

A taxonomic reassessment of native and invasive species of *Corbicula* clams (Bivalvia: Cyrenidae) from the Russian Far East and Korea

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Currently, the validity of many nominal bivalve species of the genus *Corbicula* endemic to the Russian Far East and South Korea needs a critical reassessment. In this study, we clarify the taxonomic status of *Corbicula* species of this area based on a combination of molecular genetic, conchological and anatomical data. According to our results, four *Corbicula* lineages, corresponding to the nominal species *Corbicula japonica*, *Corbicula elatior*, *Corbicula leana* and *Corbicula fluminea*, can be delineated in samples collected in the Primorye and Khabarovsk regions of Russia and South Korea. Two species endemic to the Russian Far East (i.e. *Corbicula finitima* and *Corbicula lindholmi*) are considered here as junior synonyms of the species *C. japonica*, which is widely distributed in estuarine habitats around the Japanese Archipelago, Sakhalin Island, southern Kurile Islands, Primorye and Khabarovsk regions, Korean Peninsula and China. Three nominal species described from the Lower Amur basin (*Corbicula amurensis*, *Corbicula nevelskoyi* and *Corbicula sirotskii*) appeared to be synonyms of *C. elatior*, whose range covers the Korean Peninsula, Primorye and Khabarovsk regions and, perhaps, China. We delineated several colour morphs of *C. fluminea* and *C. japonica*. The distinctness between these colour morphs can be attributed to both heritable and environmental factors.

ADDITIONAL KEYWORDS: Amur River – *Corbicula elatior* – *Corbicula japonica* – corbiculid clams – endemic species – invasive species – South Korea.

INTRODUCTION

Owing to their high invasive potential, fresh- and brackish-water clams of the genus *Corbicula* Megerle von Mühlfeld, 1811 (family Cyrenidae Gray, 1840) constitute today one of the most popular research objects for malacologists and aquatic ecologists from all

over the world (see Pigneur *et al.*, 2014; Gomes *et al.*, 2016; Vastrade *et al.*, 2022; and references therein). The native range of this genus covers tropical and subtropical regions of Africa, Asia, New Guinea and eastern Australia (Araujo *et al.*, 1993; Haponski & Ó Foighil, 2019). Owing to human activities, especially international trade and the globalization of economies, in the Anthropocene *Corbicula* clams have spread far beyond their native range (Karatayev *et al.*, 2007). The invasive *Corbicula* clams are now widespread in Asia (in regions beyond their native range) and, during the last several decades, have formed sustainable invasive populations in Europe

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and North and South America (Hedtke *et al.*, 2008; Pigneur *et al.*, 2014; Gomes *et al.*, 2016; Bepalaya *et al.*, 2018, 2021a, b; Vastrade *et al.*, 2022).

The invasive lineages of *Corbicula* have a wide spectrum of reproductive strategies that might contribute to their invasive success (Sousa *et al.*, 2014; Bepalaya *et al.*, 2021b). Among these strategies are rapid maturity, reproduction through androgenesis, hybridization and the presence of unusual ameiotic breeding systems (Byrne *et al.*, 2000; Rajagopal *et al.*, 2000; Glaubrecht *et al.*, 2003; Pigneur *et al.*, 2011; Cao *et al.*, 2017).

It is well known that invasive *Corbicula* clams can have significant negative ecological and economic impacts (Simberloff *et al.*, 2013; Oliveira *et al.*, 2015; Penãrrubia *et al.*, 2017). On the contrary, the genus *Corbicula* includes some commercial species that are popular edible animals in many Asian regions, including the Russian Far East (Zhu *et al.*, 2004; Lin *et al.*, 2012; I.N. Bolotov, pers. observ.).

Despite the decades of intense study of the genus *Corbicula*, some questions regarding the taxonomic status of certain species remain unresolved (Counts, 1989; Korniusshin, 2004; Pigneur *et al.*, 2011; Bieler & Mikkelsen, 2019). This is an outcome of a long-term tradition of application of the comparative method in this group, which has led to the multiplication of nominal species, whose descriptions were typically based on slight differences in shell shape, size and coloration (Graf, 2007). This confusing state of *Corbicula* taxonomy significantly complicates the ecological and applied research on this important group of aquatic organisms. At present, 91 species of the genus *Corbicula* are distinguished globally (Bieler & Mikkelsen, 2019; Graf & Cummings, 2021; MolluscaBase <https://www.molluscabase.org>), but the validity of many of them is dubious and needs to be resolved (Korniusshin, 2004). Herewith, the endemic species of this genus, restricted in their distribution to relatively small regions, remain the least studied (Byrne *et al.*, 2000; Glaubrecht *et al.*, 2003). The Far East represents one such region, with a number of *Corbicula* nominal species described in the 19th–20th centuries and waiting for their taxonomic reassessment. In this communication, we focus on two parts of this vast region, namely, the Russian Far East (Primorye and Khabarovsk regions) and South Korea, in order to clarify the species diversity of *Corbicula* clams in their fauna.

The reliable data on *Corbicula* species endemic to the Far East are relatively scarce. At present, as many as eight nominal species of *Corbicula* clams are included in the fauna of the Russian Far East: *Corbicula japonica* Prime, 1864, *Corbicula finitima* Lindholm, 1927, *Corbicula lindholmi* Kursalova & Starobogatov, 1971, *Corbicula amurensis* Bogatov & Starobogatov, 1994, *Corbicula nevelskoyi*

Bogatov & Starobogatov, 1994, *Corbicula sirotskii* Bogatov & Starobogatov, 1994, *Corbicula producta* Martens, 1905 and *Corbicula elatior* Martens, 1905 (Lindholm, 1927; Zatravkin & Bogatov, 1987; Counts, 1989; Glaubrecht *et al.*, 2007; Vinarski & Kantor, 2016). No attempts to assess their taxonomic status (except for *C. japonica*) through a molecular study have been undertaken, and most of these species are still known from dried shells only, sometimes from a few specimens.

For Korea, Morton (1986) considered nine species: *Corbicula fluminea* O.F. Müller, 1774, *C. japonica*, *Corbicula suifunensis* Lindholm, 1927, *Corbicula colorata* Martens, 1905, *Corbicula felnouilliana* Heude, 1887, *Corbicula vicina* Heude, 1887, *Corbicula papyracea* Heude, 1887, *Corbicula orientalis* Lamarck, 1818 and *C. elatior*. However, a decade later Lee & Kim (1997) listed only four species of the genus in the fauna of South Korea: *C. japonica*, *C. fluminea*, *C. colorata* and *Corbicula leana* Prime, 1864. Park & Chung (2003) discussed three species of *Corbicula* from South Korea: *C. papyracea*, *C. leana* and *C. fluminea*. Graf & Cummings (2021) listed six species for South Korea: *C. japonica*, *C. fluminea*, *C. colorata*, *C. felnouilliana*, *C. finitima* and *C. producta*. The difference among the four species lists published during the last 11–25 years is, in our opinion, symptomatic.

The most studied among the above-mentioned species is *C. japonica*, distributed in Japan, Korea and the Russian Far East. The phylogenetic position, phylogeography and genetic diversity of this clam were studied by a number of authors, including Okamoto & Arimoto (1986), Park & Kim (2003), Lee *et al.* (2005), Komaru *et al.* (2010), Yamada *et al.* (2014) and Vastrade *et al.*, 2022). A series of publications were devoted to the reproductive biology and population dynamics (Baba *et al.*, 1999; Byun & Chung, 2001; Oshima *et al.*, 2004; Hedtke *et al.*, 2008; Mito *et al.*, 2014). The genetic structure of *C. japonica* populations and its reproductive biology and population characteristics were also studied in the Primorye Region of Russia (Rybalkina *et al.*, 2013; Evdokimov & Matrosova, 2014; Voronoy & Zaslavskaya, 2014; Kolpakov *et al.*, 2016).

At least five nominal species endemic to the Russian Far East have been described during the last century; three of them (*C. amurensis*, *C. nevelskoyi* and *C. sirotskii*) were established in a single paper (Bogatov & Starobogatov, 1994) as a result of an examination of shells of the Far-Eastern *Corbicula* deposited in collections of the Zoological Institute of Russian Academy of Science, St. Petersburg (ZIN), based on the comparative method (for comments on this method, see Graf, 2007; Bolotov *et al.*, 2013; Vinarski & Kantor, 2016). The type localities of the three species are situated in the Lower Amur basin, Khabarovsk Region of Russia. Neither anatomical nor genetic information

on the species established in the paper by Bogatov & Starobogatov (1994) is available, which creates some doubts about their validity (Glaubrecht *et al.*, 2007).

The main goals of the present study were as follows: (1) to perform a taxonomic revision of the Russian Far East and South Korean *Corbicula* spp. based on an integrative approach combining molecular genetic, conchological and anatomical data; and (2) to assess the genetic diversity and phylogeography of *Corbicula* spp. of these areas based on DNA sequences.

MATERIAL AND METHODS

STUDY AREA AND TAXON SAMPLING

The field study was conducted within several localities of the Russian Far East (Primorye and Khabarovsk regions) and South Korea between 2014 and 2021, with emphasis on obtaining samples from the type localities of nominal species of the genus described from the Russian Far East and considered endemics of the region (Fig. 1). *Corbicula* were sampled using a hand net and dredge and fixed in 96% ethanol. A total of 243 specimens of molluscs were collected (Supporting Information, Table S1). Additionally, 89 dead specimens were collected from the bank deposits of the Amur River near the Nizhnetambovskoe settlement, Khabarovsk Region (Supporting Information, Table S1). We also examined the type specimens of *C. amurensis* ($N = 3$), *C. nevelskoyi* ($N = 3$), *C. sirotskii* ($N = 1$), *C. finitima* ($N = 1$) and *C. lindholmi* ($N = 1$) and non-type specimens of *C. producta* ($N = 5$), *C. japonica* ($N = 131$) and *C. elatior* ($N = 1$) from the ZIN collection. The syntypes of two nominal *Corbicula* species described by Eduard von Martens (*C. producta* and *C. elatior*) and Prime (*C. japonica*) were examined in the collection of the Zoological Museum of Berlin, Germany (ZMB) (for details, see Vinarski, 2016).

The majority of specimens discussed in this publication are stored in the Russian Museum of the Biodiversity Hotspots (RMBH) of the N. Laverov Federal Center for Integrated Arctic Research of the Ural Branch of the Russian Academy of Sciences (Arkhangelsk, Russia). Some voucher specimens (exclusively dried shells collected from the bank deposits) are kept in the Laboratory of Macroecology & Biogeography of Invertebrates, Saint Petersburg State University, Saint Petersburg, Russia (LMBI) (Supporting Information, Table S1).

EXTRACTION OF DNA, PCR AMPLIFICATION AND DNA SEQUENCING

The present study includes new molecular data for 43 *Corbicula* specimens (Supporting Information, Table S2). Total DNA was extracted from 96% ethanol-preserved

foot tissues using the NucleoSpin Tissue Kit (Macherey-Nagel, Duren, Germany), following the manufacturer's protocol. As the primer pairs, we used LCO 1490 and HCO2198 for the *COI* gene fragment (Folmer *et al.*, 1994), C1 and D2 for the 28S gene fragment (Jovelin & Justine, 2001) and the designed internal forward primer KR1 (5'-TTCAGCCCGGCCGCCAG-3'). The PCR mix contained ~100 ng of total cell DNA, 10 pmol of each primer, 200 μ mol of each dNTP, 2.5 μ L of PCR buffer (with 20 mmol of $MgCl_2$), 0.8 units of Taq DNA polymerase (SibEnzyme, Novosibirsk, Russia), and H_2O was added for a final volume of 25 μ L. Temperature cycling was as follows: 95 °C (4 min), 36 cycles of 95 °C (50 s), 52 °C (50 s) and 72 °C (50 s), with 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 v.3.1 reagent kit. The resulting sequences were checked manually using the sequence alignment editor BIOEDIT v.7.2.5 (Hall, 1999).

SEQUENCE ALIGNMENT AND PHYLOGEOGRAPHICAL ANALYSES

The sequences were aligned using the MUSCLE algorithm of MEGA7 (Kumar *et al.*, 2016). 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 phylogeographical analyses were performed based on a median-joining network approach using NETWORK v.4.6.1.3 software with default settings (Bandelt *et al.*, 1999). In addition, 202 sequences were obtained from NCBI GenBank (Supporting Information, Table S3).

Taking into account that the presence of cryptic hybrids is typical for the studied genus, we followed Vastrade *et al.* (2022) in using the term 'lineage' instead of 'species' for designation of the elementary taxonomic units within *Corbicula*.

MORPHOLOGICAL AND ANATOMICAL STUDIES

We measured shells of *Corbicula* following the same protocol, with three basic measurements taken from each specimen: shell length (SL), height (SH) and width (SW), in millimetres, with an accuracy of 0.1 mm. All measurements were made using digital callipers. A total of 332 specimens were collected during this study (Supporting Information, Table S1), and 143 museum specimens were measured.

The analysis of shell morphology of *Corbicula* clams included examination of the shell shape, sculpture, umbo position, shape of the hinge, and surface coloration (for details, see Bepalaya *et al.*, 2018, 2021a). Shell images were obtained using a Leica M165C stereomicroscope (Leica Microsystems,

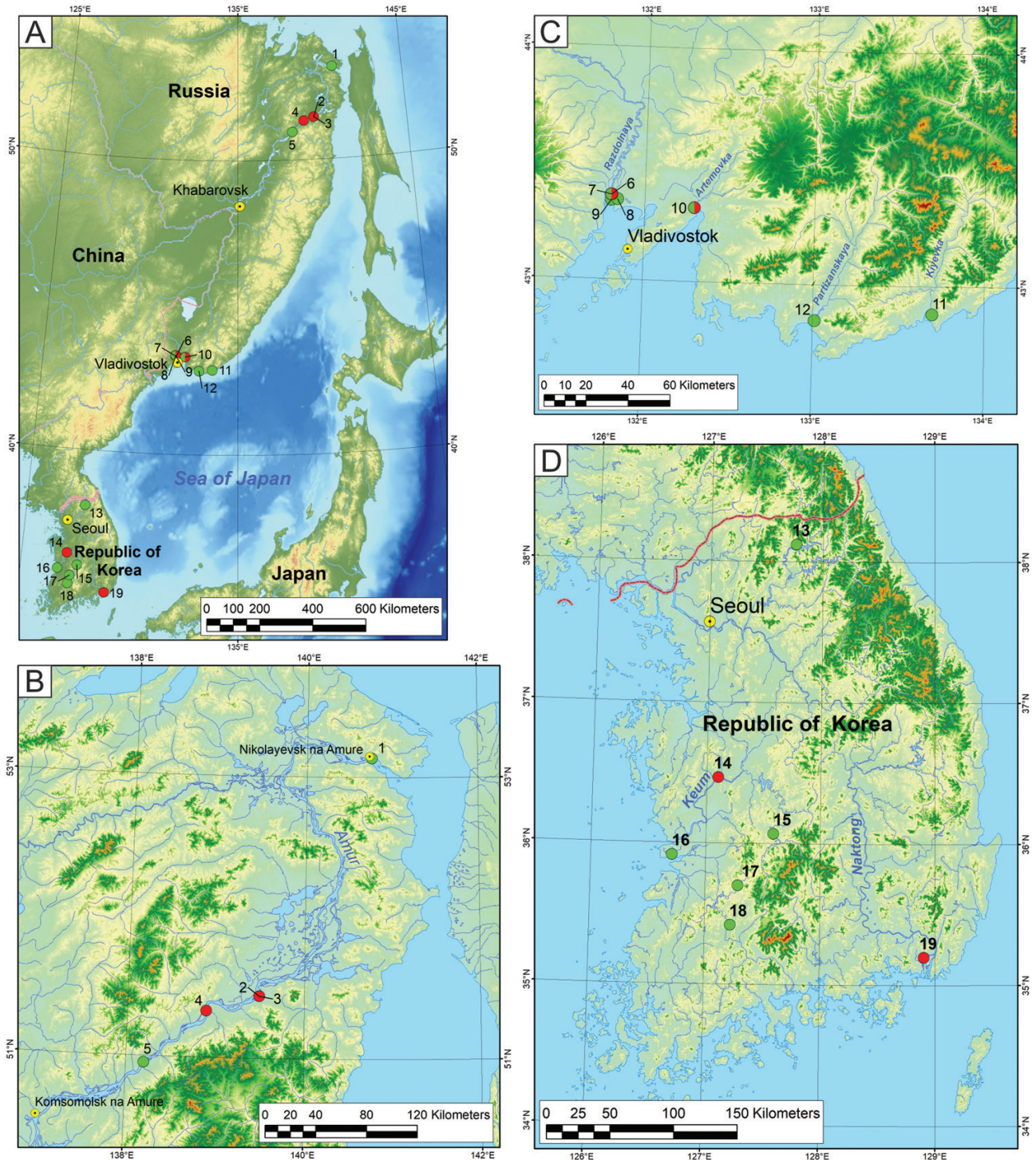


Figure 1. Maps of study localities in the Far East (A), Khabarovsk Region of Russia (B), Primorye Region of Russia (C) and South Korea (D). The green circles indicate our sampling localities, the red circles indicate the type localities for nominal *Corbicula* spp., and the green and red circles indicate our toptype samples. The sampling localities are as follows: (1) Lower Amur River near Nikolaevsk-on-Amur town; (2 and 3) Lower Amur River near Balbinski cliff, 22 km upstream of Kalinovka settlement (type locality of *Corbicula amurensis* Bogatov & Starobogatov, 1994 and *Corbicula nevelskoyi* Bogatov & Starobogatov, 1994); (4) Lower Amur River, 7 km upstream of Maxim Gorky settlement (type locality of *Corbicula*

Germany) for shells with length < 15 mm, or using a Canon EOS 80D digital camera (Canon, Japan) for shells with length > 15 mm. The ethanol-fixed individuals were dissected, and their mantle, siphons and gills were extracted for visual examination. The soft bodies were photographed using a Leica M165C stereomicroscope.

To assess the extent of conchological variation and its potential overlap in the three nominal species of *Corbicula* described from the Lower Amur basin (*C. amurensis*, *C. nevelskoyi* and *C. sirotskii*), principal components analysis was performed, using the three basic measurements (SL, SH and SW). For this analysis, measurements of 121 specimens were used. The statistical analysis, including the normality distribution tests, in addition to the visualization of the results, were conducted using the software PAST v.3.0 (Hammer *et al.*, 2001) and STATISTICA v.12 for Windows (StatSoft, USA).

GONAD HISTOLOGY

Histological examination of the gonads was performed to determine the sexual characteristics of *C. elatior*. A total of ten mature specimens were used for histological examination. Tissues were dehydrated through a graded alcohol series and embedded in paraffin. Histological sections with a thickness of 6 µm were made using a rotary microtome (HM 325; Thermo Scientific, Waltham, MA, USA). The sections were stained with Mayer's Haematoxylin and Eosin double stain for examination under a light microscope (Axio Lab.A1; Carl Zeiss, Oberkochen, Germany).

RESULTS

MITOCHONDRIAL DNA SEQUENCES

Eighteen new *COI* sequences from specimens collected from the rivers of Primorye Region were obtained during this study (Supporting Information, Table S3). All clams collected from the Artemovka River, the type locality of *C. finitima*, from the Kiparisovka River, the type locality of *C. lindholmi* (Vinarski & Kantor, 2016), and from the Razdolnaya, Kievka and Partizanskaya rivers share the single *COI* haplotype. The *COI* haplotype network reveals that these haplotypes belong to the widespread estuarine species *C. japonica* (Fig. 2). The *COI* haplotype network of *C. japonica*

reveals two distant clades. The first of these includes samples from Japan, the Korean Peninsula and the Primorye Region of Russia. A separate group is formed by samples from China and South Korea; it is separated by six or seven nucleotide substitutions from the first group.

The samples of *Corbicula* species from South Korea and the Khabarovsk Region (Lower Amur River) contained representatives of three distant genetic lineages having distinct morphotypes (Fig. 3). The first lineage belongs genetically to an invasive clade, *C. fluminea*, which has been reported from its native range (Eastern Asia) and from non-native regions (Europe, North Africa and North America). Specimens of *Corbicula* collected during our study from the lower reaches of the Amur River (Nikolaevsk-on-Amur and Nizhnetambovskoe settlement, Khabarovsk Region) represent a separate genetic lineage, whose *COI* gene sequences are identical to those found in the Seomjin River, South Korea (Park & Kim, 2003) (GenBank accession no. AF457992).

The specimens from South Korea sequenced in this study represent two distant genetic lineages (Fig. 3) having distinct morphotypes. The first lineage evidently corresponds to *C. fluminea* (= *Corbicula* clade FW5; = *Corbicula* New World's form A; Pigneur *et al.*, 2014; Vastrade *et al.*, 2022) and was found by us in the Geum River (the type locality of *C. producta*) and in the Seomjin River. The second lineage belongs genetically to another clade, *C. leana* (= *Corbicula* sp. 'form R'; = *Corbicula* clade FW1 + FW4; = *Corbicula* New World form B; Pigneur *et al.*, 2014; Vastrade *et al.*, 2022); it was registered from the Seomjin and Bukhan rivers and from an irrigation channel near the Mangyeong River.

NUCLEAR DNA SEQUENCES AND THEIR INTRAGENOMIC VARIABILITY

We obtained 28S ribosomal DNA (rDNA) gene sequences from 23 individuals (Supporting Information, Table S2), including ten individuals of *C. japonica*, seven of *C. elatior*, five of *C. leana* and one of *C. fluminea*. All studied sequences of 28S rDNA of *C. japonica* and *C. elatior* are identical. Our analyses reveal that samples of *C. leana* and *C. fluminea* discovered by us in South Korea share at least two variants of 28S in each individual (Supporting Information, Table S4). Thus, one specimen of *C. fluminea* and one of five specimens of *C. leana* genotyped

sirotskii Bogatov & Starobogatov, 1994); (5) Lower Amur River near Nizhnetambovskoe settlement; (6 and 7) Kiparisovka (Pachikheza) River (type locality of *Corbicula lindholmi* Kursalova & Starobogatov, 1971); (8 and 9) Razdolnaya River; (10) Artemovka River [type locality of *Corbicula finitima* (Lindholm, 1927)]; (11) Kievka River; (12) Partizanskaya River; (13) Bukhan River; (14) Geum River (type locality of *Corbicula producta* von Martens, 1905); (15) Geum River; (16) irrigation channel near Mangyeong River; (17 and 18) Seomjin River; and (19) Nakdong River. Locality numbers on the map correspond to the numbers in the Supporting Information (Table S1).

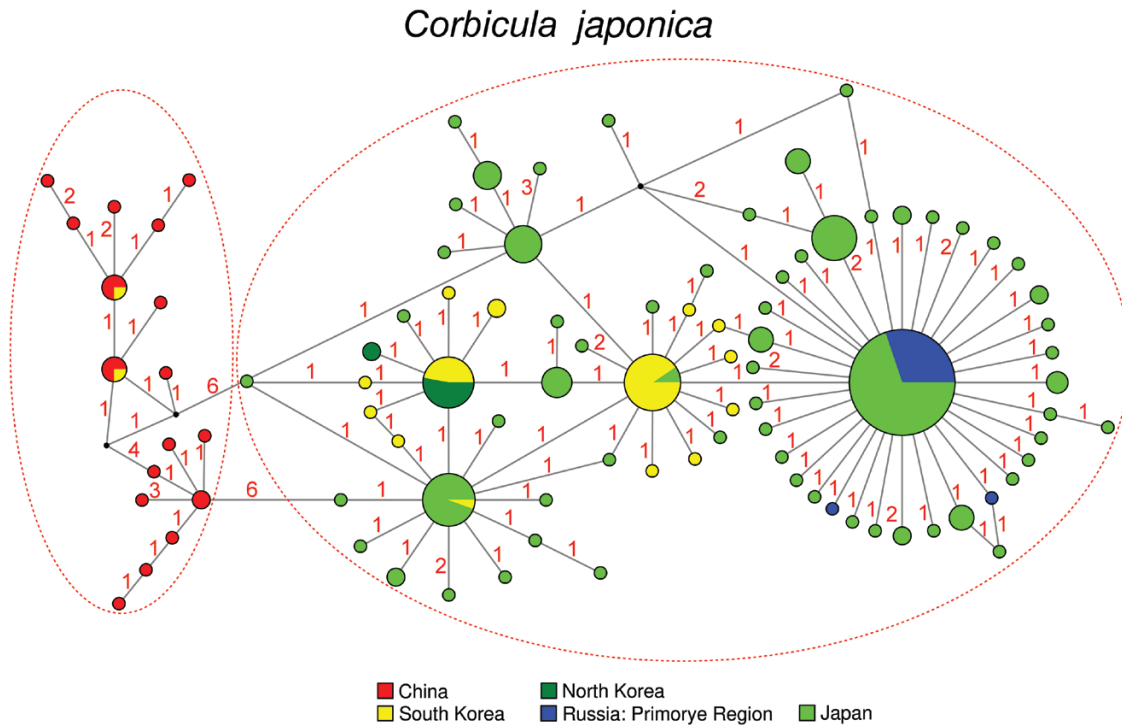


Figure 2. Median-joining network of *Corbicula japonica* based on the *COI* sequences. Circles represent different haplotypes, with the size reflecting their frequency (smallest = 1). Numbers near branches are numbers of nucleotide substitutions per site. The dataset contains 132 *COI* sequences (length = 570 bp; [Supporting Information, Tables S2 and S3; Alignment S1](#)).

displayed heterozygous chromatograph profiles. Based on the visual inspection of sequences, we assume that specimens of *C. leana* and *C. fluminea* from South Korea could contain copies of nuclear genomes originating from two *Corbicula* lineages.

Next, we compare our heterozygous 28S rDNA gene sequences with those obtained from GenBank. It is established that one of the *C. fluminea* 28S rDNA lineages revealed during this study is identical to that of *C. fluminea* from Japan (Shiga, Ritto) (Komaru, 2012; GenBank accession no. AB736278; [Supporting Information, Table S4](#)). The second 28S rDNA lineage in the same sample shows 99.61% identity (with two nucleotide substitutions) to sequences of *Corbicula* sp. (= form A/R) found in Russia (Arkhangelsk, Northern Dvina River basin; GenBank accession no. MG757362; [Bespalaya et al., 2018](#)). In addition, the first variant 28S rDNA lineage in *C. leana* shows 99.76% similarity (with three nucleotide substitutions) to *C. fluminea* from Japan (Shiga, Ritto; GenBank accession no. AB736278; Komaru, 2012), whereas the second variant of this species shows 98.83% similarity (with nine nucleotide substitutions) to *Corbicula* sp. (= form A/R) from Russia (Arkhangelsk, Northern Dvina River basin; GenBank accession no. MG757362; [Bespalaya et al., 2018; Supporting Information, Table S4](#)).

SHELL MORPHOLOGY AND ANATOMY OF *CORBICULA* CLAMS FROM THE RUSSIAN FAR EAST AND SOUTH KOREA

The analysis of the collected individuals ([Supporting Information, Table S1](#)) and museum samples ($N = 131$) of *C. japonica* indicates that this species is morphologically heterogeneous ([Figs 4, 5](#)). The appearance of the shell of young individuals ([Fig. 5A](#)) is clearly different. The average shell measurements (\pm SE; $N = 282$) are as follows: SL = 23.7 ± 0.7 mm [minimum–maximum (min–max) 4.0–45.0 mm], SH = 20.8 ± 0.6 mm (min–max 3.5–40.0 mm) and SW = 13.5 ± 0.4 mm (min–max 2.6–26.0 mm). The specific characteristics of both shell morphology and anatomy of *C. japonica* are described in detail below.

The morphological characteristics of *Corbicula* spp. from the Lower Amur basin are based on our two samples (Nizhnetambovskoe settlement and Nikolaevsk-on-Amur town; [Fig. 6](#)) and on results of the examination of the type specimens of *C. amurensis*, *C. nevelskoyi* and *C. sirotskii* ([Fig. 7](#)). The average shell measurements (\pm SE; $N = 121$) are as follows: SL = 34.5 ± 0.6 mm (min–max 11.5–45.7 mm), SH = 31.2 ± 0.5 mm (min–max 10.7–41.0 mm) and SW = 22.5 ± 0.4 mm (min–max 7.4–33.4 mm). The principal components analysis of shell variation in this set shows that there is no reliable difference between

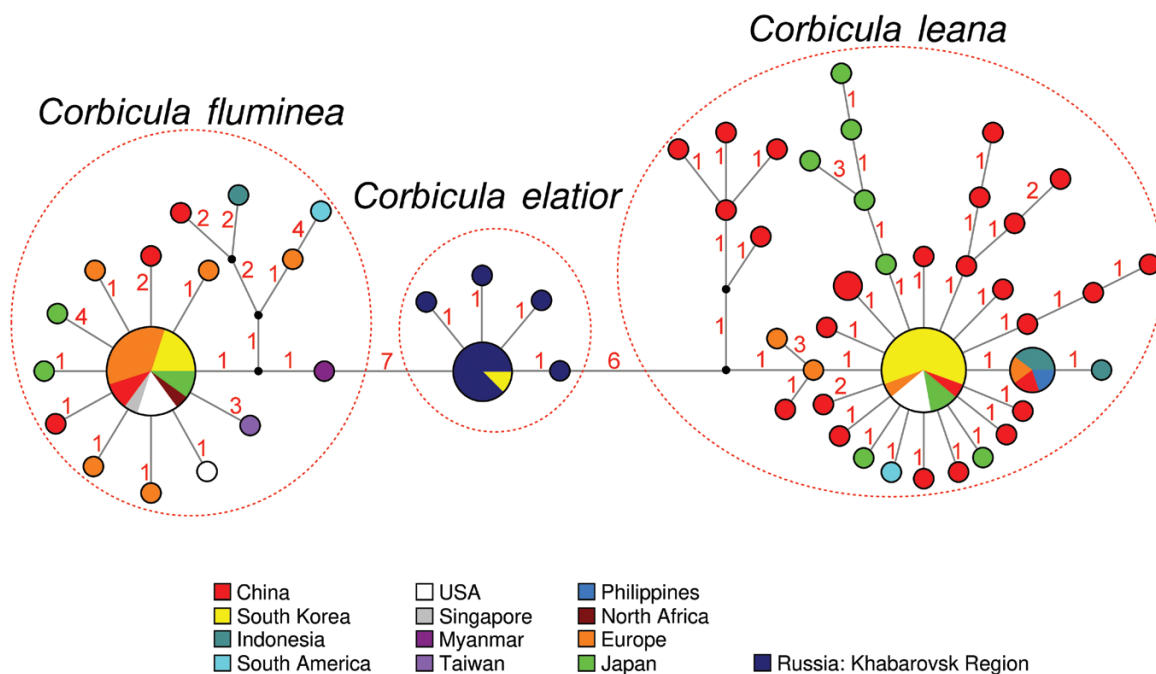


Figure 3. Median-joining network of East Asian *Corbicula* species based on the *COI* sequences. Circles represent different haplotypes, with the size reflecting their frequency (smallest = 1). Red dotted contours indicate putative species-level taxa. Numbers near branches are numbers of nucleotide substitutions per site. The dataset contains 111 *COI* sequences (length = 613 bp; [Supporting Information, Tables S2 and S3; Alignment S2](#)).

specimens belonging to different nominal species of *Corbicula*, because all individuals form a single, almost continuous cloud of points in the multivariate space (Fig. 8). The distribution normality test of morphometric parameters of *Corbicula* clams from the Lower Amur (Nizhnetambovskoe settlement and Nikolaevsk-on-Amur) and type specimens indicates that they belong to the same morphological entity, which, most probably, corresponds to a single species (Fig. 9). Slight bimodality, seen in some graphs in Figure 9, reflects, in our opinion, the heterogeneity in age of the studied sample of shells and does not correspond to two distinct taxonomic entities.

Both shell morphology and anatomy of *Corbicula* from the Lower Amur basin are described in detail below in the ‘Taxonomy’ section.

Individuals of *C. fluminea* inhabiting the Geum River are characterized by small, oval–triangular shells (Fig. 10). The average shell measurements (\pm SE; $N = 5$) are as follows: SL = 9.0 ± 1.9 mm (min–max 4.0–13.6 mm), SH = 7.7 ± 1.9 mm (min–max 3.0–11.9 mm) and SW = 5.2 ± 1.3 mm (min–max 2.0–8.0 mm). The umbo is centrally located and slightly protruding. External shell colour is yellow or olive green. The exterior exhibits concentric sculpture with regular ribs. Internal shell colour is purple. The hinge has three cardinal teeth on each valve and two crenulated lateral teeth. Siphons are of a pale yellow colour and have

small papillae with black spots and surrounding dark pigmentation. A specimen of *C. fluminea* from Seomjin River studied by us has a large, oval–triangular shell, with the following dimensions: SL = 21.0 mm, SH = 19.2 mm and SW = 13.8 mm. The internal shell colour is white, with purple marks in the area of the lateral teeth (Fig. 10F). The external shell colour is dark brown. The exterior exhibits concentric sculpture with regular ribs. Siphons have large papillae, are differently digitated and have orange coloration with black spots and dark pigmentation around. D-shaped larvae were recorded in the inner demibranchs.

Corbicula leana from the Seomjin and Bukhan rivers and an irrigation channel near Mangyeong River are characterized by large, oval or broadly triangular shells (Fig. 11). The average SL = 17.9 ± 0.9 mm (min–max 11.7–32.0 mm), SH = 16.1 ± 0.8 mm (min–max 10.3–31.0 mm) and SW = 11.0 ± 0.6 mm (min–max 7.8–23.0 mm) ($N = 31$). External shell colour is dark olive or dark brown (Fig. 11). The internal colour is purple. Individuals from the irrigation channel have matte marks. The exterior exhibits concentric sculpture with regular ribs. Siphons are conical, with a row of long papillae and with an additional row of short papillae. The outer surface of the siphons is white–yellow; on the inside, the siphons are orange. The individuals from the Seomjin River and the irrigation channel share a black pigment

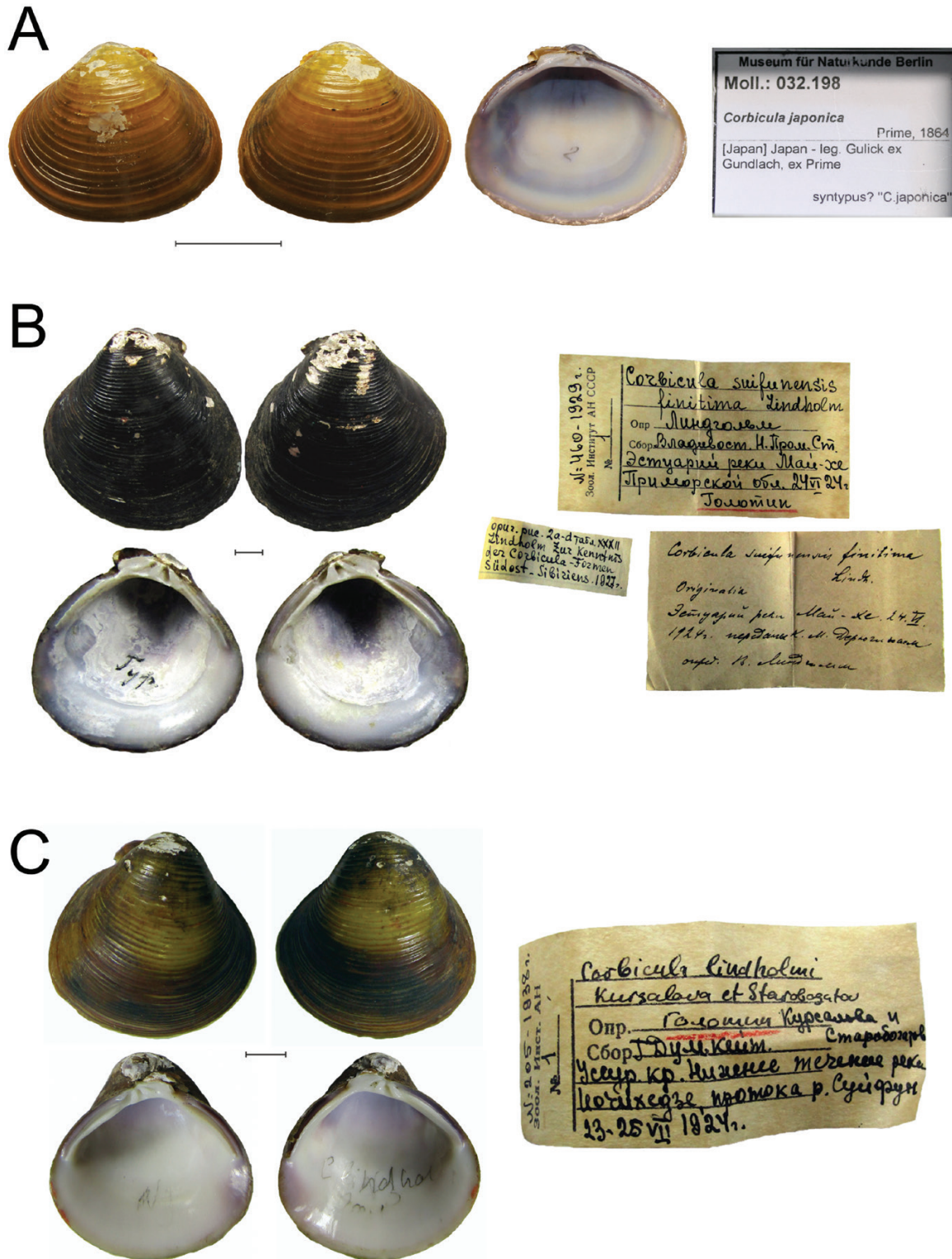


Figure 4. Samples of *Corbicula japonica* from museum collections. A, the syntype of *Corbicula japonica* Prime, 1864, with its labels: ZMB, Zoological Museum of Berlin. B, the lectotype of *Corbicula finitima* Lindholm, 1927 with its labels: ZIN; Russia, the Primorye Region, estuary of the Artemovka River (Mai-khé River). C, the lectotype of *Corbicula lindholmi* Kursalova & Starobogatov, 1971 with its labels: ZIN; Russia, Primorye Region, lower course of the Kiparisovka River (Pachikheza). Scale bars: 1 cm in A; 5 mm in B, C. Photographs: M. V. Vinarski.

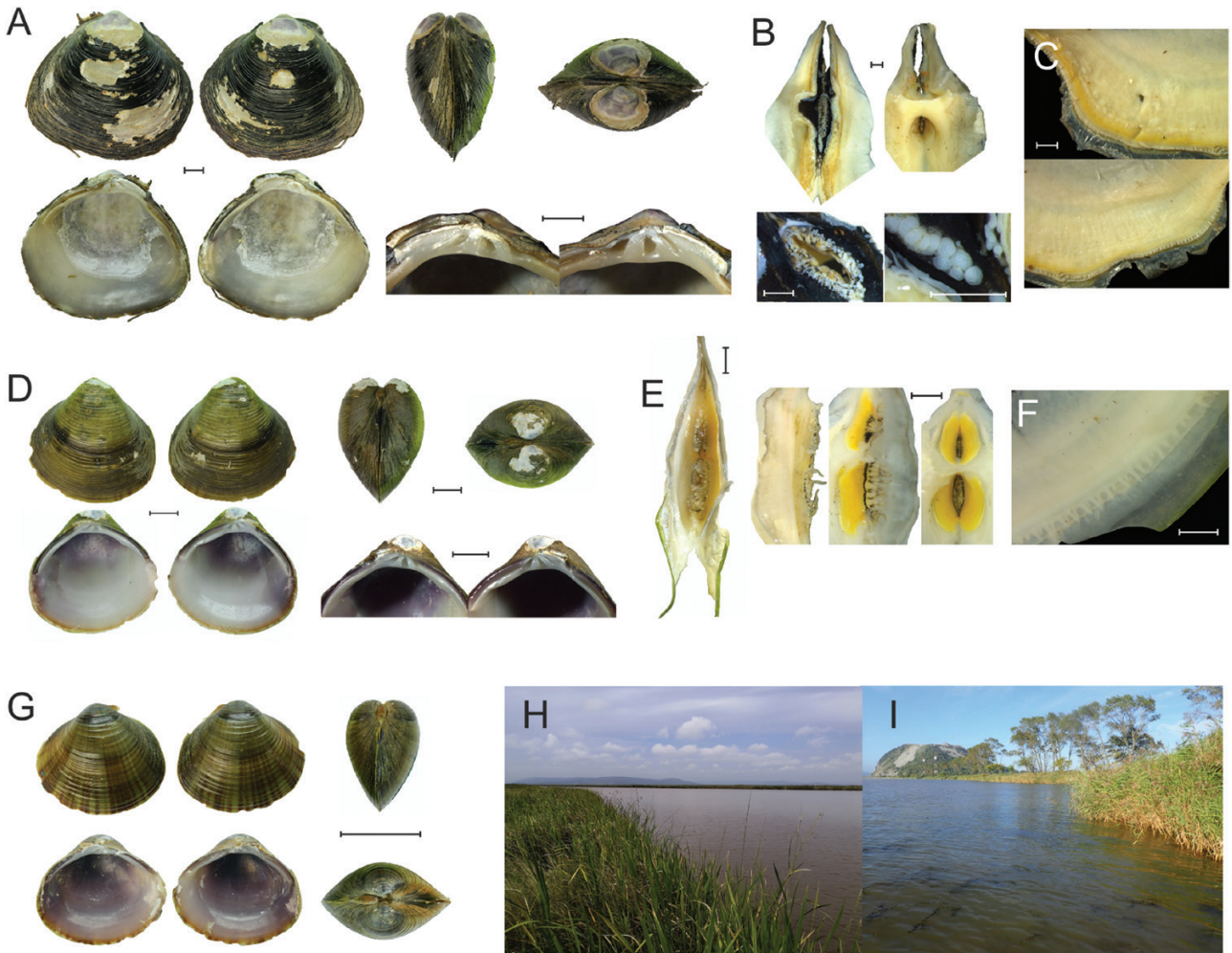


Figure 5. Morphology and anatomy of *Corbicula japonica* from the Primorye Region (Russia). A, old individuals from Artemovka River (lot no. RMBH Corb 114/2). B, general view of the siphon from outer and inner sides, and section of siphons with siphon papillae. C, outgrowths on the mantle edge. D, adult individuals from Kiparisovka River (lot no. RMBH Corb 115). E, general view of the siphons and lateral view of the siphons from outer and inner sides, and general view of the siphons from inner side. F, outgrowths on the mantle edge. G, young individuals from Partizanskaya River (lot no. RMBH Corb 118). H, habitat of *C. japonica* in Kiparisovka River. I, habitat of *C. japonica* in the Partizanskaya River. Scale bars: 5 mm in A, D; 1 mm in B, E; 2 mm in C; 0.2 mm in F; 1 cm in G. Photographs: O. V. Aksenova.

concentrated in rings internally at the base of both siphons. The larger papillae of the inhalant siphon have dark rings (Fig. 11).

HISTOLOGY

According to our histological data, *C. elatior* is dioecious. Examination of gonads in our specimens revealed the presence of either female (eggs) or male (spermatozoa) gametes in a single individual (Fig. 6L, M). Of the studied specimens, five were male and five female. Aggregations of spermatozoa were observed in the gonads of males (Fig. 6M). In the female gonads, many mature eggs were recorded (Fig. 6L). The state

of the gonads of males and females indicates that the molluscs are at the spawning stage.

TAXONOMY

FAMILY CYRENIDAE GRAY, 1840

GENUS *CORBICULA* MEGERLE VON MÜHLFELD, 1811

Type species: Tellina fluminalis O.F. Müller, 1774.

CORBICULA JAPONICA PRIME, 1864

Corbicula japonica Prime, 1864: 68 (Japan, without a precise locality)

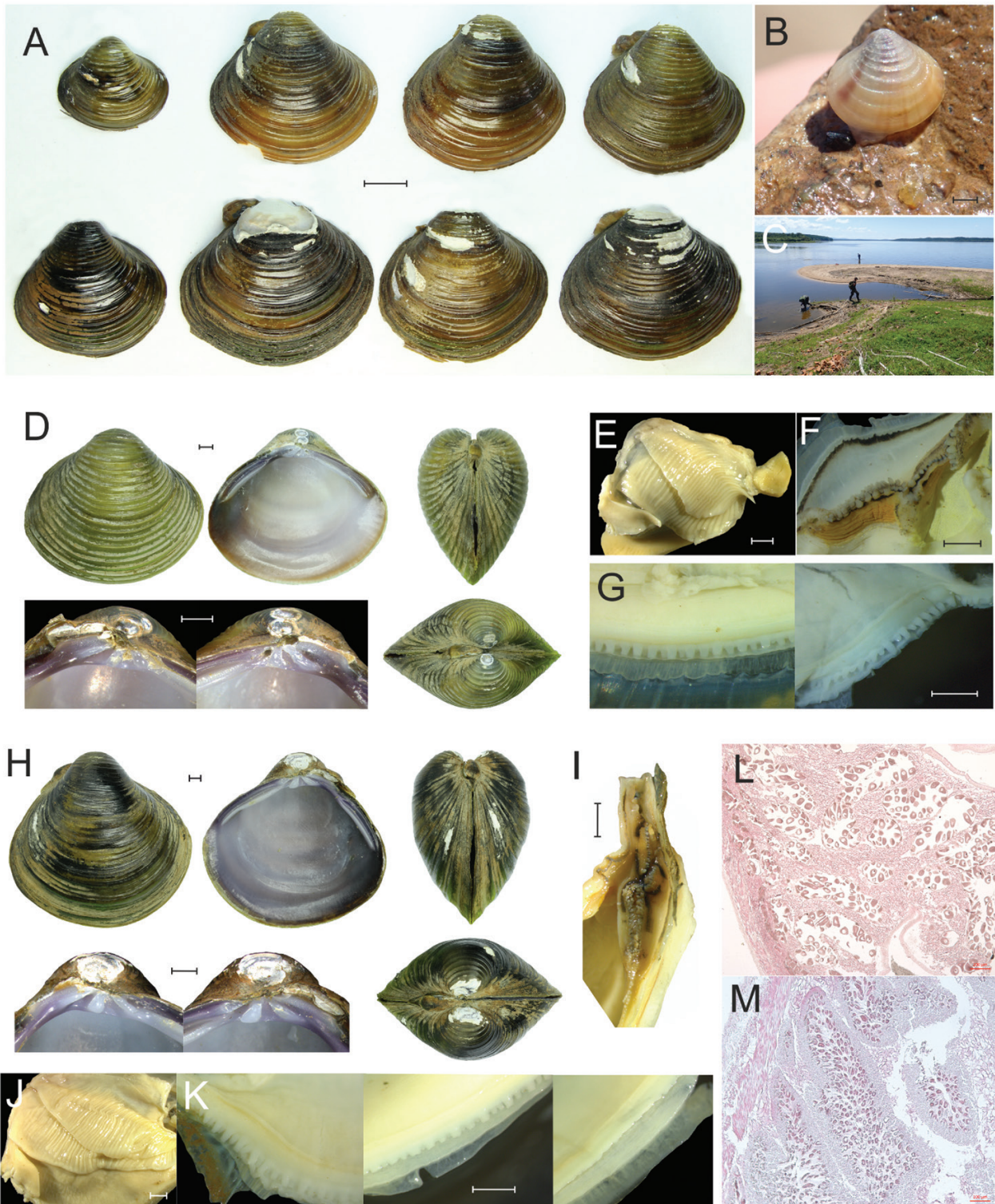


Figure 6. Morphology and anatomy of *Corbicula elatior* from the Khabarovsk Region (Russia). A, variability in shells of *Corbicula* samples from the lower course of the Amur River near the Nizhnetambovskoe settlement. B, young individuals of *C. elatior* from the Amur River near the Nizhnetambovskoe settlement. C, Amur River near the Nizhnetambovskoe settlement. D, morphology and anatomy of *Corbicula elatior* Martens, 1905 from the Lower Amur River (lot no. RMBH Corb 0015/3). E, gills. F, longitudinal section of the siphon. G, outgrowths on the mantle edge on the different part of mantle.

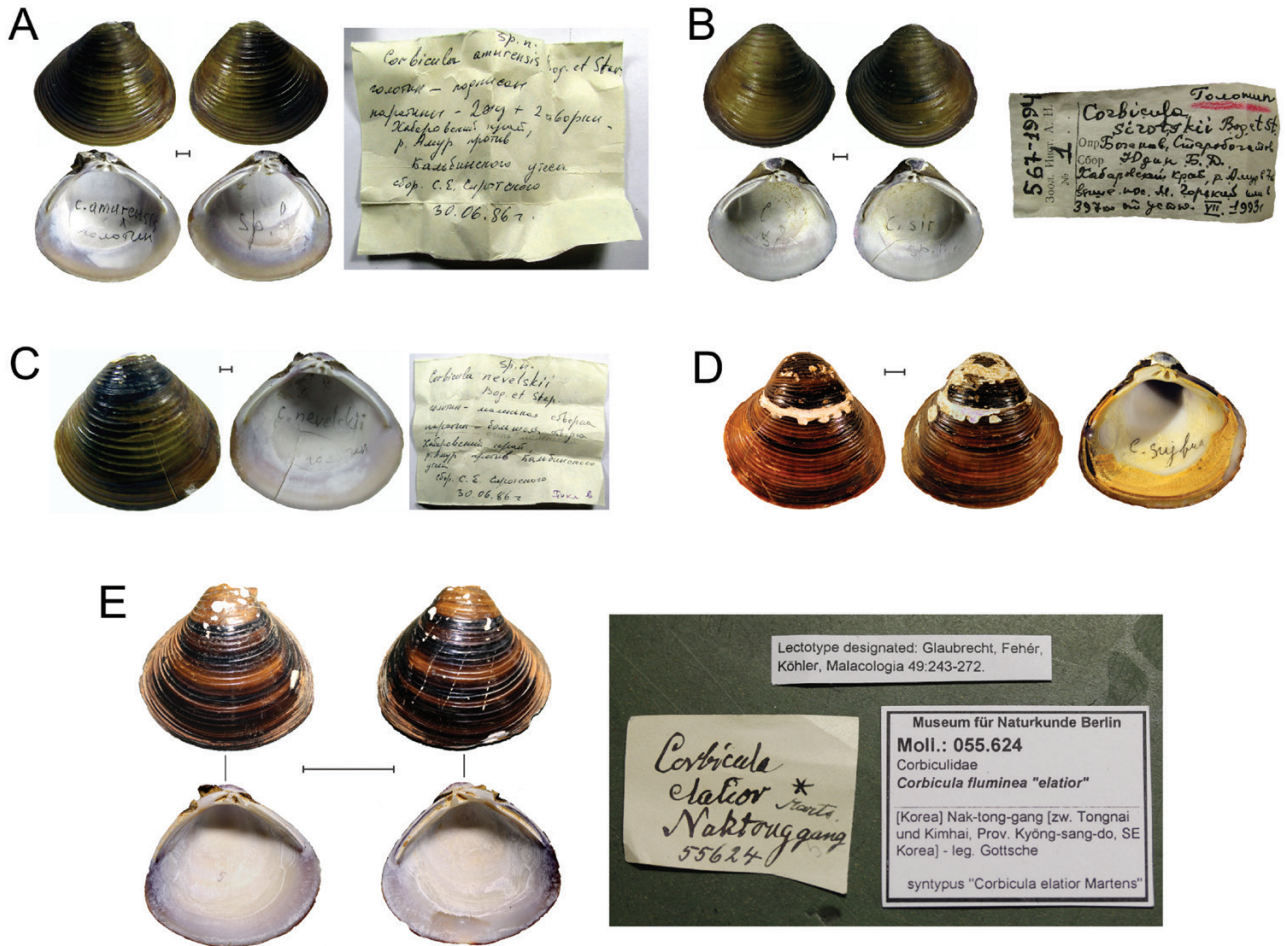


Figure 7. Samples of *Corbicula elatior* from museum collections. A, holotype of *Corbicula amurensis* Bogatov & Starobogatov, 1994 with its labels: ZIN; Russia, Khabarovsk Region, lower course of the Amur River. B, holotype of *Corbicula sirotskii* Bogatov & Starobogatov, 1994 with its labels: ZIN; Russia, the lower course of the Amur River. C, holotype of *Corbicula nevelskoyi* Bogatov & Starobogatov, 1994 with its labels: ZIN; Russia, the lower course of the Amur River. D, samples of *C. elatior* from the Razdolnaya River (ZIN RAS No. 3, 18/08/1928, A. Derzhavin leg.). E, lectotype of *Corbicula elatior* Martens, 1905 with its labels: ZMB, No. 55624: Nakdong River near Gimhae, Gyeongsangnam Prov. Scale bars: 2 mm in A–C, E; 5 mm in D. Photographs: M. V. Vinarski.

= *Corbicula biformis* Reinhardt, 1877: 70 (Japan, 'Jedo' = Tokyo)
 = *Cyrena (Corbicula) leana* von Martens, 1877: 119, non Prime, 1864 (Yokohama)
 = *Cyrena (Corbicula) transversa* von Martens, 1877: 120 (Yokohama)
 = *Cyrena yokohamensis* G.B. Sowerby II, 1877: pl. 12, fig. 55 (Yokohama)
 = *Corbicula ovalis* Reinhardt, 1878: 192, pl. 5, fig. 5, non Prime, 1860 (Japan)

= *Corbicula fuscata* var. *atrata* Reinhardt, 1878: 191, pl. 5, fig. 4 (Japan)
 = *Corbicula doenitziana* Clessin, 1879: 197, pl. 39, fig. 4 (Japan, Yokohama)
 = *Corbicula martensii* Clessin, 1879: 196, pl. 38, figs 17, 18 (Japan, Yokohama)
 = *Corbicula reiniana* Clessin, 1879: 196, pl. 39, figs 8, 9 (Japan, Yokohama)
 = *Corbicula sadoensis* Pilsbry, 1901: 406 (Japan, Sado)

H, *C. elatior* from the Lower Amur River (lot no. RMBH Corb 0015/1). I, longitudinal section of the siphon. J, gills. K, outgrowths on the mantle edge on the different parts of the mantle. L, section of the female gonad. M, section of the male gonad. Scale bars: 1 cm in A; 1 mm in B, F, G, J, K; 2 mm in D, E, H, I; 0.2 mm in L; 0.1 mm in M. Photographs: O. V. Aksenova.

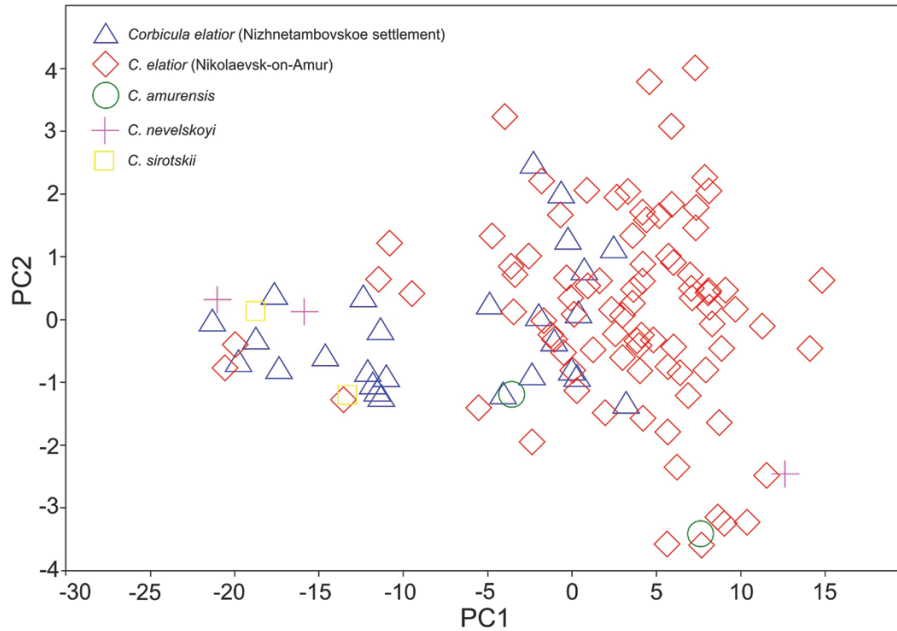


Figure 8. The principal components analysis of shell variation in *Corbicula* clams from the Lower Amur River. Principal component (PC) 1 explains 96.2% of the total variation, and PC2 2.8%.

= *Corbicula nipponensis* Pilsbry, 1907: 159, pl. 7, figs 3, 4 (Japan, Kiogawaranuma, Mutsu)

= *Corbicula nipponensis delicata* Pilsbry, 1907: 160, pl. 7, figs 11, 12 (Japan, Imaegata, Kaga)

= *Corbicula suiifuensis* var. *finitima* Lindholm, 1927: 552, pl. 32, fig. 2 [Russia, Primorye Region, estuary of the Mai-khé River (nowadays Artemovka)], **synon. nov.**

= *Corbicula fluminalis* var. *extrema* Lindholm, 1927: 550 (Russia, Primorye Region, and Sakhalin Island)

= *Corbicula fluminea* Zhadin, 1952: 317, non O.F. Müller, 1774, partim.

= *Corbicula lindholmi* Kursalova & Starobogatov, 1971: 94 [Russia, Primorye Region, the lower course of the Pachikheza River (nowadays Kiparisovka) River], **synon. nov.**

Type material: Syntypes ZMB 32.198 (two pairs of valves ex coll. Gundlach; ‘*Corbicula japonica* Prime, Japan, Gulick, Prime’); syntypes ZMB 170.411 (two pairs of valves ex coll. Dunker; ‘*Corbula japonica*, von Mr Prime selbst erhalten’) inspected during this work. According to Glaubrecht *et al.* (2007), three other specimens (presumable syntypes) are kept in the Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA (not seen).

Type locality: ‘Japonia (fide Gulick) collect. Wheatley, Jay, Browne, Cooper, Lyc. Hist. Nat., Prime and Lea’ = Japan (Glaubrecht *et al.*, 2007).

Material examined: Far East of Russia: Artemovka, Kiparisovka, Razdolnaya, Partizanskaya and Kievka

rivers, in total 194 specimens; IX.2020, Aksenova O.V., Bespalaya Yu.V., Kropotin A.V., Travina O.V., Vinarski M.V. leg. [lot nos RMBH Corb 54 and RMBH Corb 113–119], 43 specimens from the Razdolnaya and Artemovka rivers are kept in LMBI (accession numbers 21-043 and 21-045).

Description: Shell relatively large, oval–triangular (Fig. 5). The umbo is centrally located and prominent. External shell colour varies from olive or greenish brown to black. The exterior exhibits concentric sculpture with regular ribs. Internal shell coloration matte white, with pale violet or dark purple marks in the area of the umbo. Hinge of the heterodont dentition type, with three cardinal teeth on each valve and two reniculated lateral teeth. Shell sculpture of young individuals characterized by well-marked concentric ridges and pronounced transverse stripes; shell coloration is lighter than in adults. Nacre varies from pure purple to purple with wide white marks. Siphons conical, both narrow. Inhalant siphon with a row of long papillae and with an additional row of short papillae. Black pigment is concentrated in rings internally at the base of both siphons and in the edge of the mantle forming the siphons. The outer surface of the siphons is white; on the inside, the siphons are bright orange. Larger papillae of the inhalant siphon, with dark rings.

Distribution: East Asia: the Japan Sea (including some lakes and rivers near the sea), Korea, southern Sakhalin, southern Kurile Islands and the lower reaches of the Amur River (Glaubrecht *et al.*, 2003; Yamada *et al.*, 2014; Vinarski & Kantor, 2016).

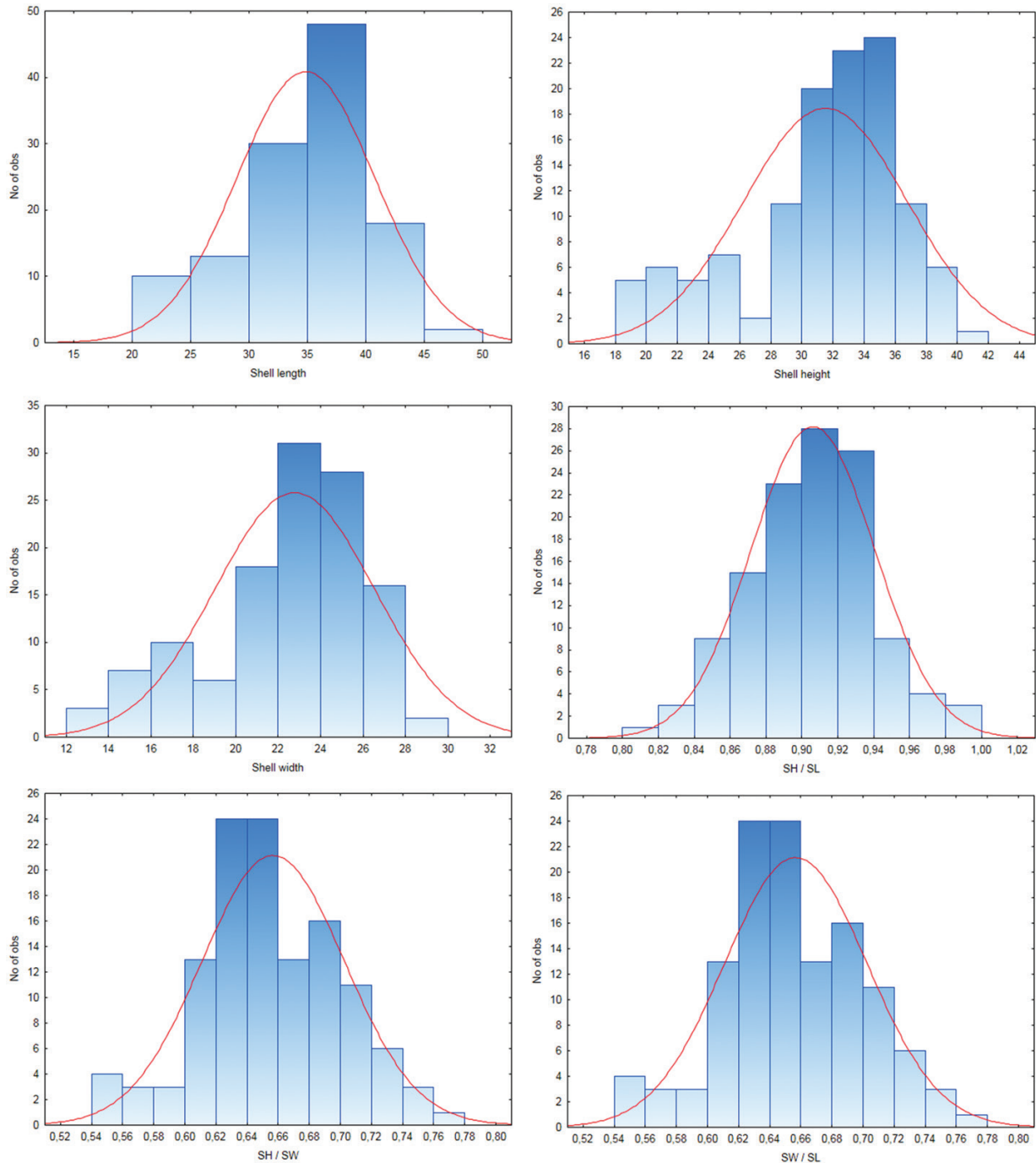


Figure 9. Frequency histograms of morphometric parameters for *Corbicula* clam samples from the Lower Amur River (Nizhnetambovskoe settlement and Nikolaevsk-on-Amur town).

CORBICULA ELATIOR VON MARTENS, 1905

Corbicula elatior von Martens, 1905: 65, pl. 2, fig. 5 (Korea, Kyongsang-namdo and Kyonggi-do provinces)

= *Corbicula suiifuensis* Lindholm, 1925: 29 [Russia, Primorye Region, Suifun (nowadays Razdolnaya) River near Razdolnoye settlement]

= *Corbicula amurensis* Bogatov & Starobogatov, 1994: 149, fig. 1D–F (Russia, Khabarovsk Region, the Lower Amur river near Balbinskiy Cliff, 22 km upstream of Kalinovka settlement and 337 km from the mouth), **synon. nov.**

= *Corbicula nevelskoyi* Bogatov & Starobogatov, 1994: 148–149, fig. 1A–C (Russia, Khabarovsk Region,

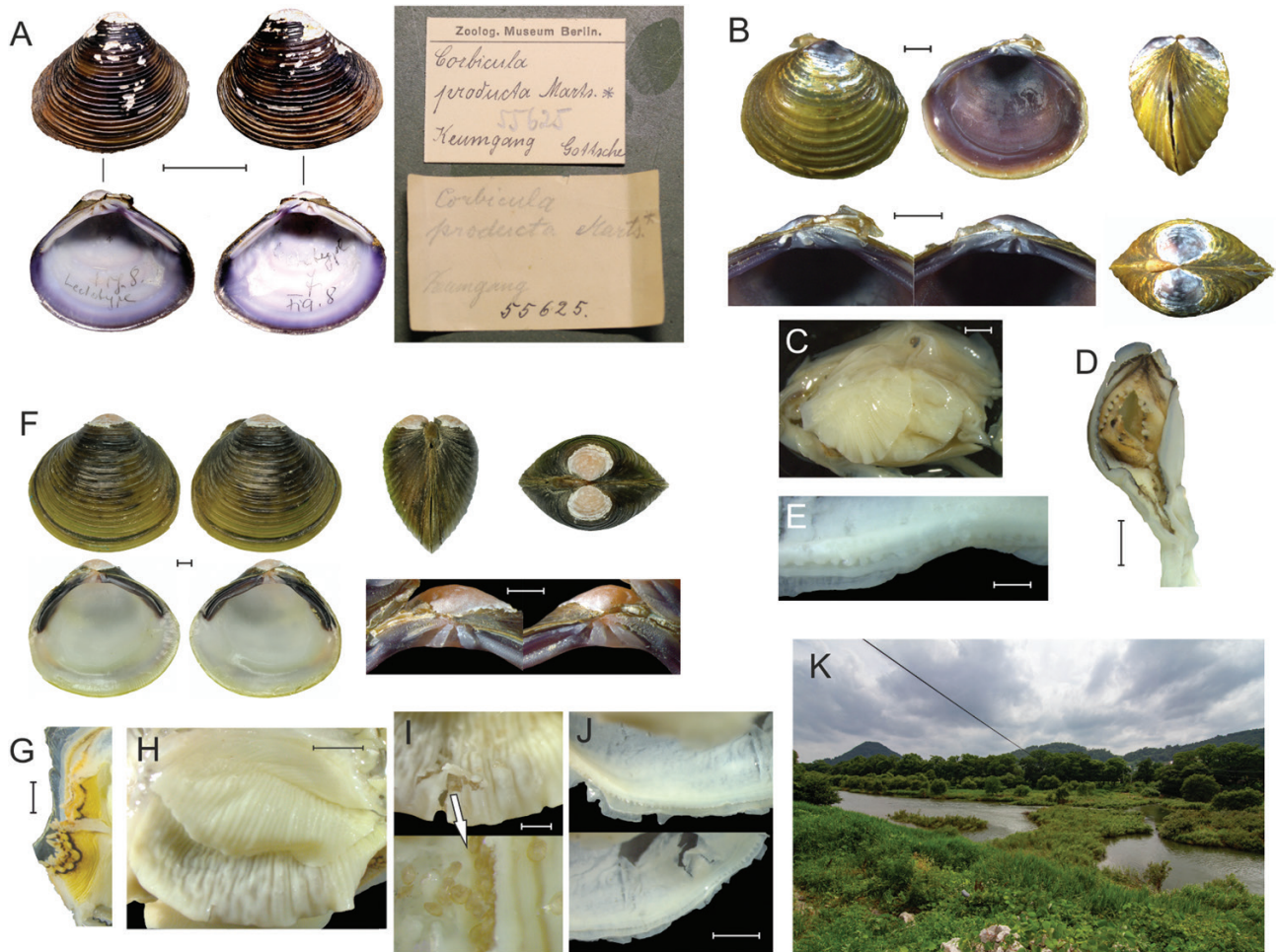


Figure 10. Morphology and anatomy of *Corbicula fluminea* from South Korea. A, lectotype of *Corbicula producta* Martens, 1905 with its labels: ZMB 55.625a; South Korea: Prov. Chungcheongnam, Geum River near Gongju. B, *C. fluminea* from Geum River (lot no. RMBH MCorb 0082.3). C, soft body and gills. D, general view of the siphon. E, outgrowths on the mantle edge. F, *C. fluminea* from Seomjin River (lot no. RMBH MCorb 0084.1). G, longitudinal section of the siphon and siphon papillae with a narrow dark stripe. H, gills. I, outgrowths on the mantle edge. J, larvae in the inner demibranch. K, habitat of *C. fluminea* in Seomjin River. Scale bars: 2 mm in A, B, F, H, J; 1 mm in C, D, G, I; 0.5 mm in E. Photographs: A, M. V. Vinarski; B–J, O. V. Aksenova; K, I. V. Vikhrev.

the Lower Amur River near Balbinskiy Cliff, 22 km upstream of Kalinovka settlement and 337 km from the mouth), **synon. nov.**

= *Corbicula sirotskii* Bogatov & Starobogatov, 1994: 149, fig. 1G–I (Russia, Khabarovsk Region, Lower Amur River, 7 km upstream of Maxim Gorky settlement and 397 km from the mouth), **synon. nov.**

Type material: The lectotype [a pair of valves; '*Corbicula elatior* Martens., Naktonggang'; designated by Glaubrecht *et al.*, 2007], ZMB 55.624; paralectotypes ZMB 38.439 (ten pairs of valves, one right valve; '*Corbicula elatior* jung, Naktonggang, mittl. Arm Korea, Gottsche'); paralectotypes ZMB 38.429 (six pairs of

valves, one right valve; '*Corbicula* No. 1, N'aktonggang, Gottsche'); paralectotypes ZMB 38.430b (three pairs of valves, one tiny right valve; '*Corbicula* no. 2, Imjingang bei Imjin 20/9 Gottsche'); paralectotype ZMB 55.626 (a pair of valves; specimen depicted in Fig. 6 as '*C. elatior*?') (Glaubrecht *et al.*, 2007).

Type locality: 'Mittlerer Arm des Naktonggang, Hauptfluss der Provinz Kyöngsangdo, zwischen Tongnai und Kimhai. Imjingang bei Imjin, Provinz Kyöngkwido, Korea'; South Korea: restricted to Naktong River near Kimhae, Kyongsang-namdo (Nakdong River near Gimhae, Gyeongsangnam Prov., 35°11'57"N, 128°54'00"E). Locality of paralectotypes: Prov. Kyonggi-do: Imjin River near Imjin (Glaubrecht *et al.*, 2007).

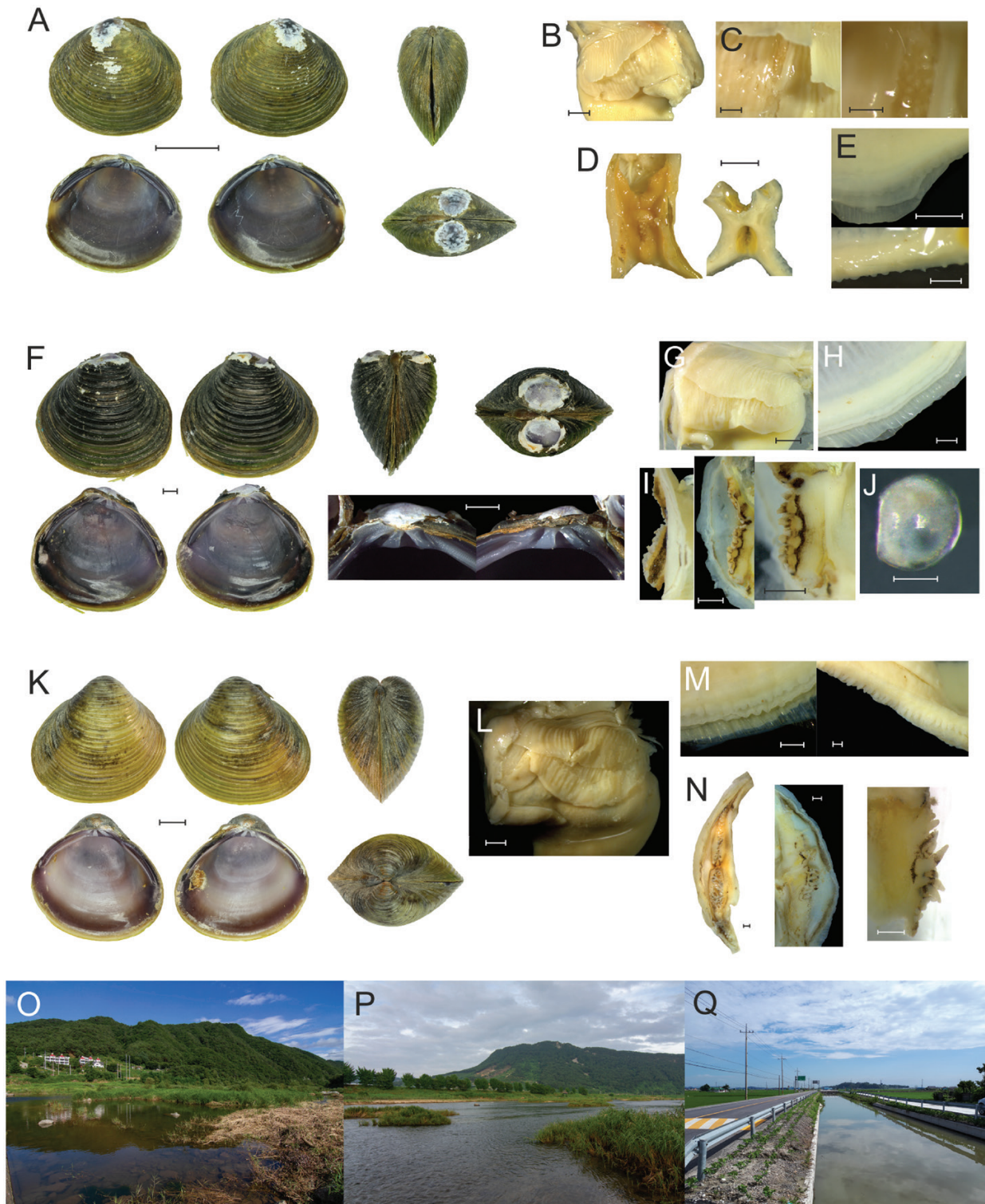


Figure 11. Morphology and anatomy of *Corbicula leana* from South Korea. A, *C. leana* from Bukhan River (lot no. RMBH MCorb 0085.4). B, gills. C, juvenile molluscs inside the gills. D, general view of the siphons from outer and inner sides. E, outgrowths on the mantle edge. F, *C. leana* from Seomjin River (lot no. RMBH MCorb 0084.2). G, gills. H, outgrowths on the mantle edge. I, longitudinal sections of the siphon and siphon papillae. J, larvae. K, *C. leana* from an irrigation channel near Mangyeong River (lot no. RMBH MCorb 120.2). L, gills. M, outgrowths on the mantle edge. N, general view of the siphon

Material examined: The type series. Our samples: Far East of Russia: lower reaches of the Lower Amur River near Nikolaevsk-on-Amur City, 53°7'12.948"N, 140°50'47.646"E, 17 July 2014, 28 specimens, Bolotov I.N. & Vikhrev I.V. leg. (lot nos RMBH Corb 15); Nizhnetambovskoe settlement, 16 September 2020, 50.952778N, 138.204444E, 89 specimens, Aksenova O.V., Kropotin A.V., Travina O.V. & Vinarski M.V. leg.; 61 specimens are stored in RMBH; 28 specimens from the same locality are kept in LMBI under accession number 21-044; Nizhnetambovskoe settlement, 7 July 2021, 50.921111N, 138.1775E, 23 specimens, Aksenova O.V., Kropotin A.V., Travina O.V. & Khrebtova I.S. leg.; one specimen from Razdolnaya River is kept in ZIN collection, accession number 3.

Description: The shell is large, triangular, and the ventral margin is rounded (Fig. 6). The umbo is insignificantly prominent and slightly offset. Sculpture is represented by well-marked deep concentric ridges; the width of the ribs and distance between them are variable in the same specimen. External shell coloration varies from dark brown, greenish brown to yellow–brown, sometimes with light or dark concentric bands. Internal shell coloration varies from matte white with pale violet marks to light purple. Hinge has a heterodont dentition type, with three cardinal teeth on each valve and two crenulated lateral teeth. Siphons conical, both narrow, with a row of short papillae. Black pigment is concentrated in rings internally at the base of both siphons and in the edge of the mantle forming the siphons. The outer surface of the siphons is white; on the inside, the siphons are bright orange. The papillae of both siphons are without dark rings. *Corbicula elatior* is dioecious.

Differential diagnosis: This species could be distinguished from the sympatric *Corbicula leana*, *C. fluminea* and *C. japonica* by the following combination of characters: larger size, significantly prominent umbo, well-marked deep concentric ridges, external shell with light or dark concentric bands, the siphons without dark pigmentation and with short papillae.

Distribution: East Asia: Amur River and the Korean Peninsula (Graf & Cummings, 2021). The records of this species in the South Primorye Region (Razdolnaya River) and China (Itunghe River) (Zatravkin & Bogatov, 1987) need to be checked.

Comments: Considering that the samples from the Lower Amur River are genetically identical to the samples from the Seomjin River (South Korea) collected by Park & Kim (2003), we also analysed the original descriptions of some nominal species described from South Korea: *C. producta*, *C. elatior*, *C. colorata* and *C. papyracea*. Presumably, *C. producta* is a junior synonym of *C. fluminea* (for details, see Discussion). According to their original descriptions (Heude, 1887; von Martens, 1905), *C. colorata* and *C. papyracea* are small clams with a flattened umbo. At the same time, the specimens of *Corbicula* from the Lower Amur River are distinguished by a relatively large shell and prominent umbo. We were unable to find any significant conchological differences between our samples of *Corbicula* from the Lower Amur and the type specimens of nominal species described by Bogatov & Starobogatov (1994) (Figs 6, 7). The original morphological description of *C. elatior* published by von Martens (1905) (Fig. 7E) corresponds well to the morphological features of our samples from the Lower Amur River. Hence, we assume that *C. elatior* represents a species endemic to the Far East of Russia and the Korean Peninsula. The nominal species *C. amurensis*, *C. nevelskoyi* and *C. sirotskii* are considered here junior synonyms of *C. elatior*.

DISCUSSION

PHYLOGEOGRAPHY OF THE NATIVE AND INVASIVE *CORBICULA* LINEAGES IN THE FAR EAST

In general, according to our molecular genetic, conchological and anatomical data, four *Corbicula* species were identified in the studied area. *Corbicula japonica* was found in the Primorye Region, *C. elatior* in the Khabarovsk Region, and *C. leana* and *C. fluminea* in South Korea.

The East Asian brackish water clam *C. japonica* is abundant in estuarine areas around the Japanese Archipelago, Sakhalin Island, southern Kurile Islands, Primorye and Khabarovsk regions, the Korean Peninsula and China (Komaru *et al.*, 2010; Yamada *et al.*, 2014; Vinarski & Kantor, 2016; M.V. Vinarski & I.N. Bolotov, pers. observ.).

The analysis of our data (Fig. 2) and literature data (Yamada *et al.*, 2014) indicates that the populations of *C. japonica* from South Korea and China represent a separate, mitochondrially isolated group, the taxonomic status of which is undetermined. These

and section of siphons, showing siphon papillae with a narrow dark stripe. O, habitat of *C. leana* in the Bukhan River. P, habitat of *C. leana* in Seomjin River. Q, habitat *C. leana* in irrigation channel near Mangyeong River. Scale bars: 1 cm in A; 2 mm in B, D, F, G, L; 1 mm in C, E, I; 0.5 mm in H, M, N; 0.1 mm in J; 5 mm in K. Photographs: A–N, O. V. Aksenova; O, P, I. V. Vikhrev; Q, A. V. Kondakov.

populations might merit classification as a subspecies of *C. japonica* or even as a separate species, but this issue requires additional research. We have no *C. japonica* from China at our disposal to solve this question here. Perhaps, this relatively large *COI* haplotype distance, with six or seven mitochondrial substitutions, can be explained by the population differentiation (restricted gene flow) by the repeated glacial and interglacial periods during the Pleistocene (Watanabe *et al.*, 2006; Motokawa, 2017). For instance, Yamada *et al.* (2014) invoked the formation of a land bridge near the southern coast of the Korean Peninsula at the Tsushima Strait during the Middle Pleistocene as an external factor that caused isolation of the ancestral populations. The dispersal of *C. japonica* within the Japanese Archipelago probably occurred from south-west to north-east and has been influenced by major oceanic currents around the archipelago (Yamada *et al.*, 2014). Recent molecular genetic data indicate that *C. japonica* dispersed from the Japanese Archipelago to nearby insular territories and the Asian mainland. The high genetic diversity of the Japanese populations compared with those from Sakhalin Island, South Korea and China (Park & Chung, 2003; Mito *et al.*, 2014; Yamada *et al.*, 2014) supports this hypothesis.

The current molecular data locate the geographical origin of the invasive lineages of *C. fluminea* [= FW5 (A/R form)] in Japan (Vastrade *et al.*, 2022). According to Pigneur *et al.* (2014), the invasive lineage FW5 is close to the Japanese sexual lineage of *C. japonica* based on the microsatellites. At the same time, recent studies have shown that the invasive clonal lineages originated from an ancestor shared with *Corbicula sandai* Reinhardt, 1878 (the sexual lineage from Lake Biwa, Japan; Haponski & Ó Foighil, 2019; Vastrade *et al.*, 2022). Presumably, the androgenetic lineages of *Corbicula* originated from a sexually reproducing ancestor, which was followed by independent nuclear capture events between sympatric lineages. Indeed, the androgenetic *Corbicula* clams are found in sympatry with sexually reproducing clams in several locations in Japan (Pigneur *et al.*, 2014; Benson & Williams, 2021; Vastrade *et al.*, 2022).

The samples collected from the Seomjin and Geum rivers (the latter is the type locality of *C. producta*) in South Korea (Fig. 10A) correspond to *C. fluminea*. Thus, *C. producta*, an endemic to the Primorye Region of Russia and the Korean Peninsula (Zatravkin & Bogatov, 1987; Glaubrecht *et al.*, 2007; Vinarski & Kantor, 2016; Graf & Cummings, 2021), is probably a junior synonym of *C. fluminea*. However, the limited number of individuals of *Corbicula* from Geum River does not allow such a conclusion to be drawn, and the status of this nominal species requires further research.

According to our results, *C. elatior* appears to be a species rather distant from other taxa within the genus, both morphologically and genetically. Given that the body of available literature is extremely scarce, it is difficult to hypothesize on the dispersal vectors of *C. elatior*. Probably, the spread of *C. elatior* occurred from the Korean Peninsula to the Far East of Russia (Primorye and Khabarovsk regions) and, perhaps, to China. Thus, Bolotov *et al.* (2020) and Lopes-Lima *et al.* (2020), who analysed the Far East fauna of freshwater mussels (family Unionidae), considered this region as a contact zone for several distinct faunas, including that of Asiatic Russia in the north, the Yellow River basin in China in the west and Japan in the south. However, the biogeographical connections between the Korean Peninsula and the Amur basin and Primorye in Russia, and the Yellow River basin in China, are unclear owing to the lack of data on the unionid mussels of North Korea (Bolotov *et al.*, 2020; Lopes-Lima *et al.*, 2020). According to Zatravkin & Bogatov (1987), *C. elatior* inhabits the Razdolnaya River in the Primorye Region of Russia. Examination of the shell morphology of the samples of *C. elatior* from the ZIN collection has revealed that their features correspond to the original description of *C. elatior* made by von Martens (1905) (Fig. 7D).

The third lineage belongs to the Far Eastern clade, *C. leana* (= *Corbicula* clade FW1 + FW4; = *Corbicula* New World form B), which has recently been recorded as invasive in other regions of the world, including Indonesia, the Philippines, China, Japan, Europe, North America, South America and South Korea (Bespalya *et al.*, 2021a; Fig. 3). According to the latest molecular data, the lineages FW1 and FW4 originated in the Asian mainland (China, Korea and Vietnam; Pigneur *et al.*, 2014; Vastrade *et al.*, 2022).

REPRODUCTIVE MODES OF *CORBICULA*

It was established that *Corbicula* is able to reproduce sexually with both sexes or through androgenesis, 'all-male asexuality' (Glaubrecht *et al.*, 2003; Hedtke *et al.*, 2008). Androgenetic *Corbicula* clams are hermaphroditic and produce biflagellate unreduced sperm, whereas sexual clams have reduced monoflagellate sperm (Lee *et al.*, 2005; Mackie, 2007; Pigneur *et al.*, 2012). Through androgenesis, all the maternal chromosomes of eggs are extruded as two polar bodies at the first meiosis (Ishibashi *et al.*, 2003). Hermaphroditic lineages of *Corbicula* have a worldwide distribution, whereas their sexual relatives have restricted ranges (Pigneur *et al.*, 2012). Currently, only a few *Corbicula* species reproducing sexually are known in the genus *Corbicula*: *Corbicula sandai* is endemic to Lake Biwa in Japan; *C. japonica* is restricted to brackish water of East Asia; and a few freshwater

sexual *Corbicula* lineages are known from Indonesia (Glaubrecht *et al.*, 2003, 2006; Yamada *et al.*, 2014).

Both *C. sandai* and *C. japonica* are dioecious. *Corbicula japonica* is characterized by the development of free-swimming veligers (Kimura *et al.*, 2004; Nanbu *et al.*, 2008). In contrast, *C. sandai* lacks planktonic larvae; this species sheds eggs and sperm in the water, and the fertilized eggs sink onto the bottom substrate (Hurukawa & Mizumoto, 1953). Indonesian *Corbicula* are dioecious, ovoviviparous, with incubation of larvae in the maternal gill (Korniushin & Glaubrecht, 2003; Glaubrecht *et al.*, 2003, 2006).

In the present study, we found one more sexual, dioecious *Corbicula* species from the lower Amur, *C. elatior*. We were not able to find any larvae in the gills of individuals of this species. Young individuals were attached to a rocky substrate by a byssus (Fig. 6B).

Given that a free-swimming larva was found only in the brackish water clam *C. japonica* (Kimura *et al.*, 2004; Nanbu *et al.*, 2008; Mito *et al.*, 2014), we assume that *C. elatior* has a benthic larva, which is characteristic of all freshwater *Corbicula* lineages studied to date (Glaubrecht *et al.*, 2003, 2006; Kimura *et al.*, 2004). However, this issue requires additional research.

THE INTRAGENOMIC VARIABILITY OF THE 28S GENE OF INVASIVE *CORBICULA* FROM THE FAR EAST

The intragenomic 28S rDNA gene variability in Korean *C. fluminea* and *C. leana* is probably attributable to a hybridization event between forms A/R, C/S and Rlc in *C. fluminea* and between forms A/R and C/S in *C. leana*. This phenomenon was described in detail in previous works (Hedtke *et al.*, 2011; Pigneur *et al.*, 2012; Bepalaya *et al.*, 2018, 2021a; Vastrade *et al.*, 2022).

The hybrid genotypes of the Korean *C. fluminea* and *C. leana* identified by us perhaps have a common origin. They probably belonged to the same ancestral species (lineages) but occurred as a result of different directions of the mitochondrial genome capture.

It was established that egg parasitism in a distinct androgenetic lineage could be accompanied by mixing of different nuclear genomes, which can occur when the maternal nuclear genome is incompletely extruded, increasing the ploidy and the diversity of hybrids (Hedtke *et al.*, 2008, 2011; Bepalaya *et al.*, 2018, 2021a; Vastrade *et al.*, 2022). It has been demonstrated that the forms A/R and C/S have a common allele 28S (Pigneur *et al.*, 2012; Vastrade *et al.*, 2022). Remarkably, despite their different biogeographical origins, both lines are found in sympatry throughout their invasive range (Bepalaya *et al.*, 2018; Vastrade *et al.*, 2022). Individuals of invasive forms B and Rlc share alleles with form A/R (Penárrubia *et al.*, 2017; Bepalaya *et al.*, 2018; Vastrade *et al.*, 2022). It is likely

that many of the androgenic lines *Corbicula* originated as a result of hybridization (Vastrade *et al.*, 2022).

THE DIVERSITY OF THE SHELL COLOUR MORPHS OF *CORBICULA*

Currently, different intraspecific colour morphs of *Corbicula* have been recorded all over the world (Hillis & Patton, 1982; Tsoi *et al.*, 1991; Park *et al.*, 2002; Houki *et al.*, 2011; Wang *et al.*, 2014; Tiemann, 2017). Individuals of *C. leana* from the South Korean populations investigated by us demonstrated purple inner shell coloration (Fig. 11). Within the Korean *C. fluminea*, we recognized purple and white morphs (Fig. 10). Besides that, we detected that the shell colour of *C. japonica* is also polymorphic. Following earlier studies, the two freshwater morphotypes of *Corbicula* were designated as *C. fluminea* (white morph) and *C. leana* (purple morph) in Korea (Lee & Kim, 1997; Park *et al.*, 2002; Houki *et al.*, 2011). At the same time, several colour morphs within *C. fluminea* were discovered (Tsoi *et al.*, 1991; Ishibashi *et al.*, 2003; Houki *et al.*, 2011). According to Wang *et al.* (2014), both *C. leana* and *C. fluminea* sympatric in Lake Datong were represented by two colour morphs: white and purple. Three coexisting shell colour types were detected in samples of *C. fluminea* collected in the Keelung River (Taiwan) (Komaru & Konishi, 1999).

An analysis of the literature data shows that both heritable and environmental factors can control variation in the shell colour of molluscs (Morton, 1987; Williams, 2017; Hsu *et al.*, 2020). The effect of environmental factors on shell coloration has been discussed in a number of papers (Morton, 1987; Tsoi *et al.*, 1991; Williams, 2017). In addition, as previous studies have suggested, the differences between *Corbicula* shell colour morphs are related to their different genetic structure, not only environmental conditions (Komaru & Konishi, 1999; Qiu *et al.*, 2001; Wang *et al.*, 2014; Hsu *et al.*, 2020). However, the molecular processes involved in the synthesis of shell colour have not yet been studied sufficiently (Williams, 2017). Wang *et al.* (2014) demonstrated an absence of distinct differences in the morphological features and the mitochondrial *COI* haplotypes between two colour morphs of each species from Lake Datong. A study of the enzyme polymorphism in *C. fluminea* demonstrated that there is no genetic differentiation between the white and purple colour morphs of *C. fluminea* from Hong Kong (Tsoi *et al.*, 1991).

We also have not observed differences in the *COI* haplotypes between the colour morphs of *C. fluminea* from South Korea and *C. japonica* from the Primorye Region. In addition, it is established that, among molluscs with unusual features of reproduction, the mechanisms underlying the heredity of traits are

quite complex (Tsoi *et al.*, 1991; Williams, 2017). That has probably led to problems in identification of potential genes involved in the production of shell colour (Williams, 2017). Therefore, this phenomenon in relationship to *C. leana* and *C. fluminea* from South Korea might also be explained by egg parasitism with nuclear genome capture (Hedtke *et al.*, 2011; Pigneur *et al.*, 2012; Bepalaya *et al.*, 2018, 2021a). Nuclear capture events might generate nuclear diversity in otherwise asexually reproducing lineages of *Corbicula* (Hedtke *et al.*, 2011). Besides that, nuclear genome capture might have contributed to polyploidy and genetic divergence among androgenetic *Corbicula* lineages (Penãrrubia *et al.*, 2017). However, this issue requires additional research.

To conclude, the results of the present study provide new and important insight into the phylogeny, taxonomy, life history, anatomical characters and biogeography of endemic *Corbicula* species from the Russian Far East and South Korea. Future studies should focus on phylogeny, biogeography and a taxonomic revision of the *Corbicula* clams throughout East and Southeast Asia, including eastern China, Japan, Taiwan, North Korea, the Indochinese and Malay peninsulas and the Indonesian Archipelago.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Table S1. Samples of *Corbicula* spp. from the Russian Far East and South Korea.

Table S2. Information on newly sequenced specimens of *Corbicula* spp. from the Russian Far East and South Korea. Materials are from the collection of the Russian Museum of Biodiversity Hotspots (RMBH), N. Laverov Federal Center for Integrated Arctic Research of the Ural Branch of the Russian Academy of Sciences (Arkhangelsk, Russia).

Table S3. Information on additional *COI* sequences of *Corbicula* clams obtained from GenBank, including taxon, accession number, region and data source.

Table S4. 28S ribosomal DNA polymorphism in selected *Corbicula* species.

Alignment S1. Set of the *COI* nucleotide sequences for median-joining network of *Corbicula japonica*.

Alignments S2. Set of the *COI* nucleotide sequences for median-joining network of *Corbicula fluminea*, *C. elatior* and *C. leana*.