Ecologica Montenegrina
ISSN 2336-9744 (online) | ISSN 2337-0173 (print)

Ecologica Montenegrina 94: 166-175 (2026)
This journal is available online at: www.biotaxa.org/em
https://dx.doi.org/10.37828/em.2026.94.10

Article

DNA barcoding and morphology reveal a broad distribution of Asian freshwater clams *Corbicula fluminea* and *C. leana* (Cyrenidae) in Vietnam

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Received 20 December 2025 | Accepted by *V. Pešić*: 15 January 2026 | Published online 21 January 2026.

Abstract
The present study provides the first confirmed records of *Corbicula fluminea* and *C. leana* in Vietnam based on DNA sequence data. Additionally, *C. blandiana*, an endemic species to the Mekong River basin, was identified. The COI sequences of *Corbicula fluminea* and *C. leana* from Vietnam are either identical or differ by one or two nucleotide substitutions from those collected in Japan, China, and Myanmar. These new DNA sequence data support our earlier hypothesis that populations of *C. leana* and *C. fluminea* in Southeast and East Asia have served as sources for their worldwide expansion.

Key words *Corbicula blandiana*, DNA barcoding, hybridization, invasive species, native range, Mekong River basin, Pearl River basin, Red River basin.

Introduction

Corbicula clams are currently attracting significant scientific interest due to their high invasive potential and unique reproductive characteristics (Pigneur *et al.* 2014; Vastrade *et al.* 2022; Bespalaya *et al.* 2025). These molluscs are widely distributed in rivers and lakes throughout Vietnam, where they serve as an important food resource for humans. Consequently, they are also studied for contamination with toxic xenobiotics (e.g., Bogatov *et al.* 2019; Donets *et al.* 2022). Despite the ecological importance of this group, several questions regarding the taxonomic status of certain species remain unresolved (Park and Kim 2003; Bespalaya *et al.* 2025). Furthermore, the endemic species within this genus from some regions, including Vietnam, remain poorly understood (Glaubrecht *et al.* 2003).

So far, 16 species of the genus *Corbicula* Megerle von Mühlfeld, 1811 have been identified in reservoirs and watercourses of Vietnam: *Corbicula blandiana* (Prime, 1864), *C. baudoni* Morlet, 1886, *C. bocourti* (Morelet, 1865), *C. castanea* (Morelet, 1865), *C. cyreniformis* Prime, 1860, *C. dautzenbergi* Prashad, 1928, *C. guidopoppei* Thach, 2023, *C. gubernatoria* Prime, 1870, *C. lamarckiana* Prime, 1867, *C. larnaudieri* Prime, 1862, *C. leviuscula* Prime, 1867, *C. luteola* Prashad, 1928, *C. messageri* Bavay & Dautzenberg, 1901, *C. moreletiana* Prime, 1867, *C. solidula* Prime, 1861, *C. tenuis* Clessin, 1887 (see Park and Kim 2003; Raschepkina and Sayenko 2017; Ngo *et al.* 2018; Seleznev *et al.* 2023; Thach 2023; Le *et al.* 2024; MolluscaBase 2025, Graf and Cummings 2025). At the same time, the valid taxonomic status of a single species, *C. blandiana*, has been confirmed by molecular genetic methods (Bespalaya *et al.* 2025).

Therefore, main objectives of the present study are: (1) to identify the species diversity of *Corbicula* clams in Vietnam using an integrative approach; and (2) to assess the genetic diversity of Vietnamese *Corbicula* spp.

Materials and Methods

Study area and field sampling

The field study was conducted within four areas of Vietnam in 2012, 2017, and 2018. The localities were as follows: (1) downstream section and delta of the Mekong River; (2) downstream section and delta of the Red River; (3) Bang River basin; and (4) Ky Cung River basin (Figs 1-2, Tables 1-2). Some samples were purchased at a local market; in these cases, information on the collection locality and habitat was obtained from the seller (see Table 1). Clams were sampled using a hand net and dredge and fixed in 96% ethanol. More than 200 specimens of molluscs were collected, and a total of 41 samples were examined.

The materials are stored in the collection of the Federal Scientific Center for Biodiversity of Terrestrial Biota of East Asia of Far Eastern Branch of the Russian Academy of Sciences (Bioresource Collection No 2797657), Vladivostok, Russia and the Russian Museum of the Biodiversity Hotspots of the N. Laverov Federal Center for Integrated Arctic Research of Ural Branch of the Russian Academy of Sciences, Arkhangelsk, Russia.

DNA extraction, PCR amplification, and DNA sequencing

The present study includes new molecular data for 18 *Corbicula* specimens (Table 2). Total DNA was extracted from 96 % ethanol-preserved foot tissues using the HiPure Tissue DNA Kit (Magen Biotechnology Co., Ltd, China), following the manufacturer's protocol. As the primer pairs, we used LCO 1490 and HCO 2198 for the COI gene fragment (Folmer *et al.* 1994), C1 and D2 for the 28S gene fragment (Mollaret *et al.* 1997). The PCR mix contained approximately 100 ng of total cell DNA, 10 pmol of each primer, 200 µmol of each dNTP, 2.5 µl of PCR buffer (with 20 mmol $MgCl_2$), 0.8 units Taq DNA polymerase (SibEnzyme Ltd., Russia), and H_2O was added for a final volume of 25 µl. Temperature cycling was as follows: 95 °C (4 min), 36 cycles of 95 °C (50 s), 52 °C (50 s), 72 °C (50 s) and a final extension at 72 °C (5 min). The forward and reverse sequencing was performed on an automatic sequencer (ABI PRISM 3730, Applied Biosystems) using the ABI PRISM BigDye Terminator ver. 3.1 reagent kit. The resulting sequences were checked manually using a sequence alignment editor BioEdit ver. 7.2.5 (Hall 1999).

Sequence alignment and phylogeographic analyses

The sequences were aligned using the MUSCLE algorithm of MEGA X (Kumar *et al.* 2018). The phylogenetic affinities of the nucleotide sequences of certain specimens were identified using the Basic Local Alignment Search Tool, BLAST (Johnson *et al.* 2008). The phylogeographic analyses were performed based on a median joining network approach using Network ver. 5.0.0.1 software with default settings (Bandelt *et al.* 1999). In addition, 488 sequences for three species were obtained from NCBI GenBank previously used in the Bespalaya *et al.* (2025).

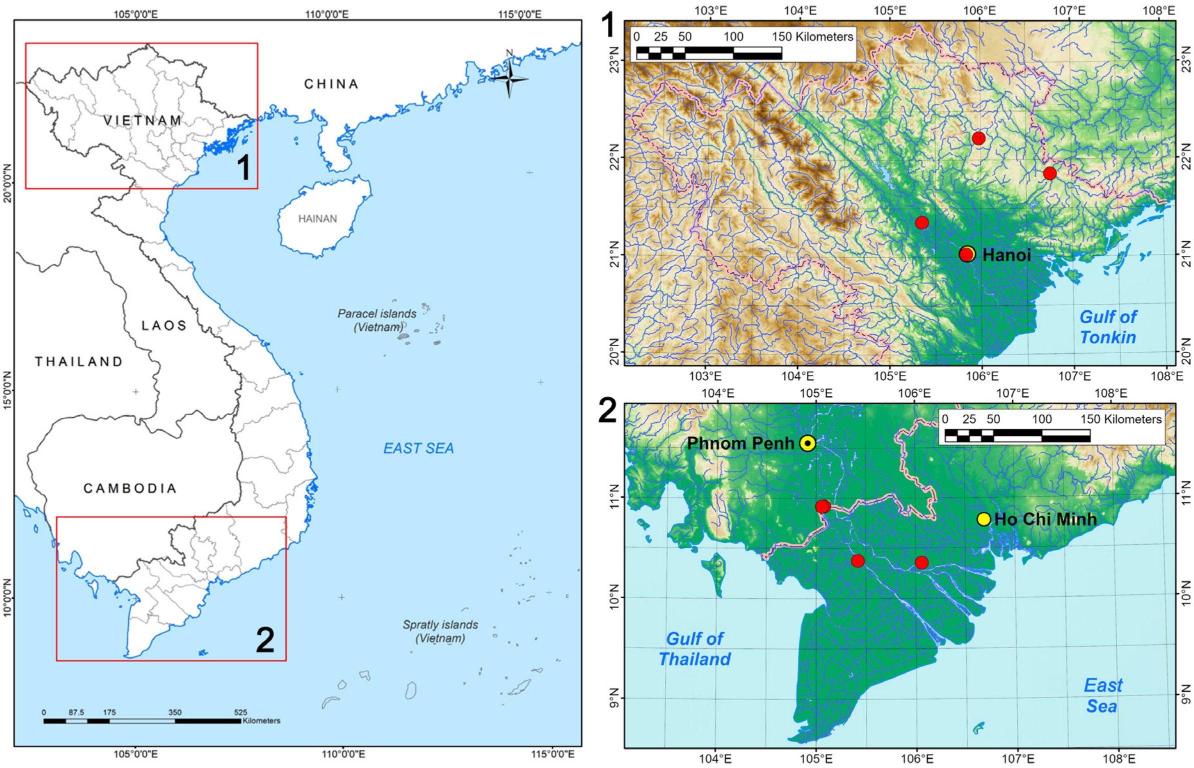

Figure 1. Collection localities of Asian *Corbicula* clams in Vietnam.

Figure 2. Habitats of *Corbicula* clams in Vietnam: (A) Binh Thien Lake; (B) Ky Cung River; (C) small channel of the Tien River; (D) small semi-mountain stream of the Upper Bang River basin. Photos: Larisa A. Prozorova.

Table 1. Geographic and ecological information on collecting localities.

Locality	Latitude	Longitude	Co-ordinate uncertainty (m)	Type of habitat	Sampling year | Museum lot code (DVO RAS)
Southern Vietnam					
Long Xuyen Ward, Hau River basin, Mekong Delta*, An Giang Province	10.3759°N	105.4185°E	2000	Large river	2018 | DVO RAS 102V2018-2
Binh Thien Lake, Hau River basin, Mekong Delta, An Giang Province	10.9206°N	105.0805°E	100	Natural lake, connected with the river	2012, 2017 | DVO RAS 10V2017-1
Small channel of the Tien River, Mekong Delta, Dong Thap Province	10.3536°N	106.0622°E	100	Small channel	2017 | DVO RAS 17V2017-1
Northern Vietnam					
Lang Son Ward, Ky Cung River basin, Lang Son Province*	21.8537°N	106.7615°E	2000	Medium-sized river	2018 | DVO RAS 62V2018-1
Viet Tri Ward, Lo River, Red River basin, Phu Tho Province *	21.3570°N	105.3526°E	5000	Large river	2017 | DVO RAS 35V2017-5
Small tributaries of the Red River, Red River Delta*	21.0278°N	105.8342°E	5000	Small tributaries	2017, 2018 | DVO RAS 52V2017-1; DVO RAS 76V2018-1,2
Upper Bang River basin, Cao Bang Province	22.2235°N	105.9810°E	100	Small semi-mountain stream	2018 | DVO RAS 60V2018

*Sample purchased at a local market. The locality and habitat information are based on verbal communication from the seller. The coordinates correspond to the city where the market is located. The coordinate uncertainty was estimated using Google Earth (https://earth.google.com) tools, based on the approximate geographic distance between the city center and the target watercourse.

Morphological and anatomical studies

The analysis of shell morphology of *Corbicula* clams included examination of the shell shape, sculpture, umbo position, shape of the hinge, and surface coloration (see Bespalaya *et al.* 2018, 2021a, 2021b, 2023). Specimens of *Corbicula* were measured for length (SL), height (SH), and width (SW) all taken at maximum diameter to the nearest 0.1 mm with dial calipers and using a Leica M165C stereomicroscope (Leica Microsystems GmbH, Germany).

Shell images were obtained using a Canon EOS 80D Digital Camera (Canon Inc., Shimomaruko, Ōta, Tokyo, Japan). The ethanol-fixed individuals were dissected; their mantle, siphons, and gills were extracted for visual examination. The soft bodies and siphons were photographed using a stereomicroscope Leica M165C (Leica Microsystems GmbH, Wetzlar, Germany). The gills of specimens from each sampling location were investigated for incubating juveniles.

Results

Shell morphology and anatomy of clams

A total of three *Corbicula* species were distinguished based on siphon anatomy and shell characters, including shell shape, size, external and internal coloration, sculpture and umbo position. These species are *C. fluminea* (Müller, 1774), *C. leana* Prime, 1867, and *C. blandiana* (Fig. 3). The average shell length (± SD) of *C. fluminea* was 21.8 ± 0.4 mm ($N = 2$), and *C. leana* was 20.8 ± 1.7 ($N = 2$). The average shell length (± SD) of *C. blandiana* was 13.7 ± 3.9 mm (min–max 10–22 mm, $N = 12$). Siphons of all *Corbicula* species studied by us are conical (Fig. 3). Siphons of *C. fluminea* are light yellow and have two rows of papillae. The siphonal papillae have black spots and well-defined dark pigmentation

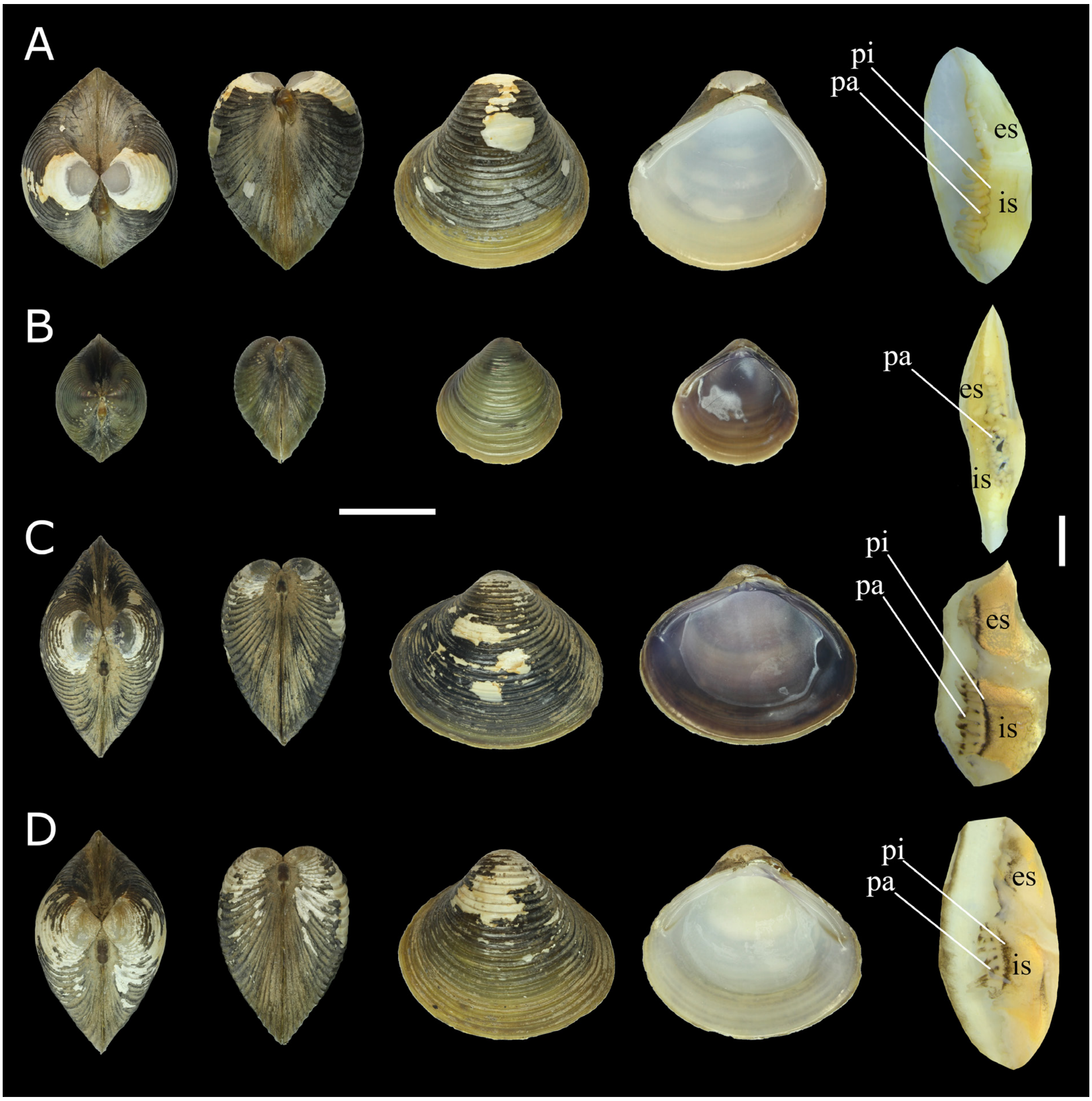

Figure 3. Morphology of *Corbicula* clams from Vietnam: (A) adult individual of *C. blandiana*, specimen RMBH MCorb-195/2 (Binh Thien Lake, Vietnam); (B) young individual of *C. blandiana*, specimen RMBH MCorb-199 (Binh Thien Lake, Vietnam); (C) *C. fluminea*, specimen RMBH MCorb-196/1 (Red River Delta, Hanoi city, Vietnam); (D) *C. leana*, specimen RMBH MCorb-196/2 (Red River Delta, Hanoi city, Vietnam). For each specimen, we illustrated complete shell in dorsal view, complete shell in lateral view (from anterior end), outer view of the right valve, inner view of the left valve, and soft body with siphons (from posterior end). Abbreviations: *es*, exhalant siphon, *is*, inhalant siphon, *pi*, pigmentation, and *pa*, papillae. Scale bars: 1 cm for shells; 1 mm for soft bodies with siphons. Photos: Alexander V. Kropotin.

around them. The siphons of *C. leana* have a row of long papillae and an additional row of short papillae with black spots (Fig. 3). Black pigment is concentrated at the base of both siphons (Fig. 3). The outer surface of the siphons of *C. blandiana* is light yellow, while the inner surface is yellow. The inhalant siphon has two rows of long and short papillae with faint dark rings at the base.

Table 2. List of sequenced specimens of *Corbicula* spp. from Vietnam, with their accession number, sample code, and locality information.

Species	Specimen voucher (RMBH)	NCBI GenBank acc. No		Locality
		COI	28S rRNA	
C. blandiana	RMBH MCorb-0194/1	PX641568	n/a	Long Xuyen Ward, Hau River basin, Mekong Delta, An Giang Province, Southern Vietnam*
C. blandiana	RMBH MCorb-0194/2	PX641569	n/a	Long Xuyen Ward, Hau River basin, Mekong Delta, Southern Vietnam*
C. blandiana	RMBH MCorb-0195/1	PX641570	n/a	Binh Thien Lake, Hau River basin, Mekong Delta, An Giang Province, Southern Vietnam
C. blandiana	RMBH MCorb-0195/2	PX641571	PX622720	Binh Thien Lake, Hau River basin, Mekong Delta, An Giang Province, Southern Vietnam
C. blandiana	RMBH MCorb-0198	PX641576	PX622721	Small channel of the Tien River, Mekong Delta, Dong Thap, Southern Vietnam
C. blandiana	RMBH MCorb-0199	PX641577	n/a	Binh Thien Lake, Hau River basin, Mekong Delta, An Giang Province, Southern Vietnam
C. fluminea	RMBH MCorb-0191/1	PX641560	PX622709 PX622710	Lang Son City, Ky Cung River basin, Lang Son Province, Northern Vietnam*
C. fluminea	RMBH MCorb-0191/2	PX641561	PX622711 PX622712	Lang Son Ward, Ky Cung River basin, Lang Son Province, Northern Vietnam*
C. fluminea	RMBH MCorb-0192/1	PX641562	PX622713 PX622714	Viet Tri City, Red River basin, Vinh Phuc Province, Northern Vietnam*
C. fluminea	RMBH MCorb-0192/2	PX641563	PX622715	Viet Tri Ward, Red River basin, Phu Tho Province, Northern Vietnam*
C. fluminea	RMBH MCorb-0192/3	PX641564	PX622716 PX622717	Viet Tri Ward, Red River basin, Phu Tho Province, Northern Vietnam*
C. fluminea	RMBH MCorb-0193/1	PX641565	n/a	Red River Delta, Northern Vietnam*
C. fluminea	MCorb-0193/2	PX641566	PX622718	Red River Delta, Northern Vietnam*
C. fluminea	RMBH MCorb-0193/3	PX641567	PX622719	Red River Delta, Northern Vietnam*
C. fluminea	RMBH MCorb-0196/1	PX641572	n/a	Red River Delta, Northern Vietnam*
C. fluminea	RMBH MCorb-0196/3	PX641574	n/a	Red River Delta, Northern Vietnam*
C. leana	RMBH MCorb-0196/2	PX641573	n/a	Red River Delta, Northern Vietnam*
C. leana	RMBH MCorb-0197	PX641575	n/a	Upper Bang River basin, Cao Bang Province, Northern Vietnam

*Sample purchased at a local market. n/a – not available.

Mitochondrial and nuclear DNA sequences

We obtained 18 new COI sequences from specimens collected in Vietnam under the framework of this study (Table 2). The COI haplotype network reveals three distant genetic lineages (Fig. 4). The first lineage corresponds to *C. fluminea*, the second to *C. leana*, and specimens from Binh Thien Lake (Mekong Delta) represent a separate genetic lineage, identified as *C. blandiana* (Fig. 4). Phylogeographic analysis indicated that the *C. blandiana* populations from Vietnam are closely related to those from Thailand.

We obtained 28S rRNA sequences from eight *Corbicula* individuals from Vietnam (Table 2). Several individuals of *C. fluminea* exhibited heterozygosity in their 28S rRNA sequences (Table 2). Consequently, five individuals of *C. fluminea* from Vietnam displayed four variants of 28S rRNA, which showed (1) 99.61% similarity (with three nucleotide substitutions) to that of *C. elatior* from Far Eastern Russia (Bespalaya *et al.* 2023; GenBank accession No. MZ427282); (2) 100% similarity to *C. lamarckiana* from Thailand (Bespalaya *et al.* 2025; GenBank accession No. PV036601); (3) 99.87% similarity (with one nucleotide substitution) to that of *C. leana* from South Korea (Bespalaya *et al.* 2023; GenBank accession No. MZ427292); and (4) 99.10% similarity (with two nucleotide substitutions, four insertions and one deletion) to that of *C. fluminalis* from European Russia (Kropotin *et al.* 2023; GenBank accession No. OR252292). Additionally, two *C. fluminea* individuals possessed 28S rRNA sequences that were not heterozygous. We were unable to amplify the 28S rRNA sequences from *C. leana* individuals.

The 28S rRNA gene sequences of *C. blandiana* from Binh Thien Lake (Mekong Delta, Hau River basin) were identical to those from Thailand (Chee River, Chae Stream, and Mun River) and other Vietnamese localities (Mekong Delta, Bassak River, and Kan Shomot River) (see Bespalaya *et al.* 2025).

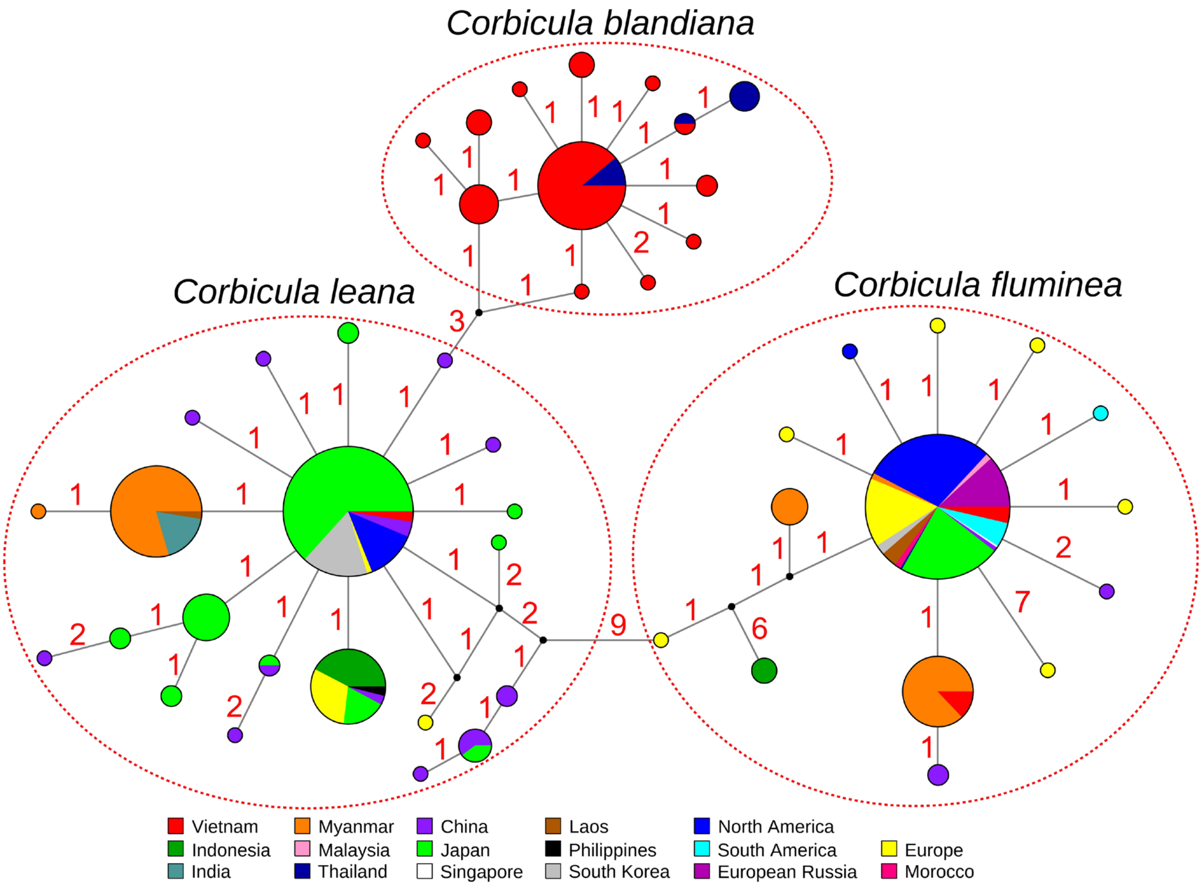

Figure 4. Median-joining network of *Corbicula* species from Vietnam based on the COI gene sequences. Circles represent different haplotypes, with the size reflecting their frequency (smallest = 1). Red dotted contours indicate confirmed species-level taxa. Numbers near branches are numbers of nucleotide substitutions per site. The dataset contains COI sequences ($N = 506$; length = 591 bp).

Discussion

Three *Corbicula* species were identified in our samples from Vietnam: *C. fluminea*, *C. leana*, and *C. blandiana* (Fig. 3). Notably, *C. blandiana* was recorded in freshwater courses of the Mekong Delta. The other two species, *C. fluminea* and *C. leana*, were found in the Red River and other rivers of North Vietnam, also under freshwater conditions.

The present study provides the first confirmed record of *C. fluminea* and *C. leana* in Vietnam based on DNA sequence data. These invasive species are widespread globally. Both *C. fluminea* and *C. leana* are native to Southeast and East Asia, with type locality China and Japan respectively, and have been reported as non-native in Europe and the Americas (Hedtke *et al.* 2008, 2011; Pigneur *et al.* 2014; Vastrade *et al.* 2022). In addition, *C. fluminea* has been recorded in North Africa (Gomes *et al.* 2016; Bespalaya *et al.* 2025).

Our COI haplotype network indicates that *C. blandiana* has a limited distribution and is likely endemic to the Mekong River basin. The COI sequences of *C. fluminea* and *C. leana* from Vietnam either share identical haplotype or differ by only one or two nucleotide substitutions from sequences obtained in Japan, China, and Myanmar (Fig. 4). These molecular data support our earlier hypothesis that Southeast and East Asia are potential sources for non-native populations of *C. leana* and *C. fluminea* on a global scale (Kropotin *et al.* 2023; Bespalaya *et al.* 2025).

The intragenomic variability observed in the 28S rRNA gene of *C. fluminea* from Vietnam is likely attributable to hybridization events between different *Corbicula* lineages, resulting from ‘nuclear genome capture’. This phenomenon has been extensively described in previous studies (Hedtke *et al.* 2008, 2011; Pigneur *et al.* 2012; Bespalaya *et al.* 2018, 2021a, 2023).

In conclusion**,** this study provides new insights into the biogeography and genetic diversity of *Corbicula* in Vietnam. Future research should focus on revising the taxonomy of Vietnamese *Corbicula* species using molecular approaches.

Acknowledgements

This research was supported by the Ministry of Science and Higher Education of the Russian Federation (project No. 125022002728-9 to Y.V.B. and A.V.Kr.; project No. 124012400285–7 to L.A.P. and V.V.B.). Field expeditions to Vietnam were supported by the “VAST17– 007” Program of the Far Eastern Branch of the Russian Academy of Sciences.

Conflicts of Interest: The authors declare no conflict of interest.

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