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RESEARCH ARTICLE

Molecular evidence confirms the presence of *Euglesa waldeni* (Bivalvia: Sphaeriidae) in Lake Baikal

Молекулярные доказательства наличия *Euglesa waldeni* (Bivalvia: Sphaeriidae) в озере Байкал

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Abstract. The malacofauna of Lake Baikal is considered predominantly endemic. For example, the list of bivalve species inhabiting the littoral zone of this lake mainly comprises endemic representatives of the family Sphaeriidae. However, the absence of molecular data has hindered their precise identification. Here, the presence of the North Palaearctic fingernail clam *Euglesa waldeni* (Kuiper, 1975) in Lake Baikal is reported for the first time. This finding is confirmed using three molecular markers, including the Folmer fragment of the mitochondrial cytochrome c oxidase subunit I (COI), 16S rRNA, and ITS1. The phylogenetic relationships of *Eu. waldeni* and its congeners were estimated based on a maximum likelihood analysis of the COI marker. Morphological characteristics of *Eu. waldeni* collected from Lake Baikal are described, and individuals identified as sexually mature, with embryos at various developmental stages, have been documented. The population density of *Eu. waldeni* has been determined in the area around Ol'khon Island.

Резюме. Малакофауна Байкала считается в основном эндемичной. На данный момент в списке видов двустворчатых моллюсков для литорали озера указаны преимущественно эндемичные представители семейства Sphaeriidae. Однако отсутствие молекулярно-генетических данных затрудняло их достоверную идентификацию. Наличие северопалеарктического вида *Euglesa waldeni* (Kuiper, 1975) в Байкале впервые подтверждено на основании последовательностей трёх молекулярных маркеров, включая фолмеровский фрагмент цитохром-с оксидазы (COI), 16S рРНК и ITS1. Филогенетические отношения *Eu. waldeni* и других видов рода *Euglesa* Jenyns, 1832 были реконструированы с использованием метода максимального правдоподобия на основании фрагмента COI. Выявлены морфологические особенности байкальских *Eu. waldeni*, отмечено присутствие половозрелых особей с эмбрионами на различных стадиях развития, определена плотность населения в районе острова Ольхон.

Key words: distribution, morphological characters, palaearctic species, endemics, COI, 16S, ITS1, Sphaeriidae, *Euglesa*

Ключевые слова: расселение, морфологические признаки, палеарктические виды, эндемики, COI, 16S, ITS1, Sphaeriidae, *Euglesa*

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Introduction

The family Sphaeriidae Deshayes, 1855 (pea clams, pill clams, fingernail clams), which currently includes 272 extant species (MolluscaBase, 2025), is the second most species-rich family of freshwater bivalves worldwide, after the Unionidae Rafinesque, 1815 (Bogan, 2008; Graf, 2013). It is widely distributed across all continents except Antarctica (Lee, 2019), and its representatives inhabit a variety of freshwater biotopes, ranging from deep ancient lakes to small pools and mires. Historically, the taxonomy of this family was based predominantly on shell characters, with limited use of some anatomical characters, such as the structure of the nephridia and ctenidia (Korniushin, 1996, 1998).

Shell morphology within this group varies considerably depending on environmental conditions, both at intra- and interspecific levels, and is currently regarded as an unreliable and potentially misleading source of taxonomic information. Consequently, a substantial proportion of Sphaeriidae species described in the past require revision based on molecular data. The same applies to the numerous records of sphaeriid species published in the existing literature. A recent integrative revision of representatives of the nominative subfamily Sphaeriinae has revealed that it comprises no fewer than 80 extant species, including 35 species of the genus *Euglesa* Jenyns, 1832 (Bespalaya et al., 2024b). It is likely that the actual global diversity of this group is somewhat higher. Despite the wide geographic distribution of the Sphaeriinae, they remain poorly studied worldwide, including in the World's deep ancient lakes. Ancient lakes are often considered "hotspots" of speciation and diversity among aquatic organisms, including molluscs (Brooks, 1950; Boss, 1978; Schultheiß et al., 2008; Cristescu et al., 2010; Clewing et al., 2020), and Lake Baikal is no exception in this regard (Kozhov, 1963; Timoshkin, 2001). The latest revision revealed sixteen endemic species of Bivalvia in Lake Baikal, all belonging to the subfamily Sphaeriinae (Slugina & Starobogatov, 1999; Vinarski & Kantor, 2016). However, molecular data for these species remain unavailable. All the referenced species are primarily found in the open littoral zones of Lake Baikal (Slugina & Starobogatov, 1999; Slugina, 2006). Palaearctic species of the Sphaeriidae, with the exception of *Pisidium dilatatum* Westerlund, 1897, have been recorded only in relatively shallow shoals and bays of the lake. The species composition of these non-endemic fingernail and pea clam species in Baikal requires further revision.

In this article, we report the first molecularly confirmed record of the cold-adapted Palaearctic species *Euglesa waldeni* (Kuiper, 1975) from the open littoral zone of Lake Baikal.

Material and methods

Field research and sampling. Three localities in Lake Baikal were surveyed in June 2021 and August 2024: Barguzinsky Bay and two open littoral sites opposite Anga Bay and off Cape Khoboy (Ol'khon Island) (Fig. 1). Molluscs, including fingernail clams, were collected from silty sand and from sandy bottoms with gravel and boulders at depths ranging from 10 m to 30 m, using a dredge at all sites and a Petersen grab sampler (0.025 m² sampling area) only at Cape Khoboy. Sampling was conducted from the decks of the research vessels G. Titov and Papanin [Centre for Collective Use, Research Vessels Centre of the Limnological Institute of the Siberian Branch of the Russian Academy of Sciences (LIN SB RAS) on Lake Baikal].

Morphological analysis. Conchological and soft-body characters of the collected fingernail clams were examined following a standard methodology (Korniushin, 1996). Primary taxonomic identification was conducted using the original

description of *Euglesa waldeni* (Kuiper, 1975) and relevant literature, including identification keys (Slugina & Starobogatov, 1999; Starobogatov et al., 2004; Piechocki & Wawrzyniak-Wydrowska, 2016; Bespalaya et al., 2024b), as well as the three paratypes of this species deposited at the Zoological Institute of the Russian Academy of Sciences (St Petersburg; ZIN). For comparison, approximately 30 collection lots of *Eu. waldeni* from northern Western Siberia were also examined. These materials are held in the malacological collections of ZIN and the Institute of Plant and Animal Ecology of the Ural Branch of the Russian Academy of Sciences (Yekaterinburg; IPAE).

Using the eyepiece micrometer of a stereomicroscope, standard measurements of shells (length, height, and width, as defined by Starobogatov et al., 2004) were taken. Two morphometric indices were calculated from these measurements: the shell convexity index (SCI = width-to-length ratio × 100) and the shell elongation index (SEI = height-to-length ratio × 100) (Bolotov et al., 2018). Embryo size stages of the examined mature specimens were determined during dissection, following the protocol developed by Bespalaya et al. (2015).

The taxonomy and nomenclature used in this paper follow MolluscaBase (2025). The Baikal specimens of *Eu. waldeni* collected and examined during this study are deposited in the authors' collections (ESB, collection of E.S. Babushkin; MVK, collection of M.V. Vinarski).

DNA extraction, amplification, and sequencing. Total DNA was extracted from pea clam foot tissue using a CTAB-chloroform method (Doyle & Doyle, 1987). Mitochondrial cytochrome c oxidase subunit I (COI) and 16S rRNA gene regions, as well as the nuclear internal transcribed spacer 1 (ITS1), were amplified and sequenced using standard primer pairs: LCO1490–mHCO2198 (Folmer et al., 1994; Hoeh et al., 2002); 294-313F–778-98R (Katana et al., 2001); and ITS1–ITS4 (White et al., 1990), respectively. The cycling protocol was as follows: initial denaturation for 5 minutes at 95 °C; 40 cycles of denaturation for 1 minute at 95 °C, primer annealing for 1 minute at 50 °C, extension for 2 minutes at 72 °C; followed by a post-elongation for 8 minutes at 72 °C. Sanger sequencing was performed using the GenSeq kit (Synthol, Russia) with the Nanofor 05 genetic analyser (Synthol, Russia) at the Collective Use Instrumentation Centre "Ultramicroanalysis" of the LIN SB RAS. All obtained sequences were deposited in GenBank under accession numbers PQ896864–PQ896865 (COI), PV088884–PV088890 (16S), and PV089530–PV089534 (ITS1).

Phylogeography and phylogenetic analysis. Genetic distances (uncorrected p-distances) were estimated using MEGA12 (Kumar et al., 2024). The obtained ITS1 and 16S rRNA sequences were analysed using the BLASTn server on the NCBI website (Altschul et al., 1990). The median-joining network of 16S rRNA haplotypes of *Eu. waldeni* (Table 1) was inferred using the "pegas" package in R (Paradis, 2010). Phylogenetic analysis was conducted using 62 unique *Euglesa* spp. COI haplotypes, comprising 65 sequences from GenBank (*Electronic supplementary material*; see Addenda) and three newly obtained in this study. IQ-TREE 2 (Minh et al., 2020) was used for phylogenetic inference, employing the TIM3+F+I+G4 model and 10,000 UltraFast bootstrap (UFBS) and SH-aLRT replicates (Minh et al., 2013) to assess tree topology. The midpoint-rooted consensus tree was visualised using FigTree v1.4.1 (http://tree.bio.ed.ac.uk/software/figtree/).

Results

Class **Bivalvia** Linnaeus, 1758

Subclass **Autobranchia** Grobben, 1894

Order **Sphaeriida** Lemer, Bieler et Giribet, 2019

Family **Sphaeriidae** Deshayes, 1855 (1820)

Subfamily **Sphaeriinae** Deshayes, 1855 (1820)

Genus ***Euglesa*** Jenyns, 1832

Euglesa waldeni (Kuiper, 1975)
(Figs 4, 5)

Type material. Holotype (not examined), **Norway**, *Finnmark Prov.*, Varanger Peninsula, Buetjörni, Lake Gednjevandet [Lake Geatnjajavri], 20.VII.1973, coll. W. Hinz (SMF 192851). *Paratypes*: same data as for holotype, 1 specimen (SMF 192852/10) (not examined); same data, 3 specimens (ZIN, No. 1) (examined).

Additional material examined. **Russia**: *Irkutsk Prov.*, Lake Baikal: opposite Anga Bay, 52°46′29.7″N

Table 1. List of 16S rRNA sequences of *Euglesa waldeni* and *Eu. nipponensis* used in the haplotype network.

NCBI GenBank accession No.	Specimen vouchers (No.)	Locality	Coordinates	Reference
EU559164	Piwa5140	Norway: Varanger Peninsula, Lake Geatnjajavri	70°30′23.0″N, 29°06′59.0″E	Schultheiß et al., 2008
KY126441	MSph52/2	Russia: Novaya Zemlya Archipelago, Svyatoe Lake	72°00′42.2″N, 52°08′11.3″E	Bespalaya et al., 2017
PV088884 PV088885 PV088887 PV088888 PV088889 PV088890	c35 c36 aa195 aa196 aa198 aa208	Russia: Lake Baikal, Anga Bay	52°46′29.7″N, 106°35′02.0″E	This study
PV088886	c65	Russia: Lake Baikal, Khoboy Cape	53°24′38.0″N, 107°47′05.2″E	This study
ON814976	MSph643	Russia: Vitim Nature Reserve	57°26′25.3″N, 116°38′44.4″E	Bespalaya et al., 2024
ON814990 ON814991 ON814992	MSph717 MSph718 MSph719	Russia: Bykovskiy Peninsula, Mamontovo Lake	71°49′37.4″N, 129°18′13.4″E	Bespalaya et al., 2024
PQ032462 PQ032467	MSph976 MSph980	Russia: Commander Islands	55°12′52.2″N, 166°02′54.3″E	Bespalaya, in press
AY093565	UMMZ266734	Japan: Honshu Island	–	Lee & Foighil, 2003
LC703792 LC703866	TUFJ_h33-3 TUFJ_h84-1	Japan: Hokkaido Island	–	Saito et al., 2022

106°35′02.0″E, 13–20 m depth, yellow silted sand, 15.VI.2021, 10 specimens, coll. Kovalenkova, Babushkin, Vinarski, Sitnikova; opposite Anga Bay, 52°46′29.7″N 106°35′02.0″E, depth of 10–30 m, yellow silted sand, 12.VIII.2024, 6 specimens, coll. Kovalenkova; off Khoboy Cape, 53°24′38.0″N 107°47′05.2″E, 12–15 m depth, stones, silted sand, 17.VI.2021, 5 specimens, coll. Kovalenkova, Babushkin, Vinarski, Sitnikova; Barguzinsky Bay, 53°26′10.3″N 108°54′56.0″E, 20 m depth, yellow silted sand, 19.VI.2021, 53 specimens, coll. Kovalenkova, Babushkin, Vinarski, Sitnikova; *Yamalo-Nenets Autonomous Prov.*, Yamal Distr.: content of gastrointestinal tract of *Coregonus pidschian* (Gmelin, 1789), 7.IX.1963, 16 specimens, coll. A. Yakovleva (IPAE645); Polkur-To Lake: content of gastrointestinal tract of *C. pidschian*: 7.IX.1963, 98 specimens, coll. A. Yakovleva (IPAE671, IPAE692); 3.VIII.1964, 97 specimens, coll. I. Brusynina (IPAE665, IPAE760); 12.VIII.1964, 169 specimens, coll. I. Brusynina (IPAE658); content of gastrointestinal tract of *C. nasus* (Pallas, 1776): 7.IX.1963, 525 specimens, coll. A. Yakovleva (IPAE656, IPAE657, IPAE660, IPAE664, IPAE669, IPAE670, IPAE672, IPAE680, IPAE686, IPAE699, IPAE700, IPAE811, IPAE4514); 2.VIII.1964, 56 specimens, coll. I. Brusynina (IPAE673); 3.VIII.1964, 309 specimens, coll. I. Brusynina (IPAE646, IPAE648, IPAE668, IPAE1437, IPAE1453); 31.III.1965, 46 specimens, coll. I. Brusynina (IPAE661); *Priuralskiy Distr.*, Khadyta River basin, floodplain lake, 20.VII.1983, 5 specimens, coll. L. Stepanov (IPAE12014); *Tazovskiy Distr.*: Gydanskaya Bay, Ekman-Burge grab, station 12/11, 21.III.1937, 2 specimens, coll. E. Burmakin (ZIN, uncatalogued); Yambuto Lake, 10.6 m depth, bottom dredge, station 3/9, 09.VIII.1937, 8 specimens, coll. E. Burmakin (ZIN, uncatalogued). **Poland**, *Lesser Poland Voivodeship*, "Żabno Municipality" [Gmina Żabno], VII.1959, 1 specimen (ZIN, No. 9).

Diagnosis. Shells of Baikal *Eu. waldeni* relatively small to medium-sized (2.2–3.0 mm in length; Table 2). Smallest mature mollusc shell containing embryos 2.2 mm in length. Shells relatively thick-walled, robust, often bearing ochre-black or black (likely ferromanganese) external deposits covering shell either partially or completely

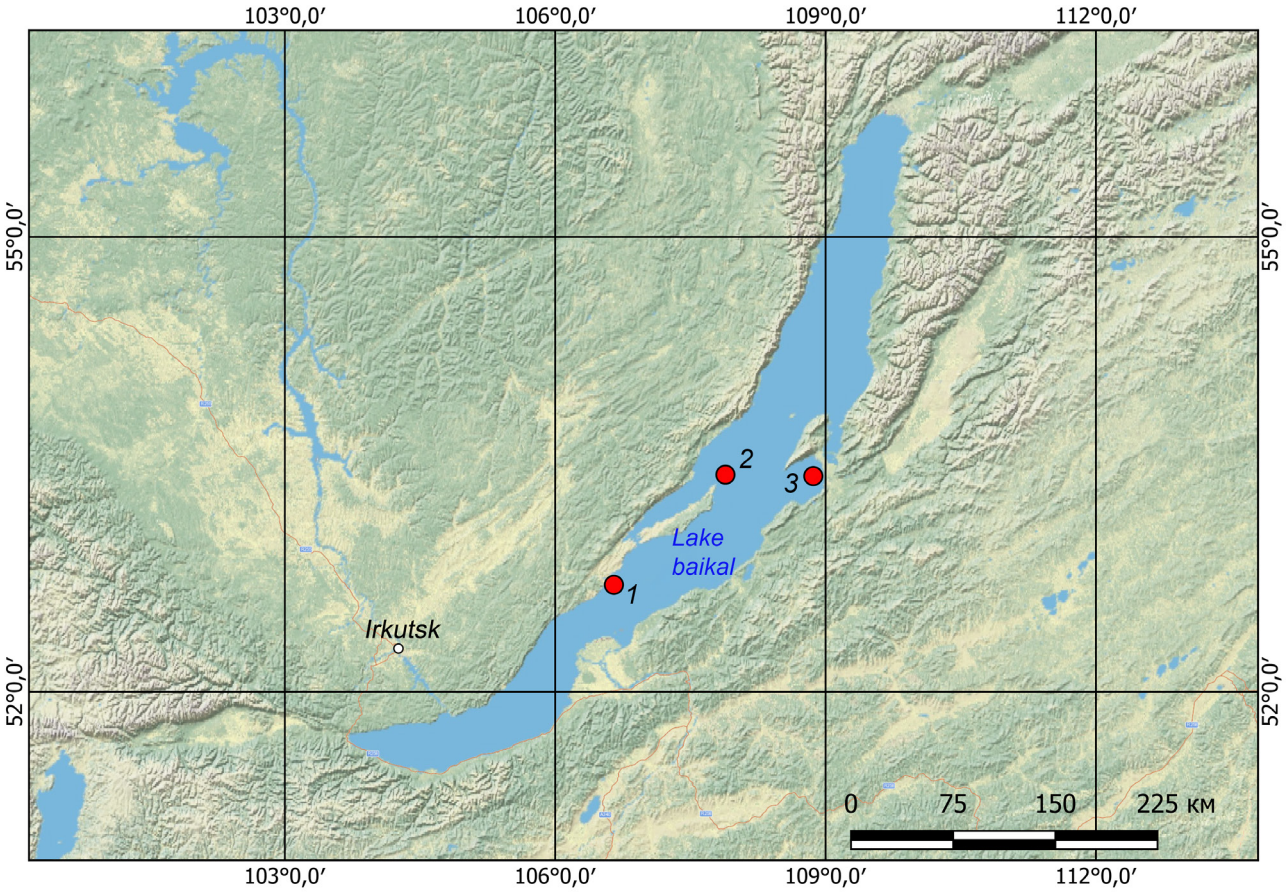

Fig. 1. Locations of the samples examined of *Euglesa waldeni* (Kuiper, 1975). Abbreviations: *1* – Anga Bay; *2* – off Khoboy Cape; *3* – Barguzinskiy Bay.

(Fig. 2). Shell pores sparse, less conspicuous in mature individuals, whereas juveniles exhibiting more densely arranged pores. Shell contour variable, generally rounded, with slightly elongated anterior margin. Umbones slightly protruding, rounded, displaced slightly posteriorly. Hinge plate broad, nearly as long as wide. Lateral teeth robust, especially AI and AII. Cardinal teeth: C3 strongly bent, with thickened, forked posterior end; C2 small, sharply bent (nearly U-shaped); C4 slightly bent, positioned obliquely behind and above C2. Ligament pit relatively short, not extending beyond umbo contour in hinge view, reaching approximately midpoint of thickness of hinge plate. Nephridia of open or closed type. Outer demibranch relatively small, originating at or beyond tenth filament from superior margin of inner demibranch.

Remarks. Among the smaller specimens, no embryos were found, so these were considered as immature. Twenty-five specimens with a shell length of 2.2 mm or greater were dissected; only eight (32%) contained embryos at various stages of development (see Table 2).

The density of *Eu. waldeni* in quantitative samples collected off Cape Khoboy reached 28.6 individuals per square metre, accounting for up to 35.8% of the total abundance of bivalves in these samples.

Phenotypic comparison. The specimens examined in this study exhibit several characteristic features when compared to the original description and illustrations of *Eu. waldeni* (Kuiper, 1975), as well as the paratype shell housed in the ZIN collection under No. 1 (Figs 3, 4A). Notably, the upper margin is not elongated, the hinge plate is not narrowed in the middle and can be quite robust (Fig. 3), and the cardinal teeth of both valves are not shortened. In general, the cardinal teeth resemble those of *Eu. casertana* (Poli, 1791), a species with a

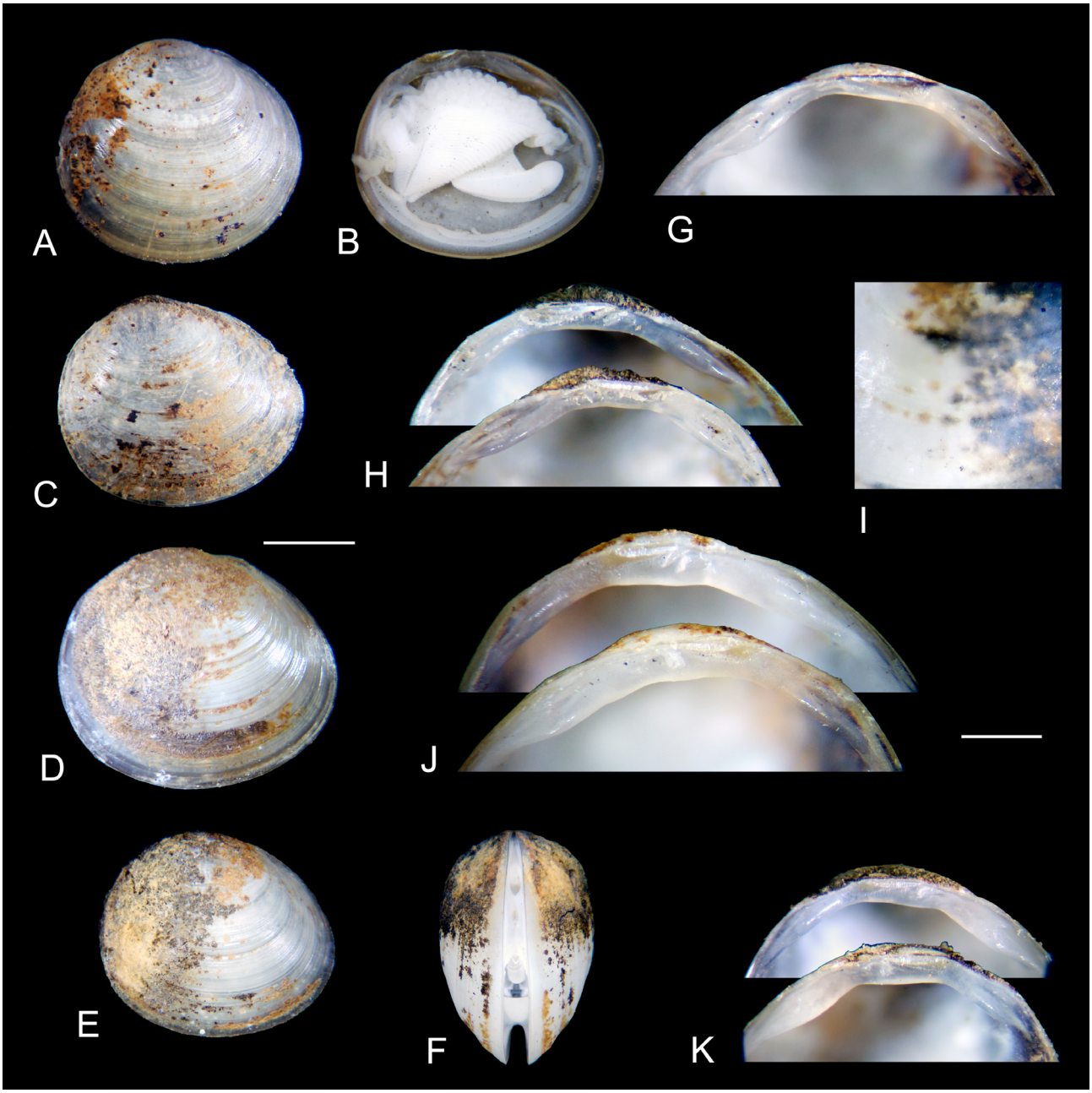

Fig. 2. *Euglesa waldeni* (Kuiper, 1975), shells of from Lake Baikal. **A**, **C**, **G**, **H**, Ust'-Anga Bay (No. 8B-21-5, 8B-21-6); **B**, **D**–**F**, **I**–**K**, Ol'khon Island, Cape Khoboy (No. 13B-21-9). Scale bars: 1 mm (A–F), 0.5 mm (G–K). Photographs by E.S. Babushkin.

worldwide distribution. The shell sculpture characters are consistent with the original description of *Eu. waldeni*. However, the shells of *Eu. waldeni* from Lake Baikal differ from those of the Holarctic species with a boreo-Alpine distribution, *Eu. lilljeborgii* (Clessin, 1886), despite Kuiper (1975) noting similarities between the two species. Moreover, *Eu. waldeni* from Lake Baikal is largely similar to the description of the Baikalian endemic *Eu. granum* (Lindholm, 1909), especially in the morphology of the hinge plate (Fig. 4B). Nevertheless, most specimens examined differ from *Eu. granum* due to variability in shell shape; for example, the most protruding points of the anterior and posterior margins are not aligned opposite the lower third of the shell height (Fig. 2A, C, D).

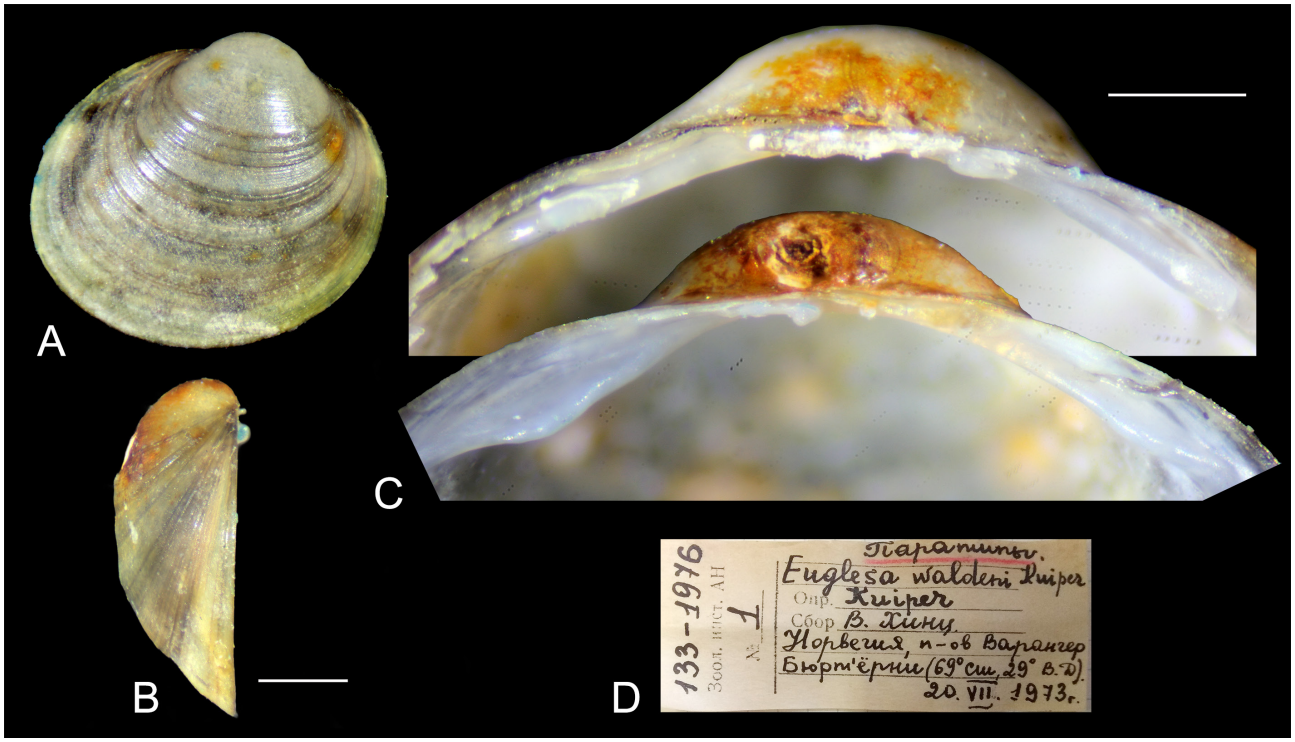

Fig. 3. *Euglesa waldeni* (Kuiper, 1975), paratype (ZIN). **A**, general appearance of left valve; **B**, left valve in posterior view; **C**, hinge plate of left valve; **D**, hinge plate of right valve; **E**, label of paratype. Scale bars: 1 mm (A, B), 0.5 mm (C, D). Photographs by E.S. Babushkin.

Molecular analysis and phylogeny. The molecular analysis of five specimens revealed that they share a single ITS1 allele identical to that of *Eu. waldeni* from the Novaya Zemlya Archipelago (GenBank accession No. KY126462) and *Eu. nipponensis* (Kuroda, 1930) from Honshu Island, Japan (AY093525). Similarly, seven specimens examined comprised a single 16S rRNA haplotype identical to that of specimens of *Eu. waldeni* from Norway, the Novaya Zemlya Archipelago, the Vitim Nature Reserve, and the Commander Islands (GenBank accession Nos EU559164, KY126441, ON814976, and PQ032467) (Fig. 5). The GenBank sequences of *Eu. waldeni* from Norway to the Commander Islands corresponded to only two haplotypes, differing by a single nucleotide substitution. One of these was found exclusively in northern Yakutia (Bykovskiy Peninsula) and the Commander Islands. All three *Eu. nipponensis* sequences are unique haplotypes that differ from the *Eu. waldeni* haplotypes by two to five substitutions.

Two unique COI haplotypes, differing by less than 0.4% divergence, were obtained from specimens collected at Khoboy Cape and Anga Bay. The COI-based phylogeny revealed that the specimens of *Eu. waldeni* from Baikal cluster within a clade containing *Eu. subtruncata* (Malm, 1855), *Eu. armillatum* (Kuiper, 1966), *Eu. costulosa* (Connolly, 1931), and *Eu. zugmayeri* (A. Weber, 1910) (UFBS = 96, SH-aLRT = 90.5) (Fig. 6). The closest relative of *Eu. waldeni* is the Palaearctic species *Eu. subtruncata*, with which it shows approximately 7% *p*-distance divergence in the Folmer region. The phylogenetic position of *Eu. casertana* is not entirely clear; however, this species belongs to a polyphyletic group comprising seven species of *Euglesa* (UFBS = 99, SH-aLRT = 95.3). The clade containing *Eu. henslowana* (Sheppard, 1825), *Eu. supina* (A. Schmidt, 1851), and *Eu. lilljeborgii* is separated by a relatively long branch from the other *Euglesa* species. Without molecular genetic data for endemic Baikal sphaeriids, including *Eu. granum*, it is impossible to assess the degree of their relationship to *Eu. waldeni*.

Distribution. The native range of *Eu. waldeni* is considered to encompass the northern Holarctic Region (Kuiper, 1975; Clarke, 1981; Kuiper

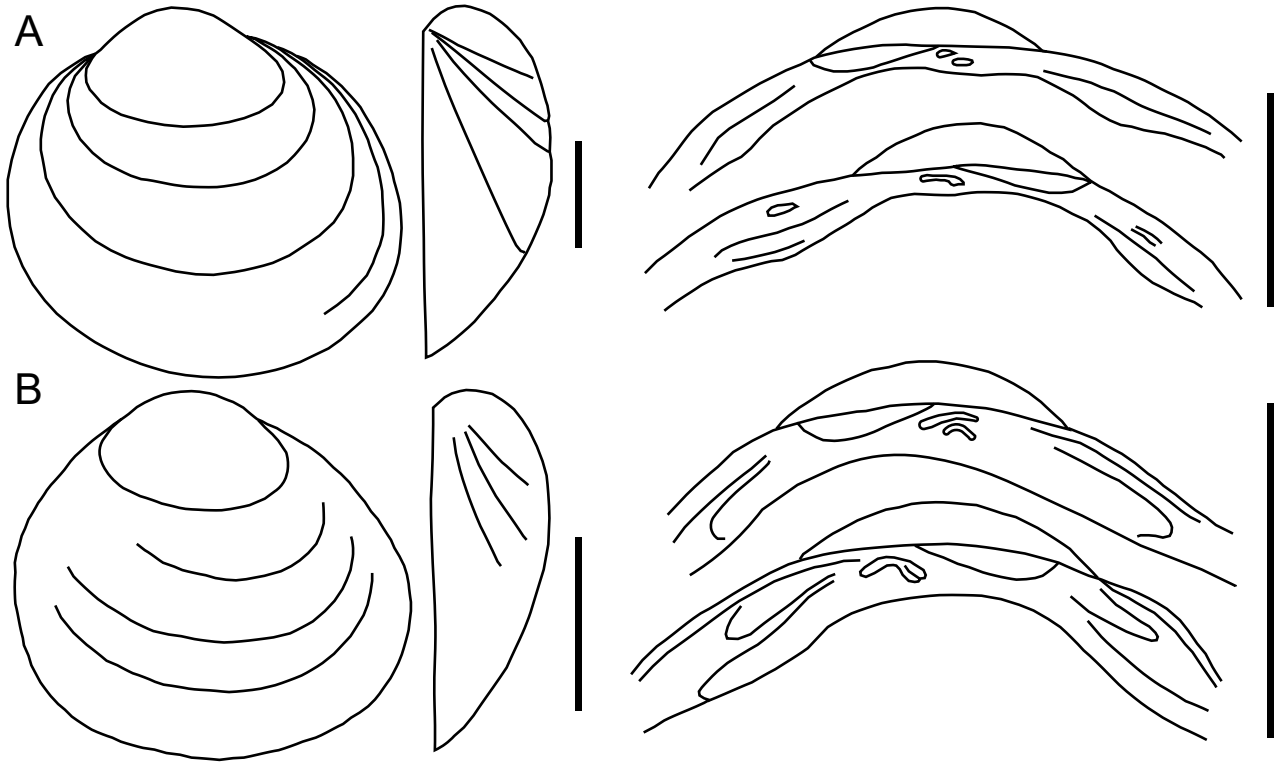

Fig. 4. General appearance of shells, posterior view of valves and hinge plates. **A**, *Euglesa waldeni* (Kuiper, 1975) (modified from Kuiper, 1975, figs 24, 25, 15); **B**, *Eu. granum* (Lindholm, 1909) (modified from Slugina & Starobogatov, 1999, fig. 32). Scale bars: 1 mm.

et al., 1989; Vinarski & Kantor, 2016; Vinarski et al., 2021). This species, along with two other sphaeriid clams, was identified in samples from the Novaya Zemlya Archipelago, which represents the northernmost known locality of freshwater molluscs worldwide (Bespalaya et al., 2017, 2021). Based on conchological data, *Eu. waldeni* has been reported from the lower reaches of the Ob and Yenisei rivers (Dolgin, 2009), as well as from alpine lakes in the Sayan Mountains (Dolgin, 2013), Lake Khuvsgul (Slugina, 2001), and the upper reaches of the Vitim River (Rozhkova et al., 1999). The natural range of this species extends eastwards to Sakhalin Island (Pietsch et al., 2012). A single report of this clam from Ukraine (Stadnichenko, 1984), while not implausible, requires further confirmation.

The catalogue of the ZIN Mollusca collection, in addition to the paratypes from the type locality, lists 26 lots of *Eu. waldeni* identified by two prominent experts in freshwater bivalve taxonomy, the late Drs Ya.I. Starobogatov and A.V. Korniushin. The sampling sites of this material are located in Norway, Poland, the Kola Peninsula, the Kolyma and Yana river basins, and the Kamchatka Peninsula, comprising a total of 173 specimens. We studied numerous lots of *Eu. waldeni* in the IPAE and ZIN collections; the identifications of this species were confirmed. One of these samples (ZIN, No. 9 in the collection catalogue) was collected in southern Poland (Gmina Żabno) in 1959. Polish authors did not record *Eu. waldeni* in their country (Piechocki, 1989; Piechocki & Wawrzyniak-Wydrowska, 2016), although they acknowledged the possibility of its presence (Piechocki & Dyduch-Falniowska, 1993). This finding extends the known range of *Eu. waldeni* into Central Europe and helps to clarify the report of this clam from Ukraine (Stadnichenko, 1984). Additionally, *Eu. waldeni* was found in uncatalogued samples from the Tazovskiy Peninsula (Western Siberia; 10 specimens) stored at ZIN. In total, 1,334 specimens of *Eu. waldeni* from northern Western Siberia were examined.

Several recent publications have reported new occurrences of *Eu. waldeni*, which have been

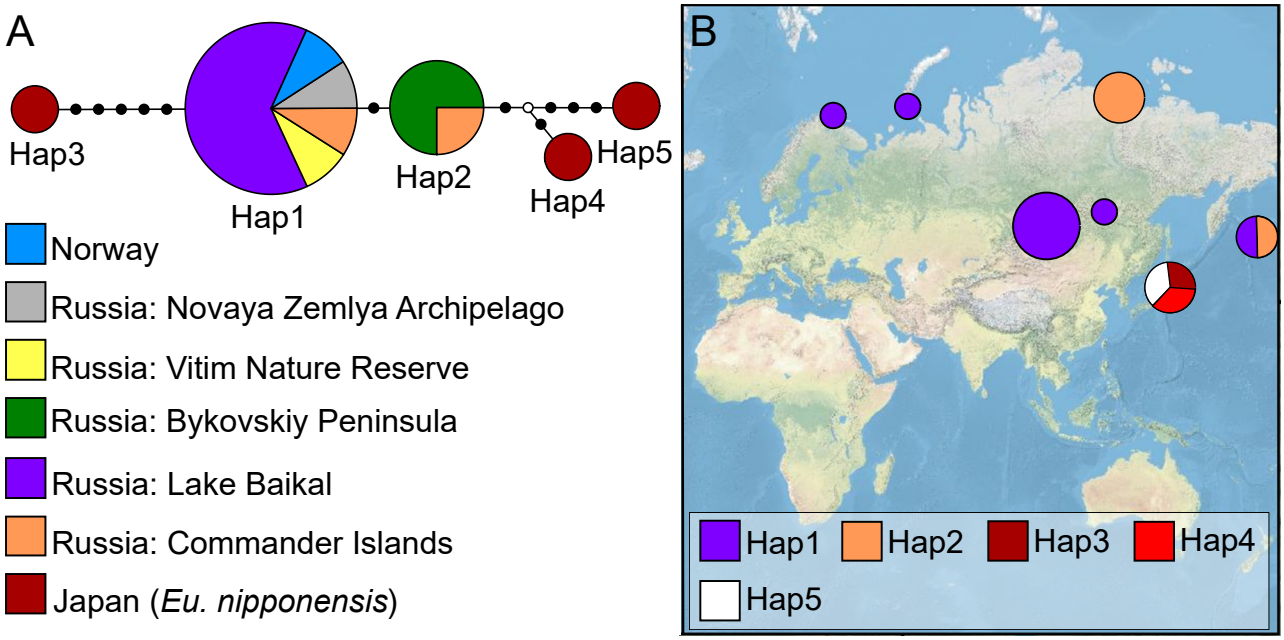

Fig. 5. Median joining network of 16S rRNA haplotypes of *Euglesa waldeni* (Kuiper, 1975) and *Eu. nipponensis* (Kuroda, 1930) **(A)** and its distribution map **(B)**. The size of each circle is proportional to the number of sequences belonging to a particular haplotype. The black dots represent mutations.

genetically confirmed. These records originate from the Subarctic and Arctic regions of Eurasia (Schultheiß et al., 2008; Bespalaya et al., 2017, 2024b), as well as central Eastern Siberia (Bespalaya et al., 2024b), Japan (Lee & Foighil, 2003; Saito et al., 2022), and the Commander Islands (Bespalaya et al., 2025). However, the presence of *Eu. waldeni* in Canada (Kuiper, 1975; Clarke, 1981), and thus in the Nearctic region more broadly, requires confirmation. Therefore, the range of this species can be described as Northern Palaearctic.

Discussion

The high conchological variability of the Sphaeriidae, resulting from the modifying influence of environmental factors (Herrington, 1962; Kornyushin, 1996; Rassam et al., 2021), complicates accurate species identification. The effectiveness of DNA barcoding for identifying pea clam species in Lake Baikal is also limited by the lack of reference sequences (Kravtsova et al., 2021; Kravtsova et al., 2025). Furthermore, Folmer primers frequently fail to amplify the cytochrome c oxidase subunit I (COI) gene of Sphaeriidae (Clewing et al., 2013). GenBank provides extensive coverage of the taxonomic diversity of Palaearctic Sphaeriidae; it currently contains nucleotide sequences for the mitochondrial large subunit ribosomal RNA (16S rRNA) gene for nearly 80 species (Bespalaya et al., 2024b). Sequences of *Eu. waldeni* from the Palaearctic region, specifically the area ranging from Norway to the Commander Islands, deposited by various research groups, correspond to only two haplotypes, differing by a single nucleotide substitution. The collection site for the sequence from Norway (EU559164) corresponds to the type locality (Lake Geatnjajavri) of this species. Notably, a multi-threshold General Mixed Yule Coalescent (GMYC) delimitation analysis by Saito et al. (2022) classified sequences of *Eu. waldeni* (from Russia and Norway) and *Eu. nipponensis* (from Japan) as belonging to a single genetic lineage. However, the sequences of *Eu. nipponensis* exhibit greater divergence among themselves than do pairs of closely related species. Since identical haplotypes of *Eu. waldeni* and *Eu. nipponensis* have not yet been found, and a detailed morphological analysis remains pending, we, in agreement with other authors (Saito et al., 2022), consider it premature to revise the taxonomic status of these species.

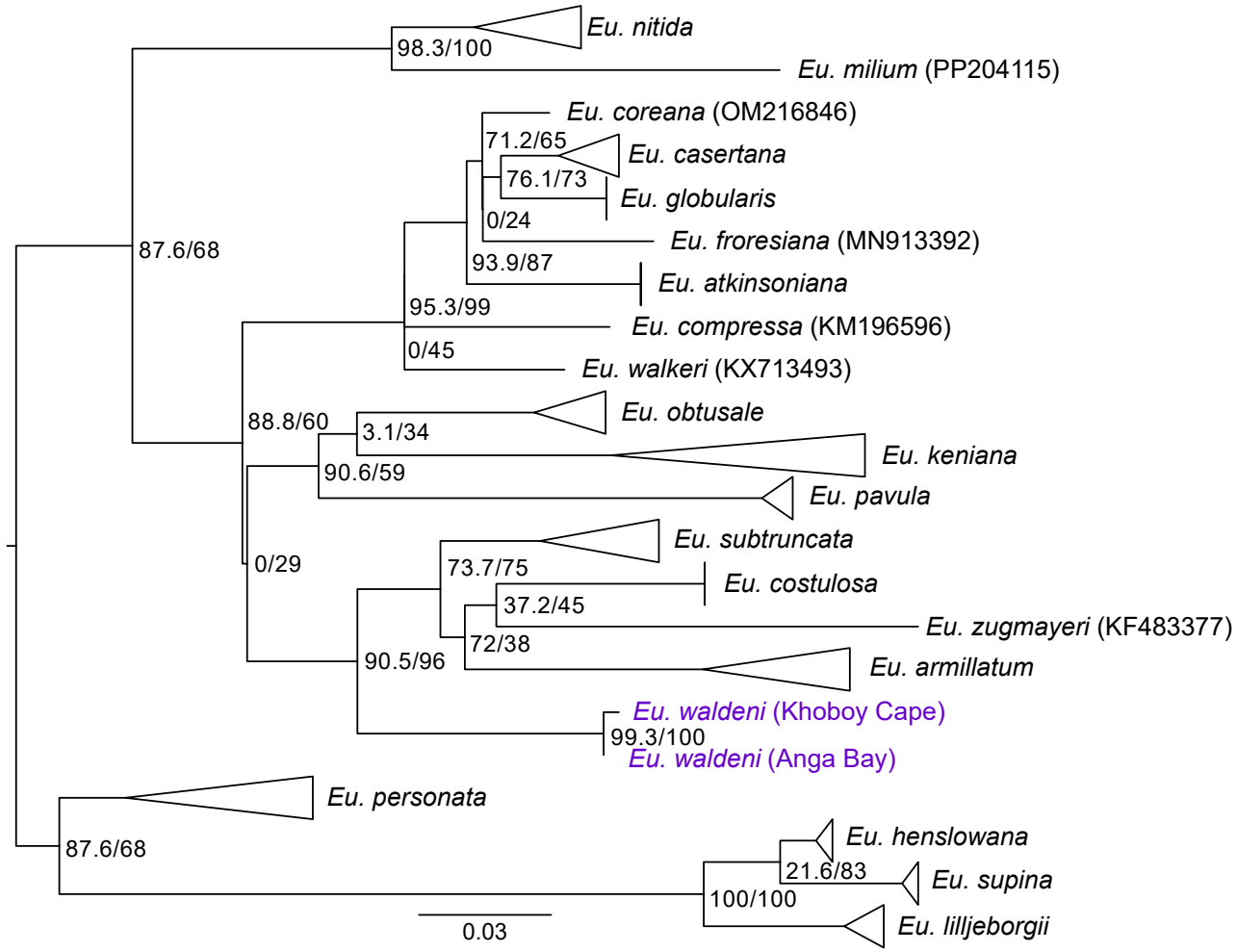

Fig. 6. Midpoint-rooted maximum likelihood (ML) tree derived from CO1 nucleotide sequences of the genus *Euglesa* Jenyns, 1832. SH-aLRT/UFBS support values are indicated at the tree nodes. The *Eu. waldeni* (Kuiper, 1975) haplotypes from Lake Baikal are highlighted in purple.

Before *Eu. waldeni* was classified as a separate species (Kuiper, 1975), these widespread Palaearctic pea clams were considered the "northern form of *P. lilljeborgii*" (= *Eu. lilljeborgii*). Kornyushin (1996) assigned *Eu. waldeni* to the genus *Henslowiana* Servain, 1888, thereby positioning it closer to *Eu. henslowana* and *Eu. lilljeborgii*. However, these species are separated by a significant genetic distance. The phylogenetic position of *Eu. waldeni*, based on COI sequences, is consistent with previous phylogenetic studies mainly based on rRNA markers (Schultheiß et al., 2008; Clewing et al., 2013; Bespalaya et al., 2017, 2024b; Saito et al., 2022).

At present, we cannot determine how long *Eu. waldeni* inhabited Lake Baikal. The fossil record documents the presence of Sphaeriidae in Baikal over an extended period. In particular, shells of sphaeriine clams have been found in the deposits of the Tankhoi Formation, which are approximately five million years old (Martinson, 1961; Rasskazov et al., 2014). Moreover, the divergence between *Eu. waldeni* and *Eu. nipponensis* is estimated to have occurred about five to 25 million years ago (Bespalaya et al., 2024b). Deep-water Lake Baikal, during global climate changes such as the low temperatures of the Ice Ages, could have served as a refugium for various filter-feeding organisms, particularly sedentary polychaetes (Pudovkina et al., 2016). Despite this, it is possible that *Eu. waldeni* is a relatively recent Palaearctic invader that entered the lake from neighbouring areas. Some cases of such a "young" invasion are known among the gastropods of Lake Baikal

Table 2. Shell morphometry in type specimens of *Euglesa* species (Slugina & Starobogatov, 1999) and in mature individuals of *Eu. waldeni* from Lake Baikal.

Species and locality	Length, mm	Height, mm	Width, mm	SEI	SCI	Maturity stages
Eu. granum (Lindholm, 1909) (P), Dagarskaya Bay, N = 2	3.0–3.3	2.9–3.0	2.0–2.1	90.90–96.67	63.63–66.67	–
Eu. korotnewi (Lindholm, 1909) (L), Listvyanka, N=1	4.0	3.8	2.6	95.00	65.00	–
Eu. minuta (Kozhov, 1936) (H), Birkhin Bay, N=1	3.0	2.5	1.6	83.33	53.33	–
Eu. platyvalva Slugina et Starobogatov, 1994 (H), Dagarskaya Bay, N=1	2.85	2.45	1.3	85.96	45.61	–
Eu. subgranum Slugina et Starobogatov, 1994 (H & P), Peschanaya Bay, N = 3	2.5–2.8	2.15–2.55	1.3–2.0	86.00–91.07	52.00–71.42	–
Eu. waldeni (Kuiper, 1975), Anga Bay, N = 5	2.30–2.85 2.56±0.10	2.00–2.40 2.18±0.07	1.35–1.60 1.47±0.05	80.77–87.50 85.25±1.26	53.85–60.38 57.48±1.13	0–3
Eu. waldeni , Off Khoboy Cape, N = 3	2.50–3.00 2.72±0.15	2.10–2.60 2.32±0.15	1.40–1.90 1.60±0.15	84.00–86.67 85.19±0.78	56.00–63.33 58.65±2.35	0–2
Eu. waldeni, Barguzinskiy Bay, N = 17	2.20–2.65 2.37±0.03	1.85–2.30 2.03±0.03	1.20–1.60 1.34±0.04	82.22–88.46 85.51±0.47	50.00–64.00 56.14±0.94	0–4
Eu. waldeni, all localities, N = 25	2.20–3.00 2.45±0.04	1.85–2.60 2.09±0.04	1.20–1.90 1.39±0.04	80.77–88.46 85.42±0.40	50.00–64.00 56.71±0.73	0–4

Note. H – holotypes; L – lectotypes; P – paratypes; N – number of specimens; SEI = height / length ratio × 100; SCI = width / length ratio × 100. Numbers above the horizontal line represent the limits, while those below the line represent the mean ± standard error.

(Sitnikova et al., 2024). The discovery of two distinct COI haplotypes of *Eu. waldeni* in Lake Baikal may indicate either multiple recent invasions or the presence of this species in the lake for several hundred thousand years. It is important to consider that the 16S rRNA and ITS1 markers may exhibit limited variability among closely related species. For example, *Eu. supina* and *Eu. henslowana* show no differences in ITS1. The presence of identical ITS1 alleles and 16S haplotypes in *Eu. waldeni* populations across 3,000–4,000 km suggests two possible explanations: the conservatism of these molecular markers or a relatively recent dispersal across its extensive range. Sphaeriine clams are capable of attaching to various aquatic animals and plants, indicating that they can disperse over long distances via waterfowl, reptiles, amphibians, and even large flying insects (Kew, 1893; Rees, 1965; Mackie, 1979; Bespalaya et al., 2020, 2024a). Viviparity, simultaneous hermaphroditism and autogamy, the ability to overwinter in a frozen state, high fecundity, and small size are believed to facilitate sphaeriid clams in dispersing and colonising high latitudes (Bespalaya et al., 2015, 2019; Vinarski et al., 2021).

Shells of *Eu. waldeni* from Lake Baikal are relatively small, with shell lengths of up to 3.1 mm. By comparison, data from other regions indicate shell lengths of 4.2–4.7 mm in Scandinavia (Kuiper, 1975) and up to 4.0 mm in Ukraine (Stadnichenko, 1984). The smaller size of *Eu. waldeni* in Baikal may represent an adaptation to specific environmental conditions of the lake. This cannot be attributed to a predominance of juvenile individuals in our samples, as approximately 40% of the dissected specimens contained embryos at various stages of development. One hypothetical explanation is juvenilisation (or neoteny) of this species in Baikal. Supporting this hypothesis is the absence of *Euglesa* species with shell lengths

greater than 3.5–4.0 mm in the lake (Slugina & Starobogatov, 1999) (Table 2). All five *Euglesa* species currently recorded in Lake Baikal are only weakly differentiated morphologically. The discovery of *Eu. waldeni*, which resembles *Eu. granum*, in Baikal suggests that local environmental conditions, by reducing conchological distinctions among pea clams, may contribute to the formation of local morphs in Palaearctic species that resemble endemic species. Further studies of the Baikal pea clams, with larger sample sizes, are required to determine whether *Eu. granum* and *Eu. waldeni* should be regarded as separate species.

The first well-documented record of the fingernail clam species *Eu. waldeni* in Lake Baikal expands our understanding of the distribution and ecology of this species. It also provides new insights into the origin, diversity, and endemism of the bivalve fauna in Lake Baikal. These topics should be the focus of future studies employing an integrative taxonomic approach.

Addenda

Electronic supplementary material. List of COI sequences of *Euglesa* species from GenBank used for maximum likelihood phylogeny. File format: PDF. Available from: https://doi.org/10.31610/zsr/2025.34.2.364

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