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A malacological study of the Ukok Plateau lakes

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Abstract. The article reports on the results of an interdisciplinary scientific expedition to the Ukok Plateau of the Kosh-Agachsky District, Altai Republic, Russia, that took place in August 2021. Freshwater molluscs were collected from the lakes Ukok and Kaldzhin-Kul. The morphological and molecular genetic analyses show that the snails collected from the two lakes are of the *Ampullaceana lagotis* species. However, the study identified a range of morphological and genetic differences between the molluscs from the two different lakes. This indicates that they represent isolates. In addition, the lack of intrapopulation variability in *A. lagotis* molluscs may indicate a relatively recent settlement of these snails in the lakes Ukok and Kaldzhin-Kul.

Keywords: Altai, Ukok Plateau, molluscs, *Ampullaceana lagotis*, Lake Ukok, Lake Kaldzhin-Kul, isolates

Малакологическое изучение озер плоскогорья Укок

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Аннотация. В августе 2021 г. в рамках комплексной экспедиции на плоскогорье Укок (Кош-Агачский район Республики Алтай) были собраны пресноводные моллюски в озерах Укок и Кальджин-Куль. На основании морфологического и молекулярно-генетического анализа улитки из обоих озер отнесены к виду *Ampullaceana lagotis*. Однако определенные морфологические и генетические отличия между моллюсками из разных озер позволяют определить их как изоляты. Кроме того, отсутствие внутрипопуляционной вариабельности моллюсков *A. lagotis* может свидетельствовать об относительно недавнем заселении улиток этого вида в озера Укок и Кальджин-Куль.

Ключевые слова: Алтай, плоскогорье Укок, моллюски, *Ampullaceana lagotis*, озеро Укок, озеро Кальджин-Куль, изоляты

Introduction

The scientific expedition that lasted from 27 to 29 August 2021 explored the Ukok and Kaldzhin-Kul lakes on the Ukok Plateau of the Kosh-Agachsky District, Altai Republic, Russia. The average absolute elevations of the Ukok Plateau range from 2,200 to 2,500 metres.

The Ukok Plateau is bounded by high mountains with altitudes of 4,000 m and higher (e. g., the 4,134 m high mountain Russky Shater of the Tavan-Bogdo-Ul Range) with the South Chuysky Ridge of the Central Altai in the north and north-east, the Karaalakhinsky Mountains in the west and the foot of the Saylyugem Mountains up to the Tarkhatinskaya Basin in the east. In the south, the Plateau is bounded by the following ranges: Saylyugem (western end), Tavan-Bogdo-Ul and Southern Altai. The Ukok Plateau is the result of erosion and denudation in the Mesozoic, the Paleogene and the Neogene (Bogachkin 1981). Some of its geomorphological structures have higher than average absolute elevations, e.g., the Kyzyltas Range (2,646 m).

The Ukok Plateau is permafrost. Its climate is extremely continental with average annual temperatures reaching –27°C in January and as low as +9.4°C in July (Kharlamova 2004). At the end of August, the water temperature in the plateau lakes is no higher than 8–9°C. The low temperatures do not encourage woody vegetation. The gently-sloping waterlogged plains of the plateau are grassland halophytic steppes as well as lowland bogs with sedge and cottongrass or tundra with sedge and kobresia grown on peat and gley soils.

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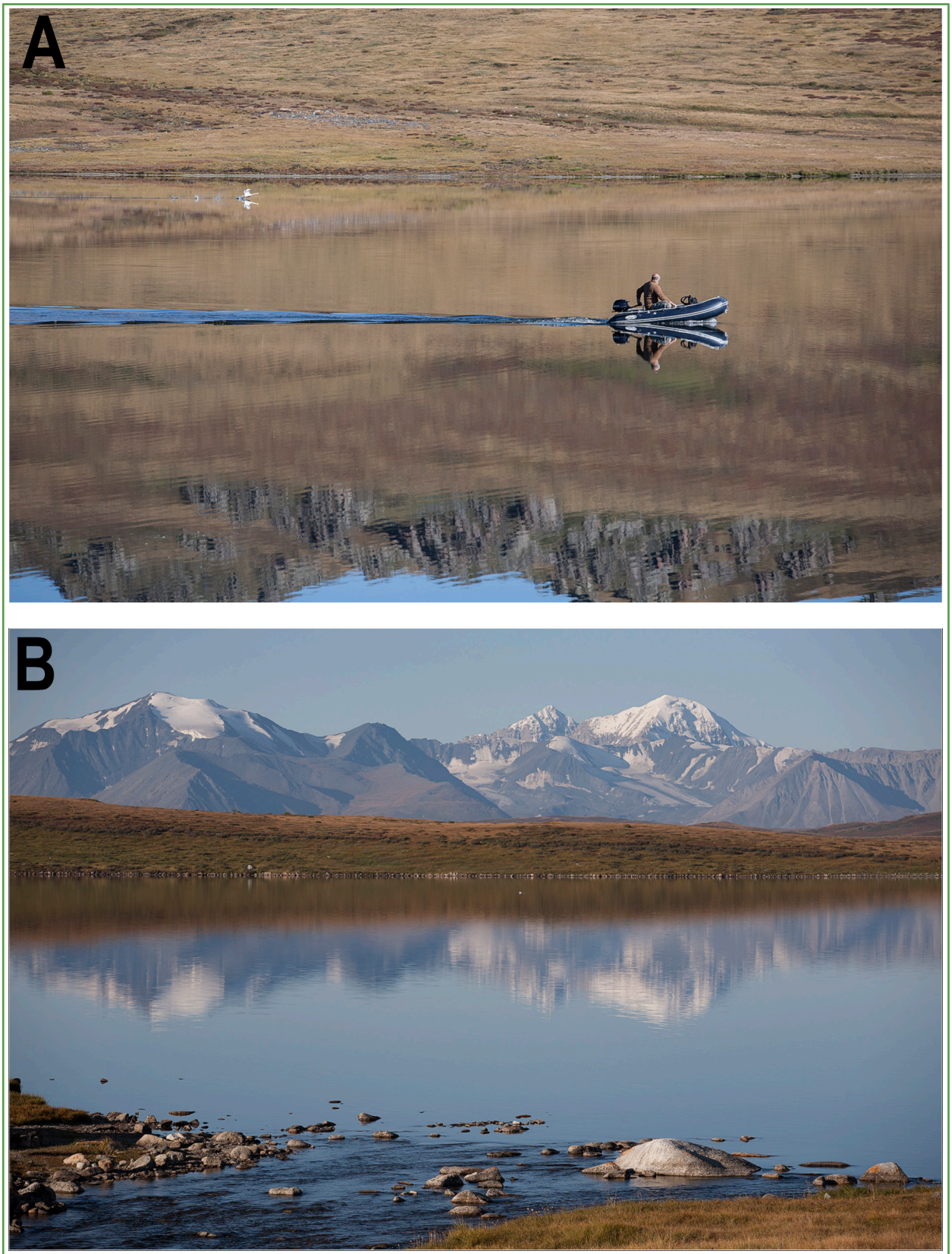

Fig. 1. *A* — Lake Ukok, *B* — Lake Kaldzhin-Kul

Рис. 1. *A* — озеро Укок, *B* — озеро Кальджин-Куль

The Ukok Plateau flora and fauna have been the subject of a range of studies. One of the most comprehensive biogeographical reviews was developed by the research team of Gorno-Altaisk State University (Bondarenko et al. 2022). The review focuses specifically on birds, fish, mammals, and, partly, invertebrates (insects only). However, the review as

Table 1

Primers used for sample genotyping

Таблица 1

Праймеры, использованные для генотипирования исследуемых образцов

Primer	Gene	Nucleotide sequence (5'–3')	Annealing temperature, °C	Reference
1 F	18S–ITS1–5.8S	TCGGATTGGTCTCGGTCTG	62.8	Prokhorova et al. 2015
1R		GCGTTCAAGATGTCGATGTTC		
2F	5.8S–ITS2–28S	TTGCAGAACACATTGAACATCG	64	
2R		GGAGTTTACCACCCGCTTTG		
HCO2198	cox1	TAAACTTCAGGGTGACCAAAAAATCA	54.1	Folmer et al. 1994
LCO1490		GGTCAACAAATCATAAAGATATTGG		

well as other available relevant sources fail to provide any information on molluscs inhabiting the Ukok Plateau water bodies. To fill the gap in the knowledge about the Ukok Plateau malacofauna, two glacial (moraine-dammed) lakes — Ukok and Kaldzhin-Kul — were chosen. It is assumed that they appeared after the degradation of the Late Pleistocene glaciation (Mikhailov 1994). The studied area is marked by earlier Upper Quaternary sediments of sand and clay with larger inclusions.

Material and methods

Collection of samples

Lake Ukok is located at 49°15′52″ N, 87°22′56″ E. Its absolute elevation is 2,416 m. It covers 2.4 sq. km. The maximum dimensions of the lake are 2.5 by 1.2 km. The shore is 8.4 km long. The lake lies in a small depression eroded by the glacier. Its slopes are mainly granite outcrops covered sporadically with shallow ground moraine (Fig. 1: *A*). The shore is alpine meadow. The Kara-Bulak River flows out of Ukok Lake to soon join the Ak-Alakha River as a drainage basin for all the rivers of the Ukok Plateau. The maximum depth of the lake is 9.6 m, the average depth is 2.5 m. In late summer the water temperature does not exceed 10°C. Its bottom is covered with algae. The samples of molluscs were taken along its left south-western shore (Fig. 1: *A*).

Lake Kaldzhin-Kul is located at 49°19′24″N, 87°27′29″ E. Its absolute elevation is 2,402 m. It covers 3.9 sq. km. The maximum dimensions of the lake are 3.7 by 2.3 km. The shore is 12.2 km long. The shores are low and marshy (Fig. 1: *B*). An anabranch from Lake Kaldzhin-Kul-Bas located a few metres higher flows into Lake Kaldzhin-Kul. The Kaldzhin River, a left tributary of the Ak-Alakha River, flows out of Kaldzhin-Kul. Molluscs were collected near the source of the Kaldzhin River (Fig. 1: *B*).

Morphological analysis

The shell structure and the reproductive system of snails were analysed using a Leica M165C stereomicroscope. Photographs were taken using a Leica DFC290 camera.

Molecular genetic analysis

For molecular genetic studies, mollusc tissues were fixed and stored in 90% ethanol. Before the DNA extraction, the samples were washed in three changes of distilled water. DNA was isolated using a commercial DNA-Sorb-C-M kit (cat. no. K1-6-50-Mod) (AmpliSens, Russia) by following the manufacturer's instructions. Genotyping was performed on an rDNA fragment (18S-ITS1-5.8S-ITS2-28S) and mitochondrial gene fragment of cytochrome c-oxidase subunit I (*cox1*). See Table 1 for nucleotide sequences of primers and appropriate annealing temperatures.

All the PCR reactions were performed with Taq DNA polymerase (Thermo Scientific) in 20 µl reaction volume of 16 µl sterilized distilled water, 2 µl of Taq10x buffer, 1 µl of DNA (10 ng/µl), 0.4 µl of each primer (10 nM)

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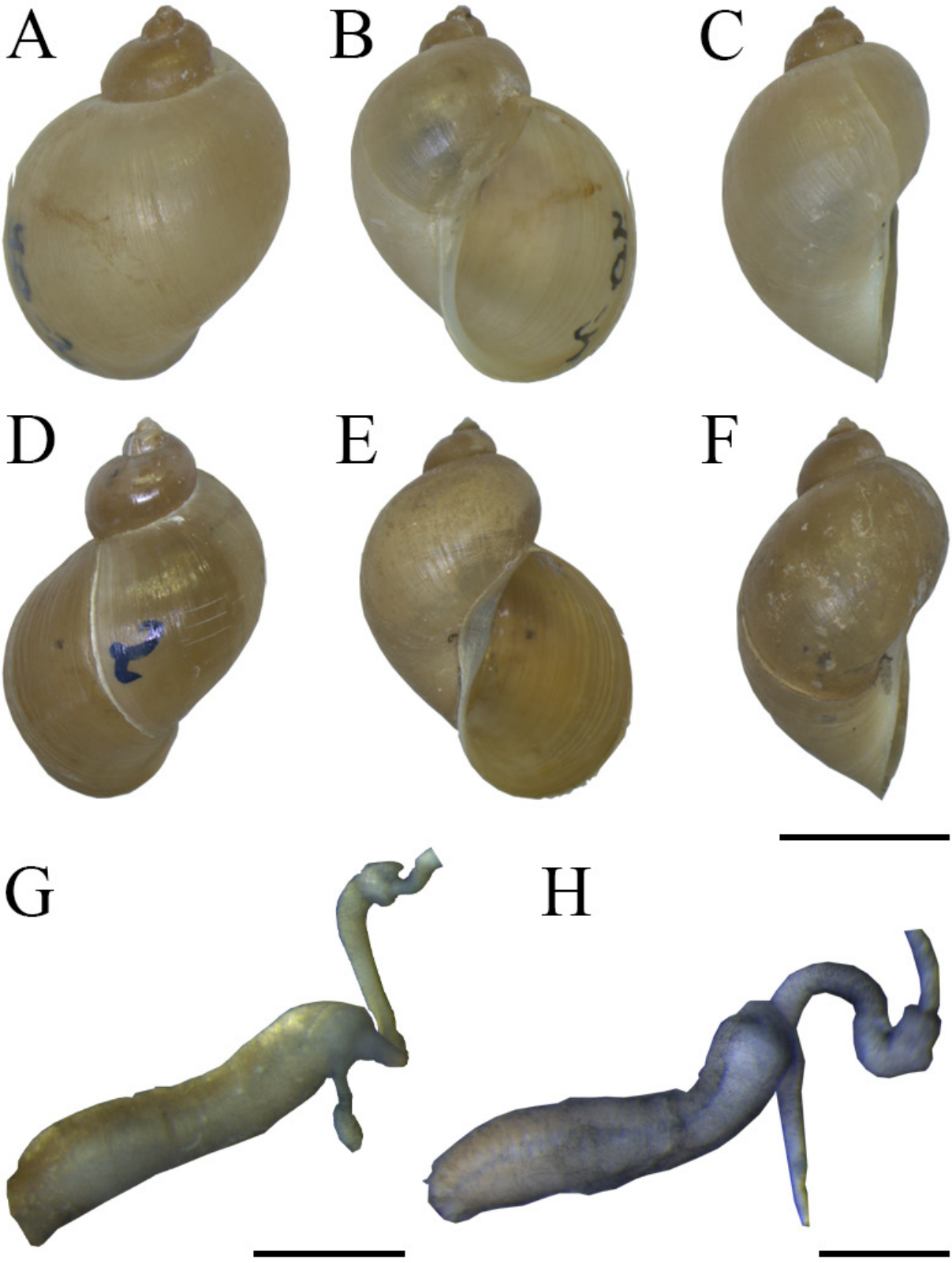

Fig. 2. *A. agotis* shell: *A–C* — mollusc shell from Lake Ukok; *D–F* — mollusc shell from Lake Kaldzhin-Kul. Copulative apparatus of *A. lagotis* molluscs: *G* — mollusc from Lake Ukok; *H* — mollusc from Lake Kaldzhin-Kul. Scale bar: *A–F* — 10 mm, *G* — 2 mm, *F* — 1 mm

Рис. 2. Раковина *A. lagotis*: *A–C* — раковина моллюска из озера Укок; *D–F* — раковина моллюска из озера Кальджин-Куль. Копулятивный аппарат моллюсков *A. lagotis*: *G* — моллюска из озера Укок; *H* — моллюска из озера Кальджин-Куль. Масштаб: *A–F* — 10 мм, *G* — 2 мм, *F* — 1 мм

Table 2

Dimensions (in mm) of *Ampullaceana lagotis* mollusc shells from different collecting sites (average values and standard errors). Statistically significant differences between the samples are marked with an asterisk

Таблица 2

Размерные характеристики (в мм) раковин моллюсков *Ampullaceana lagotis* из разных точек сбора. Указаны средние значения и ошибки среднего. Звездочкой отмечены параметры, для которых была выявлена статистически значимая разница между выборками

Parameter	Ukok Lake	Kaldzhin-Kul Lake
Number of studied molluscs. In brackets is the number of those which had their prepuce length and penial sac length measured.	11 (3)	15 (3)
Shell height*	23.83±0.72	11.76±0.73
Shell width*	16.63±0.87	8.90±0.40
Aperture height*	16.37±0.58	8.45±0.37
Aperture width*	11.12±0.53	5.63±0.24
Whorl height*	8.18±0.40	3.65±0.37
Height of the last whorl*	21.18±0.70	10.13±0.57
Prepuce length	5.35±0.73	3.13±0.07
Penial sac length	3.59±0.37	2.62±0.22
Index of the copulatory apparatus	1.48±0.07	1.21±0.10
Numbers of ITS1-5,8S-ITS2 fragment sequences annotated in GenBank	OR600215.1, OR600216.1, OR600217.1, OR600218.1, OR600226.1, OR600227.1, OR600228.1, OR600229.1	OR600208.1, OR600209.1, OR600210.1, OR600211.1, OR600212.1, OR600213.1, OR600214.1, OR600219.1, OR600220.1, OR600221.1, OR600222.1, OR600223.1, OR600224.1, OR600225.1
Numbers of *cox1* sequences annotated in GenBank	OR722466.1	OR593313.1

and 0.2 μl (5 U/μl) of Taq polymerase following the protocol described in (Prokhorova et al. 2020). The electrophoretic analysis of the PCR products was performed in 1.4% agarose gel in TBE buffer. The samples of the obtained PCR products were sequenced using an ABI PRISM 310 sequencer (Applied Biosystems). The assembly and multiple alignment of nucleotide sequences and the analysis of the chromatograms were performed with BioEdit v. 7.2.5 (Hall 1999) and MEGA v. 10.2.4 (Kumar et al. 2018). We also used the BLAST software on the NCBI server to establish the homology of nucleotide sequences (BLAST… 2023).

Phylogenetic reconstructions with the use of the maximum likelihood method were performed with MEGA v. 11 (Kumar et al. 2018; Tamura et al. 2021). Bayesian analysis was performed using BEAST v. 2.5 (Bouckaert et al. 2019) followed by a tree visualisation using TreeAnnotator v. 1.1.4 (Helfrich et al. 2018). An optimal mathematical model for calculating genetic distances was chosen with the help of the Akaike information criterion and Bayesian information criterion with the jModelTest v. 2.1.7 software (Darriba et al. 2012). The phylogenetic reconstructions from rDNA fragments (ITS1-5.8S, ITS2-28S) and a *cox1* gene fragment was performed using the General Time Reversible model with gamma correction (GTR+G) (Nei, Kumar 2000). Bootstrap branch support (BS) levels for ML and Bayesian analysis were performed with 1,000 replicates (Felsenstein 1985).

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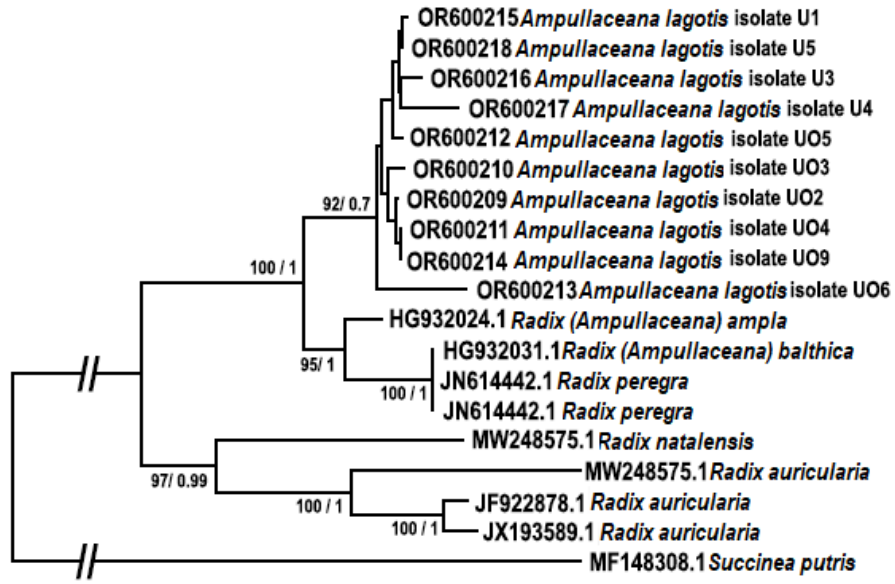

Fig. 3. Phylogenetic reconstruction based on nucleotide sequences of 18S (partial)–ITS1–5.8S (partial) rDNA (690 bp). The number at the branch nodes indicates percentage bootstrap support for 1,000 replicates for ML and posterior probability for BI. The Figure shows the numbers of the used GenBank sequences

Рис. 3. Филогенетическая реконструкция на основании 18S (частично)–ITS1–5.8S (частично) рДНК (690 п. н.). В узлах указаны бутстрепные поддержки для 1000 реплик для ML и значения апостериорных вероятностей для BI. Указаны номера использованных последовательностей в GenBank

The choice of the outgroups was mainly based on the presence and the completeness of nucleotide sequences of the studied genome regions. The following sequences from GenBank were used to construct the phylogenetic trees: *Ampullaceana ampla* (HG932024.1, LS974249.1, HG932229.1), *A. balthica* (HG932031.1, MZ400505.1, MW709280.1, MW675330.1), *A. dipkunensis* (MH189854.1), *A. fontinalis* (MH189853.1), *A. lagotis* (MT708678.1, GU574224.1, AJ319639.1, MH189939.1, MH189995.1), *A. zazurnensis* (KT852376.1, KF918625.1), *Peregriana dolgini* (KT030050.1, MH189979.1), *P. labiate* (KX056253.1), *Radix alticola* (LC659114.1), *R. auricularia* (JF922878.1, JX193589.1, MN194260.1, OP174292.1, MK779205.1), *Radix cf. plicatula* (LC659144.1), *R. euphratica* (MH189866.1), *R. labiate* (KX056263.1), *R. natalensis* (MW248575.1, HQ283270.1, MN737037.1), *R. peregra* (JN614442.1, HQ283258.1), *R. rubiginosa* (LC659107.1, KM067685.1), *R. rufescens* (LC659117.1), *Succinea erythrophana* (NC069953.1), *S. putris* (MF148308.1, MH352216.1), *S. striata* (AY841295.1).

Results and discussion

Morphological analysis

We studied the shell structure of molluscs from both lakes. As a result, the molluscs were found to belong to the same species — *Ampullaceana lagotis* Schrank, 1803. The species has a long research history. Over its course, it has been assigned to different genera. Among them are *Buccinum*, *Lymnaea*, *Radix*, and *Peregriana,* with the majority belonging to the Lymnaeidae family (Vinarski et al. 2020).

The *Ampullaceana lagotis* shell is ovoid-conical, trochospiral, dexiotropic, evolute (Fig. 2: *A*–*F*). Shell walls thin with a clear sculpturing of growth lines. Tangent line convex. Umbilical slit partly covered by a parietal lip of the aperture. Parietal depression strongly impressed. The suture of each whorl deep, oblique. Aperture oval, parietal and palatal angle sharp.

Already at the sample collection stage the Ukok Lake molluscs were found to be visibly

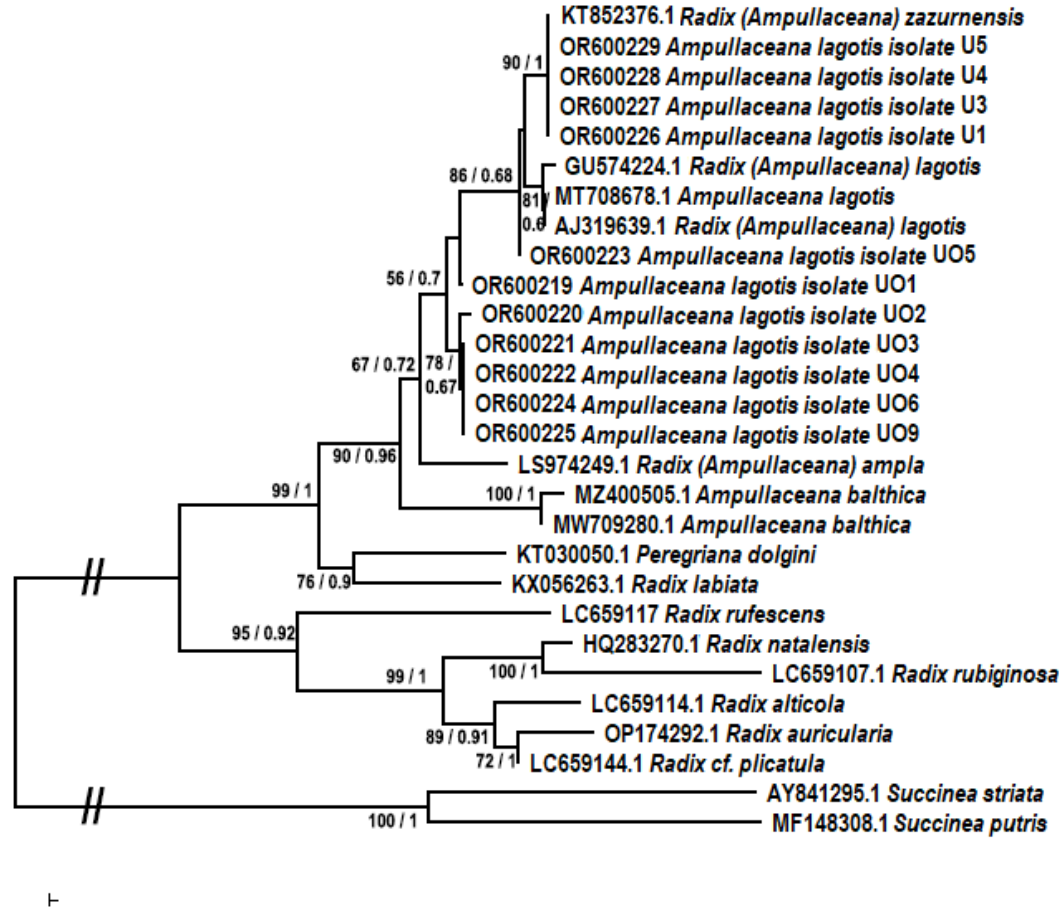

Fig. 4. Phylogenetic reconstruction based on nucleotide sequences of ITS2–28S (partial) rDNA (711 bp). The number at the branch nodes indicates percentage bootstrap support for 1,000 replicates for ML and posterior probability for BI. The Figure shows the numbers of the used GenBank sequences

Рис. 4. Филогенетическая реконструкция на основании ITS2–28S (частично) рДНК (711 п. н.). В узлах указаны бутстрепные поддержки для 1000 реплик для ML и значения апостериорных вероятностей для BI. Указаны номера использованных последовательностей в GenBank

bigger than those from Lake Kaldzhin-Kul. This observation was supported by shell measurements (Table 2; Fig. 2: *A–F*).

All the collected samples were found to have the same reproductive system typical of the *Ampullaceana* genus (Aksenova et al. 2018). The copulatory apparatus includes the prepuce and the penial sac (Fig. 2: *G–H*). The index of the copulatory apparatus of molluscs varies from 1.08 to 1.70 and does not differ significantly between molluscs from different lakes (Table 2).

Molecular genetic analysis

Genotyping resulted in nucleotide sequences of a 1515-1771 bp long rDNA fragment. It includes the 18S (partial)-ITS1-5.8S-ITS2-28S (partial) sequence and *cox1* of 656-659 bp in length (Table 2).

The obtained sequences were used in phylogenetic reconstructions of fragments 18S-ITS1-5.8S (Fig. 3), 5.8S-ITS2-28S (Fig. 4) and *cox1* (Fig. 5).

All the obtained phylogenetic sequence reconstructions of molluscs collected from the Ukok Plateau comprise a single clade and match the *Ampullaceana lagotis* specimens. However, the same clades based on the reconstruction of ITS2-28S and *cox1* include *Radix zazurnensis* sequences — KT852376.1 and KF918625.1, respectively. Later, the authors of these sequences identified the studied isolate as *Ampullaceana (Radix) lagotis* (Aksenova et al. 2016; 2017).

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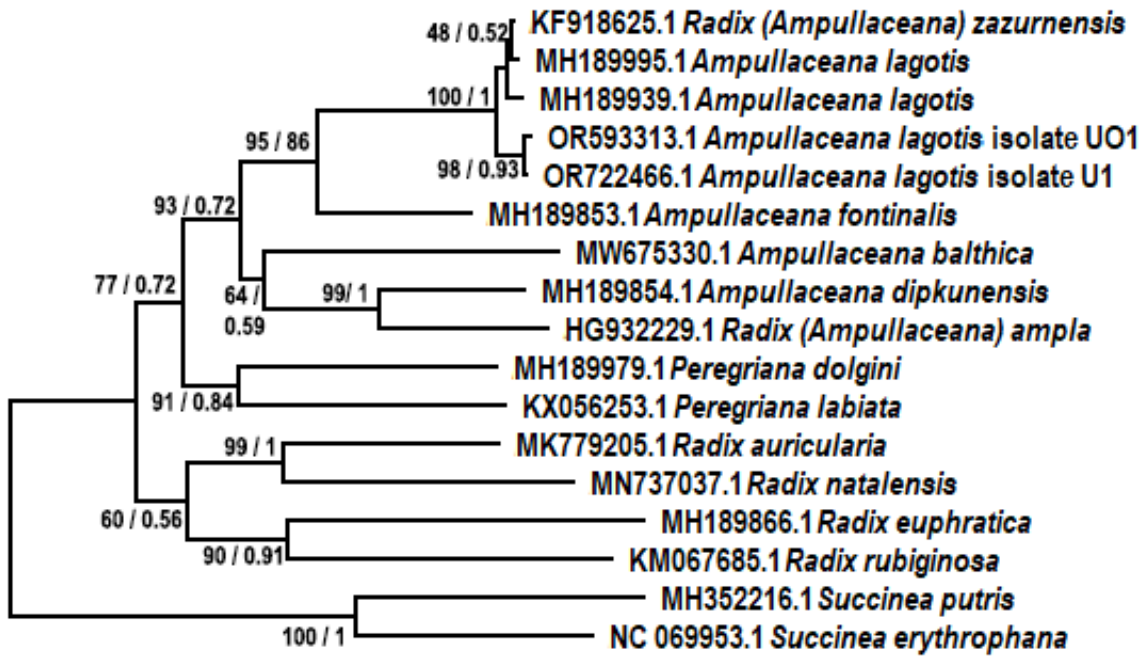

Fig. 5. Phylogenetic reconstruction based on nucleotide sequences of a fragment of the *cox1* gene (626 bp). The number at the branch nodes indicates percentage bootstrap support for 1,000 replicates for ML and posterior probability for BI. The Figure shows the numbers of the used GenBank sequences

Рис. 5. Филогенетическая реконструкция на основании фрагмента гена *cox1* (626 п. н.). В узлах указаны бутстрепные поддержки для 1000 реплик для ML и значения апостериорных вероятностей для BI. Указаны номера использованных последовательностей в GenBank

In addition, phylogenetic reconstruction of the *cox1* gene of *A. lagotis* snails from the Ukok Plateau also clusterizes with molluscs from Lake Teletskoye, genotyped as *Radix zazurnensis* (GenBank KF918624.1).

As stated before, the *Ampullaceana lagotis* species has developed a few synonyms. Of them, the most frequent in use are *Radix lagotis* (Schniebs et al. 2015; Glöer 2019) and *Lymnaea (Peregriana) lagotis* (Kruglov, Starobogatov 1983; Khokhutkin et al. 2009). All the given names were used to annotate genome sequences of molluscs in GenBank. For this reason, phylogenetic reconstructions sometimes feature two names of taxa.

The obtained nucleotide sequences and the data from GenBank were used to calculate average intraspecific and interspecific genetic distances for the *Ampullaceana* genus (Table 3, 4). The samples genotyped by us are unique for *Ampullaceana lagotis* with respect to the ITS1 fragment. The genetic distance for the fragment in question between *A. lagotis* and *A. baltica* and *A. ampla* exceeds the distance between the latter two (Table 3). Similar results were obtained for ITS2: *A. lagotis* differs more from *A. baltica* and *A. ampla* than these two species differ from each other. However, the distance between *A. lagotis* specimens collected on the Ukok Plateau and in other regions does not exceed the average interspecific distance characteristic of the *Ampullaceana* genus (Table 4).

Thus, the morphological and molecular genetic analyses show that snails collected in the lakes Ukok and Kaldzhin-Kul belong to the same species — *Ampullaceana lagotis.* At the same time, the intraspecific variability of *A. lagotis* from water bodies on the Ukok Plateau is higher than the average intraspecific distance between the representatives of this species.

The most variable of the studied genome fragments was ITS2. *A. lagotis* molluscs from Lake Kaldzhin-Kul have 618 bp long ITS2, which is characteristic of the same species

Table 3
Intraspecific and interspecific genetic distances (p-distance) for *Ampullaceana* molluscs based on the ITS1 rDNA fragment

Таблица 3
Внутривидовые и межвидовые генетические дистанции (p-distance) для моллюсков рода *Ampullaceana* по фрагменту ITS1 рДНК

ITS1 (745–748 bp)	Interspecific p-distance	Intraspecific p-distance	
		A. baltica	***A. ampla***
A. lagotis Ukok	0.0191	0.0544	0.0427
A. baltica	0.0037	—	0.0331
A. ampla	0.0019	—	—
Average p-distance	0.0162	**0.0434**	

of molluscs from other regions (see above). However, *A. lagotis* molluscs from Lake Ukok have 21-nucleotide insertion in ITS2. Previously, a similar insertion in ITS2 was found in *A. lagotis* pond snails from the Irkut River (KT852376.1).

Conclusion

Snails collected in Lake Ukok and Lake Kaldzhin-Kul have shown not only morphological, but also genetic differences. This leads us to suppose that *Ampullaceana lagotis* molluscs in two different lakes are isolates. In addition, the lack of intrapopulation variability in *A. lagotis* molluscs may indicate a relatively recent settlement of these snails in the lakes Ukok and Kaldzhin-Kul. This is confirmed by the results of geomorphological analysis. It showed that both lakes appeared after the degradation of the Late Pleistocene glaciation (Mikhailov 1994)

Previously, similar data were obtained in a study on genotypic diversity of *Radix* spp. on the Tibetan Plateau (von Oheimb et al. 2011). The study of the malacofauna of 46 lakes suggests that molluscs inhabited the water bodies at different times. Some of the studied mollusc populations have existed since before the Last Glacial Maximum. These populations are marked by considerable genotypic diversity. The other lakes were not inhabited until relatively recently. They have more genetically homogeneous populations of molluscs. The hydrobiological analysis of the region concluded that molluscs colonized the water bodies not only through the aquatic system but also through passive dispersal by birds.

Lake Kaldzhin-Kul and Lake Ukok may have been formed by different moraines and, similarly to the Tibetian Plateau water bodies, were inhabited by *Ampullaceana lagotis* snails at different times. The shallow Ukok is a moraine-dammed lake, while the deep Kaldzhin-Kul occupies a rift lined by dump moraine.

At the same time, despite the proximity of the lakes, the water-based exchange of malacofauna between them is complicated. The reason is the high current velocity of the Kara-Bulak and Kaldzhin rivers flowing out of the lakes, as

Table 4
Intraspecific and interspecific genetic distances (p-distance) for *Ampullaceana* molluscs based on the ITS2 rDNA fragment

Таблица 4
Внутривидовые и межвидовые генетические дистанции (p-distance) для моллюсков рода *Ampullaceana* по фрагменту ITS2 рДНК

ITS2 (618–639 bp)	Interspecific p-distance	Intraspecific p-distance		
		A. baltica	***A. ampla***	***A. lagotis***
A. baltica	0.0020	—	—	—
A. ampla	0.0025	0.0176	—	—
A. lagotis	0.0080	0.0243	0.0203	—
A. lagotis Ukok	0.0162	—	—	0.0132
Average p-distance	0.0071	**0.0197**		

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well as the Ak-Alakha river, of which they are tributaries. Local climate also contributes to the isolation of mollusc populations. The activity season for snails, including reproduction, is short, while different temperature dynamics of the two lakes also hinder their dispersal beyond the established habitats. The exchange of the malacofauna between the lakes by birds is also limited due to the hydrobiological specifics.

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