



Article The Anodontini of Vietnam (Mollusca: Bivalvia: Unionidae: Unioninae) with the Description of a New Species

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Abstract: The basic knowledge of freshwater bivalves in the Unionida in some regions of the world is still limited, hindering potential conservation efforts, including in Vietnam. A subset of these mussels, the freshwater bivalve tribe Anodontini, is especially difficult to properly identify morphologically due to intraspecific shell similarity. This study aims to define the species of Anodontini in Vietnam and describe their evolutionary relationships and distributions by estimating phylogenies and analyzing collected specimens. The Anodontini are represented in Vietnam by five species divided among three genera: *Sinanodonta, Cristaria,* and *Pletholophus. Sinanodonta woodiana,* a large species complex, is represented in Vietnam by *Sinanodonta jourdyi. Cristaria* is confirmed to include the widespread *Cristaria plicata* and substantiates the validity of *Cristaria truncata.* Finally, *Pletholophus tenuis,* and a species new to science. Our study is an important baseline for future studies on Vietnamese freshwater mussels and highlights the importance of surveys, molecular work, and taxonomic expertise to describe the biodiversity of understudied regions.

Keywords: Cristaria; distribution; Pletholophus; Sinanodonta; Southeast Asia; systematics; taxonomy

1. Introduction

Freshwater bivalves in the order Unionida, also recognized as freshwater mussels, are known for their unique life cycle, with a parasitic phase primarily on fish [1] and an uncommon doubly mitochondrial inheritance [2]. These animals are notorious for providing vital ecosystem functions and services [3]. They are useful for exploring past geological and hydrological events due to their stable biogeography [4]. Unfortunately, this group is among the most imperiled worldwide, with many species considered extinct or on the brink of extinction [5]. This highlights the urgency of describing their diversity, distribution, and evolution, which is reflected in the growing research and conservation attention paid to this group [6,7]. However, in many regions of the world, the necessary



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Copyright: © 2023 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (https:// creativecommons.org/licenses/by/ 4.0/). baseline knowledge to guide conservation efforts is still lacking [5]. For instance, in Asia, our understanding of the biology and systematics of these animals' ranges from poor to absent in many areas [8]. Many Asian River basins have never been surveyed and may be home to numerous undescribed genera and species (e.g., [9,10]) that may even go extinct before being described or studied [11–14]. Despite being poorly known, the freshwater mussel fauna of Asia has recently attracted intense research interest, especially in taxonomy, phylogeny, and biogeography (e.g., [8,10,15–25]). However, these efforts have been mostly regional or national, with several countries or regions being overlooked, such as Vietnam. In this country, research on freshwater mussels is limited, and only recently has a wide study on the Vietnamese freshwater bivalve fauna been published to document its diversity and distribution [26]. However, it relied solely on shell characters, which often fail to properly identify and separate species.

Species belonging to the freshwater tribe Anodontini generally present high cryptic (species that can only be distinguished molecularly) diversity and exhibit high habitat and host-fish plasticity. However, virtually nothing is reported about the habitat requirements and main life history traits of these species in Vietnam. Furthermore, until this study, the number and identity of species belonging to this tribe in Vietnam were still contentious, with previous morphological identifications not being verified molecularly. Therefore, the present study aims to overcome this issue and update the systematics, taxonomy, phylogeny, and distribution of Anodontini freshwater mussels from Vietnam based upon extensive surveys by (i) examining and defining species boundaries and distributions; (ii) estimating phylogenies with new data from additional specimens; (iii) revising species taxonomy and systematics; and (iv) discussing conservation implications based on these results.

2. Materials and Methods

2.1. Field and Tissue Sampling

Representative specimens of Anodontini were collected during extensive surveys across Vietnam from 2010 to 2016, also covering local markets where freshwater mussels are typically sold as food (Figure 1) [26]. Specimens and shells were collected as vouchers and deposited in the IEBR—Institute of Ecology and Biological Resources, Hanoi, Vietnam, and the NCSM—North Carolina Museum of Natural Sciences, U.S.A. Selected specimens were sampled for molecular analyses (Figure 2) (Supplementary Tables S1–S3). For this, a small sample of foot tissue was collected (see [27]) and placed in 95% ethanol.



Figure 1. Freshwater mussels for sale as food in local market in Hanoi, Vietnam. Photograph by Arthur Bogan, 2014.



Figure 2. Map of Vietnam, with the study area shaded in blue. White dots mark the location of collected specimens or shells.

2.2. DNA Extraction, PCR, and Sequencing

Genomic DNA was extracted from the tissue samples using a standard high-salt protocol [28]. PCRs were done for the female lineages of mitochondrial cytochrome c oxidase subunit 1, COI (annealing temperature of 48 °C), and 28S ribosomal RNA (annealing temperature of 50 °C) as described in [29]. Amplified DNA templates were purified and sequenced using the same primers by Macrogen.

2.3. Phylogenetic Analyses

In order to estimate the phylogenetic position of all the newly sequenced individuals, a preliminary COI alignment was produced, including all available Anodontini. A Bayesian Inference phylogenetic tree was produced using MrBayes 3.2.7a [30] with 20×10^6 generations sampled at intervals of 1000 generations on a single partition with the model GTR + I + G.

Based on this preliminary analysis, three genera were revealed to be present in the data set, i.e., Cristaria, Pletholophus, and Sinanodonta (Supplementary Tables S1–S3). Therefore, a concatenated COI + 28S dataset was constructed using one individual of each clade inside each genus (Table 1). Sequences from species belonging to the same three genera as well as a single representative of all previously published sequences of congeneric taxa and four other taxa as an outgroup were also included (Table 1). This data set was aligned with GUIDANCE2 [31], following [32], and analyzed using Maximum Likelihood (ML) in IQ-TREE v. 1.6.12 [33] and Bayesian inference (BI) using MrBayes 3.2.7a [30]. For the BI analyses, the best-fit models of nucleotide substitution and partition schemes were selected using PartitionFinder 2 [34] 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 1000 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 [35]. The best-fit models of nucleotide substitution and partition schemes were selected using ModelFinder [36] for the ML, and then the analyses were conducted with initial tree searches, followed by 10 independent runs and 10,000 ultrafast bootstrap replicates. Substitution saturation tests for all codon positions were performed for COI as implemented in DAMBE 6 [37].

Table 1. List of sequences used for the phylogenies of the Cristariini with respective species, countries, voucher numbers, and GenBank references selected from the combined dataset (COI + 28S rRNA). Acronyms for the voucher deposit institutions are as follows: IEBR—Institute of Ecology and Biological Resources, Hanoi, Vietnam; 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.

Species	COI	285	Country	Voucher	Studies for COI/28S
INGROUP					
Amuranodonta kijaensis	MK574204	MK574473	Russia	RMBH Biv_228	Bolotov et al., 2020 [15]
Anemina arcaeformis	MG462936	MG595463	China	NCU 16_XPWU_SU026	Huang et al., 2019 [17]
Beringiana beringiana	MT020557	MT020799	Japan	CIIMAR BIV2700	Lopes-Lima et al., 2020 [18]
Beringiana japonica	MT020576	MT020803	Japan	MHS SJSaitNam4	Lopes-Lima et al., 2020 [18]
Beringiana fukuharai	MT020567	MT020801	Japan	OMNH Mo 39101	Lopes-Lima et al., 2020 [18]
Beringiana gosannensis	MT020584	MT020802	Japan	OMNH Mo 39089	Lopes-Lima et al., 2020 [18]
Buldowskia flavotincta	MT020537	MT020804	South Korea	NNIBR IV29232	Lopes-Lima et al., 2020 [18]
Buldowskia suifunica	MK574190	MK574460	Russia	RMBH biv225_11	Bolotov et al., 2020 [15]
Buldowskia iwakawai	MT020523	MT020806	Japan	MHS AAfk080	Lopes-Lima et al., 2020 [18]
Buldowskia kamiyai	MT020525	MT020808	Japan	OMNH Mo 39097	Lopes-Lima et al., 2020 [18]
Buldowskia shadini	MK574197	MK574467	Russia	RMBH Biv_228_16	Bolotov et al., 2020 [15]
Cristaria bellua	ON704642	ON695893	Laos	RMBH Biv813_1	Konopleva et al., 2023 [38]
Cristaria clessini	MT020592	MT020810	Japan	MHS MCp-sigB	Lopes-Lima et al., 2020 [18]
Cristaria plicata	MG462956	MG595484	China	NCU 16_XPŴU_ŠU047	Ĥuang et al., 2019 [17]
Cristaria truncata	OP491287	OP499826	Vietnam	IEBR FM CT01	Konopleva et al., 2023 [38]
Pletholophus honglinhensis sp. nov.	SUBMITTED	SUBMITTED	Vietnam	NCSM 47211.01	THIS STUDY
Pletholophus tenuis	KX822658	KX822614	Vietnam	NCSM 84924.01	Lopes-Lima et al., 2017 [39]
Sinanodonta angula	MG463053	MG595580	China	16 NCU XPWU SU143	Huang et al., 2019 [17]
Sinanodonta calipygos	MT020623	MT020833	Japan	MHS SC_Shiga_4	Lopes-Lima et al., 2020 [18]
Sinanodonta cf. elliptica	MG463058	MG595585	China	16 NCU XPWU SU148	Huang et al., 2019 [17]
Sinanodonta jourdyi	SUBMITTED	SUBMITTED	Vietnam	NCSM 84916.02	THIS STUDY
Sinanodonta lauta	MT020616	MT020834	Japan	MHS SL_Shizuoka_1	Lopes-Lima et al., 2020 [18]
Sinanodonta lucida	MG463066	MG595589	China	NCU 16_XPWU_SU152	Huang et al., 2019 [17]
Sinanodonta schrenkii	MT020618	MT020837	South Korea	NNIBR IV29271	Lopes-Lima et al., 2020 [18]
Sinanodonta tumens	MT020622	MT020838	Japan	MHS fk156	Lopes-Lima et al., 2020 [18]
Sinanodonta cf. woodiana 1	MG463052	MG595599	China	NCU 16_XPWU_SU162	Huang et al., 2019 [17]
Sinanodonta cf. woodiana 2	MG463080	MG595608	China	NCU 16_XPWU_SU171	Huang et al., 2019 [17]
OUTGROUP					-
Anodonta cygnea	KX822633	KX822589	Italy		Lopes-Lima et al., 2017 [39]
Schistodesmus lampreyanus	MG463037	MG595570	China	NCU 16_XPWU_SU133	Huang et al., 2019 [17]
Margaritifera laevis	MT020707	MT020823	Japan	MHS MMt-tc01	Lopes-Lima et al., 2020 [18]
Gibbosula crassa	MH293546	MH293542	Vietnam	IEBR FM GC01	Lopes-Lima et al., 2018 [5]

Three individual COI data sets, corresponding to the three genera found, i.e., *Cristaria*, *Pletholophus*, and *Sinanodonta*, were also produced with all newly sequenced individuals, including different outgroup taxa (Supplementary Tables S1–S3). Alignments were produced in GUIDANCE2 and analyzed using ML and BI methods, following the same steps applied to the concatenated data set (above).

2.4. Species Delimitation

Three distinct methods were applied to each COI dataset, without outgroup taxa, to determine the number of molecular operational taxonomic units (MOTUs). Two are distance-based: the BIN system implemented in BOLD [40] and the automatic barcode gap discovery (ABGD) [41]; and another that uses haplotype network reconstructions in TCS 1.21 [42] with a 95% statistical parsimony connection limit. Sequence divergences (uncorrected *p*-distance) were estimated using MEGA X [43].

For the BINs system, each COI dataset was analyzed with the cluster sequences tool implemented in BOLD 4 (http://v4.boldsystems.org) (accessed 28 March 2020) [40]. The ABGD was applied to each dataset using its online version (http://wwwabi.snv.jussieu.fr/public/abgd/abgdweb.html) (accessed 28 March 2020) with the default settings and the Kimura-2-parameter (K2P) distance matrix [41].

2.5. Distribution Maps

The range of each species in the study area was mapped using the current results and previous reference works [18,26,44–46]. The distribution data were then integrated and represented as colored potential distribution maps using a level 8 HydroBASINS [47]

shapefile. For pictorial reasons, Earth topography layers made by Natural Earth http: //naturalearthdata.com (accessed 26 March 2020) were also included.

3. Results and Discussion

Here we present the diversity of the Anodontini of Vietnam, recognizing five valid Anodontini species, including the newly described *Pletholophus honglinhensis* sp. nov. We also describe their distribution, revise their taxonomy, and give guidance for future studies and conservation action.

The preliminary Bayesian inference phylogeny retrieved three clades that include Vietnamese Anodontini taxa, which were considered for further phylogenetic and species delimitation analyses. The composition, size, and parameters of the four datasets (3 COI and 1 COI + 28S) and 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. The saturation test showed significantly lower values of ISS than ISS.C (a critical value determined from the computer simulation), indicating that the evaluated (COI) data set is not site saturated and is useful for phylogenetic comparisons. Both (COI + 28S) BI and ML phylogenies presented the same topology (Figure 3). All the generic-level clades are well supported, but the relationships among some of them still lack resolution (Figure 3). In both phylogenies, the newly described species *Pletholophus honglinhensis* sp. nov. clusters with *Pletholophus tenuis, Sinanodonta jourdyi* within the *Sinanodonta* clade, and *Cristaria truncata* within the *Cristaria* clade (Figure 3).



Figure 3. Bayesian inference phylogenetic tree inferred from the combined cytochrome *c* oxidase subunit I + 28S ribosomal RNA gene fragments. The values above the branches indicate Bayesian posterior probability percentage/maximum likelihood ultrafast bootstrap values. Values over 95% for both analyses are represented by an asterisk. Sequences marked with the Vietnamese flag represent specimens collected in Vietnam.

Table 2. Number of sequences, haplotypes, and sizes of all datasets used, as well as substitution models for each partition for all phylogenetic analyses.

	6			Models							
Dataset	(New)	Haplotypes	(nt)	COLO	Codon 1	COI	Codon 2	COI 0	Codon 3		285
				BI	ML	BI	ML	BI	ML	BI	ML
COI + 28S											
Cristariini	31 (2)	-	1029	GTR + G	TN + F + G4	F81 + I	F81 + F	HKY + G	TN + F + R2	GTR	TPM3u + F
COI											
Cristaria	130	89	615	K2P + I	TNe + G4	F81 + I	F81 + F + I	HKY	HKY + F		
Pletholophus	16 (3)	8	658	HKY + I	TN + F + G4	F81 + I	F81 + F	HKY	HKY + F		
Sinanodonta	250 (9)	84	609	GTR + G	TN + F + G4	F81 + I	F81 + F	HKY + G	TPM3u + F + G4		



Molecular species delimitation for the COI individual datasets revealed the existence of five MOTUs present in the study area, here recognized as species (Figures 4–6).

Figure 4. (**A**) Bayesian Inference phylogenetic tree inferred from the cytochrome *c* oxidase subunit I (COI) gene fragment, species delimitation of *Cristaria* species, and distribution maps of the species present in the study area (marked with Vietnamese flags). 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 within each recognized MOTU were erased for clarity. Distribution maps of each species (**B**,**C**) depicting the potential distribution across the main river basins in shaded colors, the native range in blue, and the introduced range in red. White dots represent collected specimens or shells, red dots represent sequenced individuals. Sequences from the current study are represented in bold.



Figure 5. (**A**) Bayesian Inference phylogenetic tree inferred from the cytochrome *c* oxidase subunit I (COI) gene fragment, species delimitation of *Pletholophus* species, and distribution maps of species present in the study area (marked with Vietnamese flags). 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. Distribution maps for each species (**B**,**C**) depicting the potential distribution across the main river basins are in shaded colors; the known native range is in dark blue, and the questionable range is in light blue. White dots represent collected specimens or shells; red dots represent sequenced individuals. Sequences from the current study are represented in bold.



Figure 6. Bayesian Inference phylogenetic tree inferred from the cytochrome *c* oxidase subunit I (COI) gene fragment, species delimitation of *Sinanodonta* species, and distribution maps of *S. jourdyi* present in the study area (marked with a Vietnamese flag). 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 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 map of *S. jourdyi* depicting the potential distribution across the main river basins in shaded colors, the known native range in dark blue, and the questionable range in light blue. White dots represent collected specimens or shells; red dots represent sequenced individuals. Sequences from the current study are represented in bold.

From the *Cristaria* genus, 12 specimens were collected across Vietnam, but only a single *Cristaria truncata* lot was sequenced. Both COI (ML and BI) phylogenies for *Cristaria* exhibit similar topologies, retrieving five clades recovered as separate MOTUs by all species delimitation methods (Figure 4). Uncorrected *p*-distances among the delineated MOTUs (here recognized as species; see Taxonomic Account Section) ranged from 4.4% (between *C. plicata* and *C. truncata*) to 11.9% (between *C. bellua* and *Cristaria* sp.) (Table 3).

Table 3. Pairwise genetic distance matrixes among species from the three Cristariini genera present in Vietnam. 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. The lines are colored to make reading across the table easier.

Cristaria										
	C. bellua	C. clessini	C. plicata	Cristaria sp.	C. truncata					
C. bellua		0.011	0.011	0.014	0.010					
C. clessini	0.082		0.010	0.003	0.010					
C. plicata	0.087	0.080		0.011	0.008					
Cristaria sp.	0.119	0.115	0.100		0.013					
C. truncata	0.086	0.077	0.044	0.112						
Pletholophus	P. honglinhensis	P. reinianus	P. tenuis							
P. honglinhensis		0.014	0.013							
P. reinianus	0.105		0.009							
P. tenuis	0.109	0.050								
Sinanodonta	S. angula	S. calipygos	S. cf. elliptica	S. jourdyi	S. lauta	S. lucida	S. schrenkii	S. tumens	S. woodiana 1	S. woo
S. angula		0.012	0.013	0.012	0.012	0.009	0.013	0.012	0.012	0.
S. calipygos	0.114		0.012	0.012	0.010	0.014	0.012	0.010	0.010	0.
S. cf. elliptica	0.137	0.087		0.009	0.008	0.013	0.012	0.010	0.008	0.
S. jourdyi	0.128	0.088	0.049		0.009	0.013	0.011	0.011	0.009	0.
S. lauta	0.127	0.078	0.048	0.056		0.013	0.012	0.010	0.005	0.0
S. lucida	0.076	0.131	0.132	0.130	0.133		0.013	0.013	0.014	0.
S. schrenkii	0.120	0.081	0.093	0.089	0.105	0.127		0.011	0.012	0.
S. tumens	0.119	0.077	0.103	0.106	0.098	0.133	0.100		0.010	0.
S. woodiana 1	0.131	0.078	0.047	0.060	0.032	0.133	0.099	0.106		0.
S. woodiana 2	0.117	0.080	0.045	0.046	0.049	0.123	0.087	0.094	0.051	

From *Pletholophus*, 80 specimens were collected throughout Vietnam (Figure 5). Both COI ML and BI phylogenies for *Pletholophus* exhibit similar topologies, retrieving three clades recovered as separate MOTUs by all species delimitation methods (Figure 5). Uncorrected *p*-distances among the delineated MOTUs (here recognized as species; see Taxonomic Account Section) ranged from 5.0% (between *P. tenuis* and *P. reinianus*) to 10.9% (between *P. honglinhensis* sp. nov. and *P. tenuis*) (Table 3). *Pletholophus tenuis* has been recorded from the Mekong Basin in Vietnam north to the Yellow River Basin in China. Given that no molecular data is available from the distribution edges in Vietnam south of the city of Thanh Hoa and in the Yellow River Basin in China, the specific status of the *Pletholophus* specimens from these areas still needs to be confirmed. *Pletholophus honglinhensis* sp. nov. was found only in a coastal basin south of Hanoi.

From the *Sinanodonta* genus, 45 specimens were collected throughout Vietnam (Figure 6). Both COI (ML and BI) phylogenies for the *Sinanodonta* genus presented similar topologies, retrieving ten clades, defined as MOTUs by a consensus of all species delimitation methods. Only one of these MOTUs is present in Vietnam (Figure 6). Uncorrected *p*-distances among the delineated MOTUs (here recognized as species) ranged from 3.2% (between *S. lauta* (Martens, 1877) [48] and *S. cf. woodiana* 1) to 13.7% (between *S. angula* (Tchang et al., 1965) [49] and *S. cf. elliptica* (Heude, 1878) [50]) (Table 3). *Sinanodonta jourdyi* was detected throughout Vietnam, from the Pearl River Basin in the northeast to the southern coastal basins. The species has been detected in the lower Mekong Basin in Vietnam, but it is still contentious whether the species is native to this area (Figure 6).

3.1. Taxonomy of Sinanodonta, Cristaria, and Pletholophus

Dăng et al. [44] recognized three separate species of *Sinanodonta* in Vietnam, while Haas [51] included all those names as synonyms of *S. woodiana*. Later, Graf and Cummings [52] followed Haas [51] and recognized only a single *Sinanodonta* species for Vietnam, i.e., *S. woodiana*. However, *Sinanodonta woodiana* (Lea, 1834) [53] in Asia has been recently shown to be a complex of at least seven mitochondrial lineages [54]. Here, we show that only one of these lineages of *Sinanodonta woodiana* occurs in Vietnam and was previously identified as *Sinanodonta jourdyi* (Morlet, 1886) [8,26,55–59].

Cristaria Schumacher, 1817 [60] was erected to separate the type species, *Cristaria tuberculata* Schumacher, 1817 [60] (type species by monotypy), from other thin-shelled taxa with wings but with a unique hinge. Simpson [61] erected *Cristaria* (*Pletholophus*) with the type species *Symphynota discoidea* Lea, 1834 [53] (original designation). Heard [62], in

describing the comparative anatomy of *C. plicata*, made observations on *Cristaria* (*Pletholophus*) *discoidea* and mentioned anatomical distinctions between *C. discoidea* and *C. plicata*. A new *Cristaria* species restricted to northern Vietnam, *C. truncata* Đặng in Đặng et al. [44], was described based on shell characters (Figure 7). They also moved *Cristaria discoidea* out of *Cristaria*, elevating *Pletholophus* Simpson, 1900 [61] to the generic level. Graf & Cummings [52] recognized four species of *Cristaria*, including *C. truncata*, but did not recognize *Pletholophus*. He & Zhuang [63] recognized three species of *Cristaria* and placed another species of *Cristaria* erroneously in *Middendorffinaia* Moskvicheva & Starobogatov, 1973 [64] in China. Graf & Cummings [58] recognized five species in *Cristaria*, including *C. truncata*, and recognized *Pletholophus*, which included two species.



Figure 7. Shell of *Cristaria truncata*. (**A**). Outside of left valve. (**B**). Inside of right valve. [From [45] Đặng & Hồ, 2017: 208, fig. 108] Reprinted with permission from Ref. [45]. Copyright 2017, Dr. Hồ, [personal communication, February 2023].

Cristaria plicata from eastern Russia was examined using conchological, anatomical, and molecular data and found to represent a single species [65,66]. *Cristaria plicata* is distributed from eastern Russia (Amur River basin), South Korea, Japan, China, Vietnam, Cambodia, the Lao People's Republic, and Thailand [8,26,42,63,66–68]. Another unidentified species of *Cristaria* has been sequenced and was originally identified as *C. plicata* but is a separate species (Jia & Li, unpublished data, GenBank, [69]). Recently collected specimens of *C. truncata* Đặng, 1980 [44] (Figure 7) were sequenced to test the validity and placement of this species. Graf & Cummings [56,57] and MolluscaBase [70] recognized four species in *Cristaria*, including two from Vietnam, *C. plicata* and *C. truncata*.

Cristaria discoidea (Lea, 1834) [53] has been reported in China, Taiwan, Hong Kong, northern Vietnam, Cambodia, and Thailand [8,26,62,63,67]. The species has been placed in *Cristaria (Pletholophus)* by Simpson [61,71] and Haas [53], and *Pletholophus* by Đặng et al. [44]. However, both *Cristaria plicata* (Leach, 1814) [72] and *Cristaria discoidea* were overlooked by Liu et al. [73]. Historically, *Anodon tenuis* and *Unio tenuis* Gray in Griffith & Pidgeon have been dated as of 1834. It has been listed as a junior synonym of *Unio discoidea* Lea, 1834 [52] since the first edition of Lea's Synopsis [74–79] and continued by Simpson [61,71], Preston [78], Modell [79], and Haas [51]. This was the state of the synonymy until Petit and Coan (2008) [80] reviewed all the taxa described by Gray in Griffiths and Pidgeon (1833–1834) [81]. Petit and Coan [80] (p. 229) determined the date of publication for the figure of *Unio tenuis* Gray in Griffith and Pidgeon [81] (p. 595) and again as *Unio tenuis* Gray in Griffith and Pidgeon [81] (p. 595) and again as *Unio tenuis* Gray in Griffith and Pidgeon [81] (p. 595). This case

does not meet the requirements of Code 23.9 [82] for usage, and the older name has date priority and must prevail. The correct name for *Cristaria discoidea* is *Pletholophus tenuis* (Gray in Griffith and Pidgeon, 1833) [81]. The distribution of *Pletholophus tenuis* was listed by Simpson [61] as only in China; Simpson [71] listed a subspecies from Taiwan. Haas [51] (p. 389) reported it only from China, Taiwan, Tonkin, and Cambodia, with no mention of Japan. Kondo [74] mentioned only *Cristaria plicata* as present in Japan. Imai [83] documented the first record of *Cristaria discoidea* from the Nagura River system on Ishigakijima Island, Ryukyu Archipelago, Japan. The published range of *Pletholophus tenuis* included China, Taiwan, Japan, Vietnam, and Cambodia [59]. Do et al. [26] confirmed its occurrence in the northern half of Vietnam.

A subspecies, *Cristaria discoidea reiniana* Martens, 1875 [84], was recognized by [61,71]. Preston [78] listed *Pletholophus reiniana* from Lake Biwa, Japan; Modell [79] listed *Pletholophus discoidea reiniana* from central Japan; Haas [51] noted it was only known from Japan. However, *discoidea, tenuis*, and *reiniana* were not reported from Japan by Habe [85], Masuda and Uchiyam [86], or Kondo [68]. Habe [87] listed *Cristaria reiniana* as a junior synonym of *Anodonta (Sinanodonta) woodiana*, while Graf and Cummings [58] consider *Cristaria reiniana* a junior synonym of *Pletholophus tenuis*. *Cristaria reiniana* is considered a valid species [70]. The conservation status of this taxon is unknown currently, and the known distribution in Japan is very limited.

More recently, *Cristaria bellua* from the Mekong Basin was recognized as a valid species and the only species that crossed the strong biogeographical barrier of the Mekong River [38].

3.2. Systematics

Class: Bivalvia Linnaeus, 1758 [88] Order: Unionida Gray, 1854 [89] Superfamily: Unionoidea Rafinesque, 1820 [90] Family: Unionidae Rafinesque, 1820 [90] Subfamily: Unioninae Rafinesque, 1820 [90] Tribe: Cristariini Lopes-Lima, Bogan, & Froufe, 2017 [39] Genus: *Pletholophus* Simpson, 1900 [61] Species: Pletholophus honglinhensis sp. nov.

New Taxa listed with Zoobank. urn:lsid:zoobank.org:pub:D224D8EB-5305-4458-8BB3-9C8F55E7606E

Common Name: Hồng Lĩnh Asianfloater, Vietnamese Name: Trai hồng lĩnh Comparative Diagnosis:

Shells of *Pletholophus honglinhensis* sp. nov. are diagnosed by a nearly straight dorsal margin and an elongate oval shell with a marked posterior ridge and a minor secondary ridge, a lack of any surface sculpture, and a lack of anterior or posterior dorsal wings (Figure 8). The shells of *Pletholophus tenuis* are taller and rounder in outline than those of *P. honglinhensis* sp. nov. *Pletholophus honglinhensis* sp. nov. and *P. tenuis* both lack any evidence of the dorsal plications on the dorsum of *Cristaria plicata*. Pseudocardinal teeth in *P. honglinhensis* sp. nov. are elongate lamellar, and the lateral teeth are long and simple, often reduced as in *P. tenuis*. Pseudocardinal teeth are typically absent, and lateral teeth are single in specimens of *Cristaria plicata*. *Cristaria truncata* (Figure 7) is greatly inflated, lacks pseudocardinal teeth, and is truncated posteriorly as opposed to the more compressed and elongated shells and the presence of lamellate pseudocardinal teeth in *P. honglinhensis* sp. nov.



Figure 8. *Pletholophus honglinhensis* sp. nov. Holotype NCSM 47211, total shell length 74.5 mm. (**A**). Outside of right valve. (**B**). Inside of left valve. Paratype NCSM 103062.2, total shell length 77.5 mm. (**C**). Outside of right valve. (**D**). Inside of left valve. Paratype NCSM 103062.3, total shell length 90.2 mm. (**E**). Outside of right valve. (**F**). Inside of left valve.

3.3. Description

Shells reach about 91 mm in total length (Figure 8 and Table 4); the shell shape is slightly rectangular to elongate oval in outline; and the shell is inflated. The anterior shell margin is evenly rounded, the dorsal shell margin is nearly straight, the ventral margin is broadly rounded, the posterior margin is rather straight and forms either a point posteriorly where it meets the upturned ventral margin or a more rounded end, the posterior ridge is prominent but not sharp, becoming obscured in older shells, and the posterior slope is smooth with a slight secondary posterior ridge. The umbo area is not elevated above the dorsal shell margin. Umbo sculpture appears double-looped with an indentation in the middle of parallel ridges (Figure 9). Periostracum is brown to black, lacking evidence of rays; the shell surface is smooth, lacking any sculpture, and marked by growth lines. Pseudocardinal teeth in the right valve: one long, thin lamellar tooth and a long, narrow lateral tooth. In the left valve, the pseudocardinal tooth is one long, thin lamellar tooth, and the lateral teeth are straight and well developed. Anterior adductor muscle scars are deep and smooth; pedal protractor muscle scars are separate; anterior pedal retractor muscle scars are united with anterior adductor muscle scars; and posterior adductor muscle scars are very faint. The pallial line impressed anteriorly before fading posteriorly. Umbo cavities

are open and shallow. The nacre color is white, becoming bluish-iridescent toward the posterior margin.

Table 4. Measurements of	the type	series of	of P	Plethol	lophus i	hong	lini	hensis	n. s	sp
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Types	Shell Length, mm	Shell Height, mm	Shell Width mm
Holotype NCSM 47211	74.5	41.4	26.4
Paratype NCSM 103062.2	77.5	44.3	26.2
Paratype NCSM 103062.3	90.6	47.6	28.6



Figure 9. Pletholophus honglinhensis sp. nov. umbo sculpture on the holotype NCSM 47211.

Type material:

Holotype: NCSM 47211

Paratypes: NCSM 103062 (2), all from the type locality.

Type Locality: Vietnam, Bắc Trung Bộ, Hà Tĩnh Province, Market in Hồng Lĩnh. The specimens were collected from the Lam River, also known as the Cả River, in an area about eight kilometers north/northwest of Hồng Lĩnh. Latitude 18.573486 N, Longitude 105.673998 E. [Based on Google Maps. https://www.google.com/maps/place/H%E1 %BB%93ng+L%C4%A9nh,+Ha+Tinh,+Vietnam/@18.533164,105.6719373,13z/data=!3m1!4 b1!4m6!3m5!1s0\$\times\$3139ca1076ed304b:0x3572bef7b81dcdef!8m2!3d18.5299746!4d105 .7060872!16s%2Fm%2F03mct8b, accessed on 22 April 2023].

Collector: Dr. Phan Quoc Toan collected these specimens from the market in Hông Liĩnh, Hà Tĩnh Province, Vietnam, 12 July 2009.

Comparison: *Pletholophus honglinhensis* sp. nov. does not appear to have been collected before and may have been mistaken for *P. tenuis*. The shell shape of *P. honglinhensis* n. sp. is more elongated and not as tall as *P. tenuis*. The posterior ridge in *P. tenuis* is more rounded than in *P. honglinhensis* sp. nov. This new species will not be mistaken for *Cristaria plicata* because it lacks both anterior and posterior dorsal wings and the dorsal plications often seen in *C. plicata. Pletholophus honglinhensis* sp. nov. can be readily separated from *Sinanodonta jourdyi* (Morlet, 1886) [55] by being less inflated, typically having a more elongated oval shell, and lacking the heavy parallel bars of the umbo sculpture. *Sinanodonta jourdyi* lacks any evidence of hinge teeth compared with *Pletholophus* and *Cristaria. Cristaria* typically only has well-developed lateral teeth, while *Pletholophus* species both have weak lamellate pseudocardinal teeth and a single lateral tooth.

Distribution: *Pletholophus honglinhensis* sp. nov. is only known from the market in Hồng Lĩnh, Hà Tĩnh Province, Vietnam.

Conservation status: This species is known only from the type locality in Hà Tĩnh Province, Vietnam. The distribution of this species is currently unknown, so conservation status is not possible.

Etymology: The species is named after the Hồng Lĩnh Market, Hà Tĩnh Province, Vietnam, where it was collected.

Comparative shell material examined.

3.4. Pletholophus tenuis

NCSM 63599: Vietnam, Lang Son, Ky Cung River [Zhu River Basin, Pearl Basin], another stream flowing S, [0.24 air miles NNE center] Trung Thành, [Trang Dinh/Tràng Định] district]. Latitude 22.25553 N, Longitude 106.6068038 E.

NCSM 84943: Vietnam, Lang Son, Ky Cung River [Zhu River Basin, Pearl Basin], Trang Dinh, Trang Dinh District. Latitude 22.23858 N Longitude 106.5905303 E.

NCSM 85273: Vietnam, Ha Noi Province, Hong River, Phùng town, [Dan Phuomng district], [point estimated 0.21 air miles WNW Phượng Trì]. Latitude 21.087821 N, Longitude 105.6603546 E.

IEBR_QN_0001: Vietnam, Quang Ninh Province, Tien Yen River, Binh Lieu town, [Binh Lieu district]. Latitude 21.524945 N, Longitude 107.391095.

3.5. Cristaria plicata

NCSM 84956: Vietnam, Hanoi Province, Hong River, Ha Dong City, Viet Tri market Latitude 21.13333 N Longitude 105.5 E.

NCSM 100665: Vietnam, Đồng Nai Province, Cát Tiên market [point estimated 20.5 air miles SE of Đồng Xoài] Latitude 11.39935 N, Longitude 107.3306 E.

3.6. Sinanodonta jourdyi

NCSM 84916: Vietnam, Lang Son Province, Van Quan District, [Văn Quan], [0.7 air miles S center Vĩnh Lai]. Latitude 21.885499 N Longitude 106.5633499 E NCSM 84948: Vietnam, Nam Dinh Province, Day River, edge of Son la. Day River [Sông Đáy], Nam Dinh Province [Nam Định], S of Hanoi, second market on the E edge of Son La [point estimated center Son La]. Latitude 21.326944 N Longitude 103.918891 E NCSM 85282: Vietnam, Bắc Kạn Province, Nà Phặc, Ngân Sơn district, Northeast (Đông Bắc), [point estimated 1.01 air miles ENE center Na Young]. Latitude 22.385978 N, Longitude 105.9101409 E.

4. Conclusions

In this study, we unveiled the systematics, taxonomy, phylogeny, and distribution of Anodontini freshwater mussels from Vietnam, recognizing five valid species, including a species new to science, *Pletholophus honglinhensis* nov. sp. We also give guidance for future studies and conservation action.

The results reported here are an important baseline for further studies related to the conservation and biogeography of freshwater mussels at the regional and global levels. Additionally, the species delimitation provided here is key to planning and executing further ecological and physiological research on these species. Given that most of the basic life history traits and habitat requirements of freshwater mussels in Vietnam are still unknown, we advocate for investment in these fields to provide better conservation guidance. Of special concern is the complete lack of knowledge about the host fish range, which is crucial for mussels to complete their life cycle. Wider and more detailed surveys that not only provide information about the distribution but also the abundance and population structure of populations should be accomplished periodically to evaluate population trends and make more accurate conservation status assessments. The lack of such studies is hampering proper conservation status assessments, and an example is the single collection of the new

Pletholophus species from the market of Hồng Lĩnh, Hà Tĩnh Province in the Cả or Lam River Basin, south of the Red River Basin.

Furthermore, a major threat that should be considered is the overexploitation of the five species here examined, which are sold in Vietnamese markets as human food items. This activity exerts constant pressure on mussel populations and should be regulated and managed by local authorities. Other threats such as dams, agricultural practices, overharvesting, gravel/sand dredging, etc. are just some of the multiple impacts on these species that need to be addressed by developing a conservation plan for the freshwater mussels of Vietnam.

Supplementary Materials: The following supporting information can be downloaded at: https:// www.mdpi.com/article/10.3390/d15060710/s1, Table S1: List of sequences used for the phylogenetic relationships within the genus Cristaria with respective haplotypes, localities, voucher numbers or specimen codes, and GenBank references. Table S2: List of sequences used for the phylogenetic relationships within the genus Pletholophus with respective haplotypes, localities, voucher numbers or specimen codes, and GenBank references. Table S3: List of sequences used for the phylogenetic relationships within the genus Sinanodonta with respective haplotypes, localities, voucher numbers or specimen codes, and GenBank references. References [91–110] are cited in Supplementary Materials.

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Institutional Review Board Statement: This was not applicable.

Data Availability Statement: The sequences used in this study are all available from GenBank. GenBank accession numbers for all sequences used in this work are listed in Supplementary Tables S1–S3. https://www.ncbi.nlm.nih.gov/genbank/about/ (accessed on 28 Marh 2023). Shell and body vouchers and tissue snips for the new species are available at the North Carolina Museum of Natural Sciences.

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