.V. The taxonomic status of *Limnaeus gebleri* Middendorff, 1851 (Gastropoda: Pulmonata: Lymnaeidae). *Mollusca* **2009**, *27*, 149–156.
90. Starobogatov, Y.I. *Molluscan Fauna and Zoogeographic Zonation of Continental Freshwater Bodies of the World*; Nauka: Leningrad, Russia, 1970; pp. 1–372. (In Russian)
91. Speciation in ancient lakes. In *Advances in Limnology*; Martens, K., Goddeeris, B., Coulter, G., Eds.; Schweizerbart Science Publishers: Stuttgart, Germany, 1994; Volume 44, pp. 1–508.
92. Wesselingh, F. Long-Lived Lake Molluscs as Island Faunas: A Bivalve Perspective. In *Biogeography, Time, and Place: Distributions, Barriers, and Islands*; Renema, W., Ed.; Springer: Dordrecht, The Netherlands, 2007; pp. 275–314. [CrossRef]
93. Kozhov, M.M. Lake Baikal and its life. In *Monographiae Biologicae*; Springer: Dordrecht, The Netherlands, 1963; Volume 11, pp. vii+1–344. [CrossRef]
94. Wilson, A.B.; Glaubrecht, M.; Axel, M. Ancient lakes as evolutionary reservoirs: Evidence from the thalassoid gastropods of Lake Tanganyika. *Proc. R. Soc. Lond. Ser. B* **2004**, *271*, 529–536. [CrossRef]
95. Seehausen, O. African cichlid fish: A model system in adaptive radiation research. *Proc. R. Soc. Ser. B* **2006**, *273*, 1987–1998. [CrossRef]
96. Vinarski, M.V. The family Lymnaeidae in ancient lakes: A review and synthesis of data on extant and fossil taxa. In Proceedings of the SIAL 8—Speciation in Ancient Lakes: Celebrating 25 Years and Moving Towards the Future, Entebbe, Uganda, 29 July–3 August 2018; p. 66, Conference Program and Abstracts.
97. Albrecht, C.; Stelbrink, B.; Clewing, C. Patterns and Processes of Speciation in Lymnaeidae. In *The Lymnaeidae: A Handbook on Their Natural History and Parasitological Significance*; Vinarski, M.V., Vázquez, A.A., Eds.; Springer Nature: Cham, Switzerland, 2023; pp. 207–226. [CrossRef]
98. Vinarski, M.V.; Aksenova, O.V. Ecology of lymnaeid snails. In *The Lymnaeidae: A Handbook on Their Natural History and Parasitological Significance*; Vinarski, M.V., Vázquez, A.A., Eds.; Springer Nature AG: Cham, Switzerland, 2023; pp. 227–263. [CrossRef]
99. Vinarski, M.V.; Aksenova, O.V.; Bolotov, I.N.; Vázquez, A.A.; Alda, P.; Pointier, J.-P.; Hurtrez-Boussès, S. Biogeography of the Living Lymnaeidae. In *The Lymnaeidae: A Handbook on Their Natural History and Parasitological Significance*; Vinarski, M.V., Vázquez, A.A., Eds.; Springer Nature AG: Cham, Switzerland, 2023; pp. 183–206. [CrossRef]
100. Mills, E.L.; Leach, J.H.; Carlton, J.T.; Secor, C.L. Exotic Species in the Great Lakes: A History of Biotic Crises and Anthropogenic Introductions. *J. Great Lakes Res.* **1993**, *19*, 1–54. [CrossRef]
101. Sitnikova, T.Y.; Starobogatov, Y.I.; Shirokaya, A.A.; Shibanova, I.V.; Korobkova, N.V.; Adov, F.V. Gastropoda. In *Index of Animal Species Inhabiting Lake Baikal and Its Catchment Area*; Timoshkin, O.A., Ed.; Nauka: Novosibirsk, Russia, 2004; Volume 1, pp. 937–1002. (In Russian)
102. Tabata, R.; Kakioka, R.; Tominaga, K.; Komiya, T.; Watanabe, K. Phylogeny and historical demography of endemic fishes in Lake Biwa: The ancient lake as a promoter of evolution and diversification of freshwater fishes in western Japan. *Ecol. Evol.* **2016**, *6*, 2601–2623. [CrossRef]
103. Prozorova, L.A. Morphology of egg-clusters of gastropods from the Primorye Region of the USSR. *Tr. Zool. Instituta AN SSSR* **1991**, *228*, 74–110. (In Russian)
104. Vinarski, M.V.; Palatov, D.M.; Maryinskiy, V.V. Checklist of the freshwater snails (Mollusca: Gastropoda) of Mongolia. *Zootaxa* **2017**, *4317*, 45–78. [CrossRef]
105. Annandale, T.N. Aquatic molluscs of the Inle Lake and connected waters. *Rec. Indian Mus.* **1918**, *14*, 103–182. [CrossRef]
106. Annandale, T.N.; Rao, H.S. Further observations on the aquatic gastropods of the Inle watershed. *Rec. Indian Mus.* **1925**, *27*, 101–127. [CrossRef]
107. Stelbrink, B.; von Rintelen, T.; Albrecht, C.; Clewing, C.; Naga, P.O. Forgotten for decades: Lake Lanao and the genetic assessment of its mollusc diversity. *Hydrobiologia* **2019**, *843*, 31–49. [CrossRef]
108. Minelli, A. The galaxy of the non-Linnaean nomenclature. *Hist. Philos. Life Sci.* **2019**, *41*, 31. [CrossRef]
109. Popova, S.M.; Devyatkin, Y.V.; Starobogatov, Y.I. *Molluscs of the Kyzylgir Formation of the Altay Mountains*; Nauka: Moscow, Russia, 1970; pp. 1–95. (In Russian)
110. Glöer, P.; Pešić, V. *Radix skutaris* n. sp., a new species from Montenegro (Gastropoda: Lymnaeidae). *Mollusca* **2008**, *26*, 83–88.
111. Glöer, P. *The Freshwater Gastropods of the West-Palaearctis: Volume 1. Fresh- and Brackish Waters Except Spring and Subterranean Snails. Identification Key, Anatomy, Ecology, Distribution*; Selbstverlag: Hetlingen, Germany, 2019; pp. 1–399.