Freshwater mussels (Bivalvia: Unionidae) from the Rising Sun (Far East Asia): Phylogeny, systematics, and distribution

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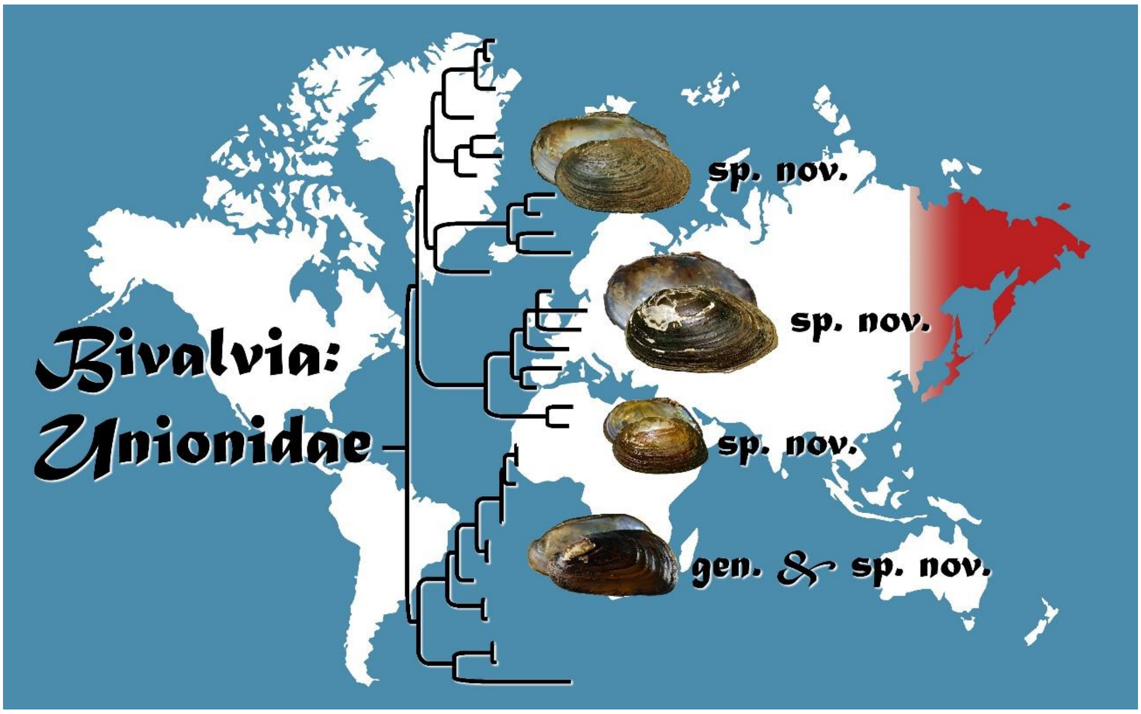
Graphical abstract



Abstract

Freshwater mussels (Bivalvia: Unionidae) is a diverse family with around 700 species being widespread in the Northern Hemisphere and Africa. These animals fulfill key ecological functions and provide important services to humans. Unfortunately, populations have declined dramatically over the last century, rendering Unionidae one of the world’s most imperiled taxonomic groups. In Far East Asia (comprising Japan, Korea, and Eastern Russia), conservation actions have been hindered by a lack of basic information on the number, identity, distribution and phylogenetic relationships of species. Available knowledge is restricted to studies on national and sub-national levels. The present study aims to resolve the diversity, biogeography and evolutionary relationships of the Far East Asian Unionidae in a globally comprehensive phylogenetic and systematic context.

We reassessed the systematics of all Unionidae species in the region, including newly collected specimens from across Japan, South Korea, and Russia, based on molecular (including molecular species delineation and a COI + 28S phylogeny) and comparative morphological analyses. Biogeographical patterns were then assessed based on available species distribution data from the authors and previous reference works.

We revealed that Unionidae species richness in Far East Asia is 30% higher than previously assumed, counting 43 species (41 native + 2 alien) within two Unionidae subfamilies, the Unioninae (32 + 1) and Gonideinae (9 + 1). Four of these species are new to science, i.e. *Beringiana gosannensis* **sp. nov.**, *Beringiana fukuharai* **sp. nov.**, *Buldowskia kamiyai* **sp. nov.**, and *Koreosolenaia sitgyensis* **gen. & sp. nov.** We also propose a replacement name for *Nodularia sinulata*, i.e. *Nodularia breviconcha* **nom. nov.** and describe a new tribe (Middendorffinaiini **tribe nov.**) within the Unioninae subfamily. Biogeographical patterns indicate that this fauna is related to that from China south to Vietnam until the Mekong River basin. The Japanese islands of Honshu, Shikoku, Kyushu, Hokkaido, and the Korean Peninsula were identified as areas of particularly high conservation value, owing to high rates of endemism, diversity and habitat loss. The genetically unique species within the genera *Amuranodonta*, *Obovalis*, *Koreosolenaia* **gen. nov.**, and *Middendorffinaia* are of high conservation concern.

Keywords: Japan; Korea; Russia; Mollusca; systematics; taxonomy; Molecular Operational Taxonomic Unit (MOTU); phylogeography.

1. Introduction

Freshwater mussels of the Unionidae family occur in freshwater habitats worldwide (Lopes-Lima et al., 2014). These bivalves are key members of aquatic ecosystems, playing important ecological roles such as nutrient cycling, increasing water purification, bioturbation and habitat provisioning (Vaughn, 2018). Unfortunately, and like many other freshwater taxa, these organisms have suffered dramatic losses both in the number of populations and individuals, with many species being on the brink of extinction (Lopes-Lima et al., 2018). In many countries, especially in North America and Europe, the number of conservation actions for these mussels have increased substantially over the latest years (Lopes-Lima et al., 2014, 2017a). However, conservation actions have been hindered by poor knowledge about their biology and a lack of accurately identified conservation units (Ferreira-Rodríguez et al., 2019; Greene, 1994). Since most current conservation programs and policies are based on species as conservation units, accurate definition of species boundaries is of extreme importance. Additionally, conservation strategies should consider the phylogenetic relationships of extant species to maximize future levels of biodiversity (Faith, 1992, Winter et al., 2013). Until the advent of molecular tools, species identification of unionid mussels used to be essentially based on shell characteristics (Lopes-Lima et al., 2017b). However, accurate identification of Unionidae species based on shell morphology alone is often difficult, due to the high phenotypic plasticity within species and morphological convergences between species (Klishko et al., 2017).

To date, the freshwater mussel diversity of Far East Asia (here restricted to Japan, Korea, and Russia east of the Transbaikalia and Lena River basin) has been described mainly at national and regional levels (e.g. Kondo, 2008; Lee et al., 2017; Vinarski and Kantor, 2016). In total, around 30 species in 14 genera and two Unionidae subfamilies (Unioninae and Gonideinae) have been recognized from Far East Asia (see Bolotov et al., Submitted; Graf and Cummings, 2019; Kondo, 2008; Lee, 2017; MolluscaBase, 2019; Sano et al., 2017). Over the last decades, important works have been dedicated to the systematics of unionid mussels in this region (e.g. Kondo, 1982, 2008; Starobogatov et al., 2004). Some of these used only morphological and/or biogeographic arguments, which have frequently shown to fail to delineate taxonomic units or species (e.g. Graf, 2007; Klishko et al., 2014, 2017). Other studies used molecular tools that have proven to be crucial in revealing evolutionary relationships and delineating species (e.g. Bolotov et al., Submitted; Klishko et al., 2014, 2017, 2018; Lee, 2017; Sano et al., 2017; Sayenko et al., 2017). However, as all of these studies are based on datasets restricted to taxa from a single region or country within Far East Asia and a very small number of taxa outside the study area, the diversity, biogeography and phylogenetic relationships of the Far East Asian Unionidae remain to be resolved in a globally comprehensive phylogenetic and systematic context. A sound, global taxonomy of these taxa will also allow for global assessments of their conservation status, which are currently restricted to national, e.g. the Japan Red Data Book (Government of Japan, Ministry of Environment, 2014) and the Korean Red List of Threatened Species (Kim et al., 2014) or regional schemes, e.g. the Red Books of the Primorye (Kostenko, 2005) and Khabarovsky Krai (Voronov, 2008) in Russia. Considering that several recently published studies profoundly changed our understanding of diversity patterns, phylogeny and biogeography of freshwater mussels in other Asian regions (e.g. Bolotov et al., 2017a, 2017b, 2018; Huang et al., 2019; Pfeiffer et al., 2018; Wu et al., 2018; Zieritz et al., 2016), similar revelations may be expected concerning the Far East Asian Unionidae.

The aims of the current study are to: i) estimate a phylogeny of the freshwater mussels from Far East Asia, including newly collected specimens from Japan, South Korea, and Eastern Russia; ii) identify species boundaries, and revise their taxonomy and systematics; iii) describe the distribution of each taxonomic unit; and iv) discuss the conservation implications of our results.

2. Materials and methods

2.1. Taxon sampling

A total of 379 Unionida specimens were collected from 186 sites across Japan, South Korea, and Russia east of Baikal Lake and Transbaikalia, and from additional locations in Asia and North America for phylogenetic comparisons (Fig. 1; Sup. Tables 1-13).

2.2. DNA extraction, amplification, and sequencing

A small foot tissue sample was collected (following Naimo et al., 1998) and placed in 99% ethanol. Whole specimens for each putative species were collected as vouchers (Sup. Tables 1-13). Genomic DNA was extracted from the tissue samples, using a standard high-salt protocol (Sambrook et al., 1989) or the Jetquick tissue DNA Spin Kit (Genomed) following the manufacturer's protocol. PCR conditions for both markers, the female lineages of mitochondrial cytochrome c oxidase subunit 1, COI (LCO22me2 + HCO700dy2; Walker et al., 2007; and LCO1490 + HCO2198; Folmer et al., 1994) and 28S ribosomal RNA (28S-RD1.3f and 28S-rD4b; Whiting, 2002) were described in Froufe et al. (2016). Annealing temperatures of 48 ºC were used for COI (LCO1490 + HCO2198) and 28S; and 50 ºC for COI (LCO22me2 + HCO700dy2). Amplified DNA templates were purified and sequenced using the same primers.

2.3. Phylogenetic analyses and species delineation

To identify the generic position of each sequenced individual, a preliminary COI alignment with all newly sequenced individuals and representatives from most previously available unionid genera was produced and analyzed with a Bayesian Inference phylogenetic approach, using MrBayes 3.2.7a (Ronquist et al., 2012) with 20×10^6 generations sampled at intervals of 1,000 generations on a single partition with model GTR + I + G. Based on this analysis, twelve COI alignments were then constructed (Sup. Tables 1-13). Nine of these alignments were composed of species for each of the following Far Eastern Asian genera, *Aculamprotula*, *Anemina*, *Beringiana*, *Cristaria*, *Inversiunio*, *Lanceolaria*, *Pletholophus*, *Sinanodonta*, and *Sinohyriopsis*. The remaining three alignments included species within each of the following genus pairs, *Lamprotula* + *Pronodularia*, *Nodularia* + *Middendorffinaia*, and *Koreosolenaia* **gen. nov.** + *Parvasolenaia*, due to uncertainties regarding the previous generic assignment of these species. No COI analyses were produced for the genera *Inversidens* and *Obovalis* due to the low number of available sequences. For each of these alignments, the ingroup included all previously published sequences of congeneric taxa; the outgroup included sequences from closely related genera and the family Margaritiferidae. All alignments were constructed with GUIDANCE2 (Sela et al., 2015), following Fonseca et al. (2017) and analyzed using Maximum Likelihood (ML) and Bayesian Inference (BI) methods, in IQ-TREE v 1.6.10 (Nguyen et al., 2014) and

MrBayes 3.2.7a (Ronquist et al., 2012), respectively. For the BI analyses, the best-fit models of nucleotide substitution and partition schemes were selected using PartitionFinder 2 (Lanfear et al., 2016) under the Bayesian Information Criterion. BI analyses were initiated with program-generated trees and four Markov chains with default incremental heating. Two independent runs of 20×10^6 generations were sampled at intervals of 1,000 generations, producing a total of 20,000 trees. Burn-in was determined upon the convergence of log-likelihood and parameter values using Tracer 1.7.1 (Rambaut et al., 2018). For the ML phylogenetic analyses, the best-fit models of nucleotide substitution and partition schemes were selected using ModelFinder (Kalyaanamoorthy et al., 2017). Maximum-Likelihood analyses were then conducted with initial tree searches, followed by 10 independent runs and 10,000 ultrafast bootstrap replicates. Three distinct methods were applied to each COI dataset, to determine the number of Molecular Operational Taxonomic Units (MOTUs). The first two are distance-based: the BIN system implemented in BOLD (Ratnasingham and Hebert, 2013) and the Automatic Barcode Gap Discovery (ABGD) (Puillandre et al., 2012). For the BINs system, the COI dataset without the outgroup was analyzed with the Cluster Sequences tool implemented in BOLD 4 (http://v4.boldsystems.org) (Ratnasingham and Hebert, 2013). The ABGD was applied to each dataset without outgroup using its online version (http://wwwabi.snv.jussieu.fr/public/abgd/abgdweb.html) with the default settings and the Kimura-2-parameter (K2P) distance matrix (Puillandre et al., 2012). The third method used haplotype network reconstructions in TCS 1.21 (Clement et al., 2000), with a 95% statistical parsimony connection limit. Sequence divergences (uncorrected *p*-distance) were estimated using MEGA X (Kumar et al., 2018).

A concatenated COI + 28S dataset was then assembled with representatives from most previously available Unionidae genera and from each of the East Asian species/MOTUs found in the COI datasets (Table 1). Sequences from species belonging to other Unionida families and *Neotrigonia* were also included as the outgroup (Table 1). This Unionida dataset was aligned with GUIDANCE2 and analyzed using ML and BI methods, following the same steps applied to individual COI datasets.

2.4. Distribution

The distribution of each species in the study area was assessed using personal data from the authors and previous reference works (Bolotov et al., Submitted; Kim et al., 2014; Kil et al., 1976; Kondo, 2008; Lee, 2017; NIBR, 2012; Seo, 2019; Vinarski and Kantor, 2016; and the NatureServe <http://www.natureserve.org> and IUCN <http://www.iucnredlist.org> databases). Distribution data were then integrated and represented as colored potential distribution maps using level 8 HydroBASINS (Lehner et al., 2013) shapefile, where very small sub-basins were grouped with their main drainage or with other small drainages (especially along the coast). Vector and raster map data from Earth topography layers made by Natural Earth <http://naturalearthdata.com> were also included for pictorial reasons.

3. Results & Discussion

3.1. Phylogenies, species delineation, and distributions

The preliminary Bayesian Inference phylogeny (data not shown) retrieved 12 clades that included Far-East Asian Unionidae taxa, which were considered for further phylogenetic and species delineation analyses.

Composition, size, and parameters of all 13 datasets (12 COI and 1 COI + 28S) together with the partition schemes and nucleotide substitution models for all analyses are presented in Table 2. No indels or stop codons were found in any of the COI datasets.

Molecular species delineation for the COI individual datasets revealed the existence of 43 (41 native + 2 alien) MOTUs that are here recognized as species, thus exceeding previous estimations of Unionidae species diversity in the region (Table 3). Four of these MOTUs require a more detailed investigation to clarify their taxonomic status: one within the genus *Nodularia* (here named *Nodularia* sp. 1) and three within *Pronodularia japanensis* (Lea, 1859) (see *Nodularia* and *Lamprotula* + *Pronodularia* sections below).

In the following, we present and discuss the revised systematics of the Far East Asian Unionidae, based on the first robust comprehensive phylogeny of this fauna (Figs. 2-4) and comparative morphological analyses. This includes the description of four new species and a new replacement species name, one genus and one tribe, and the generic reassignment of three other species (Table 3). The taxonomy of the newly described taxa is presented below in section 4. Taxonomic account and a full taxonomic revision of all the Unionidae species from Far East Asia is presented in Sup. Appendix I. Biogeographical patterns indicate that the Unionidae fauna of Far East Asia is related to that from China south to Vietnam until the Mekong River basin, which does not seem to contain any of the Far-East Asian genera (but see *Cristaria* section below).

Unionida Gray, 1854 (combined (COI + 28S) dataset)

Both ML and BI Unionida phylogenies on the combined dataset (COI + 28S) show well-supported clades for all the Unionida families (Fig. 2). All 43 Unionidae species here recognized from the study area (Table 3) are restricted to the subfamilies Unioninae Rafinesque, 1820 (33 spp.) and Gonideinae (10 spp.) (Figs. 3 and 4; Table 3). The higher-level relationships between the families here retrieved should be evaluated with caution, given that within the Unionida tree these associations have not been consistently retrieved and many contradictory hypotheses have been generated using the conventional two- or three-locus reconstructions (Pfeiffer et al., 2019), such as those in the present study. This should be attributed to the inadequacy of these molecular markers in describing the true suprafamilial phylogeny of freshwater mussels, with a recent multi-locus phylogeny producing a different topology more consistent with some of the evolutionary traits of the Unionida, e.g. clustering into distinct clades the families bearing glochidium from those with lasidium larvae (Pfeiffer et al., 2019).

Unioninae Rafinesque, 1820

The Unioninae is divided into 9 clades corresponding to 8 previously described tribes and a new tribe described here for the first time, the Middendorffinaiini **tribe nov.** (Fig. 3 and Section 4. Taxonomic account). The Unioninae is represented by five tribes in the Asian Far East (Fig. 3). Four of these tribes, Aculamprotulini, Cristariini, Lanceolariini, and Nodulariini, include species from Far East Asia and others from mainland China and Vietnam east of the Mekong River basin. The Middendorffinaiini **tribe nov.** contains a single species *Middendorffinaia mongolica* (Middendorff, 1851), which is endemic to the study region.

Aculamprotulini Huang & Wu, 2019

The combined COI + 28S phylogenies support the recently described tribe Aculamprotulini with a single genus, i.e. *Aculamprotula* (Fig. 3).

Aculamprotula Wu et al., 1999

The two (ML and BI) COI phylogenies for the *Aculamprotula* genus exhibited similar topologies, retrieving six clades, defined as MOTUs by all species delineation methods (Fig. 5). Uncorrected *p*-distances among the delineated MOTUs ranged from 3.7% (between *Aculamprotula* cf. *fibrosa* 1 and *A.* cf. *fibrosa* 2) to 11.8% (between *A. tortuosa* (Lea, 1865) and *A. scripta* (Heude, 1875)) (Sup. Table 1). The only species in this genus from the study area, *Aculamprotula coreana* (Martens, 1886), clusters within the genus clade (Figs. 3 and 5). This species was originally distributed in Daedonggang River basin in North Korea and Hangang, Geumgang, and Seomjingang River basins in South Korea (Fig. 5; Sup. Table 2). However, it has suffered a strong decline being extirpated from the Hangang River basin (Kim et al., 2014; NIBR, 2012) (Fig. 5). Sequences from GenBank submitted by various authors as *Aculamprotula fibrosa* (Heude, 1877) from China, and here labelled as *A.* cf. *fibrosa* sp. 1 and. *A.* cf. *fibrosa* sp. 2, respectively, require a more thorough study to clarify their taxonomic status.

Cristariini Lopes-Lima, Bogan and Froufe, 2017

Within Cristariini, all newly sequenced individuals from the genera *Amuranodonta*, *Anemina*, *Beringiana*, *Buldowskia*, *Cristaria*, and *Sinanodonta* cluster within the respective genera represented by well-supported clades (Fig. 3). The Cristariini is the most speciose tribe in the Asian Far East with 19 (18 native, plus one alien) valid species (Table 3).

Anemina Haas, 1969

Previous studies reported that in the study region, the species *Anemina arcaeformis* is distributed throughout East Russia, South Korea, and Japan (e.g. Graf and Cummings, 2019; Kondo, 2008; Starobogatov et al., 2004), but our results indicate that this species is restricted to Eastern South Korea and Kyushu Island in Japan (Fig. 6). Additionally, our genetic data support the existence of six further species that fall into three highly divergent clades in all phylogenies (Figs. 3 and 6; Table 3; and Sup. Table 3). The existence of these three clades within *Anemina* sensu lato, here recognized as the three valid genera *Anemina*, *Amuranodonta,* and *Buldowskia*, follows recent results from Russia (Bolotov et al., Submitted).

The *Anemina* sensu stricto clade only includes *A. arcaeformis* and *A. euscaphys* with a low divergence level (3.2% unc. *p*-distance) (Fig. 6; Sup. Table 1). The question of whether these two taxa are separate species requires further investigation when considering their low genetic divergence and the fact that ABGD did not recover them as separate MOTUs (Fig. 6).

Anemina arcaeformis is mainly distributed in China but has restricted distributions in the Ungcheoncheon Drainage in South Korea and northern Kyushu Island in Japan (Fig. 6; Sup. Table 3).

Amuranodonta Moskvicheva, 1973

The *Amuranodonta* clade is here consensually retrieved as a single MOTU (Fig. 6). This genus includes only one species, i.e. *Amuranodonta kijaensis* Moskvicheva, 1973, endemic to the Amur basin in Russia and China (Fig. 6; Sup. Table 3).

Buldowskia Moskvicheva, 1973

Buldowskia is the most speciose genus within *Anemina* sensu lato, with five species being supported based on the high divergence of COI and molecular species delineation methods (Fig. 6; Sup Table 14). The *Buldowskia* clade is further divided into five clades, consensually defined as MOTUs by all species delineation methods (Fig. 6). Uncorrected *p*-distances among the delineated MOTUs (here recognized as species) ranged from 4.7% (between *Buldowskia iwakawai* **comb. nov.** and *Buldowskia kamiyai* **sp. nov.**) to 13.7% (between *B. shadini* (Moskvicheva, 1973) and *B. suifunica* (Lindholm, 1925)) (Sup. Table 1). The phylogenetic relationships among all species are still not well resolved, but two well-supported clades were retrieved: one between *B. iwakawai* **comb. nov.** and *B. kamiyai* **sp. nov.** both native to Japan; and the other with *B. flavotincta* (Martens, 1905) and *B. suifunica* occurring in Korea and Russia, respectively (Fig. 6; Sup. Table 3).

Buldowskia iwakawai **comb. nov.** and *B. kamiyai* **sp. nov.** present a disjunct distribution, with *B. iwakawai* **comb. nov.** occurring in a single South Korean basin, several Japanese basins in western Honshu and Hokkaido Islands, and extending to southern Sakhalin in Russia. The newly described *B. kamiyai* **sp. nov.** is endemic to river basins in northeast Honshu, Japan (Fig. 6). The other well-supported clade clusters *Buldowskia flavotincta* and *Buldowskia suifunica*, which exhibit allopatric distributions in mainland East Asia (Figs. 3 and 6; Table 3; Sup. Table 3). While *Buldowskia flavotincta* is endemic to three major river basins (Hangang, Geumgang, and Nakdonggang) in South Korea (Fig. 6; Sup. Table 3), *B. suifunica* inhabits the Suifun/Razdolnaya River basin and other coastal basins between North Korea and Russia (Fig. 6; Sup. Table 3). Finally, *Buldowskia shadini* has a wider disjunct distribution throughout the Amur River basin and in the major river basins of South Korea (Fig. 6; Sup. Table 3), although data from North Korea is lacking.

Beringiana Starobogatov, 1983

Within Cristariini, the COI + 28S phylogenies retrieved *Beringiana* in a divergent well-supported clade, therefore reinforcing its separation from *Sinanodonta* (Fig. 3) following Bolotov et al. (Submitted).

Both COI ML and BI phylogenies for the *Beringiana* genus exhibit similar topologies, retrieving four clades recovered as separate MOTUs by all species delineation methods (Fig. 7). Uncorrected *p*-distances among the delineated MOTUs (here recognized as species, see Taxonomic account section) ranged from 7.6% (between *Beringiana beringiana* (Middendorff, 1851) and *Beringiana gosannensis* **sp. nov.**) to 10.7% (between *B. gosannensis* **sp. nov.** vs. *Beringiana japonica* (Clessin, 1874)) (Sup. Table 1).

The systematics of *Beringiana beringiana* has been contentious over the last 100 years. While most of the early authors had placed it under the genus *Anodonta* (e.g. Haas, 1969; Simpson 1900), recent molecular works showed that the species is not closely related to the other *Anodonta* species, with its closest relatives being members of the genus *Sinanodonta* (Lopes-Lima et al., 2017b). This has led to the reassignment of *B. beringiana* to *Sinanodonta* by e.g. Williams et al., (2017) and Graf and Cummings (2019). Subsequently, Bolotov et al. (Submitted) reassigned this species to a separate genus, i.e. *Beringiana*, based on a more comprehensive molecular and morphological dataset, and this classification is supported by our phylogenetic analyses (Fig. 7). Based on the currently available molecular data, *Anodonta japonica* Clessin, 1874 is also reassigned to the genus *Beringiana* as well as two newly described species, *Beringiana fukuharai* **sp. nov.** and *Beringiana gosannensis* **sp. nov.** (see Taxonomic account section below).

All species within this genus are native to the study area. *B. beringiana* exhibits a wide distribution range from Hokkaido Island in Japan and the Primorye Region in Russia north to Siberia East of the Lena River drainage, Kamchatka and East through the Aleutian Islands to the west coast of North America (Fig. 7; Sup. Table 4). As for the other three species, *Beringiana fukuharai* **sp. nov.** is endemic to Kyushu and southern Honshu Islands in Japan, although it has been introduced to central Honshu and Hokkaido Islands (Kondo T., pers. obs.; Fig. 7). Finally, *Beringiana gosannensis* **sp. nov.** and *B. japonica* are endemic to the western and eastern coastal areas of Honshu Island, respectively (Fig. 7; Sup. Table 4).

Cristaria Schumacher, 1817

Both (ML and BI) COI phylogenies retrieved for the *Cristaria* genus exhibit similar topologies, retrieving four clades that were defined as MOTUs by all species delineation methods (Fig. 8). Uncorrected *p*-distances among the delineated MOTUs (here recognized as species) ranged from 8.0% (between *Cristaria plicata* (Leech, 1814) and *C. clessini* (Kobelt, 1879)) to 11.5% (between *C. clessini* and *C.* cf. *radiata* Simpson, 1900) (Sup. Table 1).

The genus *Cristaria* is only represented by two species in the study region. *Cristaria plicata* is widely distributed across Asia, from East Russia to Southeast Asia (Fig. 8; Sup. Table 5). In the Asian Far East, *C. plicata* occurs in the Russian Primorye Region, South Korea in mainland Asia and the western parts of Honshu Island of Japan, while *C. clessini* is endemic to the eastern coast of the same island. Due to its ability to occupy anthropogenically altered, lentic environments, such as channels and ponds, *C. plicata* has been invading the eastern part of Honshu, now co-occurring with the endemic *C. clessini* in some regions (Kondo T., pers. obs.; Fig. 8; Sup. Table 5).

Pletholophus Simpson, 1900

Based on molecular data, the species *Cristaria tenuis* (Gray in Griffith & Pidgeon, 1833) has been recently reassigned to *Pletholophus* (Lopes-Lima et al., 2017b). The present COI + 28S phylogenies confirm this reassignment (Fig. 3).

Both ML and BI COI phylogenies for *Pletholophus* presented similar topologies, retrieving two clades that were recovered as MOTUs by all species delineation methods (Fig. 9). Uncorrected *p*-distance among the delineated MOTUs (here recognized as species) was 5.5% (Sup. Table 1).

The only species of this genus found in the study area, i.e. *Pletholophus reinianus* (Martens, 1875), is endemic to the southern Japanese islands of the Ryukyu archipelago and Kyushu, with additional restricted populations in central Honshu (Fig. 9; Sup. Table 6).

Sinanodonta Modell, 1945

Anodontine freshwater mussels are particularly difficult to separate based on morphological characters, which has led to extensive misidentifications of species within this group (Riccardi et al, in press). The genus *Sinanodonta* was erected to include Asian species previously assigned to the genus *Anodonta* Modell, 1945. Since then, several species have been assigned to *Sinanodonta*, with the most recent molecular works showing the existence of multiple taxonomic units (Bespalaya et al., 2018; Bolotov et al., 2016; Burzyński and Soroka, 2018; Huang et al., 2019; Kondakov et al., 2018; Wu et al., 2018). However, severe uncertainties regarding the true number and composition of this genus remain (e.g. Bogatov, 2007; Graf and Cummings; 2019; He and Zhuang, 2013; Kondo, 2008; MolluscaBase, 2019).

Both (ML and BI) COI phylogenies for the *Sinanodonta* genus presented similar topologies, retrieving ten clades that were defined as MOTUs by a consensus of all species delineation methods, five of which are present in the region, four native and one non-native (Fig. 10). Uncorrected *p*-distances among the delineated MOTUs (here recognized as species) ranged from 3.3% (between *S. lauta* (Martens, 1877) and *S.* cf. *woodiana* 1) to 13.4% (between *S. angula* (Tchang, Li & Liu, 1965) and *S.* cf. *elliptica* (Heude, 1878)) (Sup. Table 1).

The two Japanese endemic species *Sinanodonta calipygos* (Kobelt, 1879) and *S. tumens* (Haas, 1910) **comb. nov.** (=*S. ogurae* (Kuroda & Habe, 1987); see Sup. Appendix I) form a well-supported clade (Fig. 10). *Sinanodonta calipygos* was thought to be restricted to the Lake Biwa basin, in central Honshu, Japan (Kondo, 2008). However, due to the survey efforts for this study, a new native, genetically unique population of *S. calipygos* was found at the northern tip of the island (Fig. 10). Due to the low genetic divergence, only one of the species delineation methods separates this northern population as a distinct MOTU and we chose to keep this population included in *S. calipygos*.

Sinanodonta schrenkii (Lea, 1870) was recently separated from *S. woodiana* based on molecular data (Bolotov et al., Submitted; Sayenko et al., 2017). Our study confirms this species' separate status (Fig. 10; Sup. Table 7). The fourth *Sinanodonta* species native to the region is *S. lauta* (Figs. 3 and 10). *Sinanodonta lauta* has been introduced to central Asia in the Yenisei River where it established a population restricted to a thermally polluted river channel (Bolotov et al., Submitted; Bespalaya et al., 2018). The last *Sinanodonta* species present in the region is *Sinanodonta* cf. *woodiana* 1 (Fig. 10). Although three distinct MOTUs were recovered from sequences identified as *S. woodiana* (here named *S.* cf. *woodiana* 1, *S.* cf. *woodiana* 2, and *S.* cf. *elliptica*), only *Sinanodonta* cf. *woodiana* 1 specimens occur in the study area (Fig. 10). In the absence of sequences and specimens from the type locality, it is impossible to determine which of these three MOTUs represents the valid *Sinanodonta woodiana*, but *Sinanodonta* cf. *elliptica* is tentatively named here as such, due to the partial original identification of sequenced specimens as *S. elliptica* (Huang et al., 2019; Wu et al., 2018).

Sinanodonta tumens is endemic to Lake Biwa and effluents in central Honshu in Japan (Fig. 10). *Sinanodonta calipygos* also occurs in Lake Biwa and effluents but with a divergent lineage occurring in the Aomori region, in the northern tip of Honshu Island. *Sinanodonta calipygos* has also been widely introduced to other areas of Honshu (Fig. 10). Two other species have wider distributions: *Sinanodonta schrenkii* with a disjunctive distribution in the Amur Basin and also in western river basins of the Korean Peninsula (Fig. 10); and *Sinanodonta lauta* being present across Kyushu, Honshu and Hokkaido islands in Japan and also in southern and eastern river basins of the Korean Peninsula, extending its range to coastal rivers northwest to Vladivostok city, in Primorye Region (Fig. 10). Finally, *S.* cf. *woodiana* 1 occurs in central Honshu, Japan. This species is highly invasive, with a wide non-native range from Southeast Asia to Sunda Islands and the Philippines (Fig. 10). Without comprehensive molecular sampling of *Sinanodonta* specimens throughout China, it is difficult to say if *S.* cf. *woodiana* 1 is native or invasive to Japan. On one hand, the species could be endemic to China, with Japan being part of the invaded range, given that it only occurs in two small disjunct areas of Japan, and being sympatric with the closely related congeneric *S. lauta*. On the other, the sequences from Japanese specimens are genetically divergent from those from the Yangtze Basin in China. Therefore, if no haplotypes similar to those from the invasive range are found after comprehensively surveying China, it may indicate that *S.* cf. *woodiana* 1 is native to Japan. Until further data is available, we consider *Sinanodonta* cf. *woodiana* 1 as non-native to Japan.

Lanceolariini Froufe, Lopes-Lima & Bogan, 2017

Due to the recent synonymization of the genus *Arconaia* Conrad, 18565 under *Lanceolaria* Conrad, 1853 (Huang et al., 2019), the tribe Lanceolariini only contains the genus *Lanceolaria*. In the present COI + 28S phylogenies, all newly sequenced *Lanceolaria* species cluster within the Lanceolariini clade (Fig. 3).

Lanceolaria Conrad, 1853

Both COI ML and BI phylogenies of the *Lanceolaria* genus presented similar topologies, retrieving eight clades, defined as MOTUs by all species delineation methods, all of which present a high divergence in COI (≥5.0%) (Fig. 11; Sup. Table 1).

Uncorrected *p*-distances among the delineated MOTUs (here recognized as species) ranged from 5.0% (between *Lanceolaria lanceolata* (Lea, 1865) and *L. triformis* (Heude, 1877)) to 11.1% (between *L.* cf. *bilirata* (Martens, 1902) and *L. oxyrhyncha* (Martens, 1861)). Four *Lanceolaria* species are present in the study area. *Lanceolaria grayii* (Gray in Griffith & Pidgeon, 1833) occurs throughout east continental Asia, from China to Russia. *Lanceolaria acrorrhyncha* (Martens, 1894) is endemic to the Korean Peninsula. The other two species exhibit mutually exclusive distributions in Japan, i.e. *L. oxyrhyncha* is endemic to Honshu and Shikoku Islands, and the recently described *L. kihirai* (Kondo & Hattori, 2019) is endemic to Kyushu Island (Fig. 11; Sup. Table 8).

Nodulariini Bogatov & Zatrawkin, 1987

Our combined COI + 28S phylogenies place *Inversiunio* Habe, 1991 into the tribe Nodulariini together with the other three genera proposed by Huang et al. (2019), i.e. *Cuneopsis* Simpson, 1900, *Nodularia*, and *Schistodesmus* Simpson, 1900 (Fig. 3). However, the Nodulariini clade is not well supported and a more robust phylogeny is needed to confirm the inclusion of *Inversiunio* in this tribe. Within the Nodulariini clade, two well-supported sub-clades were retrieved, one comprising the genera *Cuneopsis*, *Inversiunio* and *Schistodesmus*, and the other one comprising the single genus *Nodularia*. Only species belonging to *Inversiunio* and *Nodularia* are represented in the study area (Fig. 3). Interestingly, *Cuneopsis pisciculus* (Heude, 1874) from China clusters with all *Inversiunio* species, thus deserving a future taxonomic re-evaluation (Fig. 3).

Inversiunio Habe, 1991

Both COI ML and BI phylogenies for the *Inversiunio* genus presented similar topologies, retrieving three clades that were defined as MOTUs by two species delineation methods (Fig. 12). A fourth MOTU was determined for *Inversiunio verrucosus* Kondo, Yang & Choi, 2007 haplotypes that were not well resolved in the phylogeny (Fig. 12). Uncorrected *p*-distances among the delineated MOTUs (here recognized as species) ranged from 2.3% (*Inversiunio reinianus* (Kobelt, 1879) and *I. yanagawensis* (Kondo, 1982)) to 8.7% (between *I. jokohamensis* (Ihering, 1893) and *I. reinianus*) (Sup. Table 1).

Using the COI molecular data only, two main clades can be distinguished: one with three species, i.e. *Inversiunio reinianus* + *I. verrucosus* + *I. yanagawensis*, and another with only *I. jokohamensis*. Within the first clade, the species boundaries are difficult to delineate based on the COI data alone since the divergences among species are low 2.3-3.0% (Sup. Table 1) and not all species delineation methods separated these three MOTUs (Fig. 12). In the present study we recognize the validity of these three species, i.e. *Inversiunio reinianus* + *I. verrucosus* + *I. yanagawensis*, based on morphological differences following Kondo et al. (2007) and Kondo (2008), instead of considering them as divergent populations within *I. reinianus*. However, additional molecular analyses on this genus are required to confirm the status of these three taxa.

The four *Inversiunio* species are endemic to the study area and have distinct distributions. While *Inversiunio verrucosus* is endemic to the Seomjingang Basin in South Korea, the three remaining species occur in distinct areas of Japan. *Inversiunio yanagawensis* is restricted to Kyushu Island, Shikoku Island and southern areas of Honshu Island, *I. reinianus* is endemic to Lake Biwa Basin and effluents in the center of Honshu Island, and *I. jokohamensis* occurs in the north of Honshu and southern Hokkaido Islands (Fig. 12; Sup. Table 9).

Nodularia Conrad, 1853 and *Middendorffinaia* Moskvicheva & Starobogatov, 1973

Until recently, the validity of the genus *Middendorffinaia* was contentious, and some authors considered this genus a junior synonym of *Unio* Retzius, 1788 or *Nodularia* (e.g. Graf and Cummings, 2019; Haas, 1969). This was rejected by recent molecular studies that recognized both genera as valid (Bolotov et al., Submitted; Klishko et al., 2019). Our study confirms the validity of the genus *Middendorffinaia*, as sequenced specimens of *Middendorffinaia mongolica* are very divergent from those of the *Nodularia* or *Unio* clades (Figs. 3 and 13; Sup. Table 1). Furthermore, the sequences of *Middendorffinaia* are not placed within the Nodulariini clade and seem to represent a new tribe named here as Middendorffinaiini (see Taxonomic account section; Fig. 3).

Both COI ML and BI phylogenies for the *Nodularia* and *Middendorffinaia* genera presented similar topologies, retrieving eight clades that were defined as MOTUs by a consensus of all species delineation methods (Fig. 13). While the species delineation methods consensually recognized a single *Middendorffinaia* species (Fig. 13), the same methods identified seven MOTUs within *Nodularia* (Fig. 13). Uncorrected *p*-distances among the delineated MOTUs within *Nodularia* ranged from 3.0% (between *N. douglasiae* (Gray in Griffith & Pidgeon, 1833) and *Nodularia* sp. 1) to 9.4% (between *N. breviconcha* **nom. nov.** and *Nodularia* sp. 1 or *N. nipponensis*) (Sup. Table 1). Four of these MOTUs are present in the study area. *Nodularia douglasiae* exhibits a wide distribution from Vietnam in the south, to Russia in the north, also occurring in two western basins of South Korea and the western basins of Kyushu and Honshu islands (Fig. 13; Sup. Table 10). *Nodularia nipponensis* (Martens, 1877) is endemic to northern Honshu and Hokkaido Island in Japan. Our taxonomic investigation revealed that the name of *Nodularia sinuolata* (Martens, 1905) is invalid and a new replacement name is here given, i.e. *Nodularia breviconcha* **nom. nov.** (see details in section 4. Taxonomic account and Sup. Appendix I). This species had already been recognized as valid by Lee (2017) and is endemic to the Korean Peninsula as is another lineage of *Nodularia* (here *Nodularia* sp. 1). We refrained from formally recognizing and describing *Nodularia* sp. 1 in the present study, due to the low level of COI divergence (Sup. Table 1) and lack of apparent distinguishing morphological characters from *N. douglasiae*. The sequenced specimens of this lineage deserve a more detailed future study to evaluate its taxonomic status. The single species within *Middendorffinaia*, i.e. *M. mongolica*, presents a wide distribution in the Amur Basin and coastal areas of Eastern Russia (Fig. 13; Sup. Table 10).

Gonideinae Ortmann, 1916

The Unionidae subfamily Gonideinae is here subdivided into five tribes, three of which (Gonideini, Lamprotulini Modell, 1942, and Chamberlainiini Bogan, Froufe & Lopes-Liima, 2017) are represented in the study area (Fig. 4). Lamprotulini and Gonideini tribes are widely distributed in the Northern Hemisphere, whilst the Chamberlainiini is restricted to Asia (Lopes-Lima et al., 2017b).

Gonideini Ortmann, 1916

Koreosolenaia **gen. nov.** and *Parvasolenaia* Huang & Wu, 2019

The combined COI + 28S phylogenies cluster *Parvasolenaia rivularis* (Heude, 1877) and *Koreosolenaia sitgyensis* **sp. nov.** in a well-supported clade (BI only) together with two other Far East Asian species, i.e. *Obovalis omiensis* (Heimburg, 1884) and *Inversidens brandtii* (Kobelt, 1879), and the South Asian *Ptychorhynchus pfisteri* (Heude, 1874), within the Gonideini tribe (Fig. 4).

Both (ML and BI) COI phylogenies of *Parvasolenaia* and *Koreosolenaia* **gen. nov.** presented similar topologies, retrieving two clades that were defined as MOTUs by all species delineation methods (Fig. 14). Uncorrected *p*-distance among the two MOTUs (here recognized as species from distinct genera, see section 4. Taxonomic account) is 11.2%.

Koreosolenaia **gen. nov.** includes a single species, i.e. *Koreosolenaia sitgyensis* **gen. & sp. nov.,** which is endemic to the Hangang, Geumgang, Nakdonggang, and Seomjingang River basins of South Korea (Fig. 14; Sup. Table 11).

Until recently, the genus *Solenaia* Conrad, 1869 included several taxa distributed across Asia from Far East Asia to India (Lopes-Lima et al., 2017b). Since then, new studies based on an improved molecular and morphological dataset split the genus into several genera with smaller ranges. The species in its western range in India and Myanmar should be reassigned to *Balwantia* Prashad, 1919 (Ivan Bolotov, pers. comm.), while some species in China and one in South Korea were reassigned to the genus *Parvasolenaia* (Huang et al., 2019). Three species were included in *Parvasolenaia,* i.e. *Parvasolenaia rivularis* and *Parvasolenaia neotriangularis* He & Zhuang, 2013 from the Yangtze basin, and *Parvasolenaia triangularis* (Heude, 1885), which has been described and collected once from the upper Yangtze at the end of the 19th century and has never been found since (He and Zhuang, 2013). Specimens collected in the early 1960s in a pond near Seoul were assigned to *Solenaia* (now *Parvasolenaia*) *triangularis* based on morphological similarities with the type figure (Yoo and Habe, 1962). Recently, phylogenetic analyses including molecular data from both *Solenaia rivularis* from the middle Yangtze and '*Solenaia triangularis'* from South Korea revealed that these two species formed a well-supported clade separate from the clade containing the other *Solenaia* species. Based on this and similarities in shell shape, *S. rivularis* and *S. triangularis,* together with *S. neotriangularis,* were then reassigned to the genus *Parvasolenaia* (Huang et al., 2019). However, our detailed analyses on the South Korean specimens of '*P. triangularis'* revealed morphological differences with the type figure of *P. triangularis* (see Taxonomic account) that indicate that these species are not the same. A separate species status of the South Korean '*P. triangularis'* is supported by what would be a highly unusual, disjunct distribution of this "species" in the upper Yangtze and South Korea, which has never been recorded in the extensively surveyed, middle sections of the Yangtze (e.g. Wu et al., 2018; Huang et al., 2019). Additionally, genetic divergence in 28S rRNA (that show none or very little variation within freshwater mussel genera: Lopes-Lima et al., 2017b; Bolotov et al., 2018) is 4.4% between *Parvasolenaia rivularis* and the South Korean '*P. triangularis*'. This strongly supports that the South Korean '*P. triangularis*' belongs to a distinct genus. Due to the facts stated above, we recognize the South Korean specimens as belonging to a new genus *Koreosolenaia* **nov. gen.** and species *Koreosolenaia sitgyensis* **gen. & sp. nov.**, formally describing them below (see section 4. Taxonomic account).

Obovalis Simpson, 1900 and *Inversidens* Haas, 1911

The monotypic genus *Obovalis* contains only the Japanese endemic *O. omiensis* (Fig. 4). Originally described as *Unio omiensis* Heimburg, 1887 it was transferred to the genus *Obovalis* by Simpson (1900) but then placed in *Pseudodon* Gould, 1844 as the subgenus *Pseudodon* (*Omiensis*) (Haas, 1969). However, our analyses revealed that the taxon is not closely related to the other *Pseudodon* species from Southeast Asia (Fig. 4), therefore supporting its reassignment back as a separate genus, i.e. *Obovalis*.

Two species are currently recognized within *Inversidens*, the Japanese endemic *I. brandtii* and *I. pantoensis* (Neumayr, 1899) from the Yunnan Region in China (Fig. 15; Sup. Table 12). There is no available molecular data from *Inversidens pantoensis* and so its placement within *Inversidens* still needs confirmation.

In our combined phylogenies, *Obovalis omiensis* and *Inversidens brandtii* are placed within a well-supported clade containing the representatives of the genera *Ptychorhynchus* Simpson, 1900, *Parvasolenaia,* and *Koreosolenaia* within the Gonideini tribe (Fig. 4).

Lamprotulini Modell, 1942

This tribe contains three genera, i.e. *Lamprotula* Simpson, 1900, *Potomida* Swainson, 1840 and *Pronodularia* (Huang et al., 2019; Lopes-Lima et al., 2017b;), as confirmed by the clustering of all representatives of these genera in a well-supported clade in our COI + 28S phylogenies (Fig. 4).

Lamprotula Simpson, 1900 and *Pronodularia* Starobogatov, 1970

Both COI ML and BI phylogenies of *Lamprotula* and *Pronodularia* genera presented similar topologies, retrieving six clades that were defined as MOTUs by all species delineation methods (Fig. 16). A seventh MOTU was determined for *Pronodularia* cf. *japanensis* (Lea, 1859) 1 haplotypes but these haplotypes were not monophyletic in the phylogenies (Fig. 16).

Uncorrected *p*-distances among the delineated MOTUs within *Lamprotula* ranged from 5.2% (between *L. leaii* (Gray in Griffith & Pidgeon, 1833) and *Lamprotula seomjinensis* (Kondo, Yang & Choi, 2007) **comb. nov.**) to 10.5% (between *L. caveata* (Heude, 1877) and *Lamprotula* sp.) (Sup. Table 1). Uncorrected *p*-distances among the delineated MOTUs within *Pronodularia* ranged from 4.1% (between *P.* cf. *japanensis* 1 and *P.* cf. *japanensis* 3) to 5.3% (between *P.* cf.

japanensis 2 and *P.* cf. *japanensis* 3) (Sup. Table 1).

Previously to this study, only one species of *Lamprotula*, i.e. *L. gottschei* (Martens, 1894), was recognized in the study region, in South Korea (e.g. Graf and Cummings, 2019). In the present study, we consider *Lamprotula gottschei* a junior synonym of *L. leaii*, due to very low divergence in COI and morphological similarities between both species, following the opinion by Haas (1969). Four species of *Lamprotula* were present in our COI dataset, supported by all species delineation methods: *L. leaii*, *L. caveata* (Heude, 1877), an unknown *Lamprotula* species (with sequenced specimens having been identified as both *L. leaii* and *L. caveata* in the GenBank database; Sup. Table 13), and *L. seomjinensis* **comb. nov.** from South Korea (Fig. 16; Sup. Table 13). The species previously named *Pronodularia seomjinensis* is here reassigned to the genus *Lamprotula* as it falls within the *Lamprotula* species clade in both the COI and COI + 28S phylogenies. The endemic Japanese *Pronodularia japanensis* is here divided into three potential species, i.e. *Pronodularia* cf. *japanensis* 1, 2, and 3 (Fig. 16; Sup. Table 13). Future taxonomic work is needed to resolve the validity and formally describe these potential species.

Five species from these two genera are present in the study area. While *Lamprotula leaii* is widely distributed from Vietnam in the south to China and Korea in the north, *L. seomjinensis* **comb. nov.** is restricted to the Seomjingang River Basin in South Korea (Fig. 16; Sup. Table 13). *Pronodularia* cf. *japanensis* 1 exhibits an interesting phylogeographic structure, with one clade being restricted to southwest Japan in Kyushu and Honshu Islands, and the other clade being restricted to Shikoku Island and the west coast of Honshu Island to the north (Fig. 16; Sup. Table 13). *Pronodularia* cf. *japanensis* 2 is endemic to the central regions of Honshu Island (Fig. 16; Sup. Table 13). Finally, *Pronodularia* cf. *japanensis* 3 only occurs in northeastern Honshu Island (Fig. 16; Sup. Table 13).

Chamberlainiini Bogan, Froufe & Lopes-Lima, 2017

This tribe contains only two genera, *Chamberlainia*, and *Sinohyriopsis* (Froufe et al., 2020; Huang et al., 2019; Lopes-Lima et al., 2017b). Our COI + 28S phylogenies retrieved a well-supported clade with representatives of these two genera (Fig. 4).

Sinohyriopsis Starobogatov, 1970

The genus *Hyriopsis* Conrad, 1853 sensu lato was recently split into *Hyriopsis* sensu stricto (for the Southeast Asian and Sundaland species) and *Sinohyriopsis* (for species east of the Mekong River basin) (Zieritz et al., 2018). Both (ML and BI) COI phylogenies for the *Sinohyriopsis* genus presented similar topologies, retrieving three clades that were defined as MOTUs by a consensus of all species delineation methods (Fig. 17). Two additional MOTUs were retrieved: *Sinohyriopsis* cf. *cumingii* (Lea,1852) 2 and *S.* cf. *cumingii* 3, but respective haplotypes were not well resolved in the phylogeny (Fig. 17). Uncorrected *p*-distances among the delineated MOTUs ranged from 2.7% (between *Sinohyriopsis schlegelii* (Martens, 1861) and *S.* cf. *cumingii* 3) to 8.9% (between *S. goliath* (Rolle, 1904) and *S.* cf. *cumingii* 1) (Sup. Table 1). Of the five defined MOTUs, only *Sinohyriopsis schlegelii* and one of the lineages of *S. cumingii* (here *S.* cf. *cumingii* 1) are present in the study area. Until the late 1960s, it was thought that *Sinohyriopsis schlegelii* was the Japanese insular form of the mainland Asian *S. cumingii* (Haas, 1969). Since then, *Sinohyriopsis schlegelii* has been recognized as separate species and considered the single *Sinohyriopsis* species endemic to Japan (Kondo, 2008; Lopes-Lima et al., 2017b). However, in the early 1990s, *Sinohyriopsis cumingii* (here the MOTU *S.* cf. *cumingii* 1: Fig. 17) was introduced to Lakes Biwa and Kasumigaura for the pearl industry, where wild populations established and hybridized with the local endemic *S. schlegelii* (Shirai et al., 2010). It is thought that only the specimens from Lake Anenuma in north Honshu currently represent pure *Sinohyriopsis schlegelii* (Shirai et al., 2010). Since no morphological specimens of *Sinohyriopsis* cf. *cumingii* 1, 2 and 3 were available to us, we refrained from further evaluating the taxonomic status of these lineages. Curiously, *Sinohyriopsis schlegelii* from Japan is more closely related to its Vietnamese congeneric *Sinohyriopsis goliath* (Rolle, 1904) **comb. nov.** than to the Chinese, Yangtze River *S. cumingii* lineages (Fig. 17). *Sinohyriopsis goliath*, previously considered a junior synonym of *S. cumingii* (Dang et al., 1980), is here erected from a synonym to a valid species (Fig. 17; Sup. Table 14).

3.2. Biogeography

The Unionidae species richness of Far East Asia is considerably higher than previously assumed, counting at least 43 rather than the 30 previously recognized species (Graf and Cummings, 2019; MolluscaBase, 2019). A south-north gradient of decreasing species diversity is apparent across the study area. Japan is the country with the highest native species richness totalling 26 species, of which 20 are endemic (when considering the three *Pronodularia* cf. *japanensis* MOTUs as valid species) (Table 3). A lower richness is observed in South Korea with 16 native and 8 endemic species (considering *Nodularia* sp. 1), and in Russia (East of Transbaikalia and the Lena River basin) with only 10 native, and no endemics (Table 3).

Phylogeographic patterns of Unionidae in Japan largely follow those described in several groups of freshwater fish (e.g. Nishimura, 1980; Watanabe, 2012). For example, the northeastern–southwestern division, a major biogeographical boundary identified for the Japanese freshwater fish fauna, is also seen in e.g. *Inversiunio* and *Nodularia* (Figs. 6 and 9), while an east-west separation is seen in other genera, e.g. *Buldowskia* and *Beringiana* (Figs. 6 and 7).

The Korean Peninsula is also an area of high levels of endemism. Biogeographic patterns here are difficult to interpret, however, probably because this region acts as a contact zone of several distinct mussel faunas, including that of Russia to the north, the Yellow River basin in China to the west and Japan to the south. This pattern is well-documented for fish taxa (e.g. Nishimura, 1980; Mizuno, 1987) but again poorly understood for freshwater mussels. *Cristaria plicata* and *Nodularia douglasiae* present wide distributions, suggesting Japanese colonization via the repeated connection of the Korean-Japan land bridge since at least the Miocene (Tominaga et al., 2016). On the other hand, it is difficult to point towards a clear direction of expansion for other freshwater mussel taxa, e.g. *Buldowskia iwakawai* **comb. nov.** or *Sinanodonta lauta*, which are present on both sides of the Korea Strait (Figs. 6 and 10). The biogeographic connections between the Korean Peninsula and the Amur and Primorye in Russia, and the Yellow River basin in China, are more unclear due to the lack of data from North Korea and China.

4. Taxonomic account

Family Unionidae Rafinesque, 1820

Subfamily Unioninae Rafinesque, 1820

Comments: This subfamily includes at least nine tribes, five of which in the study area, i.e. Aculamprotulini Huang & Wu, 2019, Cristariini Lopes-Lima, Bogan & Froufe, 2017, Lanceolariini Froufe, Lopes-Lima & Bogan, 2017, Nodulariini Bogatov & Zatrawkin, 1987 and Middendorffinaiini Lopes-Lima, Bolotov & Bogan **trib. nov.**

Distribution: Africa, Europe, Asia, North America.

Tribe Cristariini Lopes-Lima, Bogan & Froufe, 2017

Type Genus: *Cristaria* Schumacher, 1817

Type Species: *Cristaria tuberculata* Schumacher, 1817 = *Cristaria plicata* (Leach, 1814)

Comments: This tribe includes seven genera, *Anemina* Haas, 1969, *Amuranodonta* Moskvicheva, 1973, *Beringiana* Starobogatov in Zatrawkin, 1983, *Buldowskia* Moskvicheva, 1973, *Cristaria* Schumacher, 1817, *Pletholophus* Simpson, 1900, and *Sinanodonta* Modell, 1945.

Genus *Beringiana* Starobogatov in Zatrawkin, 1983

Type Species: *Beringiana beringiana* (Middendorff, 1851)

Comments: This genus includes four species, *Beringiana beringiana* (Middendorff, 1851), *Beringiana japonica* (Clessin, 1847), and two species here described, *Beringiana fukuharai* Sano, Hattori & Kondo **sp. nov.** and *Beringiana gosannensis* Sano, Hattori & Kondo **sp. nov.**

Beringiana fukuharai Sano, Hattori & Kondo sp. nov.

Type locality: Nishida (34.0741°N, 135.5396°E), Yagi-cho, Nantan City, Kyoto Prefecture, Japan.

Type material: Holotype: OMNH-Mo 39101 (Osaka Museum of Natural History, Japan; 85.5 mm × 48.9 mm × 29.1 mm) (Fig. 18A) collected at Nishida (34.0741°N, 135.5396°E), Yagi-cho, Nantan City, Kyoto Prefecture on October 15, 1994, by the late Dr. Shuuichi Fukuhara. Paratypes: 3 specimens (OMNH-Mo. 39102 to 39104) collected at the type locality on the same day, by the late Dr. Shuuichi Fukuhara.

Etymology: This species is dedicated to the late Dr. Shuuichi Fukuhara for his contribution to our knowledge of Japanese freshwater mollusks.

Diagnosis: This new species differs from congeneric species, i.e. *B. beringiana*, *B. japonica* and *B. gosannensis* **sp. nov.** by having an ovate shell, versus the elongated ovate shells in the other species. However, morphological variation in shell shape is very large in this species. So, for some specimens, accurate species identification by morphology alone is sometimes difficult. This new species is genetically distinct from the other congeneric species by multiple fixed nucleotide substitutions in the COI gene fragment (Fig. 7 and Sup. Table 1).

Description: Shell ovate, slightly inflated, medium in size, usually not exceeding 10 cm in shell length; anterior margin rounded, posterior margin slightly angulated; umbo situated at about one-fourth of shell length. Surface with concentric ridges; epidermis blackish, but greenish-brown in young shells. No cardinals or laterals; muscle scars very shallow and faint; nacre bluish-white.

Habitat and ecology: Inhabit sand-mud to mud substrata in ponds and creeks.

Distribution: Kyushu and southern Honshu islands in Japan.

Beringiana gosannensis Sano, Hattori & Kondo sp. nov.

Type locality: Gosannen (39.3656°N, 140.5504°E), Misato-cho, Senhoku-gun, Akita Prefecture, Japan.

Type material: Holotype: OMNH-Mo 39089 (Osaka Museum of Natural History, Japan; 69.3 mm × 38.1 mm × 22.7 mm) (Fig. 18B) collected at Gosannen (39.3656°N, 140.5504°E), Misato-cho, Senhoku-gun, Akita Prefecture on March 31, 1994, by the late Dr. Shuuichi Fukuhara. Paratypes: 3 specimens (OMNH-Mo. 39090 to 39092) collected at the type locality on the same day, by the late Dr. Shuuichi Fukuhara.

Etymology: This species name is derived from the name of the type locality.

Diagnosis: This new species differs from congeneric species, i.e. *B. beringiana*, *B. japonica* and *B. fukuharai* **sp. nov.** by presenting a more elongated and compressed shell. It also has a high genetic divergence from other *Beringiana* species by multiple fixed nucleotide substitutions in the COI gene fragment (Fig. 7 and Sup. Table 1).

Description: Shell elongate ovate, compressed, medium in size, usually not exceeding 10 cm in shell length; anterior margin rounded, posterior margin slightly angulated; umbo situated at about one-fifth of the shell length. Surface with concentric ridges; epidermis brownish. No cardinals or laterals; adductor muscle scars very shallow and faint; nacre bluish.

Habitat and ecology: Inhabit sand-mud to mud substrata in ponds and creeks.

Distribution: Western coastal basins of Honshu Island in Japan.

Genus *Buldowskia* Moskvicheva, 1973

Type Species: *Buldowskia suifunica* (Lindholm, 1925)

Comments: This genus includes five species, *Buldowskia flavotincta* (Martens, 1905), *Buldowskia shadini* (Moskvicheva, 1973), *Buldowskia suifunica* (Lindholm, 1925), one species reassigned from the genus *Anodonta*, i.e. *Buldowskia iwakawai* (Suzuki, 1939) **comb. nov.**, and one species here described, i.e. *Buldowskia kamiyai* Sano, Hattori & Kondo **sp. nov.**

Buldowskia kamiyai Sano, Hattori & Kondo sp. nov.

Type locality: Marumori-cho (37.9214°N, 140.7504°E), Miyagi Prefecture, Japan.

Type material: Holotype OMNH-Mo 39097 (Osaka Museum of Natural History, Japan; 52.3 mm × 31.0 mm × 21.3 mm) (Fig. 18C) collected at Marumori-cho (37.9214° N, 140.7504° E), Miyagi Prefecture on February 3, 2002, by the late Dr. Shuuichi Fukuhara. Paratypes: 3 specimens (OMNH-Mo. 39098 to 39100) collected at the type locality on the same day, by the late Dr. Shuuichi Fukuhara.

Etymology: This species is dedicated to the late Mr. Satoshi Kamiya for his contribution to our knowledge of Japanese freshwater mollusks.

Diagnosis: This species is related to the congeneric *B. iwakawai* (Fig. 6), but differed from it in shell shape; elongated with an elevated umbonal area in *B. iwakawai*, but ovate with a less elevated umbonal area in *B. kamiyai*. It also has a high genetic divergence from other *Buldowskia* species by multiple fixed nucleotide substitutions in the COI gene fragment (Fig. 6 and Sup. Table 1).

Description: Shell ovate, slightly inflated, medium in size, usually not exceeding 13 cm in shell length; anterior margin rounded, posterior margin short and blunt, dorsal and ventral lines nearly parallel; umbo situated near the center of the dorsal line, slightly elevated; epidermis dark brown. No cardinals or laterals; muscle scars very shallow and faint; nacre bluish.

Habitat and ecology: Inhabit sand-muddy to muddy substrata in ponds and creeks.

Distribution: Northeast river basins of Honshu Island in Japan.

Tribe Middendorffinaiini Lopes-Lima, Bolotov & Bogan tribe nov.

Type Genus: *Middendorffinaia* Moskvicheva & Starobogatov, 1973

Type Species: *Middendorffinaia mongolica* (Middendorff, 1851)

Description: shell shape is elongate oval. Umbo sculpture is elongated wavy ridges or knobs, weakly present in adult specimens. Pseudocardinal teeth are thickened, with the two teeth in the left valve united. Pappilae in the incurrent aperture elongate slender and in two to three rows. Based on COI sequence data *Nodularia* and *Middendorffinaia* are separate and distinct clades (Klishko et al., 2019). Molecular data presented here (COI and 28S) confirms that *Middendorffinaia* forms a clade separate from *Nodularia* and *Unio* (see Fig. 3).

Diagnosis: shell shape similar to *Nodularia* and *Unio crassus*, umbo sculpture in *Middendorffinaia* is elongate wavy ridges while *Nodularia* has W-shaped ridges or large chevron, *Unio crassus* has short or elongated wavy elevations frequently absent. *Middendorffinaia* has heavier pseudocardinal teeth in comparison with *N. douglasiae* and *U. crassus* which have thin lamellar pseudocardinal teeth and those in the left valve are separate. Both *Middendorffinaia* and *N. douglasiae* have pappilae present on the incurrent and excurrent apertures, but *U. crassus* lacks papillae in the excurrent aperture. In *Middendorffinaia* the papillae of the incurrent aperture are elongated, simple and in two to three rows while *N. douglasiae* are weakly-developed short, conic and in a single row. *Nodularia* has knobs or bumps at the base of papillae in the interior surface of the excurrent aperture on a dark background. These bumps are missing from both *Middendorffinaia* and *U. crassus*. Using COI sequence data *Middendorffinaia* and *Nodularia* were confirmed as separate genera (Klishko et al. 2019). Our molecular data presented here confirms three separate clades for *Nodularia*, *Unio* and *Middenforffinaia*, recognized as separate clades and tribes (see Fig. 3).

Comments: This tribe includes only the monotypic genus *Middendorffinaia* Moskvicheva & Starobogatov, 1973.

Distribution: East Asian Russia and China, including the Amur Basin and other coastal basins.

Tribe Nodulariini Bogatov & Zatrawkin, 1987

Type Genus: *Nodularia* Conrad, 1853

Type Species: *Nodularia douglasiae* (Griffith & Pidgeon, 1833)

Comments: This tribe includes the type genus *Nodularia*, *Cuneopsis* Simpson, 1900, *Inversiunio* Habe, 1991, and *Schistodesmus* Simpson, 1900.

Distribution: China and East Asia in the Korean Peninsula, Japan, and Russia.

Nodularia breviconcha Lee, Kim, Bogan & Kondo nom. nov.

= *Unio douglasiae* var. *sinuolatus* Martens, 1905: 57-58 (nec *Unio sinuolata* Küster, 1833: pl. 5, fig. 5).

Type locality: “Fluß Naewingang bei Hatanggyöm,230 m, Provinz Chöllado (a). Altwasser an der Mündung des westlishen Zuflusses des Imjingang, 6 km von Ichhön, Provincz Kangwöndo” [Korea] (Martens 1905:58).

Etymology: The new name for this species is derived from the relatively small size of the shell.

Comments: *Unio douglasiae* var. *sinuolatus* Martens, 1905 is a primary junior homonym preoccupied by *Unio sinuolata* Küster, 1833. *Nodularia brevichoncha* **nom. nov.** is proposed as a replacement name for *U. d.* var. *sinuolatus* Martens, 1905. The senior homonym *Unio sinuolata* Küster, 1833 is recognized today as a junior synonym of *Unio crassus* Philipsson, 1788 (Haas, 1969).

Distribution: *Nodularia breviconcha* **nom. nov**. is endemic to the Korean Peninsula

Subfamily Gonideinae Ortmann, 1916

Comments: This subfamily includes at least five tribes, three of which in the study area, i.e. Chamberlainiini Bogan, Froufe & Lopes-Lima, 2017, Gonideini Ortmann, 1916, and Lamprotulini Modell, 1942.

Distribution: North Africa, Europe, Asia, North America.

Tribe Gonideini Ortmann, 1916

Type Genus: *Gonidea* Conrad, 1857

Type Species: *Gonidea angulata* (Lea, 1838)

Comments: This tribe includes at least nine genera, three of which are represented in the study area, *Inversidens* Haas, 1911, *Obovalis* Simpson, 1900, and *Koreosolenaia* Lee, Kim, Lopes-Lima & Bogan **gen. nov.**

Genus *Koreosolenaia* Lee, Kim, Lopes-Lima & Bogan gen. nov.

Type Species: *Koreosolenaia sitgyensis* Lee, Kim, Lopes-Lima & Bogan **gen. & sp. nov.**

Comments: This tribe contains only the type species *Koreosolenaia sitgyensis* **gen. & sp. nov.**

Etymology: This genus name is a combination of the type locality country, i.e. Korea (*koreo*), its elongated or tubular shape (*solen*), and naiad (*naia*).

Diagnosis: The same as for its type species (see below).

Distribution: The same as for its type species (see below).

Koreosolenaia sitgyensis Lee, Kim, Lopes-Lima & Bogan gen. & sp. nov.

Type locality: Dalcheon Stream (Hangang River Basin) (36.931019°N 127.931339°E), Salmi-myeon, Chungju-si, South Korea.

Type material: Holotype: NNIBR-IV28166 (Nakdonggang National Institute of Biological Resources, South Korea) (Fig. 18D) collected at Dalcheon Stream (36.931019°N 127.931339°E), Salmi-myeon, Chungju-si, South Korea on 26 August 2019, by Dr. Sang Ki Kim. Paratypes: South Korea: Dalcheon Stream, Salmi-myeon, Chungju-si, 36.931019°N 127.931339°E, 26.viii.2019, 6 specimens (NNIBR-IV28167, 28168, 28172; NCSM-113451, 113452, 113453), Sang Ki Kim, Ji-Hun Song, and Seung Hyun Lee leg.; South Korea:

Pyeongchanggang River, Nam-myeon, Yeongwol-gun, 37.203117°N 128.411598°E, 4.iv.2013, 1 specimen (NNIBR-IV28173), Sang Ki Kim and Byung Soo Chae leg.; South Korea: Dalcheon Stream, Chilseong-myeon, Goesan-gun, 36.774166°N 127.841504°E, 17.ix.2012, 2 specimens (NNIBR-IV28174; NCSM 113454), Jin Hee Lee and Sang Ki Kim leg.

Etymology: The name of this species derived from the name of the wildlife protection area (Sitgye), its type locality.

Diagnosis: *Koreosolenaia sitgyensis* **sp. nov.** differs from species within *Parvasolenaia*, i.e. *P. rivularis*, and *P. triangularis* which have a straight dorsal margin. But *K. sitgyensis* **gen. & sp. nov.** and *P. neotriangularis* have a curved dorsal margin. *Koreosolenaia sitgyensis* **gen. & sp. nov.** is distinguished from *P. neotriangularis* by shell shape, which has a relatively short shell length, height to length ratio ranged from 0.487 to 0.517 (vs 0.410 to 0.460 in *P. neotriangularis,* see He and Zhuang, 2013), high anterior margin and posterior end truncated. *Koreosolenaia sitgyensis* **gen. & sp. nov.** has a high genetic divergence from *Parvasolenaia* species by multiple fixed nucleotide substitutions in the COI and 28S rRNA gene fragments (Figs. 4 and 14; Sup. Table 1).

Description: Small-sized mussel. Shell length 29.2–60.6 mm, height 15.1–30.6 mm, width 6.5–15.8 mm. Shell shape subtriangular, elongated, inequilateral, narrower anteriorly, thin, rather compressed. Anterior end rounded. Dorsal margin curved, ventral margin slightly concave. Posterior end truncated, broader than the anterior end. Umbo not prominent, slightly elevated, placed near anterior end. Surface smooth, with obscure radial ribs on the posterior slope, posterior ridge narrowly rounded, periostracum light brown to black, young shells greenish-brown. Hinge slightly elevated. Pseudocardinals absent. Nacre bluish-white.

Habitat and ecology: Gaps between stones or gravel and rocky bottom substrate in medium, flowing rivers.

Distribution: Upper reaches of the Hangang, Geumgang, Seomjingang, and Nakdonggang River basins in South Korea.

5. Conclusions

The phylogenetic and taxonomic results of the present study represent a significant advance in terms of delineating taxa and areas of conservation importance for the Far East Unionidae. For example, species from the genera *Amuranodonta*, *Obovalis*, *Koreosolenaia* **gen. nov.**, and *Middendorffinaia* are phylogenetically unique and of special conservation concern. Given that the conservation status assessments and legal protection policies generally use species as units, the redefinition of species boundaries and distributions presented here should be considered for future assessments and legal protection claims. For example, the conservation status of newly described and recognized species, e.g. within *Beringiana*, *Buldowskia*, and *Cristaria*, should now be evaluated independently with smaller ranges.

The study also highlights important diversity hotspots that should be prioritized for conservation. For example, the Honshu, Kyushu and Hokkaido islands in Japan, and the Korean Peninsula are areas of high species richness, high endemism and dramatic habitat loss for freshwater mussels, and therefore urgently require conservation attention. Other areas, such as the East Russian range, seem to be of less concern in terms of Unionidae conservation at the moment considering the general wider range of species and lower intensity of human pressure.

The present study is an excellent baseline for future research. That said, future studies including comprehensive field surveys, investigations of museum collections and molecular phylogenies based on high throughput molecular data are needed to confirm our classification and assessment of species richness of the Unionidae of this region, assess the conservation status of these species and potentially identify additional taxonomic units that deserve legal protection. Patterns of Unionidae diversity and distribution presented here will additionally be valuable for future biogeographic works and delineation of protected areas for freshwater molluscs and freshwater taxa in general.

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Figures

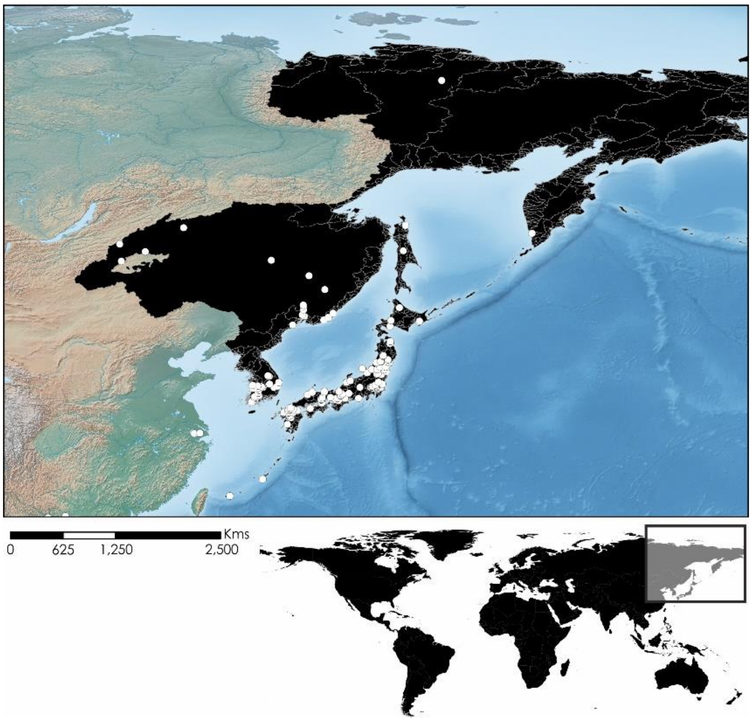


Figure 1. Map of the study area shaded in black. White dots represent the location of newly sequenced individuals or those previously sequenced with accurate GPS coordinates.

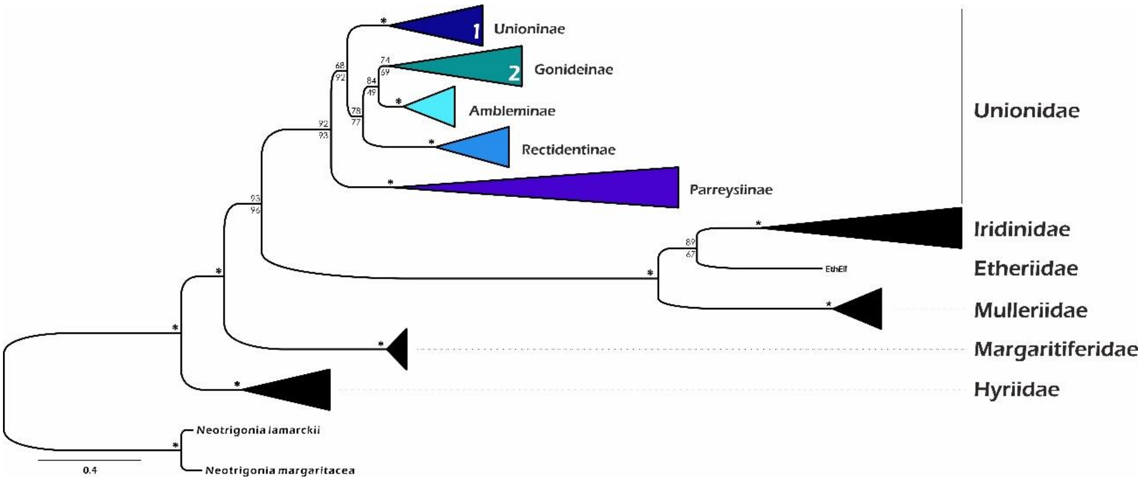


Figure 2. Bayesian consensus tree inferred from the combined cytochrome c oxidase subunit I + 28S ribosomal RNA gene fragments. The values above and below the branches indicate Bayesian posterior probability percentage and Maximum Likelihood ultrafast bootstrap values, respectively. Values over 95% are represented by an asterisk. Each subfamily was collapsed for pictorial purposes.

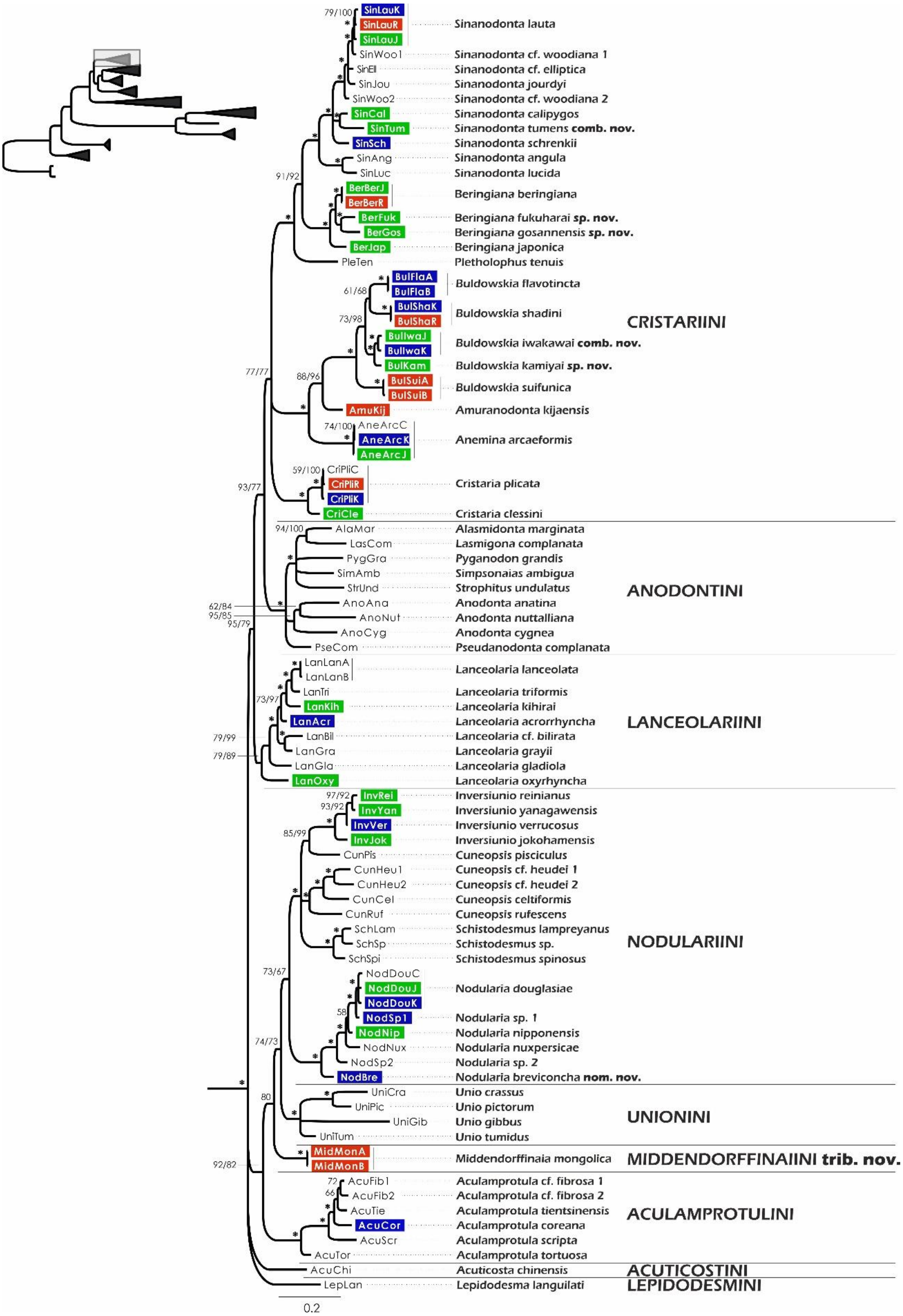


Figure 3. Uncollapsed Unioninae clade (labeled 1) from the Bayesian consensus tree inferred from the combined cytochrome c oxidase subunit I + 28S ribosomal RNA gene fragments depicted in Fig. 2. The values above the branches indicate Bayesian posterior probability

percentage/Maximum Likelihood ultrafast bootstrap values. Values over 95% are represented by an asterisk and those <50% erased for clarity. Colour of the sequence codes refer to specimens collected in Japan (green), and Korea (blue).

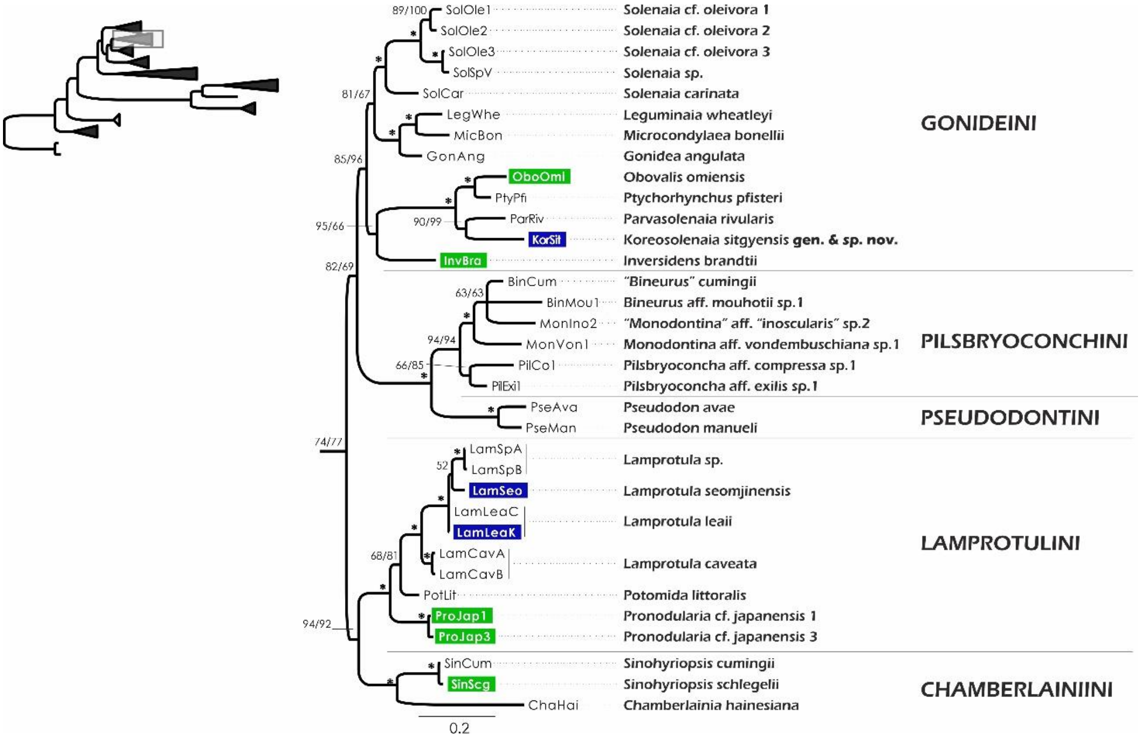


Figure 4. Uncollapsed Gonideinae clade (labeled 2) from the Bayesian consensus tree inferred from the combined cytochrome c oxidase subunit I + 28S ribosomal RNA gene fragments depicted in Fig. 2. The values above the branches indicate Bayesian posterior probability percentage/Maximum Likelihood ultrafast bootstrap values. Values over 95% are represented by an asterisk and those <50% erased for clarity. Colour of the sequence codes refer to specimens collected in Japan (green), Korea (blue), and Russia (red).

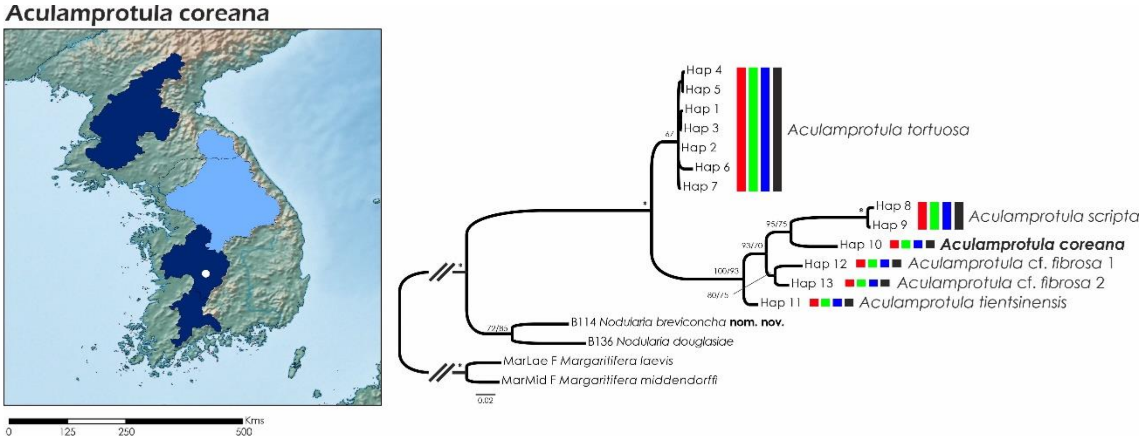


Figure 5. Bayesian Inference (BI) and Maximum likelihood (ML) phylogenetic tree inferred from the cytochrome c oxidase subunit I (COI) gene fragment, species delineation of *Aculamprotula* species, and distribution map of *Aculamprotula* species present in the study area. Support values above the branches are percent posterior probabilities/ultrafast bootstraps. Vertical bars correspond to molecular operational taxonomic units by various species delimitation methods: red – TCS (95%); green – ABGD; blue – BINS of BOLD; and black – consensus. Support values >95% for both phylogenetic analyses are represented by an asterisk, support values <50% and those within each recognized MOTU were erased for clarity. Distribution map of *Aculamprotula coreana* shows the original distribution in main river basins shaded in blue; dark blue, extant distribution; light blue, extirpated range; white dots, newly sequenced individuals.

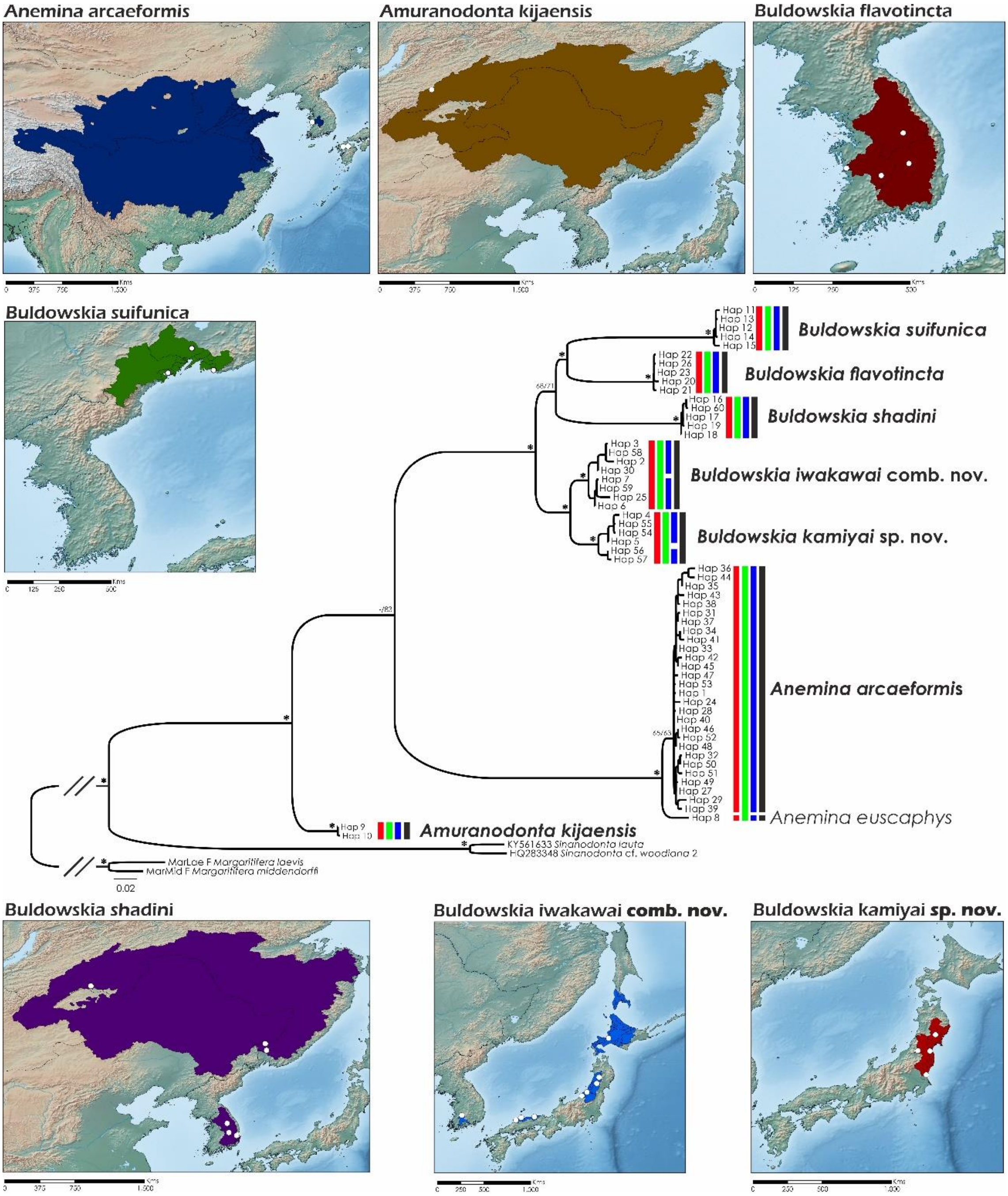


Figure 6. Bayesian Inference (BI) and Maximum likelihood (ML) phylogenetic tree inferred from the cytochrome c oxidase subunit I (COI) gene fragment, species delineation of *Anemina* sensu lato species (genera *Anemina*, *Amuranodonta*, and *Buldowskia*), and distribution maps of species present in the study area. Support values above the branches are percent posterior probabilities/ultrafast bootstraps. Vertical bars correspond to molecular operational taxonomic units by various species delimitation methods: red – TCS (95%); green – ABGD; blue – BINS of BOLD; and black – consensus. Support values >95% for both phylogenetic analyses are represented by an asterisk, support values <50% and those within each recognized MOTU were erased for clarity. Distribution maps of each species depict the potential distribution across the main river basins in shaded colors, white dots represent newly sequenced individuals.

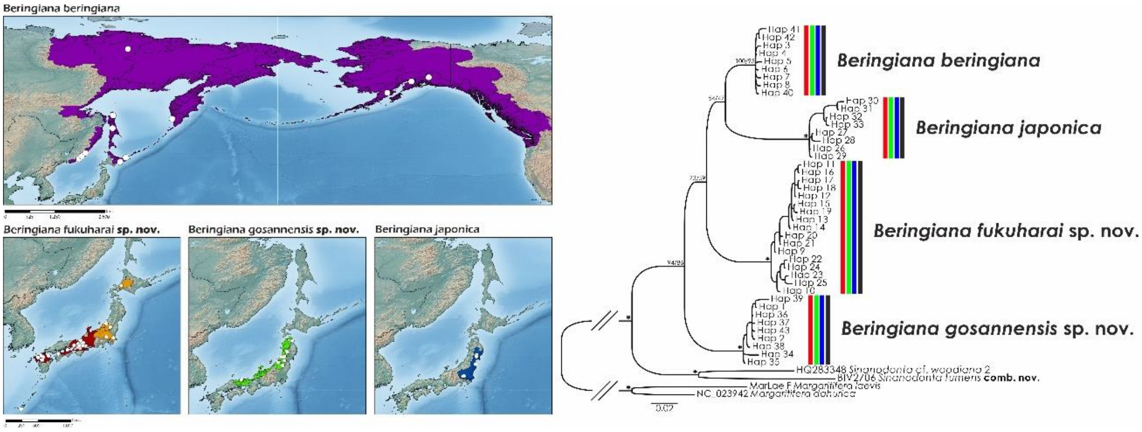


Figure 7. Bayesian Inference (BI) and Maximum likelihood (ML) phylogenetic tree inferred from the cytochrome c oxidase subunit I (COI) gene fragment, species delineation of *Beringiana* species, and distribution maps. Support values above the branches are percent posterior probabilities/ultrafast bootstraps. Vertical bars correspond to molecular operational taxonomic units by various species delimitation methods: red – TCS (95%); green – ABGD; blue – BINS of BOLD; and black – consensus. Support values >95% for both phylogenetic analyses are represented by an asterisk, support values <50% and those within each recognized MOTU were erased for clarity. Distribution maps of each species depict the potential distribution across the main river basins in shaded colors, white dots represent newly sequenced individuals. The distribution map of *Beringiana* sp. 2 shows the native range in red and introduced in orange.

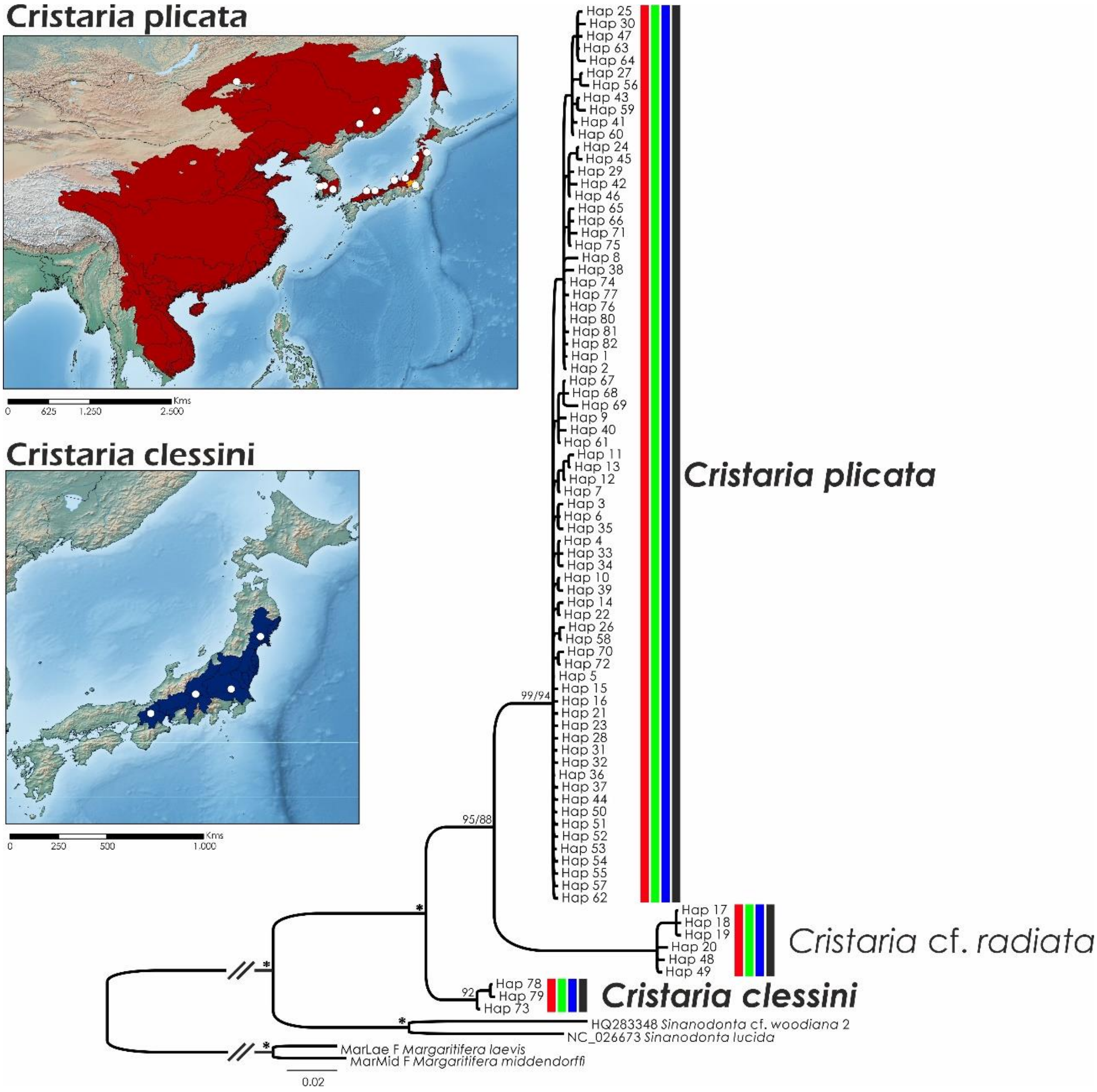


Figure 8. Bayesian Inference (BI) and Maximum likelihood (ML) phylogenetic tree inferred from the cytochrome c oxidase subunit I (COI) gene fragment, species delineation of *Cristaria* species, and distribution maps of species present in the study area. Support values above the branches are percent posterior probabilities/ultrafast bootstraps. Vertical bars correspond to molecular operational taxonomic units by various species delimitation methods: red – TCS (95%); green – ABGD; blue – BINS of BOLD; and black – consensus. Support values >95% for both phylogenetic analyses are represented by an asterisk, support values <50% and those within each recognized MOTU were erased for clarity. Distribution maps of each species depict the potential distribution across the main river basins in shaded colors, white dots represent newly sequenced individuals. The distribution map of *C. plicata* shows the native range in red and introduced in orange.

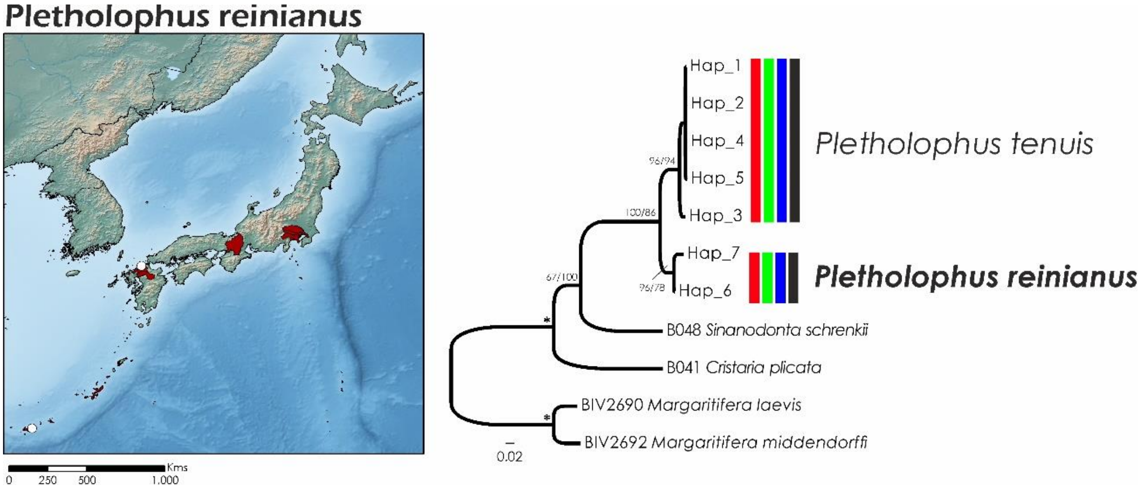
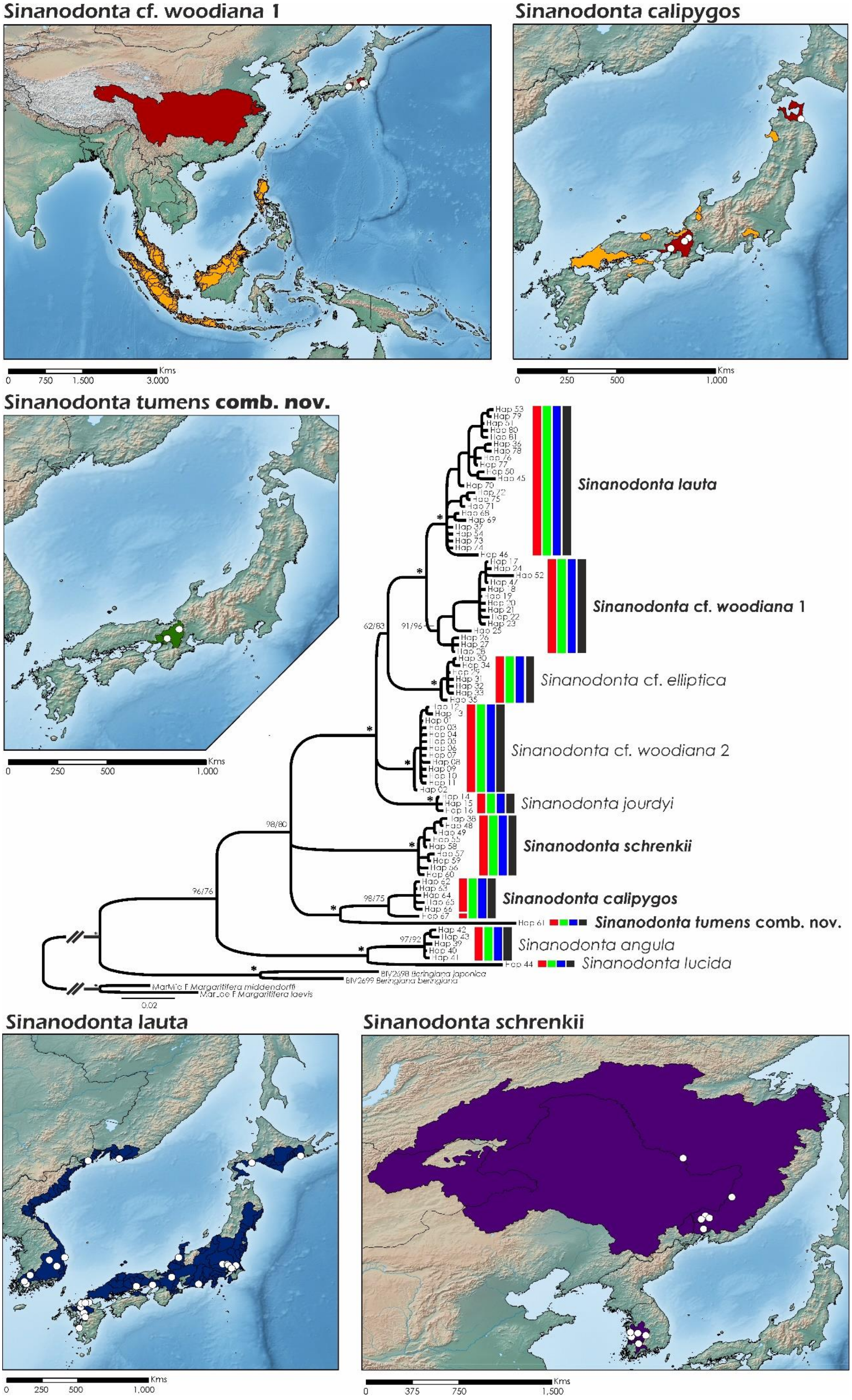


Figure 9. Bayesian Inference (BI) and Maximum likelihood (ML) phylogenetic tree inferred from the cytochrome c oxidase subunit I (COI) gene fragment, species delineation of *Pletholophus* species, and distribution maps of species present in the study area. Support values above the branches are percent posterior probabilities/ultrafast bootstraps. Vertical bars correspond to molecular operational taxonomic units by various species delimitation methods: red – TCS (95%); green – ABGD; blue – BINS of BOLD; and black – consensus. Support values >95% for both phylogenetic analyses are represented by an asterisk, support values <50% and those within each recognized MOTU were erased for clarity. Distribution maps of each species depict the potential distribution across the main river basins in shaded colors, white dots represent newly sequenced individuals.



Sinanodonta cf. woodiana 1

Sinanodonta calipygos

Sinanodonta tumens comb. nov.

Sinanodonta lauta

Sinanodonta schrenkii

Figure 10. Bayesian Inference (BI) and Maximum likelihood (ML) phylogenetic tree inferred from the cytochrome c oxidase subunit I (COI) gene fragment, species delineation of *Sinanodonta* species, and distribution maps. Support values above the branches are percent posterior probabilities/ultrafast bootstraps. Vertical bars correspond to molecular operational taxonomic units by various species delimitation methods: red – TCS (95%); green – ABGD; blue – BINS of BOLD; and black – consensus. Support values >95% for both phylogenetic analyses are represented by an asterisk, support values <50% and those within each recognized MOTU were erased for clarity. Distribution maps of each species depict the potential distribution across the main river basins in shaded colors, white dots represent newly sequenced individuals. Distribution maps of *Sinanodonta* cf. *woodiana* 1 and *S. calipygos* show the native range in red and introduced in orange.

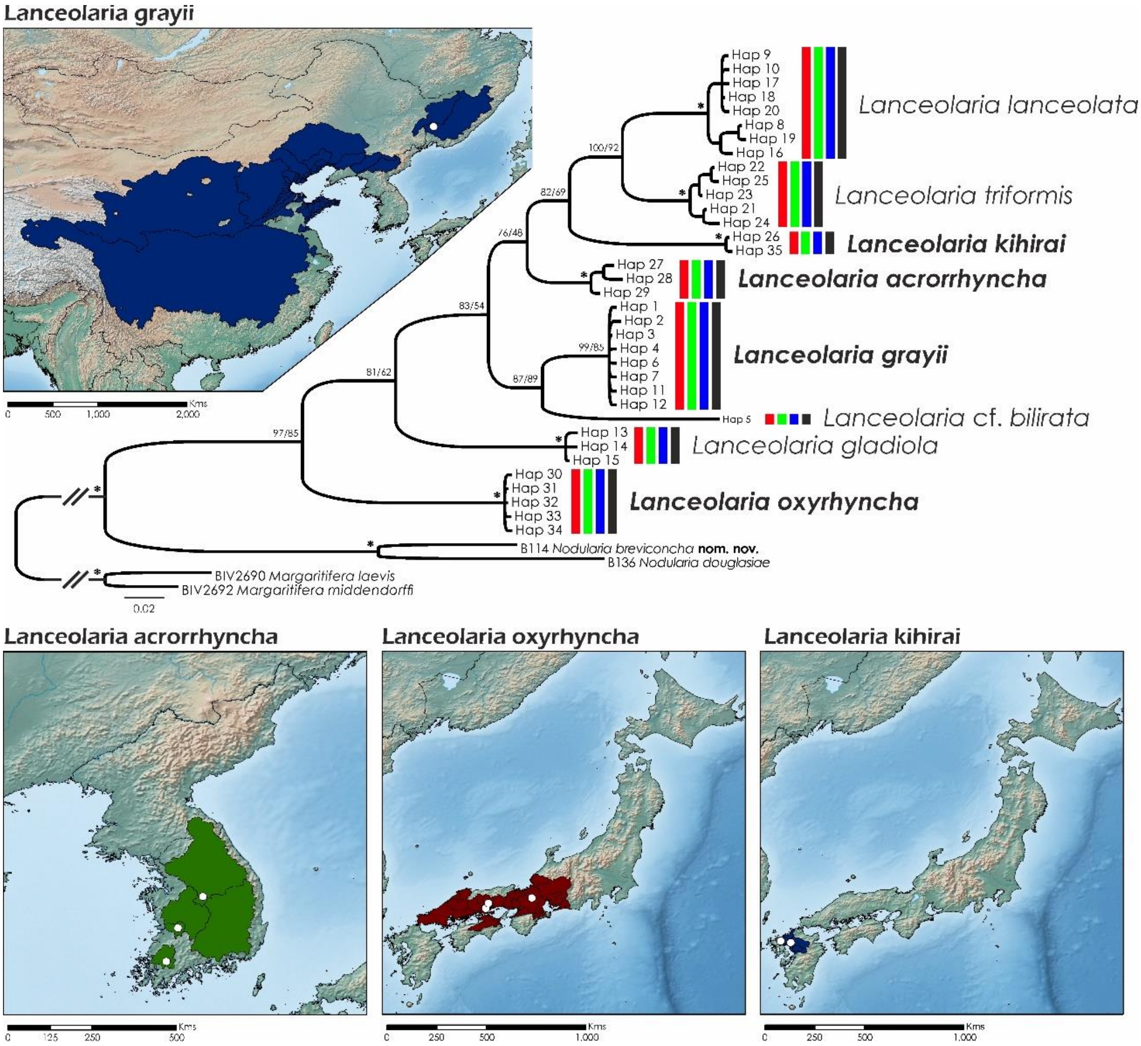


Figure 11. Bayesian Inference (BI) and Maximum likelihood (ML) phylogenetic tree inferred from the cytochrome c oxidase subunit I (COI) gene fragment, species delineation of *Lanceolaria* species, and distribution maps of species present in the study area. Support values above the branches are percent posterior probabilities/ultrafast bootstraps. Vertical bars correspond to molecular operational taxonomic units by various species delimitation methods: red – TCS (95%); green – ABGD; blue – BINS of BOLD; and black – consensus. Support values >95% for both phylogenetic analyses are represented by an asterisk, support values <50% and those within each recognized MOTU were erased for clarity. Distribution maps of each species depict the potential distribution across the main river basins in shaded colors, white dots represent newly sequenced individuals.

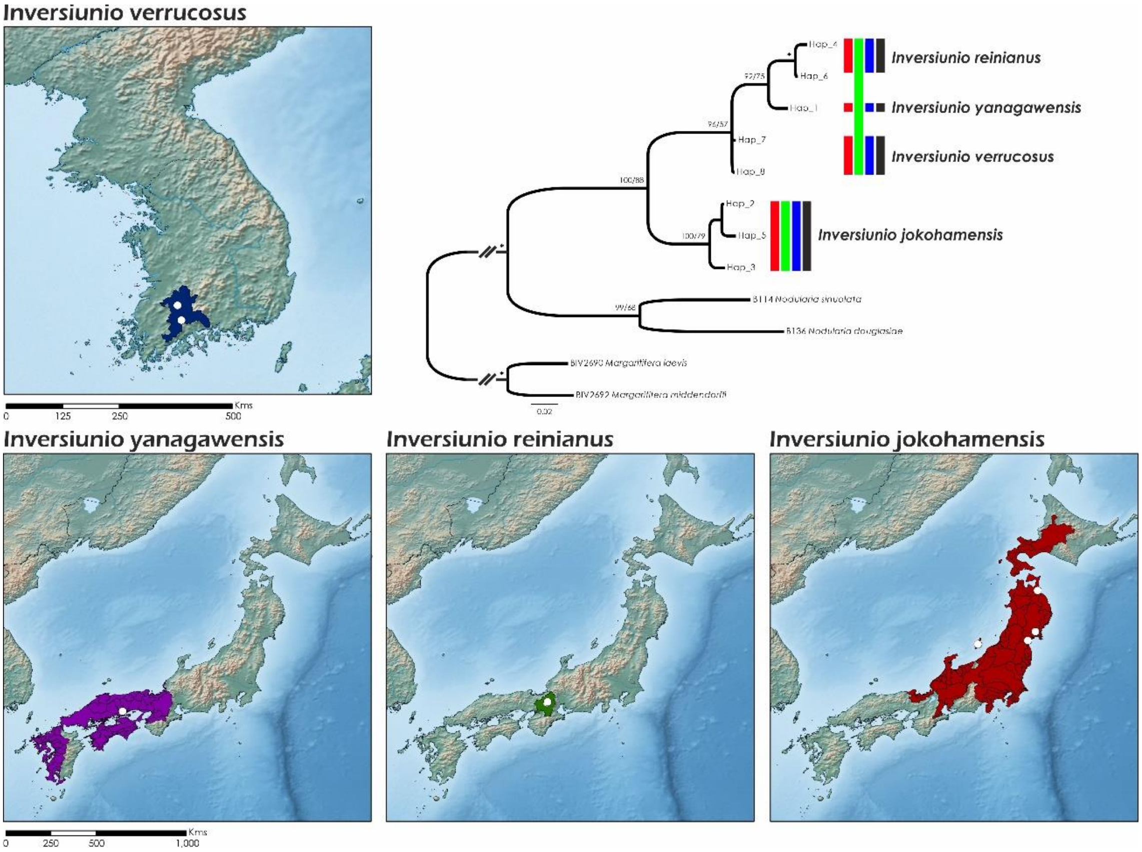


Figure 12. Bayesian Inference (BI) and Maximum likelihood (ML) phylogenetic tree inferred from the cytochrome c oxidase subunit I (COI) gene fragment, species delineation of *Inversiunio* species, and distribution maps of species present in the study area. Support values above the branches are percent posterior probabilities/ultrafast bootstraps. Vertical bars correspond to molecular operational taxonomic units by various species delimitation methods: red – TCS (95%); green – ABGD; blue – BINS of BOLD; and black – consensus. Support values >95% for both phylogenetic analyses are represented by an asterisk, support values <50% and those within each recognized MOTU were erased for clarity. Distribution maps of each species depict the potential distribution across the main river basins in shaded colors, white dots represent newly sequenced individuals.

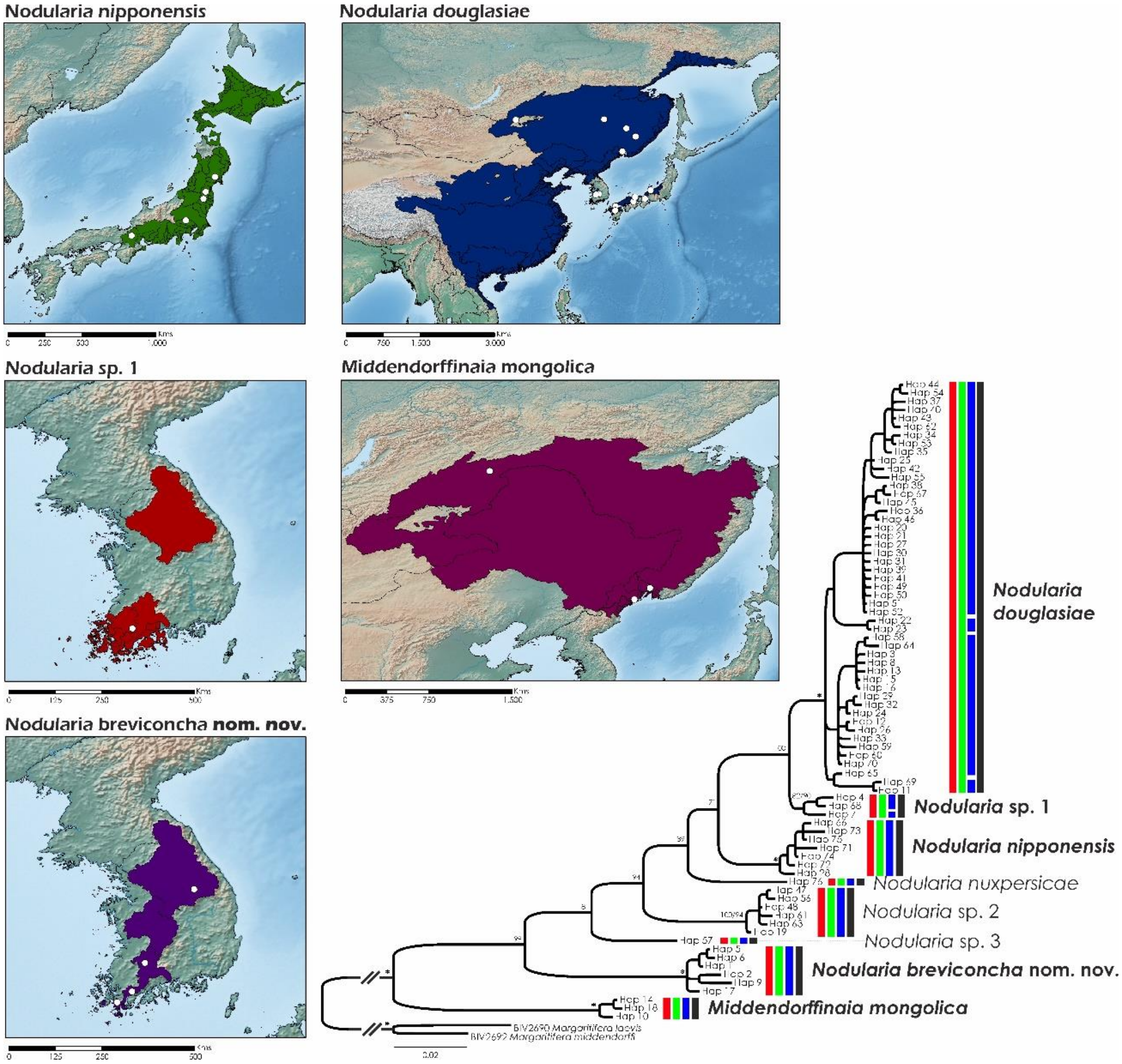


Figure 13. Bayesian Inference (BI) and Maximum likelihood (ML) phylogenetic tree inferred from the cytochrome c oxidase subunit I (COI) gene fragment, species delineation of *Nodularia* and *Middendorffinaia* species, and distribution maps of species present in the study area. Support values above the branches are percent posterior probabilities/ultrafast bootstraps. Vertical bars correspond to molecular operational taxonomic units by various species delimitation methods: red – TCS (95%); green – ABGD; blue – BINS of BOLD; and black – consensus. Support values >95% for both phylogenetic analyses are represented by an asterisk, support values <50% and those within each recognized MOTU were erased for clarity. Distribution maps of each species depict the potential distribution across the main river basins in shaded colors, white dots represent newly sequenced individuals.

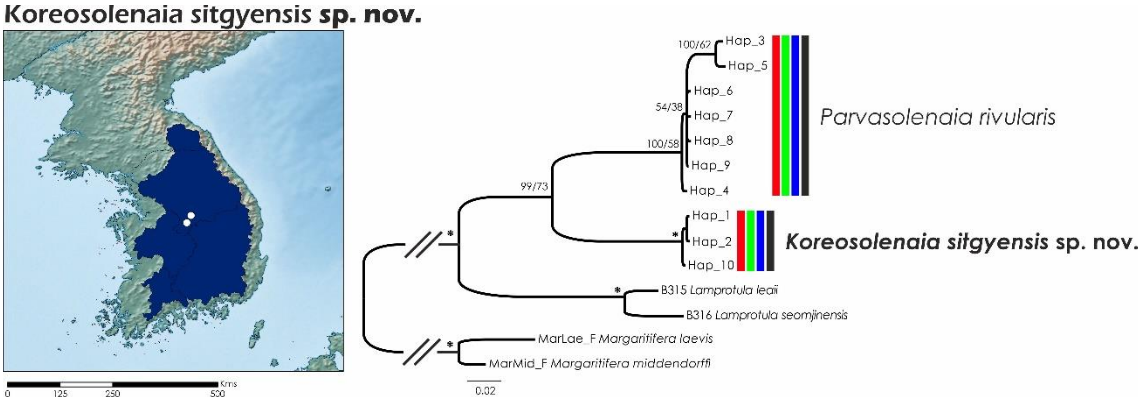


Figure 14. Bayesian Inference (BI) and Maximum likelihood (ML) phylogenetic tree inferred from the cytochrome c oxidase subunit I (COI) gene fragment, species delineation of *Koreosolenaia* and *Parvasolenaia* species, and distribution maps of species present in the study area. Support values above the branches are percent posterior probabilities/ultrafast bootstraps. Vertical bars correspond to molecular operational taxonomic units by various species delimitation methods: red – TCS (95%); green – ABGD; blue – BINS of BOLD; and black – consensus. Support values >95% for both phylogenetic analyses are represented by an asterisk, support values <50% and those within each recognized MOTU were erased for clarity. Distribution maps of each species present in the study area depict the potential distribution across the main river basins in shaded colors, white dots represent newly sequenced individuals.

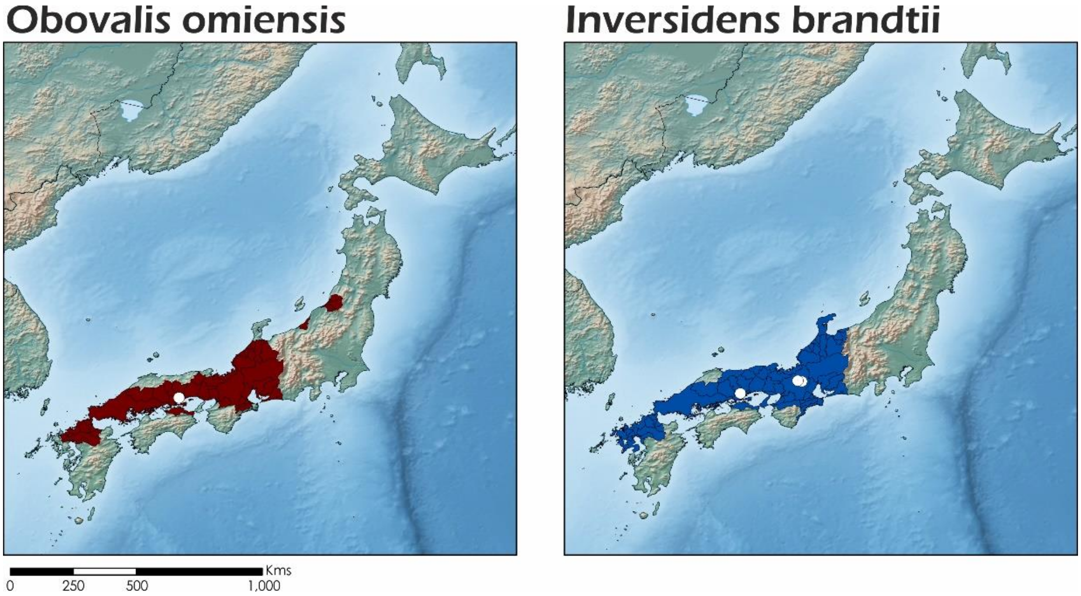


Figure 15. Distribution maps of *Obovalis omiensis* and *Inversidens brandtii*. Distribution maps of each species depict the potential distribution across the main river basins in shaded colors, white dots represent newly sequenced individuals.

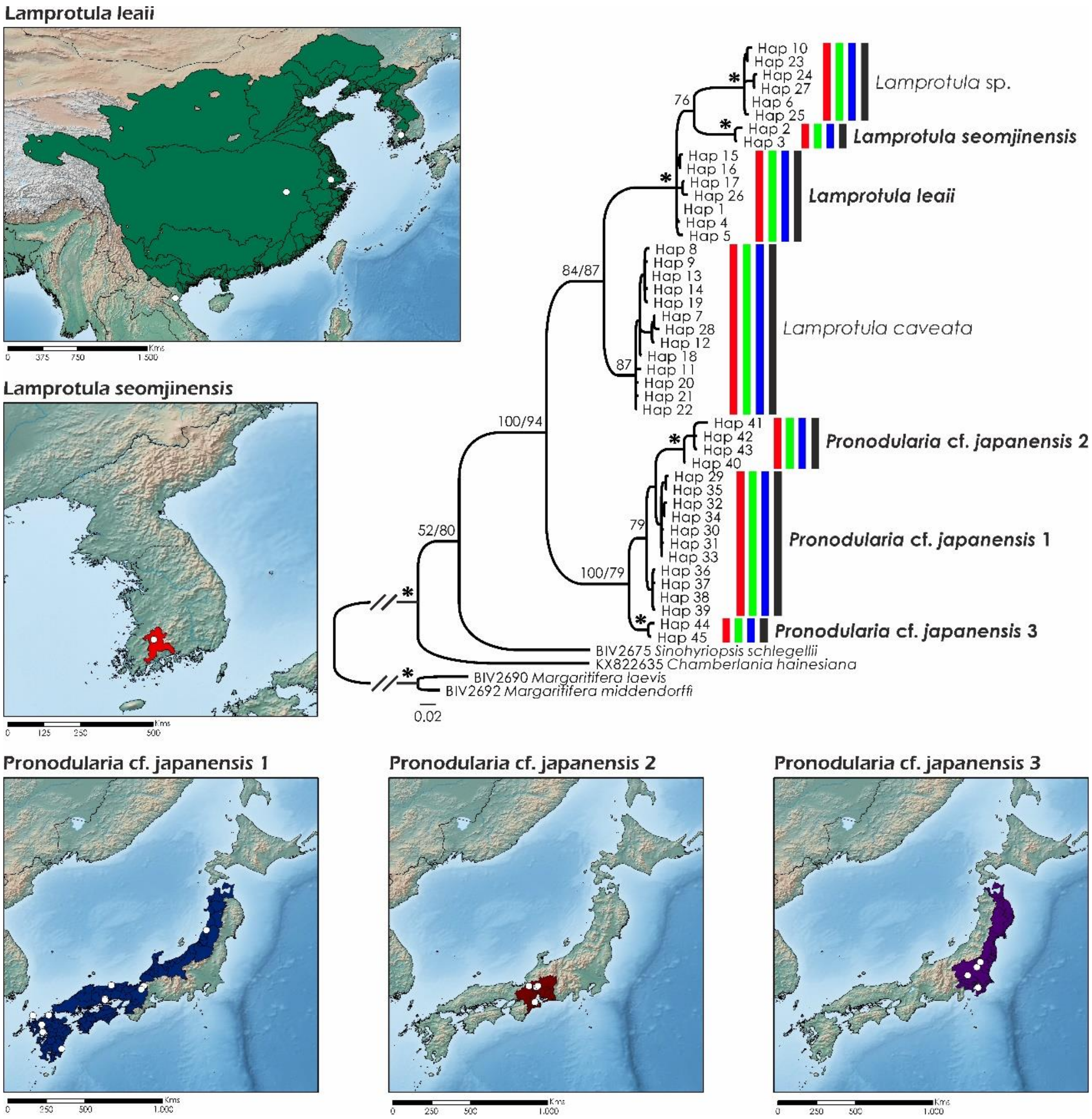


Figure 16. Bayesian Inference (BI) and Maximum likelihood (ML) phylogenetic tree inferred from the cytochrome c oxidase subunit I (COI) gene fragment, species delineation of *Lamprotula* and *Pronodularia* species, and distribution maps of species present in the study area. Support values above the branches are percent posterior probabilities/ultrafast bootstraps. Vertical bars correspond to molecular operational taxonomic units by various species delimitation methods: red – TCS (95%); green – ABGD; blue – BINS of BOLD; and black – consensus. Support values >95% for both phylogenetic analyses are represented by an asterisk, support values <50% and those within each recognized MOTU were erased for clarity. Distribution maps of each species depict the potential distribution across the main river basins in shaded colors, white dots represent newly sequenced individuals.

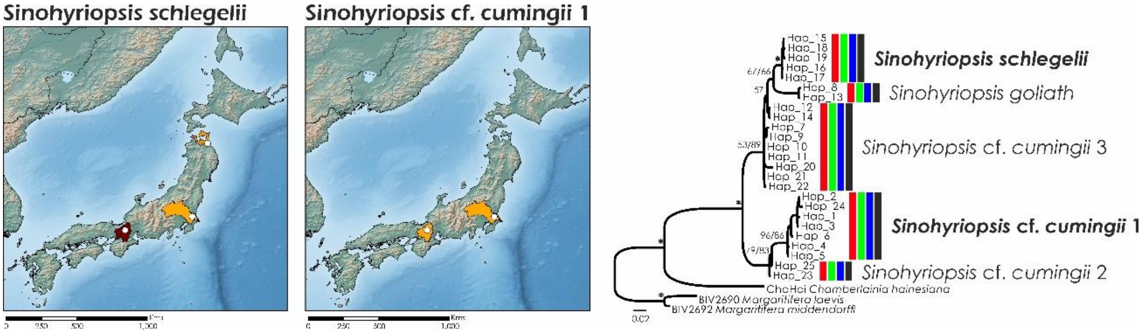
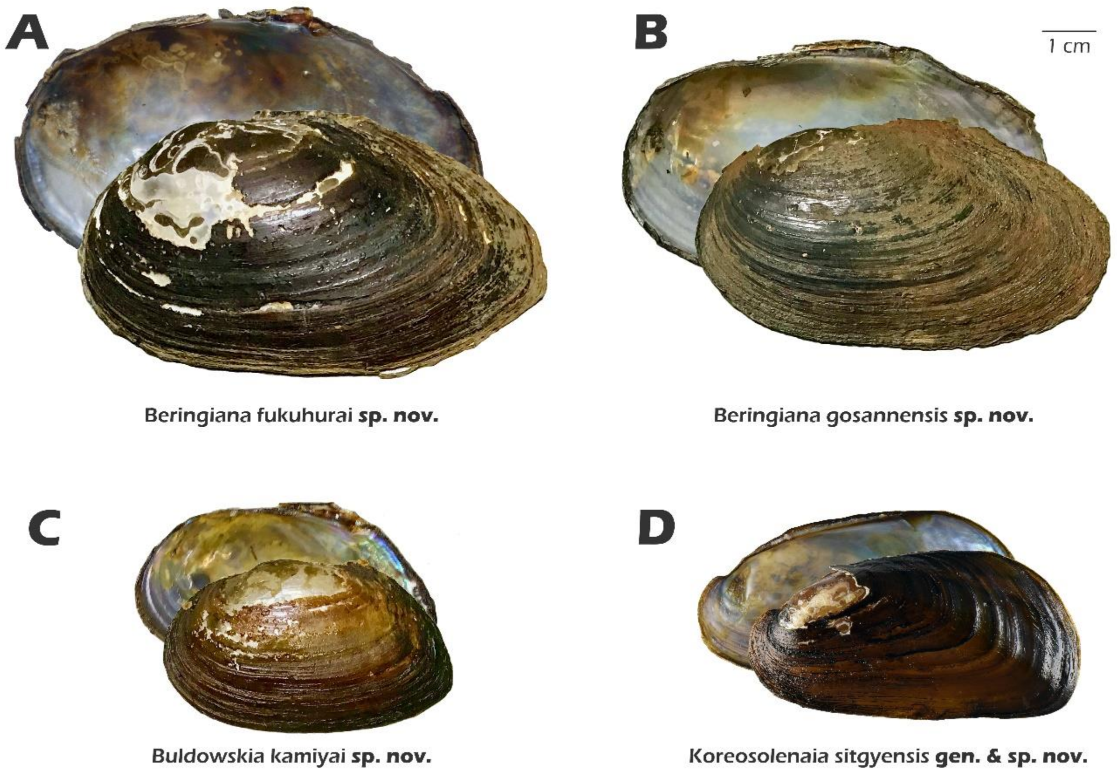


Figure 17. Bayesian Inference (BI) and Maximum likelihood (ML) phylogenetic tree inferred from the cytochrome c oxidase subunit I (COI) gene fragment, species delineation of *Sinohyriopsis* species, and distribution maps. Support values above the branches are percent posterior probabilities/ultrafast bootstraps. Vertical bars correspond to molecular operational taxonomic units by various species delimitation methods: red – TCS (95%); green – ABGD; blue – BINS of BOLD; and black – consensus. Support values >95% for both phylogenetic analyses are represented by an asterisk, support values <50% and those within each recognized MOTU were erased for clarity. Distribution maps of *Sinohyriopsis schlegelii* and *Sinohyriopsis* cf. *cumingii* 1 depict the potential distribution across the main river basins of the native range shaded in red and the introduced range in orange, white dots represent newly sequenced individuals.



Beringiana fukuhurai **sp. nov.**

Beringiana gosannensis **sp. nov.**

Buldowskia kamiyai **sp. nov.**

Koreosolenaia sitgyensis **gen. & sp. nov.**

Figure 18. Shells of the holotypes of the newly described species in this study. **A.** *Beringiana fukuharai* Sano, Hattori & Kondo **sp. nov.** (OMNH-Mo 39101); **B.** *Beringiana gosannensis*

Sano, Hattori & Kondo **sp. nov.** (OMNH-Mo 39089); **C.** *Buldowskia kamiyai* Sano, Hattori & Kondo **sp. nov.** (OMNH-Mo 39097); **D.** *Koreosolenaia sitgyensis* Lee, Kim, Lopes-Lima & Bogan **gen. & sp. nov.** (NNIBR-IV28166). OMNH – Osaka Museum of Natural History, Japan, NNIBR – Nakdonggang National Institute of Biological Resources, South Korea.

Table 1. List of sequences from the combined dataset (COI + 28S rRNA) used for the phylogenies of the Palaeoheterodonta with respective species, countries, voucher numbers, and GenBank references. Acronyms for the voucher deposit institutions as follows: ANSP – Academy of Natural Sciences of Philadelphia, U.S.A.; FMNH – Field Museum of Natural History, Chicago, U.S.A.; MCZ – Museum of Comparative Zoology Harvard, U.S.A.; MHS – Matsuyama High School; NCSM – North Carolina Museum of Natural Sciences, U.S.A.; NNIBR – Nakdonggang National Institute of Biological Resources, South Korea; NCU – Nanchang University, China; OMNH – Osaka Museum of Natural History, Japan; RMBH – Russian Museum of Biodiversity Hotspots, Arkhangelsk, Russia; UMMZ – University of Michigan Museum of Zoology, U.S.A.

Table 1. List of sequences from the combined dataset (COI + 28S rRNA) used for the phylogenies of the Palaeoheterodonta with respective species, countries, voucher numbers, and GenBank references. Acronyms for the voucher deposit institutions as follows: ANSP – Academy of Natural Sciences of Philadelphia, U.S.A.; FMNH – Field Museum of Natural History, Chicago, U.S.A.; MCZ – Museum of Comparative Zoology Harvard, U.S.A.; MHS – Matsuyama High School; NCSM – North Carolina Museum of Natural Sciences, U.S.A.; NNIBR – Nakdonggang National Institute of Biological Resources, South Korea; NCU – Nanchang University, China; OMNH – Osaka Museum of Natural History, Japan; RMBH – Russian Museum of Biodiversity Hotspots, Arkhangelsk, Russia; UMMZ – University of Michigan Museum of Zoology, U.S.A.

Reference	Species	COI	28S	Country	Voucher	Studies for COI/28S
UNIONIDAE						
AcuChi	*Acuticosta chinensis*	MG462921	MG595448	China	NCU 16_XPWU_SU011	Huang et al 2019
AcuCor	*Aculamprotula coreana*	Submitted	Submitted	South Korea	NNIBR IV29230	This study
AcuFib1	*Aculamprotula* cf. *fibrosa* 1	MG462909	MG595438	China	NCU 16_XPWU_SU001	Huang et al 2019
AcuFib2	*Aculamprotula* cf. *fibrosa* 2	MG462910	MG595439	China	NCU 16_XPWU_SU002	Huang et al 2019
AcuScr	*Aculamprotula scripta*	MG462911	MG595441	China	NCU 16_XPWU_SU004	Huang et al 2019
AcuTie	*Aculamprotula tientsinensis*	MG462913	MG595437	China	NCU 16_XPWU_SU000	Huang et al 2019
AcuTor	*Aculamprotula tortuosa*	MG462916	MG595443	China	NCU 16_XPWU_SU006	Huang et al 2019
AlaMar	*Alasmidonta marginata*	AF156502	AF400688	USA	UMMZ 265695	Graf & O'Foighil 2000/Graf 2002
AmbPli	*Amblema plicata*	U56841	AF305385	USA		Hoeh et al 1998/Graf 2002
AmuKij	*Amuranodonta kijaensis*	MK574204	MK574473	Russia	RMBH Biv_228	Bolotov et al SubmittedA
AneArcC	*Anemina arcaeformis*	MG462936	MG595463	China	NCU 16_XPWU_SU026	Huang et al 2019
AneArcK	*Anemina arcaeformis*	Submitted	Submitted	South Korea	NNIBR IV29241	This study
AneArcJ	*Anemina arcaeformis*	Submitted	Submitted	Japan	MHS AAfk067	This study
AnoAna	*Anodonta anatina*	KX822632	KX822588	Russia		Lopes-Lima et al 2017b
AnoCyg	*Anodonta cygnea*	KX822633	KX822589	Italy		Lopes-Lima et al 2017b
AnoNut	*Anodonta nuttalliana*	KX822634	KX822590	USA		Lopes-Lima et al 2017b
BerBerJ	*Beringiana beringiana*	Submitted	Submitted	Japan	MHS fk036	This study
BerBerR	*Beringiana beringiana*	Submitted	Submitted	Russia	RMBH biv_169	This study
BerJap	*Beringiana japonica*	Submitted	Submitted	Japan	MHS MSl-snA	This study

BerGos	*Beringiana gosannensis* **sp. nov.**	Submitted	Submitted	Japan	OMNH Mo 39089	This study
BinCum	"*Bineurus*" *cumingii*	KP795025	KP795008	Laos	UMMZ 304648	Pfeiffer & Graf 2015
BinMou1	*Bineurus* aff. *mouhotii* sp.1	KX865876	KX865747	Laos	RMBH biv_182_2	Bolotov et al 2017a
BerFuk	*Beringiana fukuharai* **sp. nov.**	Submitted	Submitted	Japan	OMNH Mo 39101	This study
BulFlaA	*Buldowskia flavotincta*	Submitted	Submitted	South Korea	NNIBR IV29232	This study
BulFlaB	*Buldowskia flavotincta*	Submitted	Submitted	South Korea	NNIBR IV29244	This study
BulSuiA	*Buldowskia suifunica*	MK574190	MK574460	Russia	RMBH biv225_11	Bolotov et al SubmittedA
BulSuiB	*Buldowskia suifunica*	MK574193	MK574463	Russia	RMBH biv227_3	Bolotov et al submittedA
BulIwaJ	*Buldowskia iwakawai* **comb. nov.**	Submitted	Submitted	Japan	MHS AAfk080	This study
BulIwaK	*Buldowskia iwakawai* **comb. nov.**	Submitted	Submitted	South Korea	NNIBR B100	This study
BulKam	*Buldowskia kamiyai* **sp. nov.**	Submitted	Submitted	Japan	OMNH Mo 39097	This study
BulShaK	*Buldowskia shadini*	Submitted	Submitted	South Korea	NNIBR IV29248	This study
BulShaR	*Buldowskia shadini*	MK574197	MK574467	Russia	RMBH biv_228_16	Bolotov et al SubmittedA
ChaHai	*Chamberlainia hainesiana*	KX822635	KX822592	Thailand		Lopes-Lima et al 2017b
CoeAeg	*Coelatura aegyptiaca*	JN243892	JN243870	Egypt		Whelan et al 2011
ConCon	*Contradens contradens*	MF352289	MF352406	Malaysia		Bolotov et al 2017b
CriCle	*Cristaria clessini*	Submitted	Submitted	Japan	MHS MCp-sigB	This study
CriPliC	*Cristaria plicata*	MG462956	MG595484	China	NCU 16_XPWU_SU047	Huang et al 2019
CriPliK	*Cristaria plicata*	Submitted	Submitted	South Korea	NNIBR IV29256	This study
CriPliR	*Cristaria plicata*	KX822637	KX822594	Russia		Lopes-Lima et al 2017b
CunCel	*Cuneopsis celtiformis*	MG462964	MG595488	China	NCU 16_XPWU_SU051	Huang et al 2019
CunHeu1	*Cuneopsis* cf. *heudei* 1	MG462970	MG595494	China	NCU 16_XPWU_SU057	Huang et al 2019
CunHeu2	*Cuneopsis* cf. *heudei* 2	MG462973	MG595497	China	NCU 16_XPWU_SU060	Huang et al 2019
CunPis	*Cuneopsis pisciculus*	MG462977	MG595504	China	NCU 16_XPWU_SU067	Huang et al 2019
CunRuf	*Cuneopsis rufescens*	MG462982	MG595510	China	NCU 16_XPWU_SU073	Huang et al 2019
EllCom	*Elliptio complanata*	EU448173	JF899181	USA		Unpublished/Distel et al 2011
EnsSag1	*Ensidens* aff. *sagittarius* sp.1	KP795033	KP795015	Cambodia	UMMZ 304651	Pfeiffer & Graf 2015
GonAng	*Gonidea angulata*	DQ272371	AF400691	USA		Gustafson & Iwamoto 2005/Graf 2002
HyrBia	*Hyriopsis bialata*	KX822643	KX822600	Thailand		Lopes-Lima et al 2017b

InvBra	*Inversidens brandtii*	Submitted	Submitted	Japan	MHS MIb-sig01	This study
InvJok	*Inversiunio jokohamensis*	Submitted	Submitted	Japan	MHS Ij21-28	This study
InvRei	*Inversiunio reinianus*	Submitted	Submitted	Japan	MHS MIr-sig02	This study
InvVer	*Inversiunio verrucosus*	Submitted	Submitted	South Korea	NNIBR IV29236	This study
InvYan	*Inversiunio yanagawensis*	Submitted	Submitted	Japan	MHS MIy-okX	This study
LamCar	*Lampsilis cardium*	AF120653	AF305386	USA		Giribet & Wheeler 2002/Graf 2002
KorSit	*Koreosolenaia sitgyensis* **sp. nov.**	Submitted	Submitted	South Korea	NCSM 113454	This study
LamCavA	*Lamprotula caveata*	MG462991	MG595518	China	NCU 16_XPWU_SU081	Huang et al 2019
LamCavB	*Lamprotula caveata*	MG462992	MG595522	China	NCU 16_XPWU_SU085	Huang et al 2019
LamCor	*Lamellidens corrianus*	JN243903	JN243881	Myanmar		Whelan et al 2011
LamLeaC	*Lamprotula leaii*	MG463000	MG595527	China	NCU 16_XPWU_SU090	Huang et al 2019
LamLeaK	*Lamprotula leaii*	Submitted	Submitted	South Korea	NNIBR IV29237	This study
LamSpA	*Lamprotula* sp.	MG463001	MG595529	China	NCU 16_XPWU_SU092	Huang et al 2019
LamSpB	*Lamprotula* sp.	MG462997	MG595524	China	NCU 16_XPWU_SU087	Huang et al 2019
LamSeo	*Lamprotula seomjinensis*	Submitted	Submitted	South Korea	NNIBR IV29238	This study
LanAcr	*Lanceolaria acrorrhyncha*	Submitted	Submitted	South Korea	NNIBR IV29260	This study
LanBil	*Lanceolaria* cf. *bilirata*	KX822650	KX822607	Vietnam		Lopes-Lima et al 2017b
LanGla	*Lanceolaria gladiola*	MG463007	MG595535	China	NCU 16_XPWU_SU098	Huang et al 2019
LanGra	*Lanceolaria grayii*	MG463010	MG595537	China	NCU 16_XPWU_SU100	Huang et al 2019
LanKih	*Lanceolaria kihirai*	Submitted	Submitted	Japan	MHS MLs-fk01	This study
LanLanA	*Lanceolaria lanceolata*	MG462949	MG595480	China	NCU 16_XPWU_SU043	Huang et al 2019
LanLanB	*Lanceolaria lanceolata*	MG462953	MG595481	China	NCU 16_XPWU_SU044	Huang et al 2019
LanOxy	*Lanceolaria oxyrhyncha*	Submitted	Submitted	Japan	MHS MLo-sig01	This study
LanTri	*Lanceolaria triformis*	MG463014	MG595541	China	NCU 16_XPWU_SU104	Huang et al 2019
LasCom	*Lasmigona compressa*	AF156503	DQ191414	USA	UMMZ 265696	Graf & O'Foighil 2000/Graf & Cummings 2006
LegWhe	*Leguminaia wheatleyi*	KX822651	KX822608	Turkey		Lopes-Lima et al 2017
LeoBha	*Leoparreysia bhamoensis*	JN243900	JN243876	Myanmar		Whelan et al 2011
LepLan	*Lepidodesma languilati*	MG463015	MG595544	China	NCU 16_XPWU_SU107	Huang et al 2019
MicBon	*Microcondylaea bonellii*	KX822652	KX822609	Italy		Lopes-Lima et al 2017b

MidMonA	*Middendorffinaia mongolica*	MH974548	MK574554	Russia	RMBH biv_229_2	Klishko et al 2019/Bolotov et al SubmittedA
MidMonB	*Middendorffinaia mongolica*	MH974551	MK574557	Russia	RMBH biv_99_3	Klishko et al 2019/ Bolotov et al SubmittedA
MonIno2	"*Monodontina*" aff. "*inoscularis*" sp.2	KP795027	KP795010	Cambodia	UMMZ 304349	Pfeiffer & Graf 2015
MonVon1	*Monodontina* aff. *vondembuschiana* sp.1	KX865861	KX865733	Thailand	RMBH biv_122	Bolotov et al 2017a
NodDouC	*Nodularia douglasiae*	KX822653	KX822610	China		Lopes-Lima et al 2017b
NodDouJ	*Nodularia douglasiae*	Submitted	Submitted	Japan	MHS MNd-fk01	This study
NodDouK	*Nodularia douglasiae*	Submitted	Submitted	South Korea	NNIBR IV29231	This study
NodNip	*Nodularia nipponensis*	Submitted	Submitted	Japan	MHS Un26-02	This study
NodNux	*Nodularia nuxpersicae*	KX822654	KX822611	Vietnam		Lopes-Lima et al 2017b
NodBre	*Nodularia breviconcha* **nom. nov.**	Submitted	Submitted	South Korea	NNIBR IV29233	This study
NodSp1	*Nodularia* sp. 1	Submitted	Submitted	South Korea	NNIBR IV29266	This study
NodSp2	*Nodularia* sp. 2	MG463023	MG595560	China	NCU 16_XPWU_SU123	Huang et al 2019
OboOmi	*Obovalis omiensis*	Submitted	Submitted	Japan	MHS MPo-okA	This study
ParRiv	*Parvasolenaia rivularis*	MG463101	MG595627	China	NCU 16_XPWU_SU190	Huang et al 2019
PhyMod	*Physunio modelli*	KX865883	KX865754	Thailand	RMBH biv 125_2	Bolotov et al 2017a
PilCo1	*Pilsbryoconcha* aff. *compressa* sp.1	KX865871	KX865743	Thailand	RMBH biv 125_1	Bolotov et al 2017a
PilExi1	*Pilsbryoconcha* aff. *exilis* sp.1	KP795024	KP795007	Cambodia	UMMZ 304647	Pfeiffer & Graf 2015
PleTen	*Pletholophus tenuis*	KX822658	KX822614	Vietnam		Lopes-Lima et al 2017b
PotLit	*Potomida littoralis*	JN243905	JN243883	France		Whelan et al 2011
ProJap1	*Pronodularia* cf. *japanensis* 1	Submitted	Submitted	Japan	MHS MPj-ok02	This study
ProJap3	*Pronodularia* cf. *japanensis* 3	Submitted	Submitted	Japan	MHS PJST-10	This study
PseAva	*Pseudodon avae*	KX865858	KX865730	Myanmar	RMBH biv_110_5	Bolotov et al 2017a
PseCom	*Pseudanodonta complanata*	KX822661	KX822617	Ukraine		Lopes-Lima et al 2017b
PseMan	*Pseudodon manueli*	MF352228	MF352358	Myanmar	RMBH biv_246_1	Bolotov et al 2017b
PtyPfi	*Ptychorhynchus pfisteri*	MG463036	MG595564	China	NCU 16_XPWU_SU127	Huang et al 2019
PygGra	*Pyganodon grandis*	AF231734	AF305384	USA		Bogan & Hoeh 2000/Graf & O'Foighil 2000
QuaQua	*Quadrula quadrula*	AF156511	DQ191417	USA		Graf & O'Foighil 2000/Graf & Cummings 2006
RadMou	*Radiatula mouhoti*	MF352234	MF352363		RMBH biv_248_1	Bolotov et al 2017a
RecSum	*Rectidens sumatrensis*	KX822664	KX822620	Malaysia		Lopes-Lima et al 2017b

SchLam	*Schistodesmus lampreyanus*	MG463037	MG595570	China	NCU 16_XPWU_SU133	Huang et al 2019
SchSp	*Schistodesmus* sp.	MG463043	MG595571	China	NCU 16_XPWU_SU134	Huang et al 2019
SchSpi	*Schistodesmus spinosus*	MG463046	MG595573	China	NCU 16_XPWU_SU136	Huang et al 2019
SimAmb	*Simpsonaias ambigua*	KX822666	KX822622	USA	NCSM30607	Lopes-Lima et al 2017b
SinAng	*Sinanodonta angula*	MG463053	MG595580	China	16 NCU XPWU SU143	Huang et al 2019
SinCal	*Sinanodonta calipygos*	Submitted	Submitted	Japan	MHS SC_Shiga_4	This study
SinCum	*Sinohyriopsis cumingii*	MG463086	MG595613	China	NCU 16_XPWU_SU176	Huang et al 2019
SinEll	*Sinanodonta* cf. *elliptica*	MG463058	MG595585	China	16 NCU XPWU SU148	Huang et al 2019
SinJou	*Sinanodonta jourdyi*	KX822668	KX822625	Vietnam		Lopes-Lima et al 2017b
SinLauJ	*Sinanodonta lauta*	Submitted	Submitted	Japan	MHS SL_Shizuoka_1	This study
SinLauK	*Sinanodonta lauta*	Submitted	Submitted	South Korea	NNIBR IV29267	This study
SinLauR	*Sinanodonta lauta*	KY561633	KY561665	Russia	RMBH biv_191_1	Bolotov et al 2017a
SinLuc	*Sinanodonta lucida*	MG463066	MG595589	China	NCU 16_XPWU_SU152	Huang et al 2019
SinScg	*Sinohyriopsis schlegelii*	Submitted	Submitted	Japan	MHS Hs21-02	This study
SinSch	*Sinanodonta schrenkii*	Submitted	Submitted	South Korea	NNIBR IV29267	This study
SinTum	*Sinanodonta tumens* **comb. nov.**	Submitted	Submitted	Japan	MHS fk156	This study
SinWoo1	*Sinanodonta* cf. *woodiana* 1	MG463052	MG595599	China	NCU 16_XPWU_SU162	Huang et al 2019
SinWoo2	*Sinanodonta* cf. *woodiana* 2	MG463080	MG595608	China	NCU 16_XPWU_SU171	Huang et al 2019
SolCar	*Solenaia carinata*	MG463087	MG595616	China	NCU 16_XPWU_SU179	Huang et al 2019
SolOle1	*Solenaia* cf. *oleivora* 1	MG463091	MG595618	China	NCU 16_XPWU_SU181	Huang et al 2019
SolOle2	*Solenaia* cf. *oleivora* 2	MG463093	MG595620	China	NCU 16_XPWU_SU183	Huang et al 2019
SolOle3	*Solenaia* cf. *oleivora* 3	MG463092	MG595619	China	NCU 16_XPWU_SU182	Huang et al 2019
SolSpV	*Solenaia* sp.	KY561639	KY561670	Vietnam	RMBH biv_89_1	Bolotov et al 2017a
StrUnd	*Strophitus undulatus*	AF156505	DQ191415	USA		Graf & O'Foighil 2000/Graf & Cummings 2006
TraNes	*Trapezoideus nesemanni*	KX865906	KX865777	Myanmar	RMBH biv_144_14	Bolotov et al 2017a
UniCra	*Unio crassus*	KC703878	KC703644	France		Prié & Puillandre 2014
UniGib	*Unio gibbus*	KX822671	KX822629	Morocco		Lopes-Lima et al 2017b
UniPic	*Unio pictorum*	KC429109	KC429447	Europe		Sharma et al 2013
UniTum	*Unio tumidus*	KX822672	KX822630	Ukraine		Lopes-Lima et al 2017b

IRIDINIDAE						
AspPfe	*Aspatharia pfeifferiana*	KC429107	JN243863	Zambia		Sharma et al 2013/Whelan et al 2011
ChaWah	*Chambardia wahlbergi*	JN243886	JN243864	Zambia	ANSP 419403	Whelan et al 2011
ETHERIIDAE						
EthEll	*Etheria elliptica*	KP184897	KP184873	Zambia	FMNH 343930	Graf et al 2015
MULLERIIDAE						
LamEns	*Lamproscapha ensiformis*	KP795021	KP795004	Peru	ANSP 416342	Pfeiffer & Graf 2015
MycSil	*Mycetopoda siliquosa*	JN243887	JN243865	Peru	ANSP 416344	Whelan et al 2011
HYRIIDAE						
HyrDep	*Hyridella depressa*	KP184903	KP184879	Australia		Graf et al 2015
VelAmb	*Velesunio ambiguus*	KP184915	KP184892	Australia		Graf et al 2015
MARGARITIFERIDAE						
MarLae	*Margaritifera laevis*	Submitted	Submitted	Japan	MHS MMt-tc01	This study
MarMid	*Margaritifera middendorffi*	Submitted	Submitted	Japan	MHS OMEB630	This study
TRIGONIIDAE						
NeoLam	*Neotrigonia lamarckii*	KC429105	KC429443	Australia		Sharma et al 2013
NeoMar	*Neotrigonia margaritacea*	KP068122	KP068171	Australia	MCZ 379090	González & Giribet 2015

Table 2. The number of sequences, haplotypes, and sizes of all datasets used, as well as substitution models for each partition for all phylogenetic analyses. * were not used for phylogenetic analyses due to the low sample size.

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Dataset	Sequences (new)	Haplotypes	Size (nt)	Models							
				COI codon 1		COI codon 2		COI codon 3		28S	
				BI	ML	BI	ML	BI	ML	BI	ML
COI + 28S											
Unionida	145	--	1100	GTR+I+G	TN+F+I+G4	F81+I	F81+F+I	GTR+G	TIM+F+ASC+R4	GTR+I+G	GTR+F+I+G4
COI											
Aculamprotula	28(3)	13	651	GTR+G	TRN+G	F81+I	F81+I	HKY	HKY	-----	-----
Anemina	92(48)	60	618	GTR+G	TN+F+G4	F81+I	TPM3+F+I	GTR+G	TN+F+G4	-----	-----
Beringiana	122(107)	43	612	GTR+G	TN+F+G4	F81+I	F81+F+I	GTR	TIM2+F	-----	-----
Cristaria	110(35)	82	618	GTR+G	TRN+G	F81+I	F81+I	HKY	HKY	-----	-----
*Inversidens**	4(4)	2	612	-----	-----	-----	-----	-----	-----	-----	-----
Inversiunio	16(16)	8	597	GTR+I	TN+F+I	F81+I	TN+F+I	GTR+I	HKY+F+I	-----	-----
Lamprotula + *Pronodularia*	75(32)	45	603	GTR+G	TN+F+I	F81+I	TN+F+I	HKY+G	HKY+F+G4	-----	-----
Lanceolaria	54(20)	35	603	GTR+G	TN+F+G4	F81+I	F81+F	HKY+G	TPM3+F	-----	-----
Nodularia + *Middendorffinaia*	129(22)	76	612	GTR+G	TN+F+G4	F81+I	F81+F	HKY+G	TIM2+F+R2	-----	-----
Koreosolenaia + *Parvasolenaia*	26(8)	10	651	GTR + I	TN+F+I	F81+I	TN+F+I	GTR + I	TPM3+F+I	-----	-----
*Obovalis**	1(1)	1	648	-----	-----	-----	-----	-----	-----	-----	-----
Pletholophus	14(13)	7	615	GTR + I	TNe+R2	F81	F81+F	HKY	HKY+F	-----	-----
Sinanodonta	241(65)	81	609	GTR+I+G	TN+F+G4	F81	F81+F	HKY+G	TPM3+F+G4	-----	-----
Sinohyriopsis	35(3)	25	648	GTR+G	TN+F+G4	F81	F81+F	GTR	TIM2+F	-----	-----

Table 3. List of species within the study region, closest related taxa and country-level presence for Japan, South Korea, and Russia (considering only the region east of Transbaikalia and Lena River basin). [+]Taxa that need validation and formal description.

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Taxon	Mean COI *p*-distance % (nearest neighbour)	Countries		
		S. Korea	Russia	Japan
UNIONINAE				
Aculamprotulini Huang & Wu, 2019				
Aculamprotula coreana (Martens, 1886)	6.8 (*Aculamprotula fibrosa* 2)	Endemic		
Cristariini Lopes-Lima, Bogan & Froufe, 2016				
Amuranodonta kijaensis (Moskvicheva, 1973)	---- (No congeneric species)		Native	
Anemina arcaeformis (Heude, 1877)	3.2 (*Anemina euscaphys*)	Native		Native
Beringiana beringiana (Middendorff, 1851)	7.6 (*Beringiana gosannensis*)		Native	Native
Beringiana japonica (Clessin, 1874)	8.7 (*Beringiana beringiana*)			Endemic
Beringiana gosannensis **sp. nov.**	7.6 (*Beringiana beringiana*)			Endemic
Beringiana fukuharai **sp. nov.**	8.1 (*Beringiana beringiana*)			Endemic
Buldowskia iwakawai (Suzuki, 1939) **comb. nov.**	4.7 (*Buldowskia kamiyai*)	Native		Native
Buldowskia kamiyai **sp. nov.**	4.7 (*Buldowskia iwakawai*)			Endemic
Buldowskia suifunica (Lindholm, 1925)	10.7 (*Buldowskia iwakawai*)		Native	
Buldowskia shadini (Moskvicheva, 1973)	11.1 (*Buldowskia iwakawai*)	Native	Native	
Buldowskia flavotincta (Martens, 1905)	10.6 (*Buldowskia iwakawai*)	Endemic		
Cristaria plicata (Leach, 1814)	8.0 (*Cristaria clessini*)	Native	Native	Native
Cristaria clessini (Kobelt, 1879)	8.0 (*Cristaria plicata*)			Endemic
Pletholophus reinianus (Martens, 1875)	5.5 (*Pletholophus tenuis*)			Endemic
Sinanodonta lauta (Martens, 1877)	3.3 (*Sinanodonta* cf. *woodiana* 1)	Native	Native	Native
Sinanodonta schrenkii (Lea, 1870)	7.8 (*Sinanodonta calipygos*)	Native	Native	
Sinanodonta calipygos (Kobelt, 1879)	7.3 (*Sinanodonta tumens*)			Endemic

Sinanodonta tumens (Haas, 1910) **comb. nov.**	7.3 (*Sinanodonta calipygos*)			Endemic
Sinanodonta cf. *woodiana* 1 (Lea, 1834)	3.3 (*Sinanodonta lauta*)			Non-Native
Lanceolariini Froufe, Lopes-Lima & Bogan, 2017				
Lanceolaria grayii (Griffith & Pidgeon, 1833)	6.3 (*Lanceolaria acrorrhyncha*)		Native	
Lanceolaria acrorrhyncha (Martens, 1894)	6.0 (*Lanceolaria triformis*)	Endemic		
Lanceolaria oxyrhyncha (Martens, 1861)	9.4 (*Lanceolaria acrorrhyncha*)			Endemic
Lanceolaria kihirai **(**Kondo and Hattori, 2019)	7.3 (*Lanceolaria acrorrhyncha*)			Endemic
Nodulariini Bogatov & Zatrawkin, 1987				
Inversiunio jokohamensis (Ihering, 1893)	6.6 (*Inversiunio verrucosus*)			Endemic
Inversiunio reinianus (Kobelt, 1879)	2.3 (*Inversiunio yanagawensis*)			Endemic
Inversiunio verrucosus Kondo et al., 2007	2.6 (*Inversiunio yanagawensis*)	Endemic		
Inversiunio yanagawensis (Kondo, 1982)	2.3 (*Inversiunio reinianus*)			Endemic
Nodularia douglasiae (Griffith & Pidgeon, 1833)	3.0 (*Nodularia* sp. 1)	Native	Native	Native
Nodularia nipponensis (Martens, 1877)	4.9 (*Nodularia* sp. 1)			Endemic
Nodularia breviconcha Lee, Kim, Bogan & Kondo. **nom. nov.**	7.9 (*Nodularia* sp. 3)	Endemic		
Nodularia sp. 1^{+}	3.0 (*Nodularia douglasiae*)	Endemic		
Middendorffinaiini Lopes-Lima, Bolotov & Bogan **trib. nov.**				
Middendorffinaia mongolica (Middendorff, 1851)	---- (No congeneric species)		Native	
GONIDEINAE				
Gonideini Ortmann, 1916				
Inversidens brandtii (Kobelt, 1879)	---- (No congeneric species)			Endemic
Koreosolenaia sitgyensis **sp. nov.**	---- (No congeneric species)	Endemic		
Obovalis omiensis (Heimburg, 1884)	---- (No congeneric species)			Endemic

Lamprotulini Modell, 1942			
Lamprotula leaii (Martens, 1894)	5.2 (*Lamprotula seomjinensis*)	Native	
Lamprotula seomjinensis (Kondo et al., 2007) **comb. nov.**	5.2 (*Lamprotula leaii*)	Endemic	
Pronodularia cf. *japanensis* 1 (Lea, 1859)$^{+}$	4.1 (*Pronodularia* cf. *japanensis* 3)		Endemic
Pronodularia cf. *japanensis* 2 (Lea, 1859)$^{+}$	4.5 (*Pronodularia* cf. *japanensis* 1)		Endemic
Pronodularia cf. *japanensis* 3 (Lea, 1859)$^{+}$	4.1 (*Pronodularia* cf. *japanensis* 1)		Endemic
Chamberlainiini Bogan, Froufe and Lopes-Lima, 2017			
Sinohyriopsis cf. *cumingii* 1 (Lea, 1852)	3.8 (*Sinohyriopsis cf. cumingii* 2)		Non-Native
Sinohyriopsis schlegelii (Martens, 1861)	2.7 (*Sinohyriopsis cumingii* 3)		Endemic

Supplementary Table 1. Pairwise genetic distance matrixes among species from 8 generic clades and three with combined genera (*Amuranodonta* + *Anemina* + *Buldowskia*), (*Lamprotula* + *Pronodularia*), and (*Nodularia* + *Middendorffinaia*). Mean uncorrected *p*-distance among species of cytochrome oxidase subunit I (COI) gene fragment (below the diagonal) and associated standard error (above the diagonal in blue). Taxa occurring in the study region are represented in bold.

Supplementary Table 2. List of sequences used for the phylogenetic relationships within the genus *Aculamprotula* with respective haplotypes, localities, voucher numbers or specimen codes, and GenBank references. Acronyms for the voucher deposit institutions as follows: MHS – Matsuyama High School, Japan; NCU – Nanchang University, China; NNIBR – Nakdonggang National Institute of Biological Resources, South Korea.

Supplementary Table 3. List of sequences used for the phylogenetic relationships within the genera *Anemina*, *Amuranodonta*, and *Buldowskia* with respective haplotypes, localities, voucher numbers or specimen codes, and GenBank references. Acronyms for the voucher deposit institutions as follows: CIIMAR – Interdisciplinary Centre of Marine and Environmental Research, Porto, Portugal; MHS – Matsuyama High School, Japan; NCU – Nanchang University, China; NNIBR – Nakdonggang National Institute of Biological Resources, South Korea; OMNH – Osaka Museum of Natural History, Japan; RMBH – Russian Museum of Biodiversity Hotspots, Arkhangelsk, Russia.

Supplementary Table 4. List of sequences used for the phylogenetic relationships within the genus *Beringiana* with respective haplotypes, localities, voucher numbers or specimen codes, and GenBank references. Acronyms for the voucher deposit institutions as follows: CIIMAR – Interdisciplinary Centre of Marine and Environmental Research, Porto, Portugal; MHS – Matsuyama High School, Japan; NNIBR – Nakdonggang National Institute of Biological Resources, South Korea; OMNH – Osaka Museum of Natural History, Japan; RMBH – Russian Museum of Biodiversity Hotspots, Arkhangelsk, Russia.

Supplementary Table 5. List of sequences used for the phylogenetic relationships within the genus *Cristaria* with respective haplotypes, localities, voucher numbers or specimen codes, and GenBank references. Acronyms for the voucher deposit institutions as follows: CIIMAR – Interdisciplinary Centre of Marine and Environmental Research, Porto, Portugal; MHS – Matsuyama High School, Japan; NCU – Nanchang University, China; NNIBR – Nakdonggang National Institute of Biological Resources, South Korea; RMBH – Russian Museum of Biodiversity Hotspots, Arkhangelsk, Russia.

Supplementary Table 6. List of sequences used for the phylogenetic relationships within the genus *Pletholophus* with respective haplotypes, localities, voucher numbers or specimen codes, and GenBank references. Acronyms for the voucher deposit institutions as follows: MHS – Matsuyama High School, Japan; NCSM – North Carolina Museum of Natural Sciences, U.S.A.; NNIBR – Nakdonggang National Institute of Biological Resources, South Korea.

Supplementary Table 7. List of sequences used for the phylogenetic relationships within the genus *Sinanodonta* with respective haplotypes, localities, voucher numbers or specimen codes, and GenBank references. Acronyms for the voucher deposit institutions as follows: CIIMAR – Interdisciplinary Centre of Marine and Environmental Research, Porto, Portugal; MHS – Matsuyama High School, Japan; NCU – Nanchang University, China; NNIBR – Nakdonggang National Institute of Biological Resources, South Korea; OMNH – Osaka Museum of Natural History, Japan; RMBH – Russian Museum of Biodiversity Hotspots, Arkhangelsk, Russia.

Supplementary Table 8. List of sequences used for the phylogenetic relationships within the genus *Lanceolaria* with respective haplotypes, localities, voucher numbers or specimen codes, and GenBank references. Acronyms for the voucher deposit institutions as follows: CIIMAR – Interdisciplinary Centre of Marine and Environmental Research, Porto, Portugal; MHS – Matsuyama High School, Japan; NCSM – North Carolina Museum of Natural Sciences, U.S.A.; NCU – Nanchang University, China; NNIBR – Nakdonggang National Institute of Biological Resources, South Korea.

Supplementary Table 9. List of sequences used for the phylogenetic relationships within the genus *Inversiunio* with respective haplotypes, localities, voucher numbers or specimen codes, and GenBank references. Acronyms for the voucher deposit institutions as follows: MHS – Matsuyama High School, Japan; NCSM – North Carolina Museum of Natural Sciences, U.S.A.; NCU – Nanchang University, China; NNIBR – Nakdonggang National Institute of Biological Resources, South Korea.

Supplementary Table 10. List of sequences used for the phylogenetic relationships within the genera *Nodularia* and *Middendorffinaia* with respective haplotypes, localities, voucher numbers or specimen codes, and GenBank references. Acronyms for the voucher deposit institutions as follows: CIIMAR – Interdisciplinary Centre of Marine and Environmental Research, Porto, Portugal; MHS – Matsuyama High School, Japan; NCSM – North Carolina Museum of Natural Sciences, U.S.A.; NCU – Nanchang University, China; NNIBR – Nakdonggang National Institute of Biological Resources, South Korea; RMBH – Russian Museum of Biodiversity Hotspots, Arkhangelsk, Russia; UF – Florida Museum of Natural History, University of Florida, U.S.A.

Supplementary Table 11. List of sequences used for the phylogenetic relationships within the genera *Koreosolenaia* and *Parvasolenaia* with respective haplotypes, localities, voucher numbers or specimen codes and GenBank references. Acronyms for the voucher deposit institutions as follows: MHS – Matsuyama High School, Japan; NCSM – North Carolina Museum of Natural Sciences, U.S.A.; NCU – Nanchang University, China; NNIBR – Nakdonggang National Institute of Biological Resources, South Korea.

Supplementary Table 12. List of sequences within the genera *Inversidens* and *Obovalis* with respective localities, voucher numbers or specimen codes, GenBank references. Acronyms for the voucher deposit institutions as follows: CIIMAR – Interdisciplinary Centre of Marine and Environmental Research, Porto, Portugal; MHS – Matsuyama High School, Japan.

Supplementary Table 13. List of sequences used for the phylogenetic relationships within the genera *Lamprotula* and *Pronodularia* with respective haplotypes, localities, voucher numbers or specimen codes, and GenBank references. Acronyms for the voucher deposit institutions as follows: CIIMAR – Interdisciplinary Centre of Marine and Environmental Research, Porto, Portugal; MHS – Matsuyama High School, Japan; NCU – Nanchang University, China; NNIBR – Nakdonggang National Institute of Biological Resources, South Korea; OMNH – Osaka Museum of Natural History, Japan; UMMZ – University of Michigan Museum of Zoology, U.S.A.

Supplementary Table 14. List of sequences used for the phylogenetic relationships within the genus *Sinohyriopsis* with respective haplotypes, localities, voucher numbers or specimen codes, and GenBank references. Acronyms for the voucher deposit institutions as follows: CIIMAR – Interdisciplinary Centre of Marine and Environmental Research, Porto, Portugal; MHS – Matsuyama High School, Japan; NCU – Nanchang University, China; RMBH – Russian Museum of Biodiversity Hotspots, Arkhangelsk, Russia.

Supplementary Appendix I. Taxonomic review and list of the original descriptions and type species of the Unionidae from Far East Asia and other Asian species addressed in the current study.