



Morphology and habitat of *Euglesa casertana* populations in Yakushima Island, Japan, with implications for its taxonomic status (Mollusca: Sphaeriidae)

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Abstract

A population of sphaeriid clams with a manuscript name “*Pisidium habei* Kuroda” has long been believed to be an undescribed species endemic to the UNESCO World Natural Heritage, Yakushima Island, Southern Japan. Although the known distribution of this taxon was restricted in one narrow high-altitude area of the island, one highland and two lowland populations were discovered in this study. We investigated the morphological and genetic characteristics of previously known and newly discovered populations, and conducted a brief survey of habitat temperature and population density. The examined specimens exhibited variations in external and internal shell morphologies within and among populations, with most falling within the range of the cosmopolitan *Euglesa casertana* (Poli, 1791). The four populations shared similar 16S haplotypes, which were closest to those of *E. casertana* from Northern Japan. Based on the phylogenetic position and morphological relationships, the *Euglesa* populations in Yakushima Island with the unavailable manuscript name “*Pisidium habei*” should be regarded as regional populations of *E. casertana*. In the lowland habitats of Yakushima Island, water temperatures rose up to 27.1 °C during summer. The significant differences in aquatic environments among the four surveyed localities indicate that Yakushima Island harbors diverse habitats for *E. casertana*, suggesting that its distribution range in Southern Japan and the surrounding East Asian region potentially includes wider environments than previously assumed. Taxonomic accounts and distributions of many sphaeriids remain uncertain in Japan, and thus, taxonomic and faunal studies employing integrative approaches are required.

Keywords Anatomy · Endangered species · Diagnosis · Mitochondrial haplotype · Taxonomic revision

Introduction

The family Sphaeriidae Deshayes, 1855 (1820) is a family of tiny freshwater bivalves with more than 240 species distributed worldwide, except in Antarctica (Korniushin 2006; Graf 2013; Lee 2019; Graf and Cummings 2026). Members of Sphaeriidae inhabit various aquatic environments, such as shallow marshes, fast-flowing streams, rice paddies, highland ponds, and deep lakes, and the ranges of many sphaeriid species extend globally (Korniushin 1996a; Killeen et al. 2004; Clewing et al. 2013; Groh et al. 2020). The extensive distribution and habitat range of this family have been explained by their ability

to passively disperse over long distances and colonize a wide range of environments (Lee 2019; Bernal et al. 2020). Understanding of the species richness and phylogenetic relationships of Sphaeriidae species has been improved through historical taxonomic revisions focusing on regional fauna and recent global genetic studies (e.g. Kuiper 1983; Piechocki 1989; Korniushin 2001; Clewing et al. 2022; Saito et al. 2022; Bernal et al. 2024). On the other hand, there are regions where many species with uncertain taxonomic accounts remain, such as Japan (Saito et al. 2022).

“*Pisidium habei* Kuroda” is one of the taxa of Japanese Sphaeriidae with ambiguous taxonomic position. Kuroda (1955) reported a population of Sphaeriidae from Japan’s southernmost high moor located in the UNESCO World Natural Heritage, Yakushima Island (vicinity of locality 1

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in Fig. 1). Kuroda (1955) believed this population to be an undescribed species and tentatively provided it a manuscript name “*Pisidium habeï*”. Subsequent surveys conducted by several researchers confirmed that “*Pisidium habeï*” is endemic to a narrow area in the high-altitude regions of the island (Kuroda 1963; Habe 1991; Yukita 2000; Tomiyama et al. 2003). Due to its rarity, this taxon has been assessed as a threatened species (CR + EN) by the prefectural Red List (Tomiyama et al. 2003). However, the morphological differences between this Yakushima population and other congeners have not been clarified, and its distinctiveness has relied on its unique habitat confined to the insular high mountains (Kuroda 1955; Yukita 2000). Detailed morphological characteristics and diagnoses of “*Pisidium habeï*” have not been provided by the previous studies; consequently, its taxonomic account has long been uncertain.

In recent years, major morphological characteristics of the shell and soft body of “*Pisidium habeï*” have been briefly reported (Ieyama 2024). The study identified this taxon by a combination of several characteristics, such as a centrally

positioned umbo, deep surface striae, and relatively long perisiphonal suture, while showing partial similarities to *Euglesa casertana* (Poli, 1791) and *E. globularis* (Clessin, 1873). In contrast, phylogenetic analyses using sequences obtained from the habitat of “*Pisidium habeï*” (vicinity of locality 1) have placed them within the clade consisting of *E. casertana* (Saito et al. 2022). These sequences were identified as being derived from *E. casertana* by subsequent analysis (Bespalaya et al. 2024). Accordingly, contradictions arise between studies regarding the distinctiveness of “*Pisidium habeï*”, although knowledge of the morphological and genetic characteristics of this taxon has been fragmentarily accumulated.

Several new populations of *Euglesa* clams resembling “*Pisidium habeï*” were recently discovered by the authors in both highland and lowland areas of Yakushima Island (localities 2–4 in Fig. 1). We clarified morphological and genetic characteristics of previously known and newly discovered populations in Yakushima Island with providing new insights into its taxonomic account and natural history.

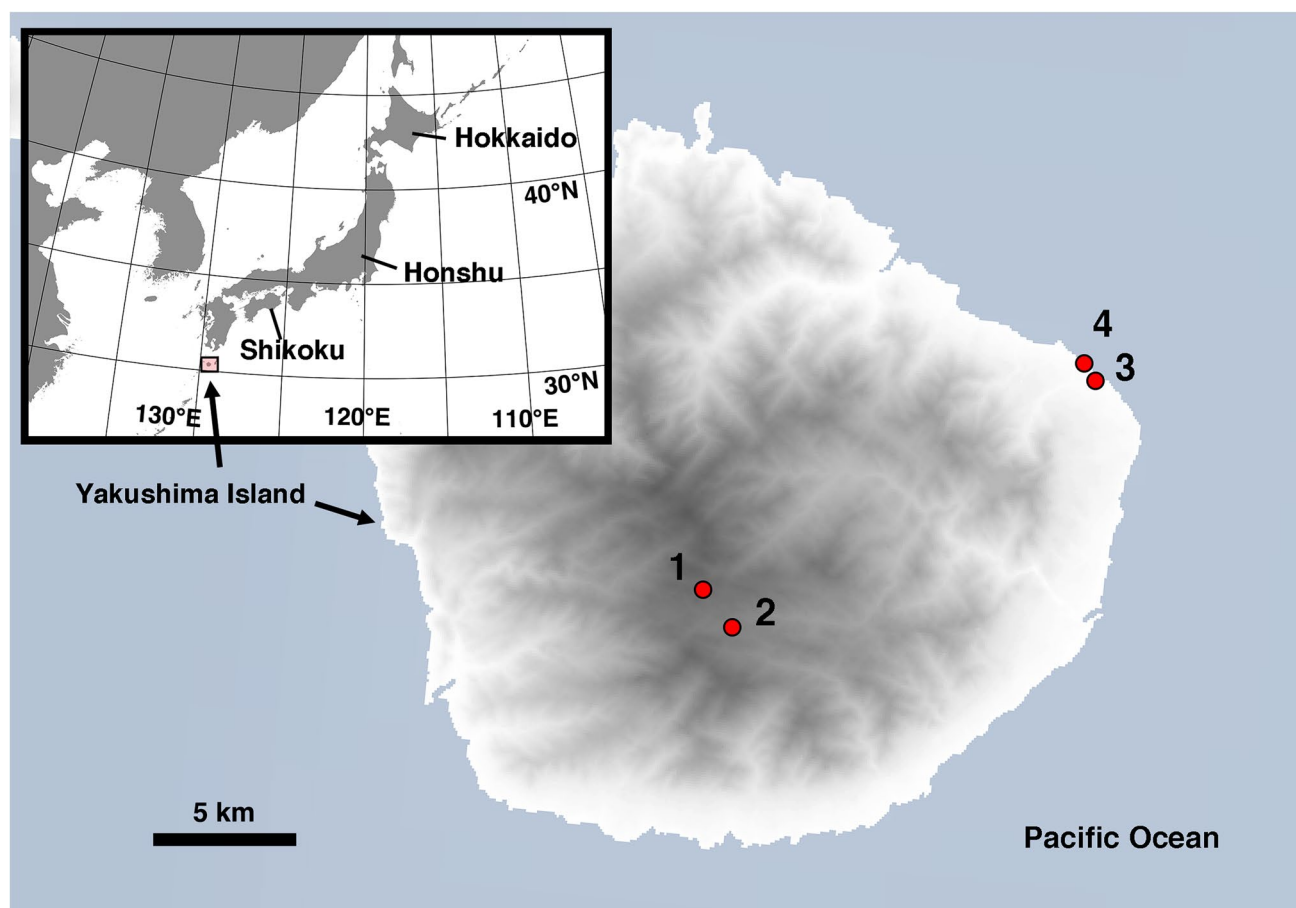


Fig. 1 Map showing the four collection localities of *Euglesa casertana* in Yakushima Island, Japan. The map was drawn using data from Reuter et al. (2007) and Amante and Eakins (2009)

Materials and methods

Field survey

Specimens examined in this study were collected from four localities in Yakushima Island, Japan (Fig. 1; Online resource: Table S1). Among them, locality 1 is vicinity of the site where the specimens of “*Pisidium habe*” was collected by Kuroda (1955), in which the manuscript name “*Pisidium habe*” was proposed. Localities 1 and 2 are situated within both Special Protection Zones designated under the Natural Parks Act of Japan, and the UNESCO World Natural Heritage site, and within areas designated as a Special Natural Monument under the Law for the Protection of Cultural Properties. Taxon sampling was conducted with permissions issued by the Agency for Cultural Affairs under the Law for the Protection of Cultural Properties (permission #: Bunkacho No. 4–2172, issued on 17 April 2020), the Ministry of the Environment under the Natural Parks Act (permission #: Kankyu-Yaku-Jikyo No. 2006121, issued on 12 June 2020), and the Forestry Agency for access to national forests (permission #: Protected Forest Survey Permission 33, issued on 11 August 2020).

In lowland locality 3, the habitat of *Euglesa* clams was surveyed eight times during the daytime (12:00–17:00) from July to November 2025 to observe rough fluctuations in water level and water temperature. Because points with relatively high and low water levels were present in this locality, the temperatures were measured at both points. Similar surveys were conducted at locality 4 in October and November 2025. The temperatures were measured using a solar-powered digital thermometer (MonotaRO Co.,Ltd., Japan).

The density of living animals was calculated at localities 1–3 using 1–5 quadrat surveys at each locality. At localities 1 and 2, sediment samples were collected to a depth of 5 cm using 15 × 15 cm quadrats, and all *Euglesa* individuals were counted on site. All individuals exceeding the permitted

number were released back into the wild on conservation grounds. Abundance was subsequently converted to the number of individuals per square meter. Sediment samples were collected to a depth of 5–10 cm using a 1 m square quadrat at locality 3.

Specimen preparation and morphological examination

The shells and soft bodies were separated after boiling for three seconds in water at 95 °C referring the methods by Fukuda et al. (2008). The shells were dried, and the entire soft bodies were preserved in 99% ethanol. Newly collected specimens were deposited at the Zoological Collection of Kyoto University, Japan (voucher #: KUZ Z6428–Z6439).

Morphological examinations were conducted according to the methods described by Mansur and Meier-Brook (2000) and Korniusshin and Glaubrecht (2002). Shell specimens from all localities were examined using a YS05T stereomicroscope (Micronet Inc., Japan). The number of specimens used for morphological examination is listed in Table 1. Among them, two specimens from locality 1 and five specimens from locality 3 were observed using a JSM-6510LV scanning electron microscope (JEOL Ltd.) after coating with platinum using a JEC-3000FC (JEOL Ltd.). The overall morphologies of the soft bodies were examined in each of the three specimens from localities 1 and 3. In addition, the lengths of the perisiphonal suture were measured in six specimens from locality 3. According to the known changes in character states accompanying growth, larger specimens within each population were used for morphological examination (Korniusshin 1996b; Korniusshin and Glaubrecht 2002).

The following shell measurements and indices were also obtained from digital images according to Kuiper (1983), Ituarte (1996), and Korniusshin (2001) using ImageJ v1.51 (Schneider et al. 2012): commissural index (commissural

Table 1 Measurements of *Euglesa casertana* collected from four localities in Yakushima Island, Japan

Locality # specimen #	1 3	2 3	3 13	4 11
Shell length (L) (mm)	3.6–4.6	3.3–3.6	3.2–4.1	3.2–4.0
Shell height (H) (mm)	3.2–4.0	2.8–3.1	2.9–3.6	2.8–3.5
Shell width (W) (mm)	2.1–3.1	1.8–2.1	2.0–2.9	1.7–2.5
Height index (H/L)	0.84–0.88	0.85–0.86	0.87–0.91	0.86–0.89
Convexity index (W/H)	0.89–0.90	0.90–0.92	0.68–0.91	0.90–0.92
Commissural index (commissural height/H)	0.89–0.90	0.90–0.92	0.85–0.92	0.90–0.92
Hinge length ratio (hinge length/L)	0.54–0.61	0.49–0.58	0.57–0.60	0.51–0.56
Hinge height ratio (hinge height/H)	0.058–0.068	0.064–0.068	0.055–0.075	0.059–0.070
Ligament-length index (ligament length/L)	0.19–0.26	0.24–0.26	0.23–0.27	0.21–0.25
Perisiphonal suture length/L	0.106–0.133	-	0.108–0.146	-

height/shell height; HK/H), convexity index (shell width/height; W/H), height index (shell height/length; H/L), hinge height ratio (hinge height/shell height; Hih/H), hinge length ratio (hinge length/shell length; Hil/L), ligament length, ligament-length index (ligament length/shell length; Li/L), shell length, shell height, and shell width.

Genetic analysis

Genomic DNA was extracted from 1–3 specimens from the four localities in Yakushima Island (Online resource: Table S1) according to the methods described by Sawada et al. (2021). Fragments of the mitochondrial 16S and nuclear 28S rRNA (28S) genes were used for genetic analysis based on the high availability of these two regions in Sphaeriinae (Bespalaya et al. 2024). Polymerase chain reaction (PCR) was performed referring the methods by Saito et al. (2022) with the primer sets and conditions described in Online resource: Table S2. The PCR products were purified using Exonuclease I and Antarctic Phosphatase (both New England Biolabs, USA), and outsourced to Eurofins Genomics K.K. (Japan) for sequencing. The sequences obtained in this study were deposited in the International Nucleotide Sequence Database (INSD) Collaboration through the DNA Databank of Japan (accession #: LC921253–LC921267).

Molecular phylogenetic trees of the concatenated sequences of 16S and 28S, and the 16S haplotype network were reconstructed. According to the phylogenetic relationships within Sphaeriinae (Bespalaya et al. 2024), the sequences of 10 sphaeriid species retrieved from GenBank were included in the present analyses (Online resource: Table S1). The identification of the GenBank sequences followed those by Bespalaya et al. (2024). Sequences were aligned using MAFFT v7 (Katoh et al. 2019) for each gene, with a LINS-I strategy. The non-conserved positions of the two genes were trimmed using Gblocks v1.0 (Castresana 2000; Talavera and Castresana 2007) with the following settings: a minimum number of sequences for a flank position – 50% of the number of sequences + 1; allowed gap positions – ‘With half’ for phylogenetic analysis, ‘None’ for haplotype analysis; default settings for the other parameters. The trimmed lengths of each dataset were as follows: 419 bp for 16S in haplotype analysis, 505 bp for 16S and 741 bp for 28S in phylogenetic analysis.

Phylogenetic trees of the concatenated sequences were estimated using maximum likelihood (ML) and Bayesian inference (BI). ML and BI trees were reconstructed using IQ-TREE v3.0.1 (Wong et al. 2025) and MrBayes v3.2.7 (Ronquist and Huelsenbeck 2003; Altekar et al. 2004), respectively. The following best-fit models were calculated based on the Bayesian information criterion and the greedy algorithm using ModelFinder implemented in IQ-TREE (Kalyaanamoorthy

et al. 2017) for ML and using PartitionFinder v2.1.1 (Lanfear et al. 2017) for BI. The evolutionary models were selected separately for 16S and 28S. The optimal models were TPM3u + F + R2 for 16S and HKY + F + G4 for 28S (ML); SYM + I + G for 16S and 28S (BI). The branch support of ML was assessed using 200 nonparametric bootstrap (BS) replicates. Four Markov chains in eight independent runs were conducted for five million generations, and the tree was sampled every 100 generations in the BI. After confirming the parameter estimates and convergence using Tracer v1.7.2 (Rambaut et al. 2018) (effective sample sizes $> 10^4$; average standard deviation of split frequencies < 0.006), the first half million trees were discarded from the analysis.

The haplotype network of 16S sequences was calculated using statistical parsimony with PopART v1.7 (Leigh and Bryant 2015).

Results

Morphological description

Shell (Figs. 2, 3)

Measurements shown in Table 1. Shell small [shell length 3.7 ± 0.3 (average $\pm$ standard deviation), shell height 3.3 ± 0.2 , shell width 2.2 ± 0.3 mm], thin, oval to triangular, high, laterally compressed (localities 1, 2, 4) or slightly inflated (locality 3) (H/L 0.87 ± 0.02 , W/H 0.80 ± 0.12). Anterior margin more protruded than posterior margin, typically rounded (Fig. 2a–h, o, p), rarely strongly protruding (Fig. 2m, n). Posterior margin rounded, gently truncated. Dorsal margin has slightly angular sloping shoulders. Ventral margin strongly curved. Umbo almost central or subcentral, slightly shifted toward posterior side, angled anteriorly, located at approximately 55% of shell length, broad, slightly swollen toward dorsal side (HK/H 0.90 ± 0.01). Sculpture on outer surface distinct, relatively regular, with concentric ribs outside umbonal region (Figs. 2a, c, e, g, 3g, h). Folds of periostracum absent. Surface of umbonal region almost smooth, with fine irregular radial folds (Fig. 3g). Outer surface has dull sheen, colored light blue-gray to light brown typically without color bands, or rarely with irregular broad dark brown concentric bands (Fig. 2a, c, e, g). Inner surface mat, colored blue-gray to light yellow–brown with irregular milky white spots (Fig. 2b, d, f, h). Shell visible beige before separating light beige-colored soft body (Fig. 2i–l). Pores distinguishable on inner shell surface, dense throughout entire surface, its openings variable in size (approximately 2–10 μ m between pores), excluding hinge and shell edge,

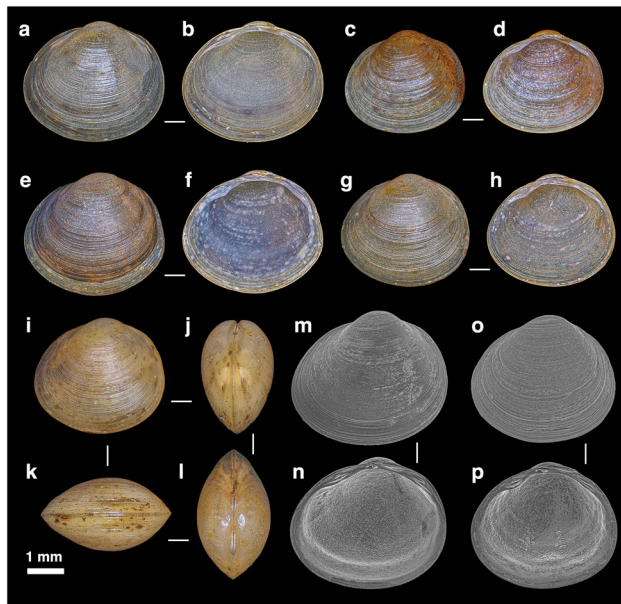


Fig. 2 Shell specimens of *Euglesa casertana*. **a–h** Empty shells from localities 1 (**a, b**), 2 (**c, d**), 3 (**e, f**), and 4 (**g, h**); **i–l** specimen before separating the soft body from locality 4; **m–p** scanning electron microscope images of empty shells from localities 1 (**m, n**) and 3 (**o, p**). Lateral (**a–i, m–p**), posterior (**j**), ventral (**k**), and dorsal (**l**) views

approximately 20–50 μm in diameter (Fig. 3i, j). Scars of inner radial muscles obscure, usually invisible, small, partially separated from pallial line (Fig. 2n, p).

Hinge (Fig. 3e–j)

Hinge plate relatively broad (H_{ih}/H 0.07 ± 0.005), relatively long (H_{il}/L 0.56 ± 0.03). Inner left cardinal tooth (c2) short, thin, moderately to strongly arched dorsoventrally, (Fig. 3a, c, e), strongly protruding laterally (Fig. 3f). Outer left cardinal (c4) relatively long, thin, oblique, typically almost straight entirely (Fig. 3c, e), or rarely weakly arched ventrally (Fig. 3a), c4 usually unparallel to c2 (Fig. 3a, c), but rarely almost parallel (Fig. 3e). Right cardinal tooth (c3) relatively long, thin, moderately to strongly arched dorsoventrally; posterior end bifurcating (Fig. 3b, d). Left lateral teeth (a2, p2) long, thick (Fig. 3c, e), with nearly central blunt cusps, strongly protruding laterally (Fig. 3f). Right lateral teeth (a1, a3, p1, p3) long, thick with small grains at central portions (Fig. 3b, d). Anterior teeth (a1–a3) usually stronger than posterior ones (p1–p3). Ligament not introverted, relatively broad, moderately long (L_{il}/L 0.24 ± 0.02), not protruding externally (Fig. 3a–e).

Mantle cavity (Fig. 4a)

Foot wide, elongated, with deep groove on its ventral side and shallow lines on lateral sides, connected to anterior and

posterior foot retractors. Anterior foot retractor adheres shell near labial palp. Distal portion of posterior foot retractor locates between posterior adductor muscle and nephridia (Fig. 5d). Anterior and posterior adductor muscles located at higher position of cavity. Digestive organs surrounded by foot and ctenidia. Labial palps at anterodorsal of mantle cavity connect to oesophagus. Intestine originating from midgut simply coiled, runs along ventral side of stomach, curving sharply near dorsal margin of mantle cavity behind posterior side of stomach, penetrating through pericardium, passing dorsal sides of nephridia and posterior adductor muscle, reaching anal on upper side of exhalant siphon. Gonad relatively large, surrounded by intestine, pericardium, and brood pouch.

Mantle edge (Fig. 4b)

Only exhalant siphon present with one pair of retractors (sr1). Branchial opening located at ventral side of exhalant siphon, with one pair of lower retractors (sr3). Lower retractor fibers of st3 connected near perisiphonal suture. Perisiphonal suture short ($12.3\% \pm 0.01\%$ of shell length), its posterior end corresponds to branchial opening. Pedal slit long. Inner radial mantle muscles long, thin, organized in eight to nine strong bundles, perpendicular to mantle margin. Bundles of equally developed. Outer radial mantle muscles short. Peripheral mantle edge thickened.

Ctenidium and brood pouch (Fig. 4a)

Inner and outer demibranches present. Inner demibranch large, occupies a relatively large portion of mantle cavity surface, with ascending and descending lamellae. Ascending lamella relatively low, approximately one-third heights of descending lamella. Outer demibranch weakly developed, only with ascending lamella, its anterior edge placed at 12th to 15th filaments of inner one. Brood pouch developing along edge of ascending lamella of inner demibranch, occupies greatest part of ctenidium on later stages of development with three to four shelled embryos per brood pouch. Several small individual pouches with 1–2 filaments aggregate, connecting to pouch with six to seven filaments in early stages of development.

Digestive system (Fig. 4a, c)

Mouth locates at base of outer lamellae of labial palps. Outer palps with anteriorly projecting angles, forming V-shaped incision between palps. Six to seven and five to six ridges distinguishable on ventral surface of outer lips and dorsal surface of inner lips, respectively. Oesophagus runs along dorsal edge of mantle cavity, between dorsal elevation of digestive glands, connecting to dorsal side of stomach. Stomach almost totally embedded in digestive glands, not

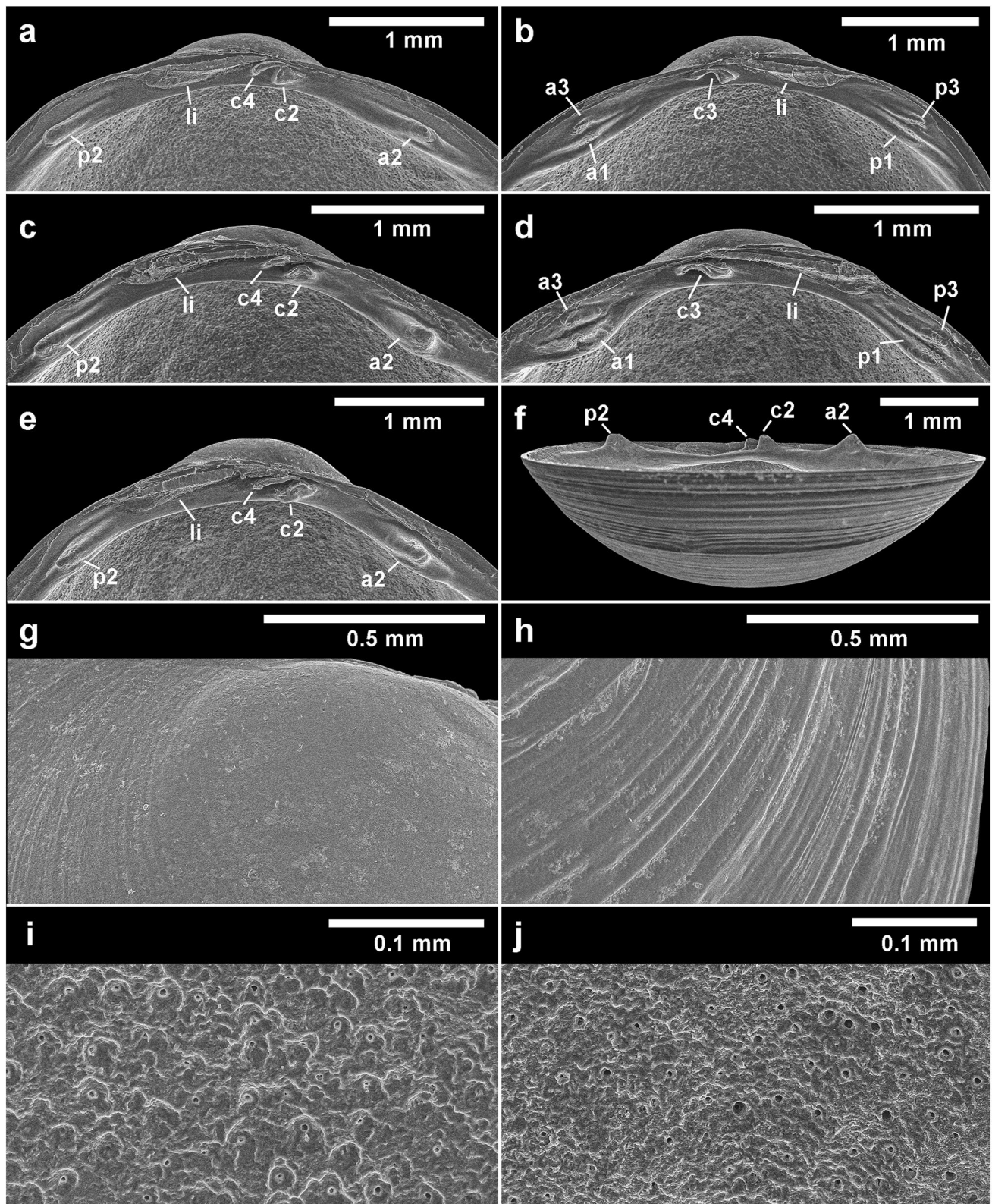


Fig. 3 Scanning electron microscope images of *Euglesa casertana*. **a–d** Hinge plates showing the right (**b, d**) and left (**a, c, e**) valves from the lateral view, and the left valve from the ventral view (**f**); **g, h** outer surfaces of the umbonal region (**g**) and shell edge (**h**); **i, j** inner surface of the umbonal region with dense pores. **a, b, f, i** Specimens from locality 1; **c–e, g, h, j** specimens from locality 3. Abbreviations: a1 – inner anterior lateral tooth of the right valve, a2 – anterior lateral tooth of the left valve, a3 – outer anterior lateral tooth of the right valve, c2 – inner cardinal tooth of the left valve, c3 – outer cardinal of the right valve, c4 – outer cardinal tooth of the left valve, li – ligament, p1 – inner posterior lateral tooth of the right valve, p2 – posterior lateral tooth of the left valve, p3 – outer posterior lateral tooth of the right valve

separated from midgut, stretched posteriorly, with narrow sorting area and dorsal hood on its roof. Anterior fold slightly elevated, with smooth surface. Anterior ridge (r1) branches off from posterior one (r2), connecting to minor typhlosole (t2) near boundary between stomach and midgut. Major typhlosole (t1) thick, slightly elevated, U-shaped. Minor typhlosole (t2) turning posteriorly at its proximal end. Intestine coil has single loop.

Nephridium (Fig. 4d–f)

Nephridium closed, with pericardial duct completely covered by dorsal lobe. Course of pericardial duct relatively fixed, typically with two loops, rarely with three loops, its tip forming narrow funnel. Pericardial duct curves dorsoventrally in V-shape near funnel, then folds ventrally in sagittal plane, curving in U-shape before reaching lateral loop. U-shape arch absent in nephridium with two loops. Lateral loop visible from dorsal side of nephridium after removing posterior adductor muscle, connecting to anteroventral side of dorsal lobe. Anterior portion of lateral loop partially or completely covered by dorsal lobe. Dorsal lobe almost square, connecting to distal loop at its dorsal portion toward ventral direction of nephridium. Course of distal duct stable, with single U-shape loop, opening to excretory sac at basal portion of nephridium. Excretory sac relatively small, not extending anterior side of dorsal lobe.

Habitat

The habitats of each locality were surrounded by forests, and no aquatic environments suitable for the habitation of sphaeriids were observed in the surroundings. The environment of the four collection localities of *Euglesa* clams was diverse (Online resource: Table S1; Fig. 5): peat substrate mixed with sand in a shallow high moor at an altitude of 1,630 m (locality 1), peat substrate mixed with sand in a small shallow stream at 1,400 m (2), mud substrate mixed with small pebbles and woodchips in a shallow fallow paddy field at 8 m (3), and mud substrate mixed with gravel in a small shallow stream at 21 m (4). Individuals

of *Odhneripisidium* Kuiper, 1962 was found at locality 3. No other sphaeriid species were collected at localities 1, 2, and 4.

The water temperatures of lowland habitats measured from July to November are shown in Tables 2, 3. Although no water flows into the paddy fields at locality 3, the habitats did not completely dry up even during the summer season (Fig. 5c, d). The water temperature in the habitat increased to a maximum of 27.1 °C as the surrounding ground surface temperature increased. Living animals of *Euglesa* clams were consistently observed at both high and low water points.

Living animals were collected only at quadrats containing peat, and was not observed on sandy substrates in localities 1 and 2 (Table 4). Large variations in the density of individuals were detected between the five quadrats at localities 1 and 2.

Genetic relationships

Topologies of the 1,246 bp concatenated ML tree (Online resource: Fig. S1) and BI tree (not shown) were similar. Monophyly of the clade consisted of *E. casertana*, *E. florensiana* (B. Rensch, 1934), *E. hallae* (Kuiper, 1983), *E. compressa* (Prime, 1852), and *E. walkeri* (Sterki, 1895) was strongly supported [BS = 89, Bayesian posterior probabilities (BPP) = 1.00], although the clade of *E. casertana* was not recovered with strong supports. Both trees strongly supported the monophyly of the sequences from the four localities on Yakushima Island (BS = 100, BPP = 0.99) within the branch composed of *E. casertana* sequences.

One to two nucleotide mutations were calculated in the 16S haplotypes from Yakushima Island (Fig. 6). The haplotypes of the island were most similar to those of Japanese *E. casertana* from Hokkaido and Honshu among the large haplotypic variations within the species. The closest haplotypes of Yakushima specimens and Japanese *E. casertana* were separated by eight mutation steps. While haplotypes of Yakushima specimens were unique to the Island, haplotypes from northern Japan, Europe, and North America were scattered in the network, indicating the geographically unstructured haplotype relationships.

Discussion

The morphological and haplotype characteristics of “*Pisidium habei*” examined in the present study were consistent with those of previous studies. Based on the specimens from locality 1, Ieyama (2024) described the major morphological characteristics of this undescribed species, and indicated that the combination of the following character states distinguishes it from *E. casertana* and

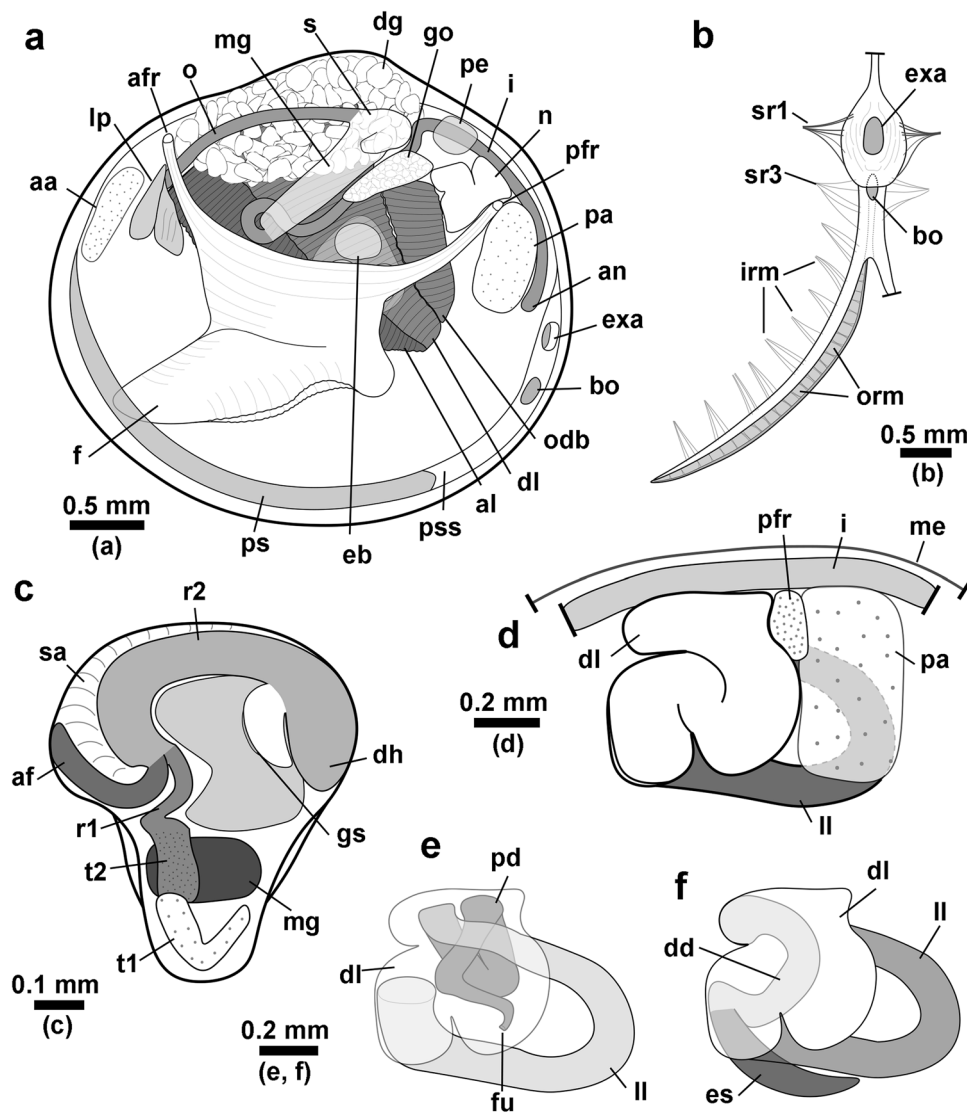


Fig. 4 Schematic illustrations of the anatomical characteristics of *Euglesa casertana*. **a** Mantle cavity after removing the mantle lobe, ctenidium, and digestive glands of left hemisphere; **b** mantle edge; **c** inner structure of the stomach from the dorsal view after removing the stomach roof and style sac in the midgut; **d–f** left nephridium from the lateral view showing the dorsal lobe and lateral loop (**d**), pericardial duct and funnel (**e**), and distal duct and excretory sac (**f**). Abbreviations: aa – anterior adductor muscle, af – anterior fold, afr – anterior foot retractor, al – ascending lamella of inner demibranch, an – anus, bo – brantial opening, dd, distal duct, dg – digestive gland,

dl – descending lamella of inner demibranch, dh – dorsal hood, dl – dorsal lobe, eb – embryo, es – excretory sac, exa – exhalant siphon, f – foot, fu – funnel, go – gonad, gs – gastric shield, i – intestine, irm – bundles of inner radial mantle muscles, ll – lateral loop, lp – labial palp, me – mantle edge, mg – midgut, n – nephridium, o – oesophagus, odb – outer demibranch, orm – bundles of inner radial mantle muscles, pa – posterior adductor muscle, pd – pericardial duct, pe – pericardium, ps – pedal slit, pfr – posterior foot retractor, pss – perisiphonal suture, r1 – r2 – fold of stomach wall, s – stomach, sr1, sr3 – siphonal retractors, t1 – major typhlosome, t2 – minor typhlosome

other congeners: centrally positioned umbo, deep surface striae, narrow hinge, weakly arched c2, and relatively long perisiphonal suture. The specimens from the four localities exhibited characteristics typical of “*Pisidium habe*”, while showing variations within and between populations in shell width, umbonal position, arch strength of c2, and hinge width. Based on the morphological similarity and identity of collection sites between the previous (Kuroda

1955; Yukita 2000; Ieyama 2024) and present studies, the examined specimens from locality 1 were identical to “*Pisidium habe*”, which has long been distinguished as an undescribed species. According to the morphological characteristics shared by the specimens from the four localities, specimens from localities 2–4 were also identified as this species. The specimens from the four localities showed unique haplotypes very close to that from locality

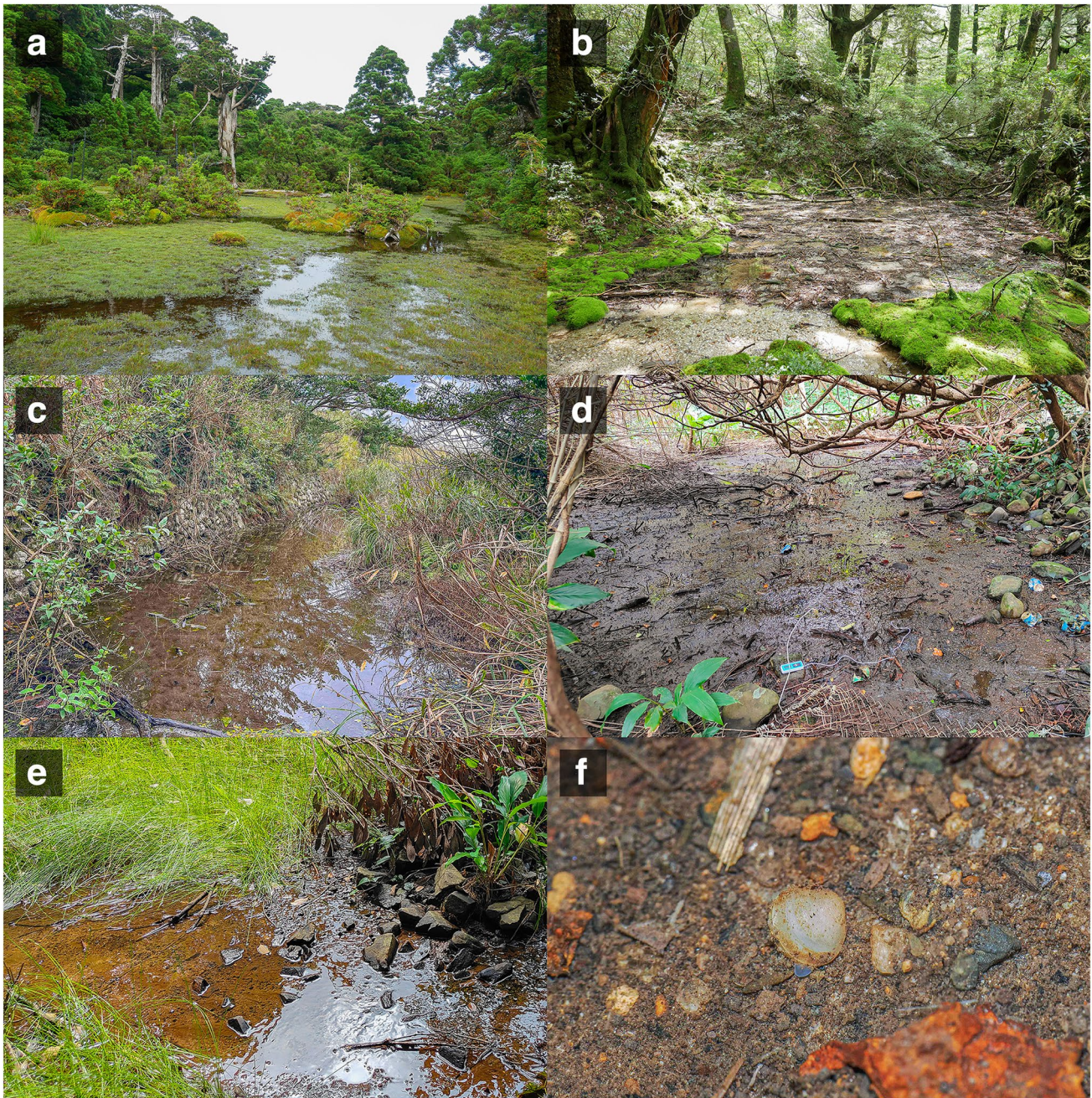


Fig. 5 Habitat of *Euglesa casertana*. **a** High moor at an altitude of 1,630 m (locality 1); **b** small stream at an altitude of 1,400 m (locality 2); **c, d** high water level point (**c**) and low water level point (**d**) of the

fallow paddy field at an altitude of 8 m (locality 3); **e** small stream at an altitude of 21 m (locality 4); **f** living animal at locality 3

1 obtained by Saito et al. (2022), and they were similar to the Japanese haplotypes of *E. casertana*. Although the monophyly of the clade of *E. casertana* was not sufficiently supported in the present phylogeny, the sequences of Yakushima specimens were included in the branch formed by the sequences of *E. casertana*, consistent with previous results (Saito et al. 2022; Bespalaya et al. 2024).

Significant morphological variation was detected in the shell, hinge, perisiphonal suture, ctenidia, and nephridia of *E. casertana* (Odhner 1929; Piechocki 1989; Killeen et al. 2004). However, the species can typically be distinguished by the combination of the following characteristics: oval shell outline, distinctly curved c2, c4 unparallel to c2, short perisiphonal suture and outer demibranch, 6–9 bundles of

Table 2 Water temperatures in lowland habitats (locality 3) of *Euglesa casertana* and ground surface temperature around habitats in Yakushima Island, Japan

Survey date	Time	Weather	Ground surface (°C)	High-water habitat		Low-water habitat (°C)	
				Water temperature (°C)	Approximate water level (cm)	Water temperature (°C)	Approximate water level (cm)
05 Jul. 2025	17:00	Cloudy	28.9	23.4	5	26.4	< 1
17 Jul.	17:00	Cloudy	28.1	22.6	10	25.8	< 1
02 Aug.	13:00	Sunny	29.7	23.2	10	26.5	1
16 Aug.	14:30	Sunny	31.0	23.8	10	27.1	1
13 Sep.	12:00	Cloudy	28.8	23.7	10	26.2	1
27 Sep.	15:00	Sunny	28.4	24.9	10	26.0	1
18 Oct.	14:15	Cloudy	26.9	23.9	10	24.8	1
11 Nov.	14:15	Cloudy	21.1	19.9	10	18.6	1

Table 3 Water temperatures in lowland habitats (locality 4) of *Euglesa casertana* and ground surface temperature around habitats in Yakushima Island, Japan

Survey date	Time	Weather	Ground surface (°C)	Water temperature (°C)	Approximate water level (cm)
18 Oct. 2025	14:30	Cloudy	25.9	24.3	10
11 Nov.	14:30	Cloudy	21.1	19.2	10

Table 4 Density of living animals of *Euglesa casertana* at three localities in Yakushima Island, Japan. The surveys at Locality 1 and 2 were conducted in 15 × 15 cm quadrats, and the results were converted to the number of individuals per square meter. A 1 m square quadrat was used at locality 3

Locality #	Survey date	Quadrat #	Substrate	Specimen # (/m ²)
1	03 Sep. 2020	1	peat	44.4
1		2	peat	0
1		3	peat	222.2
1		4	peat with sand	177.8
1		5	sand	0
2	03 Sep. 2020	1	peat	488.9
2		2	peat	2266.7
2		3	peat with sand	266.7
2		4	sand	0
2		5	sand	0
3	21 Feb. 2025	1	mud with pebble	146

inner radial mantle muscle, and closed nephridia (Odhner 1929; Piechocki 1989; Korniusshin 1996b; Korniusshin and Hackenberg 2000; Korniusshin and Glaubrecht 2002). The examined Yakushima specimens tended to possess a

narrower hinge than the typical form of *E. casertana*. For the other diagnostic characteristics, in contrast, some of these specimens exhibited characteristics typical of *E. casertana* among the variation between individuals (Korniusshin and Hackenberg 2000; Killeen et al. 2004). Perisiphonal suture length of “*Pisidium habe*” [around 15% of SL by Ieyama (2024) and $12.3\% \pm 0.01\%$ by this study] was also included in its intraspecific range of *E. casertana* (12%–21%) measured with the same method (Ieyama 2025).

An enormous number of forms have been described for *E. casertana* because of its significant morphological diversity and extensive distribution (Kuiper 1983; Graf and Cummings 2026; MolluscaBase 2026). The arrangement of its synonymy was conducted based on both morphological and molecular evidence (Korniusshin 1996a, b; Vinarski and Kantor 2016; Bepalaya et al. 2024). On the other hand, previous and present genetic analyses have detected significant genetic diversity within this species, including geographically unstructured relationships in mitochondrial haplotypes from Japan, Europe, and the USA (Saito et al. 2022; Bepalaya et al. 2024; Fig. 6). Therefore, a global revision based on a well-resolved nuclear phylogeny and covering most names synonymized under *E. casertana* is required for this species, as suggested by these previous studies. Under the current classification, the *Euglesa* populations in Yakushima Island with the manuscript name “*Pisidium habe*” should be regarded as regional populations of *E. casertana* based on its phylogenetic position and morphological similarity to *E. casertana*. This manuscript name has unavailable according to the Article 13.1.1. of the Code (International Commission on Zoological Nomenclature 1999) because a description intended to differentiate this taxon was not provided by Kuroda (1955). In addition, since none of the subsequent studies referring to “*Pisidium habe*” meet the requirements for the criteria of availability (Articles 13.1.1., 16.1., and 16.4.), this manuscript name has consistently been unavailable (Kuroda 1963; Habe 1991; Yukita 2000; Tomiyama et al. 2003; Ieyama 2004, 2005).

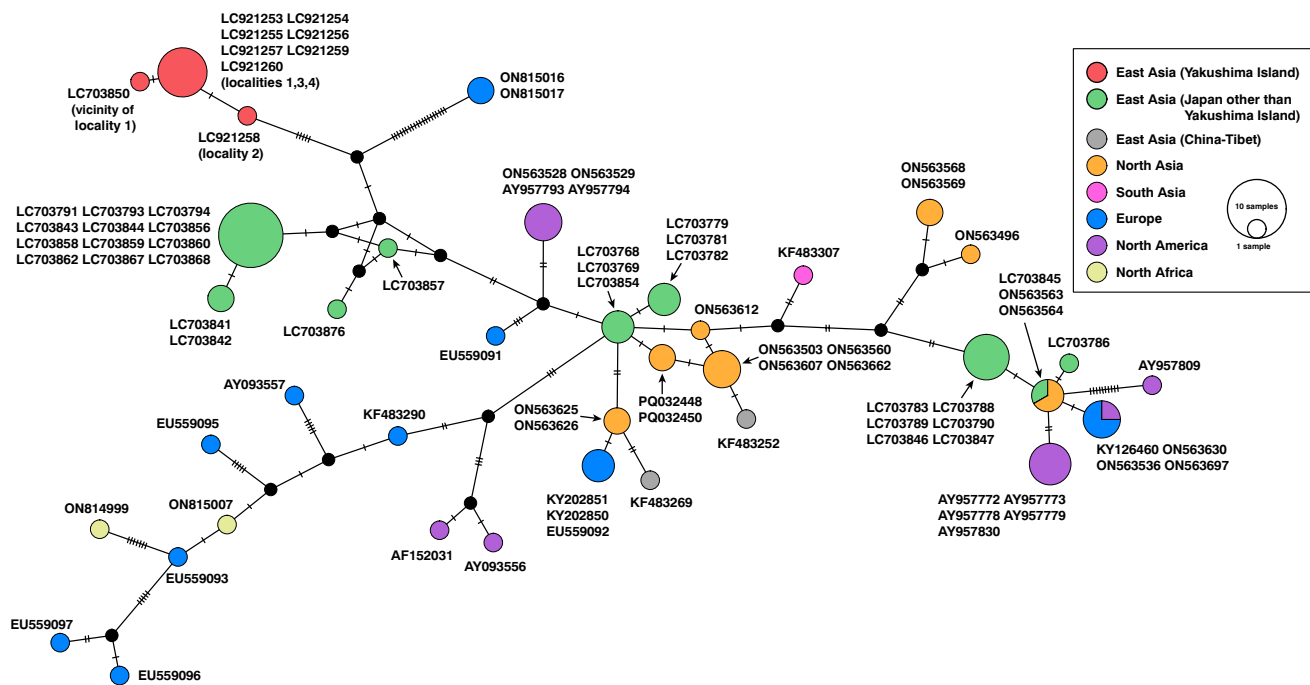


Fig. 6 Statistical parsimony network showing the relationships between the 16S haplotypes detected in *Euglesa casertana*. Each connection indicates a single mutation, and the hatch marks represent missing intermediate haplotypes

Euglesa casertana is a cosmopolitan species distributed across every continent except Antarctica, from polar regions to the tropics (Kuiper 1964, 1983; Kuiper et al. 1989; Van Damme et al. 2016). This species is widespread in Europe and North America, and sporadic in other regions (Van Damme et al. 2016). The distribution patterns of *E. casertana* in Japan were considered to vary according to latitude prior to this study. While common in lowland environments in Hokkaido and northeastern Honshu (Fig. 1), it is restricted to high altitudes (approximately 700 m or above) in western Honshu and Shikoku, with the southern limit in Yakushima Island (1,630 m) (Yukita 2000; Tomiyama et al. 2003; Inaba et al. 2011; Oyagi and Ieyama 2017; Saito et al. 2022). From the low-latitude regions of East Asia to South Asia, it is recorded only at high elevations, limited to localities with evident elevation data: Taiwan (3,048 m), China-Tibet (above 4,000 m), and Nepal (1,615 and 2,600 m) (Kuroda 1941; Subba Rao 1989; Clewing et al. 2013; Van Damme et al. 2016).

The discovery of lowland habitats (localities 3 and 4) in this study revealed that *E. casertana* can inhabit low-altitude areas even near 30°N latitude in East Asia. This species was consistently observed in shallow waters where temperatures rose to a maximum of 27.1 °C, indicating its tolerance to high temperatures. This suggests that *E. casertana* exhibits high ecological tolerance as previously observed (Kuiper and Wolff 1970; Kuiper 1983), and its distribution range in Southern Japan and the surrounding East Asian region is not limited to high-altitude areas and potentially extends far more widely than previously

assumed. The underestimation of its range may be attributable to the insufficiency of previous surveys, and therefore, further investigations of habitats in this region and ecological characteristics of *E. casertana* are required.

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Author contributions NS: conceptualization, data curation, formal analysis, funding acquisition, writing-original draft; SK: data curation, investigation, writing-review and edition; AU: data curation, investigation, writing-review and edition; SI: data curation, investigation, resources, writing-review and edition; YI: data curation, investigation, resources, writing-review and edition; TS: data curation, writing-review and edition; OK: data curation, investigation, resources, writing-review and edition.

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Data availability Specimens examined in this study were deposited at the Zoological Collection of Kyoto University, Japan (voucher #: KUZ Z6428–KUZ Z6439). The sequences obtained in this study were deposited in the INSD Collaboration (accession #: LC921253–LC921267). Other raw data that support this study will be shared upon reasonable request from the corresponding author.

Declarations

Ethical approval Survey sites of this study are partially situated within Special Protection Zones designated under the Natural Parks Act of Japan and the UNESCO World Natural Heritage site, and within areas designated as a Special Natural Monument under the Law for the Protection of Cultural Properties. Field survey and taxon sampling was conducted with permissions issued by the Agency for Cultural Affairs under the Law for the Protection of Cultural Properties (permission #: Bunkacho No. 4–2172, issued on 17 April 2020), the Ministry of the Environment under the Natural Parks Act (permission #: Kankyu-Yaku-Jikyo No. 2006121, issued on 12 June 2020), and the Forestry Agency for access to national forests (permission #: Protected Forest Survey permission 33, issued on 11 August 2020). The studied species is not legally protected, and no specific collection permissions were required.

Conflict of interest The authors declare no competing interests.

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References

- Altekar G, Dwarkadas S, Huelsenbeck JP, Ronquist F (2004) Parallel Metropolis coupled Markov chain Monte Carlo for Bayesian phylogenetic inference. *Bioinformatics* 20:407–415. <https://doi.org/10.1093/bioinformatics/btg427>
- Amante C, Eakins BW (2009) ETOPO1 1 Arc-minute global relief model: procedures, data sources and analysis. NOAA technical memorandum NESDIS NGDC-24. National Geophysical Data Center, NOAA. <https://doi.org/10.7289/V5C8276M>. Accessed 20 March 2026
- Bespalaya Y, Bulakhova N, Gofarov M, Kondakov A, Tomilova A, Berman D (2020) Occurrence of the mollusc species *Euglesa globularis* (Clessin, 1873) in North-East Asia (Magadan, Russia) with data on dispersal mechanism and vectors. *Limnologia* 85:125832. <https://doi.org/10.1016/j.limno.2020.125832>
- Bespalaya YV, Vinarski MV, Aksenova OV, Babushkin ES, Gofarov MY, Kondakov AV, Konopleva ES, Kropotin AV, Mabrouki Y, Ovchankova NB, Palatov DM, Sokolova SE, Shevchenko AR, Travina OV, Taybi AF, Soboleva AA, Zubrii NA, Bolotov IN (2024) Phylogeny, taxonomy, and biogeography of the Sphaeriinae (Bivalvia: Sphaeriidae). *Zool J Linn Soc* 201:305–338. <https://doi.org/10.1093/zoolinnean/zlad139>
- Castresana J (2000) Selection of conserved blocks from multiple alignments for their use in phylogenetic analysis. *Mol Biol Evol* 17:540–552. <https://doi.org/10.1093/zoolinnean/zlad139>
- Clewing C, Bössneck U, von Oheimb PV, Albrecht C (2013) Molecular phylogeny and biogeography of a high mountain bivalve fauna: the Sphaeriidae of the Tibetan Plateau. *Malacologia* 56:231–252. <https://doi.org/10.4002/040.056.0213>
- Clewing C, Geertz T, Rassam H, Woldekiros TH, Albrecht C (2022) Freshwater diversity at a biogeographic edge zone: the high-mountain pea-clams of Ethiopia. *Syst Biodivers* 20:1–15. <https://doi.org/10.1080/14772000.2021.2005706>
- Fukuda H, Haga T, Tatara Y (2008) Niku-nuki: a useful method for anatomical and DNA studies on shell-bearing. *Zoosymposia* 1:15–38
- Graf DL (2013) Patterns of freshwater bivalve global diversity and the state of phylogenetic studies on the Unionoida, Sphaeriidae, and Cyrenidae. *Am Malacol Bull* 31:135–153. <https://doi.org/10.4003/006.031.0106>
- Graf DL, Cummings KS (2026) The freshwater mussels (Unionoida) of the world (and other less consequential bivalves). MUSSEL Project Web Site. <http://www.mussel-project.net/>. Accessed 20 March 2026
- Groh K, Bössneck U, Clewing C, Albrecht C, Richling I (2020) A new pill clam from an unusual habitat: the interstitial *Pisidium interstitialis* n. sp. (Bivalvia: Sphaeriidae) from southwestern and Central Germany. *J Mollusc Stud* 86:104–119. <https://doi.org/10.1093/mollus/eyz036>
- Habe T (1991) Catalogue of Japanese non-marine aquatic mollusks 3. Hitachiobi 56:3–7
- Ieyama H (2024) Morphology of *Pisidium Habei*. *Maigo* 31:3–6
- Ieyama H (2025) Comparison of adductor muscles of pea mussels. *Maigo* 32:16–22
- Inaba O, Kayane S, Ikezawa H, Ieyama H (2011) *Pisidium* (Bivalvia: Sphaeriidae) collected from Ibaraki Prefecture, Japan. *Chiribotan* 41:89–92
- International Commission on Zoological Nomenclature (1999) International code of zoological nomenclature. International Trust for Zoological Nomenclature, London, UK
- Iuarte C (1996) Argentine species of *Pisidium* Pfeiffer, 1821, and *Musculium* Link, 1807 (Bivalvia: Sphaeriidae). *Veliger* 39:189–203
- Kalyaanamoorthy S, Minh BQ, Wong TKF, von Haeseler A, Jermin LS (2017) ModelFinder: fast model selection for accurate phylogenetic estimates. *Nat Methods* 14:587–589. <https://doi.org/10.1038/nmeth.4285>
- Katoh K, Rozewicki J, Yamada KD (2019) MAFFT online service: multiple sequence alignment, interactive sequence choice and visualization. *Brief Bioinform* 20:1160–1166. <https://doi.org/10.1093/bib/bbx108>
- Killeen I, Aldridge D, Oliver G (2004) Freshwater bivalves of Britain and Ireland. Field Studies Council, Telford
- Korniushin AV (1996a) Morphological and anatomical characteristics of *Pisidium casertanum* (Poli) from the Lake Biwa (Japan) (Bivalvia: Eulamellibranchiata: Pisidiidae). *Malak Abh* 18:53–57
- Korniushin AV (1996b) Dvustvorchatye molluski nadsemeystva pisidioidea palearktiki: fauna, sistematika, filogeniya (Bivalve molluscs of the superfamily Pisidioidea in the Palaearctic Region: fauna, systematics, phylogeny). Schmalhausen Institute of Zoology, Kiev
- Korniushin AV (2001) Taxonomic revision of the genus *Sphaerium* sensu lato in the Palaearctic Region, with some notes on the North American species (Bivalvia: Sphaeriidae). *Arch Molluskenkd* 129:77–122. <https://doi.org/10.1127/arch.moll/129/2001/77>

- Korniushin AV (2006) Non-unionoid freshwater bivalves. In: Sturm CF, Pearce TA, Valdés A (eds) The mollusks: a guide to their study, collection, and preservation. The American Malacological Society, Los Angeles and Pittsburgh
- Korniushin AV, Glaubrecht M (2002) Phylogenetic analysis based on the morphology of viviparous freshwater clams of the family Sphaeriidae (Mollusca, Bivalvia, Veneroida). Zool Scr 31:415–459. <https://doi.org/10.1046/j.1463-6409.2002.00083.x>
- Korniushin AV, Hackenberg E (2000) Verwendung konchologischer und anatomischer Merkmale für die Bestimmung mitteleuropäischer Arten der Familie Sphaeriidae (Bivalvia). mit neuem Bestimmungsschlüssel und Diagnosen. Malak Abh 20:45–72
- Kuiper JGJ (1964) Contribution to the knowledge of the South African species of the genus *Pisidium* (Lamellibranchiata). Ann S Afr Mus 48:77–95
- Kuiper JGJ (1983) The Sphaeriidae of Australia. Basteria 47:3–52
- Kuiper JGJ, Wolff WJ (1970) The Mollusca of the estuarine region of the rivers Rhine, Meuse and Scheldt in relation to the hydrography of the area III the Genus *Pisidium*. Basteria 34:1–42
- Kuiper JGJ, Økland KA, Knudsen J, Koli L, von Proschwitz T, Valovirta I (1989) Geographical distribution of the small muscels (Sphaeriidae) in North Europe (Denmark, Faroes, Finland, Iceland, Norway and Sweden). Ann Zool Fennici 26:73–101
- Kuroda T (1941) A catalogue of molluscan shells from Taiwan (Formosa), with description of new species. Mem Fac Sci Taihoku Imp Univ 22:65–216
- Kuroda T (1963) A catalogue of the non-marine mollusks of Japan: a congratulatory publication on the 77th birthday of Dr. Tokubei Kuroda. The Malacological Society of Japan, Tokyo
- Kuroda T (1955) Land shell fauna of Yaku Island. Venus 18:145–157. https://doi.org/10.18941/venusjmc.18.3_145
- Lanfear R, Frandsen PB, Wright AM, Senfeld T, Calcott B (2017) PartitionFinder 2: new methods for selecting partitioned models of evolution for molecular and morphological phylogenetic analyses. Mol Biol Evol 34:772–773. <https://doi.org/10.1093/molbev/msw260>
- Lee T (2019) *Sphaeriidae* Deshayes, 1855 (1820). In: Cummings K, Lydeard C (eds) Freshwater mollusks of the world. A distribution atlas. Johns Hopkins University Press, Baltimore, pp 197–201
- Leigh JW, Bryant D (2015) Popart: full-feature software for haplotype network construction. Meth Ecol Evol 6:1110–1116. <https://doi.org/10.1111/2041-210X.12410>
- Mansur MCD, Meier-Brook C (2000) Morphology of *Eupera* Bourguignat 1854, and *Byssanodonta* Orbigny 1846 with contributions to the phylogenetic systematics of Sphaeriidae and Corbiculidae (Bivalvia: Veneroida). Arch Molluskenkd 128:1–59. <https://doi.org/10.1127/arch.moll/128/2000/1>
- MolluscaBase eds (2026) MolluscaBase. <https://www.molluscabase.org>. Accessed 20 March 2026
- Odhner N (1929) Die Molluskenfauna des Tåkerns. K Sven Vetenskapsakad Handl 8:1–130
- Oyagi A, Ieyama H (2017) *Pisidium* (Bivalvia: Sphaeriidae) collected from Shimokita Peninsula, Aomori Prefecture, Japan. Chiribotan 47:87–89
- Piechocki A (1989) The Sphaeriidae of Poland (Bivalvia, Eulamellibranchia). Ann Zool 42:249–320
- Rambaut A, Drummond AJ, Xie D, Baele G, Suchard MA (2018) Posterior summarization in Bayesian phylogenetics using Tracer 1.7. Syst Biol 67:901–904. <https://doi.org/10.1093/sysbio/syy032>
- Reuter HI, Nelson A, Jarvis A (2007) An evaluation of void-filling interpolation methods for SRTM data. Int J Geogr Inf Sci 21:983–1008. <https://doi.org/10.1080/13658810601169899>
- Ronquist F, Huelsenbeck JP (2003) MrBayes 3: Bayesian phylogenetic inference under mixed models. Bioinformatics 19:1572–1574. <https://doi.org/10.1093/bioinformatics/btg180>
- Saito T, Fujimoto K, Uchida S, Yamazaki D, Hirano T, Sano I, Ye B, Kagawa O, Shariar MS, Do VT, Morii Y, Prozorova L, Chiba S (2022) Uncovering overlooked diversity using molecular phylogenetic approach: a case of Japanese sphaeriid clams (Bivalvia: Sphaeriidae). Mol Phylogenet Evol 173:107508. <https://doi.org/10.1016/j.ympev.2022.107508>
- Sawada N, Hwang CC, Harl J, Nakano T (2021) Integrative taxonomy of insular land snails of the genus *Sicradiscus* Páll-Gergely, 2013 (Gastropoda, Plectopylidae) with description of a new species. J Zool Syst Evol Res 59:1798–1815. <https://doi.org/10.1111/jzs.12553>
- Schneider CA, Rasband WS, Eliceiri KW (2012) NIH image to ImageJ: 25 years of image analysis. Nat Methods 9:671–675. <https://doi.org/10.1038/nmeth.2089>
- Subba Rao MV (1989) Handbook: freshwater molluscs of India. Zoological Survey of India, Calcutta
- Talavera G, Castresana J (2007) Improvement of phylogenies after removing divergent and ambiguously aligned blocks from protein sequence alignments. Syst Biol 56:564–577. <https://doi.org/10.1080/10635150701472164>
- Tomiyama K, Yukita Y, Kawabe K, Sakashita Y (2003) *Pisidium* (*Pisidium*) sp. Kagoshima red data book. Kagoshima Prefecture, Kagoshima, p 346
- Vinarski M, Kantor Y (2016) Analytical catalogue of fresh and brackish water molluscs of Russia and adjacent countries. A. N. Severtsov Institute of Ecology and Evolution of Russian Academy of Sciences, Moscow
- Wong T, Ly TN, Ren H, Baños H, Roger A, Susko E, Bielow C, De Maio N, Goldman N, Hahn M, Huttley G, Lanfear R, Minh B (2025) IQ-TREE 3: Phylogenomic inference software using complex evolutionary models. EcoEvoRxiv <https://doi.org/10.32942/X2P62N>
- Van Damme D, Killeen I, Mackie G, Madhyastha A, Seddon MB, Kebapçı U (2016) *Pisidium casertanum*. The IUCN Red List of Threatened Species 2016. <https://www.iucnredlist.org/species/pdf/42430200>. Accessed 20 March 2026
- Yukita Y (2000) Mollusca of Kagoshima prefecture. Shunendoh Shuppan, Kagoshima

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