BioInvasions Records (2025) Volume 14, Issue 1: 67–77

Research Article

Rediscovery of introduced Korean *Semisulcospira* from Lake Sotonasakaura, Japan and implication for its identity (Mollusca: Gastropoda)

Naoto Sawada[1], Taichiro Toyama[2], Takuto Miyai[3] and Taiji Kurozumi[4]

[1]*Department of Zoology, Graduate School of Science, Kyoto University, Kyoto 606-8502, Japan*
[2]*Fisheries Promotion Division, Department of Agriculture Forestry and Fisheries, Ibaraki Prefectural Government, Ibaraki 310-8555, Japan*
[3]*Oshikiri Ichikawa City, Chiba, 272-0107, Japan*
[4]*Natural History Museum and Institute, Chiba 260-8682, Japan*

Corresponding author: Naoto Sawada (sawada@zoo.zool.kyoto-u.ac.jp)

Citation: Sawada N, Toyama T, Miyai T, Kurozumi T (2025) Rediscovery of introduced Korean *Semisulcospira* from Lake Sotonasakaura, Japan and implication for its identity (Mollusca: Gastropoda). *BioInvasions Records* 14(1): 67–77, https://doi.org/10.3391/bir.2025.14.1.07

Received: 14 September 2023
Accepted: 9 January 2025
Published: 10 February 2025

Handling editor: Darren Yeo
Thematic editor: Kenneth Hayes

Abstract

Assessments of the current status of non-native species and verification of its identity are essential for establishing their impacts on native ecosystems and determining their origins. True taxonomic accounts and recent conditions of non-native *Semisulcospira* snails introduced into the Tone River system in Japan, which were morphologically identified as "*S.* cf. *forticosta*" (Martens, 1886), have not been investigated. We rediscovered living snails of the introduced *Semisulcospira* snails in Lake Sotonasakaura in the lower reaches of the Tone River system. Although the identities of the most introduced snails could not be determined due to their mitochondrial DNA polymorphisms, molecular phylogenetic analysis confirmed that the population in Lake Sotonasakaura includes true *S. forticosta* indigenous to South Korea. The centre of its current distribution seemed to be in the lake and the snails may have been brought into the lake along with other non-native freshwater molluscs. The large morphological variation observed in the snails suggests a previously overlooked morphological variation of *S. forticosta* or the inhabitation of other Korean species in the Tone River system. Thus, further attempts to verify the identity of non-native snails are required, along with assessments of their dispersal and competition with other congeners.

Key words: DNA barcoding, establishment, freshwater snail, Semisulcospiridae, shell morphology

Introduction

Human-mediated introduction and subsequent dispersal of non-native freshwater molluscs are progressing globally, with serious impacts on ecosystems, such as changes in nutrient cycling and competition with native species (Strayer et al. 2011; Preston et al. 2022; Alonso et al. 2023). The negative effects of introduced freshwater molluscs on native ecosystems have been documented in various taxa (Carlsson et al. 2004; Moslemi et al. 2012; Modesto et al. 2021).

Many non-native freshwater organisms have been recorded in the Tone River system, including in Lake Kasumigaura, which is located in the Kanto region of eastern Honshu Island, Japan (Kasebayashi 1994; Nemoto et al.

2003; Hagiwara et al. 2021). The establishment and spread of introduced fishes, molluscs, and plants have been progressing as a result of the accidental release of seedlings and intentional disposal of living food animals in the lake (Ito 2007; Yanai et al. 2008; Kim et al. 2019).

Among the fauna that have been introduced to the Tone River system are freshwater snails of the genus *Semisulcospira*. Although the genus is native to East Asia, including Japan, anthropogenic introductions of *Semisulcospira* species have occurred within the country. For example, species indigenous to Lake Biwa in central Honshu have been introduced and established in neighbouring lakes and rivers (Kitahara 2015; Sawada et al. 2020; Preston et al. 2022). In the Tone River system, Kurozumi and Okamoto (2002) recorded the presence of introduced *Semisulcospira*. Based on the longitudinal ribs and fewer basal cords of the snails, the study and the subsequent prefectural list of introduced species tentatively identified them as "*Semisulcospira* cf. *forticosa* (Martens, 1886)", a species native to South Korea (Chiba Prefecture List Making Committee for Endangered and Alien Species 2012).

Although "*S.* cf. *forticosta*" has been assumed to be established in the Tone River system (Chiba Prefecture List Making Committee for Endangered and Alien Species 2012), the species has not been recorded since Kurozumi and Okamoto (2002). Thus, the establishment and dispersal conditions of snails, along with their identity, remains largely unclear. Furthermore, large intraspecific variation in shell morphology has hampered the correct identification of *Semisulcospira* species (Davis 1969; Sawada and Fuke 2022), and molecular identification is crucial for Korean species (Köhler 2017). Therefore, this study aimed to assess the current status of "*S.* cf. *forticosta*" in the Tone River system and verify its identity.

Materials and methods

Field survey and specimen preparation

Field surveys were conducted in the lower reaches of the Tone River system. Three lakes, Lake Kasumigaura (also known as Lake Nishiura), Lake Kitaura, and Lake Sotonasakaura, are located there, including the study area (Figure 1A). Lakes Kasumigaura and Kitaura are connected to Lake Sotonasakaura and the latter lake flows into the Hitachi-Tone River (Figure 1B). The Hitachi-Tone River joins the Tone River, which flows from the west into the Pacific Ocean. While most of the lower reaches of the water system are surrounded by rice fields, Lakes Kasumigaura and Sotonasakaura and The Hitachi-Tone River are partially facing urban areas (Geospatial Information Authority of Japan 2024).

In this study, we selected 14 sites in the Tone River system to be surveyed for "*S.* cf. *forticosta*" in 2019–2022, based on the proximity to previous sites surveyed in 2000 and 2005, and the possibility that the previous surveys captured snails that flowed from upstream (Figure 1; Supplementary material Table S1; Kurozumi and Okamoto 2002; Taiji Kurozumi *unpublished data*).

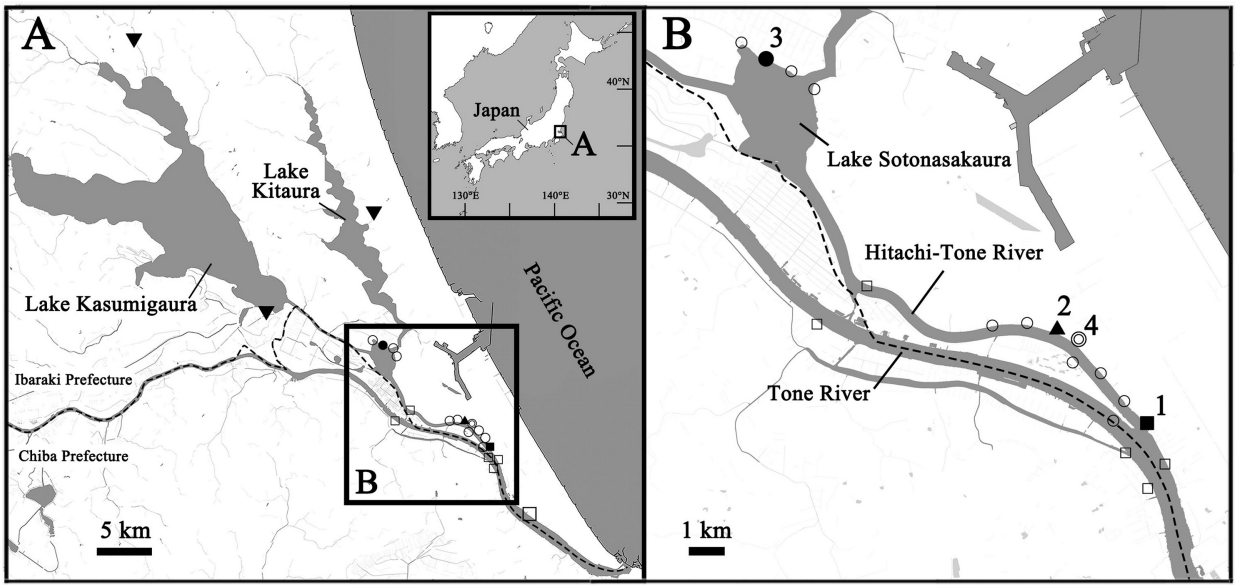

Figure 1. A: Map of the lower reaches of the Tone River water system showing survey sites of *Semisulcospira* snails in surveys conducted in 2000, 2005, and 2019–2022. B: Enlarged map of the Tone and Hitachi-Tone Rivers and Lake Sotonasakaura. The numbered sites indicate where "*S.* cf. *forticosta*" was found, and their detailed localities are provided in Supplementary material Table S1. Closed square, collection site of "*S.* cf. *forticosta*" in 2000; open squares, uncollected sites in 2000; closed triangle, collection site of "*S.* cf. *forticosta*" in 2005; closed circle, collection site of living specimens of "*S.* cf. *forticosta*" and *S. reiniana* in 2022; double circle, collection site of a dead specimen of "*S.* cf. *forticosta*" in 2022; closed inverted triangles, sites where *S. reiniana* were recorded in 2019–2022; open circles, sites where *Semisulcospira* species were not recorded in 2019–2022. The survey results in 2000 and 2005 are in accordance with the unpublished data of Taiji Kurozumi.

We surveyed each site for 2–4 person-hours and collected snails using hand and scoop nets. The presence/absence of *Semisulcospira* species was recorded. All living and dead "*S.* cf. *forticosta*" snails encountered in this study and some of the other freshwater molluscs found together were collected.

Twelve mature female specimens of "*S.* cf. *forticosta*" were selected from the newly collected snails to examine protoconchs with their parents based on the formation of their reproductive organs (Itagaki 1960). Teleconch, protoconch, and radula specimens were prepared and cleaned according to Sawada and Fuke (2022). In addition, teleoconchs and protoconchs of five mature females of *Semisulcospira reiniana* (Brot, 1876) collected with "*S.* cf. *forticosta*" were also examined for morphological comparison. Newly collected *Semisulcospira* specimens were deposited in the Zoological Collection of Kyoto University (KUZ Z5021–Z5023, Z5128, Z5139). Three voucher specimens of "*S.* cf. *forticosta*" collected by Kurozumi and Okamoto (2002) and in a subsequent survey in 2005 were also measured (Natural History Museum and Institute, Chiba; CBM-ZM125674, CBM-ZM125675, and CBM-ZM147569). The freshwater molluscs collected by the present surveys were identified according to Masuda and Uchiyama (2010), and their scientific names were obtained from MolluscaBase (2023).

Genetic analyses

The phylogenetic positions of the 12 specimens of "*S.* cf. *forticosta*" were estimated using a mitochondrial marker, a fragment of the cytochrome *c* oxidase subunit I (COI) gene. Genomic DNA was extracted from the muscle

Table 1. Specimen list examined in this study with voucher numbers, accession numbers of International Nucleotide Sequence Database (INSD) for COI sequences, clade names, and references. The clade names correspond to those of the Figure 3 in the present study. Acronyms: CBM, Natural History Museum and Institute, Chiba; KUZ, Zoological Collection of Kyoto University; ZMB, Malacological Collection of the Museum für Naturkunde, Berlin, Germany.

Species	Voucher #	INSD accession #	Clade	References
Semisulcospira forticosta	KUZ Z5022	LC778144	C3	This study
Semisulcospira sp.	KUZ Z5021, Z5023	LC778137–LC778143, LC778146	A1	This study
Semisulcospira sp.	KUZ Z5128	LC778145, LC778147, LC778148	A2	This study
Semisulcospira sp.	CBM-ZM 125674	–	–	Kurozumi and Okamoto 2002; this study
Semisulcospira sp.	CBM-ZM147569	–	–	Taiji Kurozumi *unpublished data*; this study
Semisulcospira forticosta	ZMB 114741b	KY675021	A	Köhler 2017
Semisulcospira reiniana	ZMB 114708b, ZMB 114722a	KT820612, KT820636	A	Köhler 2017
Semisulcospira decipiens	ZMB 114718b, ZMB 114765a	KT820565, KT820569	A	Köhler 2017
Semisulcospira kurodai	ZMB 114713b	KT820575	A	Köhler 2017
Semisulcospira multigranosa	ZMB 114762a, ZMB 114770b, ZMB 114775b	KT820615, KT820619, KT820621	A	Köhler 2017
Semisulcospira nakasekoae	ZMB 114732b	KT820623	A	Köhler 2017
Semisulcospira reticulata	ZMB 114592	KT820553	A	Köhler 2017
Semisulcospira libertina	ZMB 114717	KT820614	B	Köhler 2017
Semisulcospira coreana	ZMB 114729b, ZMB 114733c, ZMB 114744a	KY674993, KY674996, KY675001	C1	Köhler 2017
Semisulcospira gottschei	ZMB 111992, ZMB 112961, ZMB 114725c	KY675038, KT820549, KT820550	C2	Köhler 2017
Semisulcospira forticosta	ZMB 111991, ZMB 114761b, ZMB 114774a	KY675026, KY675028, KT820548	C3	Köhler 2017
Semisulcospira libertina	ZMB 111988, ZMB 114705a	KT820580, KT820607	C4	Köhler 2017
Semisulcospira libertina	ZMB 114589, ZMB 114740a	KT820582, KT820599	C5	Köhler 2017
Hua jacqueti	ZMB 114165	KT820543	out group	Köhler 2017
Juga nigrina	ZMB 106257	KT820544	out group	Köhler 2017

tissues of the feet based on the methods described by Okamoto et al. (2006) using a protein precipitation solution (Promega Corporation). With the primers LCO1490 and HCO2198 (Folmer et al. 1994), the polymerase chain reaction, nucleotide sequencing, and alignment of a 658 bp section of the COI gene were conducted following the methods by Sawada et al. (2021), modifying the annealing temperature to 48 °C. The sequences were deposited in the International Nucleotide Sequence Database Collaboration through the DNA Databank of Japan (LC778137–LC778148).

Phylogenetic trees were reconstructed using maximum likelihood (ML) with IQ-TREE v1.6.12 (Nguyen et al. 2015). The sequences used for molecular phylogenetic analyses are listed in Table 1. The comparative sequences obtained by Köhler (2017) were downloaded from GenBank. The best-fit models for each partition of the COI sequence were calculated based on the Bayesian information criterion and greedy algorithm using ModelFinder implemented in IQ-TREE (Kalyaanamoorthy et al. 2017): TVM+F+R2 for the 1st position, TNe+G4 for the 2nd position, and HKY+F+I for the 3rd position.

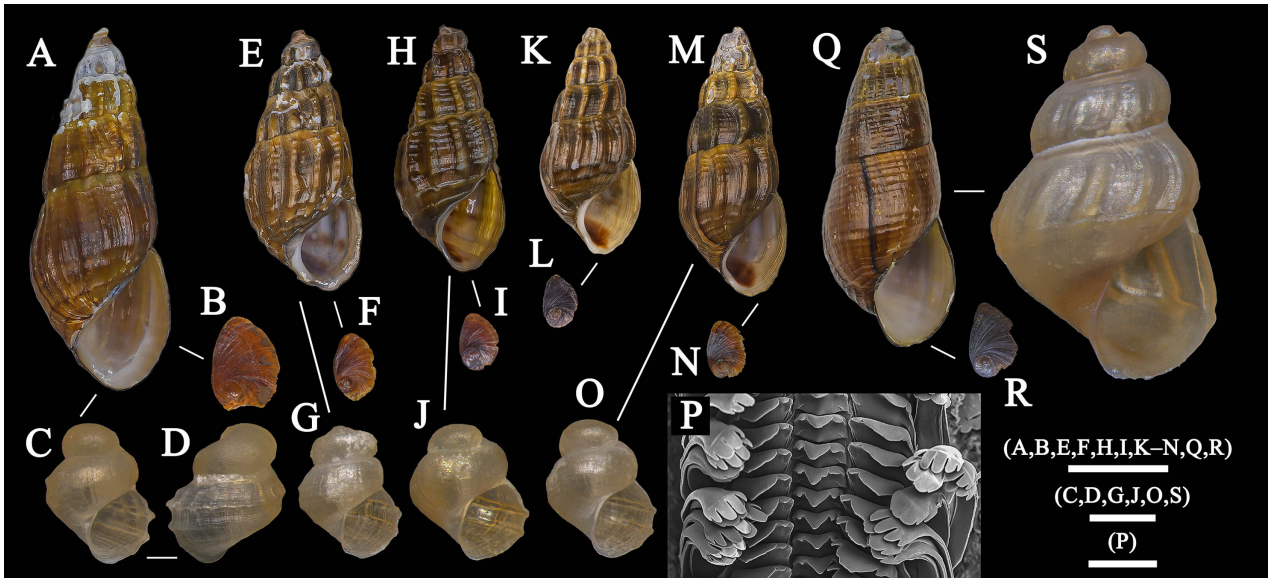

Figure 2. *Semisulcospira* specimens collected from the Tone River water system. A–D, P: "*S.* cf. *forticosta*" collected in 2005 (CBM-ZM 147569); C–O: "*S.* cf. *forticosta*" in the clades C3 (E–G; KUZ Z5022), A1 (H–L; KUZ Z5022), and A2 (N–O; KUZ Z5128) collected in 2022; Q–S: *S. reiniana* collected with "*S.* cf. *forticosta*" in 2022 (KUZ Z5139). Scale bars: 10 mm, teleoconch (A, E, H, K, M, Q), operculum (B, F, I, N, R); 0.5 mm, protoconch (C, D, G, J, O, S), radula (P). Photo by Naoto Sawada.

The branch support of the ML phylogenetic tree was assessed by 1,000 non-parametric bootstrap replicates. The name of each clade in the tree was identified according to Köhler (2017).

Morphological examination

The teleoconch specimens of "*S.* cf. *forticosta*" and sympatric *S. reiniana* were photographed using a Nikon D7500 camera fitted with a Tamron SP 90 mm f/2.8 1:1 macro-lens. Images of the protoconchs were obtained using a Leica MC170 HD digital camera mounted on a Leica M125C microscope. The extracted radulae of "*S.* cf. *forticosta*" were photographed with a Hitachi TM1000 scanning electron microscope. Measurements were obtained from digital images using ImageJ v1.51k (Schneider et al. 2012). Thirteen morphological characters of teleoconchs and protoconchs were measured following Köhler (2017) and Sawada and Nakano (2021): teleoconch, basal cord number, body whorl length, longitudinal rib number of penultimate whorl, spire angle, spiral cord number of body whorl and penultimate whorl, shell length, shell width, whorl number; protoconch, protoconch number, shell length, shell width, whorl number.

Results

Field survey

The living "*S.* cf. *forticosta*" snails was recorded at locality #3 in Lake Sotonasakaura on 26 February and 15 October in 2022 (Table S1; Figure 2). More than 50 snails, including juveniles, were observed on rocks and sand along the lake coast each day at the locality. The species were found with

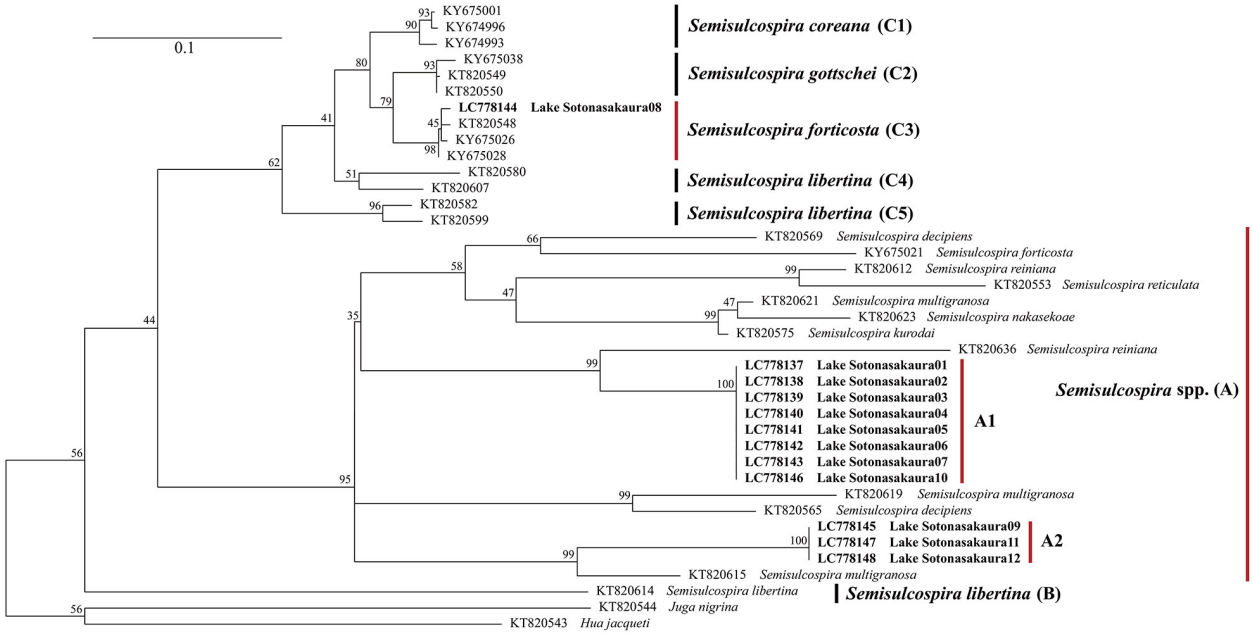

Figure 3. Maximum likelihood (ML) tree for 658 bp COI sequences. Numbers on the nodes indicate the ML bootstrap values. Information on the specimens used is presented in Table 1.

S. reiniana, *Sinotaia quadrata histrica* (Gould, 1859), *Parafossarulus* sp., *Limnoperna fortunei* (Dunker, 1857), and *Corbicula fluminea* (Müller, 1774). A fresh dead shell of "*S.* cf. *forticosta*" was also found at locality #4, another site along the Hitachi-Tone River in Nitsukawa, lower reaches of Lake Sotonasakura, approximately 1 km from the previous site (locality #2), on 12 February 2022. This species was not recorded at the other 12 sites surveyed in this study. *Semisulcospira reiniana* was observed in the other three localities (Figure 1).

Genetic analyses

Three mitochondrial haplotypes were identified in 12 specimens from Lake Sotonasakaura. The reconstructed ML tree well supported the monophyly of clades A, C1–3, and C5, respectively. The tree showed that one specimen of "*S.* cf. *forticosta*" was positioned in the clade consisting of *S. forticosta* (clade C3), while the other 11 snails were included in the clade A with Japanese congeners (Figure 3). Among them, eight and three specimens represented identical haplotypes (herein A1 and A2, respectively). The close relationships between the A1 haplotype and *S. reiniana* from Lake Biwa and between the A2 haplotype and *S. multigranosa* (Boettger, 1886) [currently *S. davisi* Sawada and Nakano, 2021 according to Sawada and Nakano (2021)] from the lake were strongly supported in clade A.

Morphological examination

The previous voucher and most of the newly collected specimens of "*S.* cf. *forticosta*" in the clade A1, A2, and C3 were morphologically similar to each other in possessing an elongated teleoconch with distinct 3–5 basal cords,

Table 2. Differential diagnoses of three Korean *Semisulcospira* species described by Köhler (2017) and the characteristics of "*S.* cf. *forticosta*" collected from Lake Sotonasakaura, Japan. The clade names correspond to those of the Figure 3 in the present study. Acronym: CBM, Natural History Museum and Institute, Chiba; KUZ, Zoological Collection of Kyoto University.

Species / specimen	Spiral cord number on body whorl	States of longitudinal sculptures	States of spiral sculpture
S. coreana (clade C1)	> 10	weakly nodulated	fine, weakly nodulated
S. gottschei (C2)	5–7	strongly nodulated	coarse, strongly nodulated
S. forticosta (C3)	0	smooth	lacked
KUZ Z5022 (C3)	11	weakly nodulated	fine, weakly nodulated
KUZ Z5021, Z5023 (A1)	9–14	almost smooth to strongly nodulated	fine, weakly to strongly nodulated
KUZ Z5128 (A2)	13–15	weakly nodulated	fine, weakly nodulated
CBM-ZM 125674	15	weakly nodulated	fine, weakly nodulated
CBM-ZM147569	15–16	weakly nodulated	fine, weakly nodulated

10–12 distinct longitudinal ribs on penultimate whorls, and 11–15 fine spiral cords on the body whorls (Table 2; Figure 2; Table S2). Additionally, several specimens with less than 10 distinctively nodulated spiral cords or with partially smooth longitudinal ribs were included in clade A1. Small, beige-coloured protoconchs with two prominent keels in the central part of whorls were also common in the lower whorls of the specimens. The radulae of the previous voucher specimens possessed a large, pointed central denticle and two to three minor cusps on each side of the rachidian and lateral teeth. Four to five rounded denticles were found in the interior and exterior marginal teeth. The specimens of *S. reiniana* represented 8–9 basal cords, weak longitudinal ribs on upper whorls, and fine spiral cords on penultimate to body whorls of elongated teleoconchs. The species possessed larger protoconchs than "*S.* cf. *forticosta*", with distinct longitudinal ribs and one keel in the lower part of the whorls.

Discussion

Assessing the distribution and evaluating the taxonomic account is necessary to clarify the status of "*S.* cf. *forticosta*" in the Tone River system. Three Korean *Semisulcospira* species, *S. forticosta*, *S. gottschei* (Martens, 1886), and *S. coreana* (Martens, 1886), exhibit similar protoconch and radula morphologies (Ko et al. 2001; Köhler 2017). They can be discriminated at the species level by spiral cord number on the body whorl and the states of longitudinal and spiral sculptures on teleoconchs (Table 2; Köhler 2017). The small protoconchs, pointed rachidian teeth, and broad cusps of the lateral teeth of the introduced snails supported that they belonged to the Korean species. In addition, the specimens of "*S.* cf. *forticosta*" and sympatric *S. reiniana* were clearly discriminated by the number and status of teleoconch sculptures, and the size and sculptures of protoconchs.

One mitochondrial sequence obtained from the newly collected "*S.* cf. *forticosta*" was included in clade C3, which was previously identified as *S. forticosta* (Köhler 2017). According to the original description of the Korean species (Martens 1886) and the revision of their type materials (Köhler 2017), the absence of spiral sculpture typically distinguishes *S. forticosta* from *S. coreana* and *S. gosttchei*. However, the newly collected C3 specimen

possessed 11 weak spiral cords on its body whorl, which is characteristic of *S. coreana*. Specimens with similar features to the C3 specimens were also included in the specimens of clades A1 and A2, with variation in the number and distinctness of spiral cords in the A1 specimens. According to the C3 haplotype detected in the "*S.* cf. *forticosta*" snails, it is clear that the true *S. forticosta* is included in the introduced population of Lake Sotonasakaura and that the population represents greater morphological variations than had previously been observed in the species. On the other hand, large morphological variation detected in the clade A specimens may be caused by the inclusion of other Korean species, and thus, the present study could not determine whether all the specimens from Lake Sotonasakaura are conspecific.

Most specimens collected from Lake Sotonasakaura possessed COI haplotypes included in the clade A. Köhler (2017) treated this clade as the "unusual clade" together with the clade B, and subsequently, they were defined by Miura et al. (2020) as the mt-B clade that was incongruent with nuclear phylogeny. This deeply divergent lineage has been estimated to have originated from Lake Biwa endemics and introgressed into Japanese and Korean riverine species without the formation of hybrid swamps (Miura et al. 2020). As mitochondrial DNA polymorphisms, both native and introgressed haplotypes have been retained in Japanese and Korean species, including *S. forticosta* (Köhler 2017; Miura et al. 2020; Figure 3). Furthermore, both haplotypes have been detected from the same site in several Japanese populations (Miura et al. 2020). Therefore, the close relationships among the "*S.* cf. *forticosta*", *S. reinina*, and *S. multigranosa* (currently *S. davisi*) in the clade A is more likely to be attributed to the mitochondrial polymorphism retained in the introduced snails, than interspecific hybridisation between the native and introduced species. While further studies on the proportion of the native and introgressed haplotypes in the native *S. forticosta* and the fitness of the snail with each haplotype are needed, the rates of the haplotypes of "*S.* cf. *forticosta*" observed in Lake Sotonasakaura may reflect the proportion of each haplotype possessed by "*S.* cf. *forticosta*" when their introduction occurred.

The establishment and dispersal conditions of "*S.* cf. *forticosta*" have not been investigated since its first record (Kurozumi and Okamoto 2002). During the present field surveys, numerous living snails, including juveniles, were discovered; thus, it appears that populations of the introduced "*S.* cf. *forticosta*" were already established in the Tone River system. In contrast to the initial record of the species in the Hitachi-Tone River, the living snails were not observed in that vicinity and was collected upstream of Lake Sotonasakaura in the present study. Although the number of survey sites was limited in this study, these occurrence records suggest that the current distribution of the species is likely to be centred in the lake.

Seedlings, discarded exotic aquarium fish, and game fish introduced into Lake Kasumigaura have led to the proliferation of numerous non-native

fish species (Yanai et al. 2008). In the lake, a freshwater mussel species, *L. fortunei* has estimated to be introduced into the lake together with intentionally disposed *Corbicula* clams imported from China (Ito 2007). It has been reported that living *Semisulcospira* snails were mixed into Chinese cyrenid clams sold in supermarkets (Kurozumi 2001; Masuda and Uchiyama 2010). *Corbicula* clams are also consistently imported from Korea to Japan, with approximately 2,000 tons imported in 1998 before the initial record of "*S.* cf. *forticosta*" (Nakamura 2000). Based on surveys conducted in 2008–2010, lots originating in the northeast and south of Korea were recorded (Akasaki and Enomoto 2011). According to the possibility of transportation of *Semisulcospira* species via other edible freshwater molluscs, the introduction pathway of "*S.* cf. *forticosta*" may have a similar pattern to that of *L. fortunei* in Kasumigaura.

Native *Semisulcospira* species, such as *S. reiniana* and *S. libertina* (Gould, 1859), are widely distributed in the lower reaches of the Tone River system (Miyadi 1932; Iwasaki and Tonooka 1997). Co-occurrence of the introduced "*S.* cf. *forticosta*" and *S. reiniana* was observed in Lake Sotonasakaura. Decreases in the native species and populations of *Semisulcospira*, owing to the introduction of Lake Biwa congeners, have been observed in several places in Japan (personal observation by the first author). Consequently, it is important to assess the negative effects of the introduced "*S.* cf. *forticosta*" on the ecosystem of the Tone River system, including competition with its congeners and possible decreases in native species.

Authors' contribution

SN designed the present study and conducted the morphological and genetic analyses. All authors performed sample collection. All authors have drafted, read, and approved the final manuscript.

Acknowledgements

We are grateful to Frank Köhler (Australian Museum) for helpful comments on the identification of *Semisulcospira* snails. We are also grateful to constructive suggestions by Darren CJ Yeo and two anonymous reviewers. We would like to thank Tokuya Yano, Takashi Hosoda, and Akihiro Tanno for assisting during field survey. We thank Toshiaki Nishimura, Osamu Masuda, and Yoshiro Kitahara for providing information on introduced *Semisulcospira* snails. We are grateful to Takumi Saito (Masaryk University) for assisting with the identification of *Parafossarulus* sp. Furthermore, we thank Taiga Kato (Kyoto University; KU) for his assistance with the morphological examination and Takafumi Nakano (KU) and Taro Jonishi (KU) for their constructive comments on the manuscript and figures. We thank Editage for English language editing.

Funding declaration

The present study was supported by JSPS KAKENHI grant no. JP21J22917 and JP20H05811.

References

Akasaki T, Enomoto Y (2011) Determination of the origins of imported *Corbicula* (shijimi) clams from the Korean Peninsula and its surrounding areas. *Reports of the Central Customs Laboratory* 51: 85–91

Alonso Á, Collado GA, Gérard C, Levri EP, Salvador RB, Castro-Díez P (2023) Effects of the invasive aquatic snail *Potamopyrgus antipodarum* (Gray, 1853) on ecosystem properties and services. *Hydrobiologia*, https://doi.org/10.1007/s10750-022-05116-z

Carlsson NOL, Brönmark C, Hansson LA (2004) Invading herbivory: the golden apple snail alters ecosystem functioning in asian wetlands. *Ecology* 85: 1575–1580, https://doi.org/10.1890/03-3146
Chiba Prefecture List Making Committee for endangered and Alien Species (2012) Alien species in Chiba Prefecture, First Edition. Chiba Prefecture List Making Committee for endangered and Alien Species. Chiba, Japan, 340 pp
Davis GM (1969) A taxonomic study of some species of *Semisulcospira* in Japan (Mesogastropoda: Pleuroceridae). *Malacologia* 7: 211–294
Folmer O, Black M, Wr H, Lutz R, Vrijenhoek R (1994) DNA primers for amplification of mitochondrial cytochrome *c* oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology* 3: 294–299
Hagiwara T, Shirai A, Morosawa T, Kumagai M, Arai S (2021) Establishment of freshwater pearl mussels *Sinohyriopsis* spp. in Lake Kasumigaura, Ibaraki Prefecture, Japan. *Izunuma-Uchinuma Wetland Researches* 15: 139–149, https://doi.org/10.20745/izu.15.0_139
Itagaki H (1960) Anatomy of *Semisulcospira bensoni* a freshwater gastropod. *Venus* 21: 4–6, https://doi.org/10.18941/venusjjma.21.1_41
Ito K (2007) Spatial distribution of golden mussel, *Limnoperna fortunei*, in Lake Kasumigaura, Ibaraki Prefecture, Japan. *Japanese Journal of Benthology* 62: 34–38, https://doi.org/10.5179/benthos.62.34
Iwasaki J, Tonooka T (1997) Natural environment of Kajinashi River – water quality and fishes distribution. *Bulletin of Ibaraki Prefectural Freshwater Fisheries Experimental Station* 33: 81–85
Kalyaanamoorthy S, Minh BQ, Wong TKF, von Haeseler A, Jermiin LS (2017) ModelFinder: fast model selection for accurate phylogenetic estimates. *Nature Methods* 14: 587–589, https://doi.org/10.1038/nmeth.4285
Kasebayashi N (1994) Fish fauna of Kasumigaura and its trends. In: Kasumigaura Information Centre Research Committee (ed), Fish of Kasumigaura. Kasumigaura Information Centre, Amicho, Japan, pp 117–133
Kim J, Yano T, Nakanishi R, Tagami H, Nishihiro J (2019) Artificial wave breakers promote the establishment of alien aquatic plants in a shallow lake. *Biological Invasions* 21: 1545–1556, https://doi.org/10.1007/s10530-019-01915-z
Kitahara Y (2015) Record of *Semisulcospira* (*Biwamelania*) *habei* Davis from Tanukiko Lake, Fujinomiya City, Shizuoka Prefecture, Japan. *Hyogo Freshwater Biology* 66: 15–18
Ko JH, Lee JS, Kwon OK (2001) Study on radulae of seven species of the family Pleuroceridae in Korea. *The Korean Journal of Malacology* 17: 105–115
Köhler F (2017) Against the odds of unusual mtDNA inheritance, introgressive hybridisation and phenotypic plasticity: systematic revision of Korean freshwater gastropods (Semisulcospiridae, Cerithioidea). *Invertebrate Systematics* 31: 249–268, https://doi.org/10.1071/IS16077
Kurozumi T (2001) Living snails of Chinese *Semisulcospira cancellata* mixed into *Corbicula* clams sold at a supermarket in Chiba City. *Chiribotan* 32: 4
Kurozumi T, Okamoto M (2002) Some newly introduced molluscs in southern Kanto Region. *Venus* 61: 111
Martens E von (1886) Vorzeigungen einiger der von Dr. Gottsche in Japan und Korea gesammelten Land- und Süsswasser-Mollusken. *Sitzungs-Berichte der Gesellschaft Naturforschender Freunde zu Berlin* 1886: 76–80
Masuda O, Uchiyama R (2010) Freshwater Molluscs of Japan 2. Freshwater Molluscs of Japan, Including Brackish Water Species. Pisces Ecological Field Guide Series 2. Second Edition. Pisces Publishers, Yokohama, Japan, 239 pp
Miura O, Urabe M, Mori H, Chiba S (2020) Ancient drainage networks mediated a large-scale genetic introgression in the East Asian freshwater snails. *Ecology and Evolution* 10: 8186–8196, https://doi.org/10.1002/ece3.6523
Miyadi D (1932) Studies on the bottom fauna of Japanese lakes. III. Lakes of the Kwanto Plain. *Japanese Journal of Zoology* 4: 1–39
Modesto V, Dias E, Ilarri M, Lopes-Lima M, Teixeira A, Varandas S, Castro P, Antunes C, Sousa R (2021) Trophic niche overlap between native freshwater mussels (Order: Unionida) and the invasive *Corbicula fluminea*. *Aquatic Conservation: Marine and Freshwater Ecosystems* 31: 2058–2071, https://doi.org/10.1002/aqc.3618
Moslemi JM, Snider SB, MacNeill K, Gilliam JF, Flecker AS (2012) Impacts of an invasive snail (*Tarebia granifera*) on nutrient cycling in tropical streams: the role of riparian deforestation in trinidad, West Indies. *PLoS ONE* 7: e38806, https://doi.org/10.1371/journal.pone.0038806
Nakamura M (ed) (2000) The Japanese Fishery of Cyrenid Clams: Current Status and Problems. Tatara Shobo, Yonago, Japan, 266 pp
Nemoto T, Sugiura H, Komaru A (2003) Distribution of non-native *Corbicula* in the Tone River and Kasumigaura-Kitaura. *Report of Freshwater Fisheries Experiment Station, Ibaraki Prefecture* 38: 32–41

Nguyen L-T, Schmidt HA, von Haeseler A, Minh BQ (2015) IQ-TREE: A fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. *Molecular Biology and Evolution* 32: 268–274, https://doi.org/10.1093/molbev/msu300

Okamoto T, Motokawa J, Toda M, Hikida T (2006) Parapatric distribution of the lizards *Plestiodon* (Formerly *Eumeces*) *latiscutatus* and *P. japonicus* (Reptilia: Scincidae) around the Izu Peninsula, Central Japan, and its biogeographic implications. *Zoological Science* 23: 419–425, https://doi.org/10.2108/zsj.23.419

Preston D, Crone E, Miller-ter Kuile A, Lewis C, Sauer E, Trovillion D (2022) Non-native freshwater snails: a global synthesis of invasion status, mechanisms of introduction, and interactions with natural enemies. *Freshwater Biology* 67: 227–239, https://doi.org/10.1111/fwb.13848

Sawada N, Fuke Y (2022) Systematic revision of the Japanese freshwater snail *Semisulcospira decipiens* (Mollusca: Semisulcospiridae): implications for diversification in the ancient Lake Biwa. *Invertebrate Systematics* 36: 1139–1177, https://doi.org/10.1071/IS22042

Sawada N, Nakano T (2021) Revisiting a 135-year-old taxonomic account of the freshwater snail *Semisulcospira multigranosa*: designating its lectotype and describing a new species of the genus (Mollusca: Gastropoda: Semisulcospiridae). *Zoological Studies* 60: 7, https://doi.org/10.6620/ZS.2021.60-07

Sawada N, Toyohara H, Miyai T, Nakano T (2020) Further records of introduced *Semisulcospira* snails in Japan (Mollusca, Gastropoda): implications for these snails' correct morphological identification. *BioInvasions Records* 9: 310–319, https://doi.org/10.3391/bir.2020.9.2.16

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. *Journal of Zoological Systematics and Evolutionary Research* 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. *Nature Methods* 9: 671–675, https://doi.org/10.1038/nmeth.2089

Strayer DL, Cid N, Malcom HM (2011) Long-term changes in a population of an invasive bivalve and its effects. *Oecologia* 165: 1063–1072, https://doi.org/10.1007/s00442-010-1792-0

Yanai T, Arayama K, Tominaga A (2008) The introduction process in alien fishes found from Lake Kasumigaura and Kitaura. *Bulletin of Ibaraki Prefectural Freshwater Fisheries Experimental Station* 41: 47–54

Web sites, online databases and software

Geospatial Information Authority of Japan (2024) GSI Maps. https://maps.gsi.go.jp/ (accessed 12 January 2024)

MolluscaBase (eds) (2023) MolluscaBase. https://www.molluscabase.org/ (accessed 20 August 2023)

Supplementary material

The following supplementary material is available for this article:

Table S1. Details of the introduced *Semisulcospira* collected from four localities during the investigation conducted in 2000–2022, including the previous study.

Table S2. Measurements and counts of 13 shell morphological and four radular characters of *Semisulcospira* specimens collected from Lake Sotonasakaura, Japan.

This material is available as part of online article from:
http://www.reabic.net/journals/bir/2025/Supplements/BIR_2025_Sawada_etal_SupplementaryMaterial.xlsx