អ្នកជំនាញខាងបាណកសាស្ត្រឥណ្ឌូចិន
The Indochina Entomologist
OPEN ACCESS
New Taxa
ICE, 1 (30): 289–304 (2025)
ISSN (Online) 3065-1107
www.indochinaentomologist.com

https://doi.org/10.70590/ice.2025.01.30
http://zoobank.org/urn:lsid:zoobank.org:pub:B69CD762-AF81-484F-B424-12BCF59F49B3

A new genus and two new species of freshwater mussel Unioninae (Bivalvia: Unionida) endemic to Yunnan of SW China

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Abstract: The ancient plateau lakes of Yunnan have long been known for their high diversity of mollusks. However, in recent times, human-induced pollution and habitat destruction have led to a severe decline in the diversity of Unionidae species. Since 2000, no living native Unionidae species have been discovered. This study, based on previous research records, conducted a comprehensive survey of the Unionidae species in the ancient plateau lakes of Yunnan. Only one living native freshwater mussel, *Mimo guoliangi* **gen. nov. sp. nov.**, was found. Molecular analysis using mitochondrial, nuclear gene fragments (COI and 28S) and mitochondrial genome confirmed the species' validity. Additionally, through morphological descriptions, this study identifies a possibly extinct species from Lake Fuxian: *Mimo jiaoyue* **gen. nov. sp. nov.**

Keywords: Plateau Lakes, taxonomy, Southwest China, Yunnan-Guizhou Plateau

中国西南部云南省特有蚌科（双壳纲：蚌目）一新属与两新种描述

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摘要：云南古高原湖泊一直以来就以其丰富的软体动物多样性而闻名。然而近年来，人为污染和栖息地破坏导致蚌科物种多样性严重下降。自 2000 年以来，没有发现任何现存的本土蚌科物种。本研究在前人研究记录的基础上，对云南古高原湖泊中的蚌科物种进行了全面调查，仅发现一种现存的本土淡水蚌 *Mimo guoliangi* **gen. nov. sp. nov.**。利用线粒体、核基因片段（COI 和 28S）和线粒体基因组进行分子分析，证实了该物种的有效性。此外，通过形态学描述，本研究在抚仙湖中鉴定了一个可能已经灭绝的物种：*Mimo jiaoyue* **gen. nov. sp. nov.**。

Accepted by Cheng-Bin WANG: 12.II.2025; published online: 12.II.2025

关键词：高原湖泊，分类学，西南地区，云贵高原

Citation: Xiang H-Q, Lu Y-Z, He Y-M & Li C-Y 2025: A new genus and two new species of freshwater mussel Unioninae (Bivalvia: Unionida) endemic to Yunnan of SW China. *The Indochina Entomologist*, 1 (30): 289–304. [向泓铨，鲁怡之，何岳铭 & 李重晔 2025: 中国西南部云南省特有蚌科（双壳纲：蚌目）一新属与两新种描述. 中南半岛昆虫学家, 1 (30): 289–304.] https://doi.org/10.70590/ice.2025.01.30

Introduction

The ancient plateau lakes of Yunnan, China, are known for their exceptionally high diversity of mollusks (Zhang *et al.* 1997; Du *et al.* 2011). Eight species of freshwater mussels, endemic to these plateau lakes, have been previously recorded in Yunnan. Unfortunately, due to pollution and habitat destruction, no living individuals of *Rhombuniopsis* (Haas 1920) species have been recorded since 2000, and they may be entirely extinct (Du *et al.* 2011; Xiang *et al.* 2024). Between 2020 and 2024, the research team conducted multiple surveys of all the ancient plateau lakes with freshwater mussels in Yunnan and the surrounding water systems. A new genus and two new species were found in this research. We conducted phylogenetic analysis based on multiple gene loci, including mitochondrial gene fragments cytochrome c oxidase subunit I (COI), nuclear large ribosomal subunit (28S) and mitochondrial genome, established a new genus and new species: *Mimo guoliangi* **gen. nov. sp. nov.** In addition, through morphological description, this study identified a possibly extinct species in Fuxian Lake: *Mimo jiaoyue* **gen. nov. sp. nov.**

Material and methods

Specimen sampling

Specimens were collected during eleven field surveys conducted in October–December 2024 (Xiang & He), July 2024 (He), March–June 2024 (Xiang & He), January 2024 (Xiang & He), January 2024 (Xiang), December 2023 (Xiang), January–July 2023 (Xiang & He), January 2022 (Xiang & He), January–March 2022 (Zhang & Xiang), May–July 2021 (Xiang), and May 2020 (Xiang), respectively, in altogether 23 lakes of the Yunnan Plateau of China (Lakes Dianchi, Fuxian, Xingyun, Erhai, Chenghai, Bitahai, Lashihai, Yangzonghai, Cibi, Jianhu, Changhu, Yuehu, Guangtangzi, Lugu, Yilong, Lulianghai, Xihu, Haixihai, Babuhai, Changqiaohai, Datunhai and Qilu) and surrounding areas, including rivers or creeks, and ruins of wells or hills for fossil and subfossil specimens (Fig. 1). The shell sizes of other species from the genera *Sinanodonta* Modell, 1945 and *Beringiana* Starobogatov, 1983 were measured by Hong-Quan Xiang and Ge Guo.Type specimens are deposited at the Museum of Biology, Nanchang University (**NCU**), China, and the private collections of Hong-Quan Xiang. Length (L) and Breadth (B) of shell is measured with calipers to a precision of 1 mm. Shells were photographed in consistent orientation using a NikonZ7 digital camera.

DNA extraction, PCR, sequencing and phylogenetic analyses

Total genomic DNA was isolated from a small piece of tissue taken from the foot of each ethanol-preserved specimen using a Trelief TM Animal Genomic DNA kit (Tsingke®). Partial sequences of COI and 28S rDNA were amplified using the following primers: LCO22me2 and HCO700dy2 for COI (Walker *et al.* 2007), D23F and D4RB for 28S (Park &Foighil 2000). Each PCR reaction was performed in a total volume of 20 μL, including 9 μL of PCR mix, 8 μL of double distilled water, 1 μL of each primer and 1 μL of the DNA template. The PCR conditions were as follows: initial denaturation at 95°C for 3 min; 35 cycles of denaturation at 95°C for 40 sec, annealing at 55°C for 30 sec and extension at 72°C for 30 sec; and final extension at 72°C for 7 min. Both ends of sequences were obtained by automated sequencing using Applied Biosystems 3730 in Sangon Biotech Co. Ltd. (Shanghai, China).

F-type mitogenomes were obtained in this study, Qualified genomic DNA samples were dispatched to Novogene (Beijing, China) for library construction and sequencing. After discarding low quality reads, clean reads were obtained and assembled de novo by CLC Genomic Workbench v. 12.0. Contigs identified as mitogen ome sequences were checked manually for overlap at the beginning and end, resulting in a circular mitogenome. The newly produced mitogenome was checked manually and annotated with Geneious v.11.0 (Kearse *et al.* 2012). The initial annotation of the mitogenome was carried out using the MITOS web server (Bernt *et al.* 2013). ARWEN (Laslett & Canbäck 2008) was also used to identify the locations of all tRNA genes. The annotations for two rRNA genes were further refined based on the positions of neighbouring genes. Open Reading Frame Finder (http://www.ncbi. nlm.nih.gov/orffinder/) and BLAST searches (http:// blast.ncbi.nlm.nih.gov/) were used to identify 13 protein-coding genes (PCGs).

Two datasets were constructed in this study: (1) datasets A (COI+28S; Table 1); (2) datasets B (F-type mitogenomes including 12 PCGs excluding ATP8, and two rRNA genes; Table 2). Sequences were aligned using MAFFT v. 7.505 based on the L-INS-i method (Katoh & Toh 2008). Pairwise distances between species were calculated using MEGA X (Kumar *et al.* 2018). The best substitution model was selected using the corrected Bayesian Information Criterion (BIC) in MODELFINDER v. 2.2.0 (Kalyaanamoorthy *et al.* 2017). For Bayesian analysis, two runs were performed simultaneously with four Markov chains starting from a random tree. Bayesian inference and maximum likelihood analysis were performed using MrBayes v. 3.2.7 (Ronquist *et al.* 2012) and IQTREE v. 2.2 (Minh *et al.* 2020), respectively, with reference to the selected model of sequence evolution. Bayesian posterior probabilities (BPPs) of nodes were determined using Metropolis-coupled Markov chains (one cold chain) for 2,000,000 generations, with sampling every 1000 generations. The first 25% of sampled trees were discarded as burn-in when the standard deviation of split frequencies of the two runs was less than 0.01; the remaining trees were then used to create a 50% majority-rule consensus tree and to estimate BPPs. Node support for maximum likelihood analysis was determined using 1000 rapid bootstrap (BS) replicates.

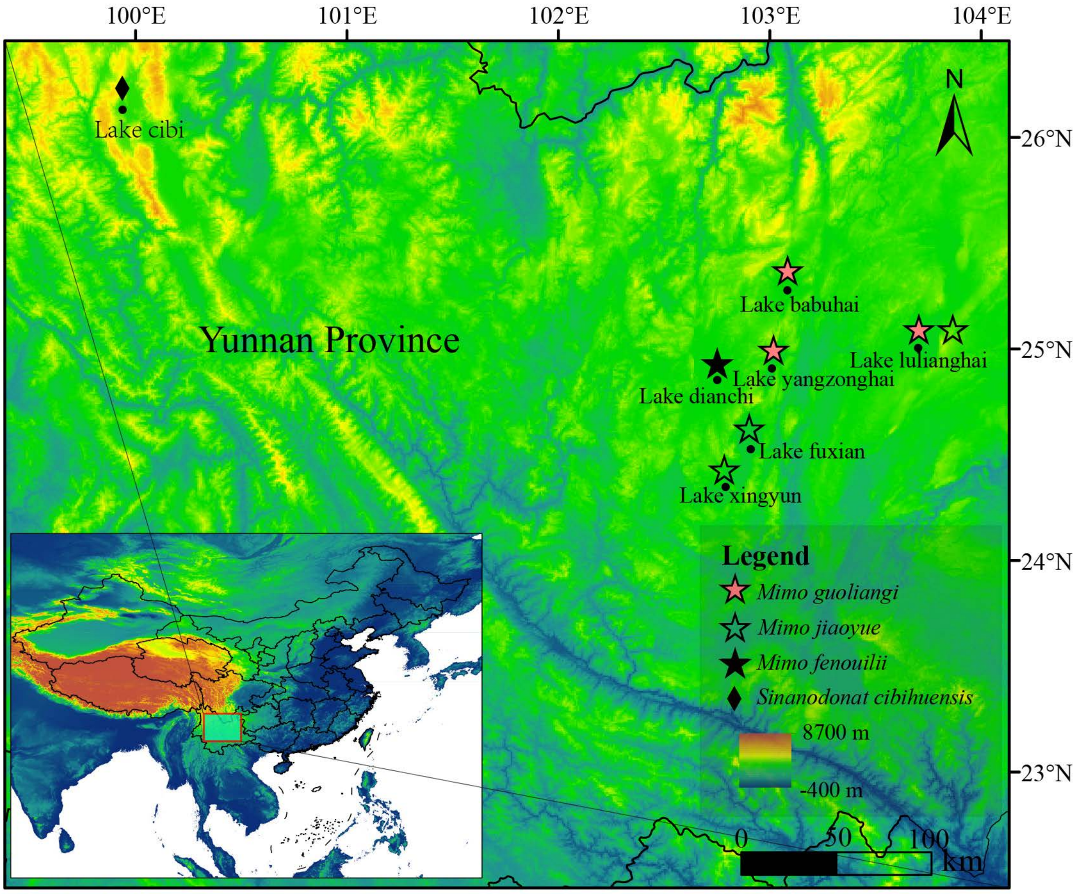

FIGURE 1. Map of the ancient plateau lakes and rivers in the Yunnan Province, south-west China, showing the sampling sites, adapted from Zhang *et al*. (2015).

TABLE 1. List of COI and 28S rRNA sequences used in this study, including the species, GenBank accession number and collecting location.

Species	COI	28S rDNA	Country
Scabies scobinatus (Gould, 1843)	MG288632	MG552824	Thailand
Pletholophus honglinhensis (Bogan, Do, Froufe & Lopes-Lima, 2023)	OR912962	OR913009	Vietnam
Pletholophus tenuis (Griffith & Pidgeon, 1833)	KX822658	KX822614	Vietnam
Pletholophus guangzhouensis (Dai, Chen, Huang & Wu, 2024)	PP945818	PP956591	China
Cristaria bellua (Morelet, 1866)	ON704642	ON695893	Laos
Cristaria clessini (Kobelt, 1879)	MT020592	MT020810	Japan
Cristaria truncata (Dang, Thai & Pham, 1980)	OP491287	OP499826	Vietnam
Cristaria plicata (Leach, 1814)	MG462956	MG595484	China
Anemina arcaeformis (Heude, 1877)	MG462936	MG595463	China
Amuranodonta kijaensis (Moskvicheva, 1973)	MK574204	MK574473	Russia
Buldowskia suifunica (Lindholm, 1925)	MK574190	MK574460	Russia
Buldowskia kamiyai (San, Hattori & Kondo, 2020)	MT020525	MT020808	Japan
Buldowskia iwakawai (Suzuki, 1939)	MT020523	MT020806	Japan
Buldowskia shadini (Moskvicheva, 1973)	MK574197	MK574467	Russia
Buldowskia flavotincta (Martens, 1905)	MT020537	MT020804	South Korea
Beringiana gosannensis (San, Hattori & Kondo, 2020)	MT020584	MT020802	Japan
Beringiana fiukuharai (San, Hattori & Kondo, 2020)	MT020567	MT020801	Japan
Beringiana japonica (Clessin, 1874)	MT020576	MT020803	Japan
Beringiana beringiana (Middendorff, 1851)	MT020557	MT020799	Japan
Sinanodonta lucida (Heude, 1877)	MG463066	MG595589	China
Sinanodonta angula (Tchang, Li & Liu, 1965)	MG463053	MG595580	China
Sinanodonta woodiana (Lea, 1834)	MG463080	MG595608	China
Sinanodonta pacifica (Heude, 1878)	MG463052	MG595599	China
Sinanodonta lauta (Martens, 1877)	MT020616	MT020834	Japan
Sinanodonta schrenkii (Lea, 1870)	MT020618	MT020837	South Korea
Sinanodonta tumens (Haas, 1910)	MT020622	MT020838	Japan
Sinanodonta calipygos (Kobelt, 1879)	MT020623	MT020833	Japan
Mimo guoliangi **gen. nov. sp. nov.** 1	PV091226	PV090864	China
Mimo guoliangi **gen. nov. sp. nov.** 2	PV091227	PV090865	China
Mimo guoliangi **gen. nov. sp. nov.** 3	PV091228	PV090866	China

TABLE 2. Complete mitogenome sequences used in this study.

Species	GenBank number
Quadrula quadrula	NC_013658
Lanceolaria gladiola	KY067441
Lanceolaria grayana	KJ495725
Arconaia lanceolata	KJ144818
Anodonta exulcerata	MN594533
Anodonta cygnea	MG385135
Cristaria plicata	FJ986302
Anemina euscaphys	KP187851
Anemina arcaeformis	KF667530
Beringiana fukuharai	LC592410
Sinanodonta lucida	KF667529
Sinanodonta woodiana	HQ283347
Sinanodonta tumens	LC592406
Mimo guoliangi **gen. nov. sp. nov.**	This study

Results

Molecular analyses

The GTR+I+G4+F model was selected as the best-fit of nucleotide substitution by the BIC criterion. The phylogenetic tree supported the validity of the new species and new genus within Unionidae. Both BI and ML methods produced identical topology, *Sinanodonta* and *Mimo* **gen. nov.** each formed a monophyletic group with are sister clades to each other based on datasets A (BPP=0.713, BS=57) (Fig. 6) and datasets B (BPP=1, BS=100) (Fig. 7).

The genetic distances of COI sequences between *Mimo* **gen. nov.**, *Sinanodonta*, *Amuranodonta* Moskvicheva, 1973, *Anemina* Haas, 1969, *Beringiana*, *Buldowskia* Moskvicheva, 1973, *Cristaria* Schumacher, 1817, *Pletholophus* Simpson, 1900 and *Scabies* Haas, 1911 species shown in Table 3; the COI p-distances between *Mimo* **gen. nov.** and its closest relative, viz. the *Sinanodonta*, are 9.6%–14.3%.

Systematics

Family Unionidae Rafinesque, 1820

Subfamily Unioninae Rafinesque, 1820

Tribe Cristariini Lopes-Lima, Bogan & Froufe, 2017

Genus *Mimo* Xiang, Lu, He & Li gen. nov.

https://zoobank.org/3EA9DEB2-8138-4337-941C-8FA524C9C10F

Type species. *Mimo guoliangi* **gen. nov. sp. nov.**

Diagnosis. Shell medium size, moderately thick. Dorsal margin slightly curved downwards; ventral margin curved. Foot approximate rectangle. Pigmentation of the incurrent and excurrent aperture not obvious; excurrent aperture relatively smooth, with little small round papillae. Mantle light yellow or white, edge with weak dense and elongated protrusions, arranged in one rows.

Etymology. The genus name "Mimo" is derived from the name of an extinct ancient ethnic group in Yunnan, with the largest branch, "Dian", becoming the long-used abbreviation for Yunnan throughout history. The word is of the feminine gender. We suggest the Chinese common name as "靡莫蚌".

Remarks. Despite *Mimo* **gen. nov.** resembles *Sinanodonta*. It differs from *Sinanodonta* in having a very round shell, pigmentation of the incurrent and excurrent aperture not obvious; excurrent aperture relatively smooth, with little small round papillae (Fig. 8).

Distribution. This genus has only been found in Lake Lulianghai, Fuxian, Xingyun, Yangzonghai and Babuhai in Yunnan Province for the time being.

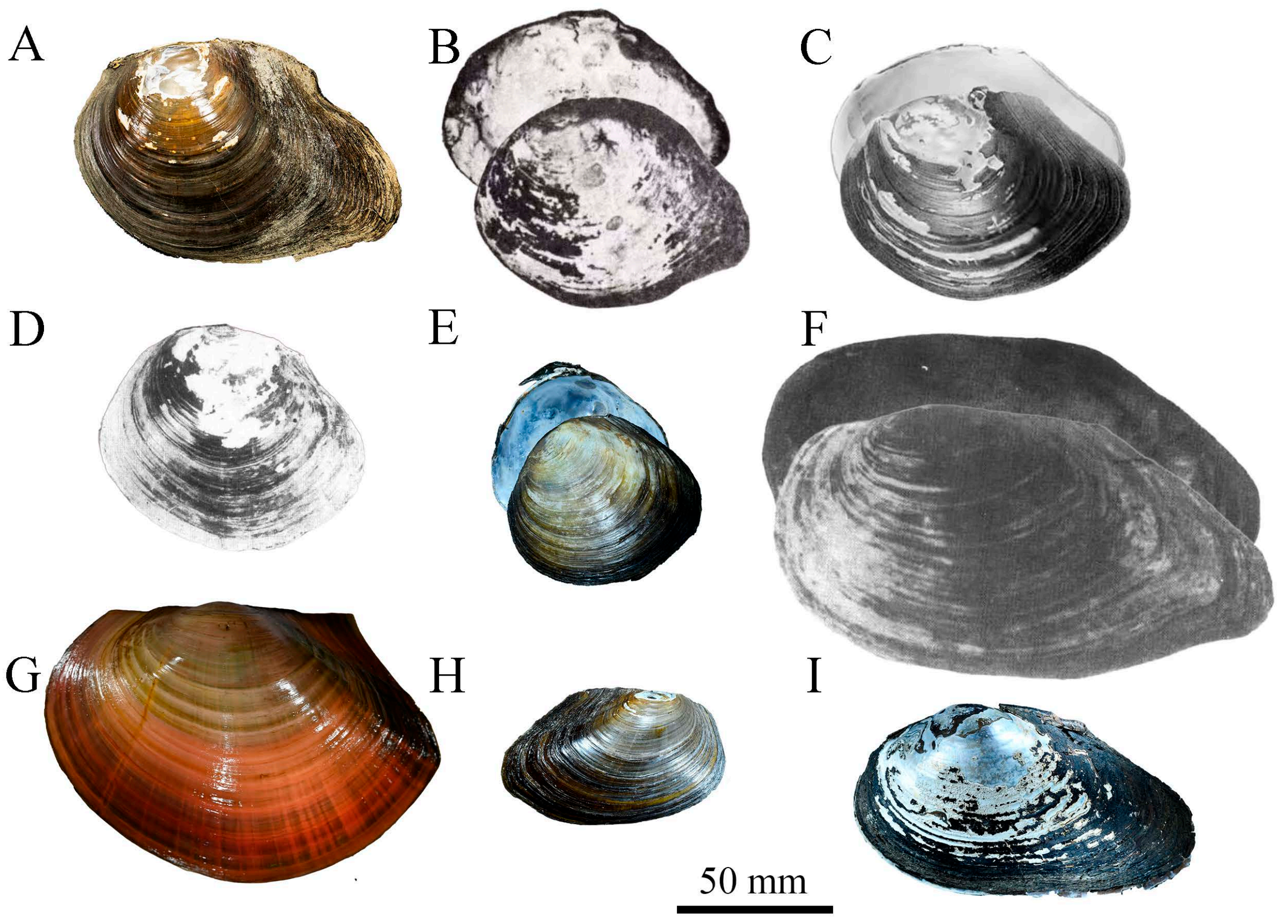

FIGURE 2. **A** *Mimo guoliangi* **gen. nov. sp. nov.**, holotype, Lake Lulianghai **B** *M. fenouilii* (Now *M. guoliangi* **gen. nov. sp. nov.**), Zhang 1949, Lake Yangzonghai **C** *M. fenouilii* **comb. nov.**, holotype, Lake Dianchi **D** *Anodonta lateriplana*, Huang & Zhang 1986, holotype, Lake Dianchi **E** *M. jiaoyue* **gen. nov. sp. nov.**, holotype, Lake Fuxian **F** *Sinanodonta cibihuensis*, Huang & Zhang 1984, holotype, Lake Cibi **G** *S. woodiana*, Lake Erhai **H** *S. woodiana*, Lake Fuxian **I** *Beringiana fukuharai*, Japan. Scale bars = 50 mm.

Mimo guoliangi **Xiang, Lu, He & Li gen. nov. sp. nov.**

https://zoobank.org/A0B6AC0F-91EA-46AA-89E8-F58548897BEB

Figs. 2A, 3, 4

Material examined. Holotype: NCU(Collection NCUHB 2501), shell length 114 mm, shell breadth 33 mm, Lake Luliang, Qujing City, Yunnan Province, China, 25°00'20"N, 103°41'41"E, March 2024 collected by Yue-Ming He and Hong-Quan Xiang.

Paratypes: 17 specimens, NCU(Collection NCUHB2502–18), shell length 72–116 mm, shell width 19–33 mm, locality and habitat same as holotype.

Additional material examined: 1 specimen, NCU(Collection NCUHB2519), shell height 79 mm, shell width 22 mm, Lake Babuhai, Yanglin town, Songming County, Kunming, Yunnan Province, China, 25°16'37"N, 103°5'35"E, January 2024 collected by Hong-Quan Xiang (Fig. 1).

Etymology. To Liang Guo, a renowned freshwater mussel and insect enthusiast from Fujian, and also the author of the book "Unionoida" in China. The recommended Chinese name is "郭氏靡莫蚌".

Diagnosis. Shell medium size, moderately thick, very flat. Anterior rounded, short, posterior little long and wide. Dorsal margin slightly curved downwards; ventral margin curved; mature individuals often with one weak pseudocardinal teeth. Hinge long. Foot approximate rectangle. Pigmentation of the incurrent and excurrent aperture not obvious; excurrent aperture relatively smooth, with little small round papillae. Mantle light yellow or white, edge with weak dense and elongated protrusions, arranged in one rows.

Description. Shell medium size, moderately thick, very flat; shell surface black or yellow-green, with the thick growth lines. Umbo not inflated, below or even with the hinge line and often eroded. Anterior rounded, short, posterior little long and wide. Dorsal margin slightly curved downwards, with a distinct obtuse angle in the lower of posterior margin; ventral margin curved; mature individuals often with one weak and short degenerated pseudocardinal teeth, without lateral teeth. Hinge long. Ligament strong. Mantle muscle scars obvious. Mantle light yellow or white, edge with weak dense and elongated protrusions, arranged in one rows. Anterior adductor muscle scars oval, deep and rough; posterior adductor muscle scars oval, shallow and rough. Foot approximate rectangle. Pigmentation of the incurrent and excurrent aperture not obvious; papillae in the incurrent aperture short and cylindrical, arranged in two rows; excurrent aperture relatively smooth, with little small weak round papillae. the size of inner gills exceeding that of outer gills. labial palps medium-thick, flat elliptical. Nacre white.

Remarks. *M. guoliangi* **gen. nov. sp. nov.** has a very flattened shell, relatively smooth excurrent aperture with few small round papillae, weak pseudocardinal teeth in mature individual which differ obvious *Sinanodonta* species.

Habitat and distribution. This species has only been found in Lake Yangzonghai, Babuhai and Lulianghai in Yunnan Province for the time being. In Lake Babuhai, this species is alongside with *Rhombuniopsis songmeng* (Xiang, He & Zhang 2024). Living specimens were only found in a reservoir near Lake Lulianghai. Both living individuals had severely corroded shells, and no juvenile empty shells or living specimens were found in this water body.

Mimo jiaoyue **Xiang, Lu, He & Li gen. nov. sp. nov.**

https://zoobank.org/C92C41C6-7D63-4B91-B557-E26F871CE10A

Figs. 2E, 5

Material examined. Holotype: NCU(Collection NCUHB2601), shell length 68 mm, shell breadth 37mm, Lake Fuxian, Yousuo Town, 24°37'53"N, 102°54'30"E, July 2024 collected by Yue-Ming He.

Paratypes: 10 specimens, NCU(Collection NCUHB2602–11), shell length 50–76 mm, shell width 23–37 mm, December 2024 (Xiang & He), July 2024 (He), March–June 2024 (Xiang & He), locality and habitat same as holotype.

Additional material examined: 1 specimen fossil, NCU(Collection NCUHB2612), shell length 60 mm, Lake Luliang, Qujing City, Yunnan Province, China, 25°01'06"N, 103°40'53"E, July 2021 collected by Hong-Quan Xiang (Fig. 1).

Etymology. The species name "jiaoyue" is derived from an ancient Chinese term for the moon, used to describe the shell's shape as being as round as the bright moon in the night sky. The recommended Chinese name is "皎月靡莫蚌".

Diagnosis. Shell round, medium size, moderately thick, very inflated. Anterior and posterior rounded, short and wide. Dorsal margin slightly curved downwards; ventral margin curved; without pseudocardinal teeth and lateral teeth. Hinge short.

Description. Shell round, medium size, moderately thick, very inflated; shell surface yellow-green, with the thin growth lines. Umbo inflated, below or even with the hinge line and often eroded. Anterior and posterior rounded, short and wide. Dorsal margin slightly curved downwards; ventral margin curved; without pseudocardinal teeth and lateral teeth. Hinge short. Ligament strong. Mantle muscle scars not obvious. Anterior adductor muscle scars irregular, shallow and smooth; posterior adductor muscle scars not obvious. Nacre white.

Remarks. *Mimo jiaoyue* **gen. nov. sp. nov.** it differs from *Mimo guoliangi* **gen. nov. sp. nov.** in having a very inflated shell (Fig. 8), hinge short, without one weak pseudocardinal teeth and posterior rounded. In addition, *Mimo jiaoyue* **gen. nov. sp. nov.** shell round, this is rare within the tribe Cristariini.

Habitat and distribution. This species has only been found in Lake Fuxian and Xingyun; fossil in Lake Lulianghai in Yunnan Province for the time being.

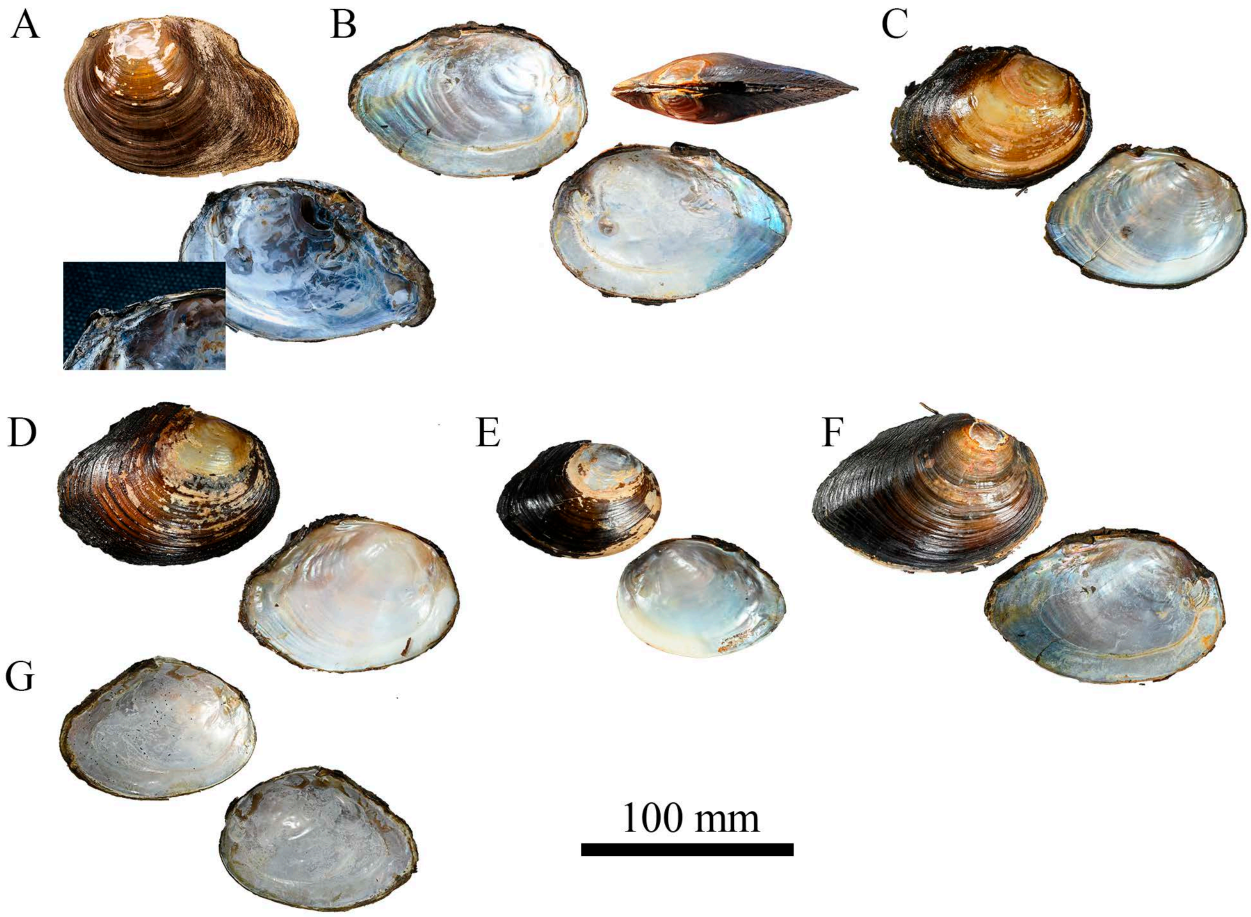

FIGURE 3. Shell of *Mimo guoliangi* **gen. nov. sp. nov.**: **A** Holotype collected from Lake Lulianghai, shell length 114 mm **B**–**D** Specimens collected from Lake Lulianghai, shell length 116 mm, 96 mm and 110 mm **E** Specimens collected from Lake Babuhai, shell length 79 mm **F**–**G** Specimens collected from Lake Lulianghai, water depth 5 m, shell length 116 mm and 97 mm. Scale bars = 100 mm.

Mimo fenouilii Heude, 1878 comb. nov.

Fig. 2C

Diagnosis. Shell sub-compressa, medium size, moderately thick. Anterior and posterior rounded. Dorsal margin short and curved downwards; ventral margin curved; without pseudocardinal teeth and lateral teeth. Nacre white.

Remarks. *Mimo fenouilii* it differs from *Mimo guoliangi* **gen. nov. sp. nov.** in inflated shell (Fig. 8), without one weak pseudocardinal teeth. Unlike *Mimo jiaoyue* **gen. nov. sp. nov.**, *Mimo fenouilii* does not have a round shell and posterior little long.

Habitat and distribution. This species has only been found in Lake Dianchi.

Discussion

Similar to *Rhombuniopsis* species, those species discovered of genus *Mimo* **gen. nov.** are all found exclusively in ancient highland lakes. However, The survival status of freshwater mussels in the highland ancient lakes of Yunnan Province is concerning. The modern pollution and destruction of the shoreline have caused them to lose their essential habitat (Cui *et al.*, 2008; Xiang *et al.* 2024). Due to increased pollution, the dissolved oxygen levels in Lake Fuxian have decreased even further (Zhang *et al.* 2023), making it unlikely that any surviving populations remain in the deeper parts of the lake. The discover of *Mimo guoliangi* **sp. nov.** has significant implications for understanding and conserving the unique species of the ancient plateau lakes in Yunnan.

For the previously published *Anodonta lateriplana* (Huang & Zhang, 1986) (Fig. 2D), *A. lateriplana* was found in Lake Dianchi, the same location as *M. fenouilii* **comb. nov.**, and has a completely identical shell morphology, after reviewing the original literature, no description of this species was found in the main text; it only appears as the Latin name "*Anodonta lateriplana* sp. nov." in the picture of the paper. Furthermore, an investigation of all other publications by the same author from the same year revealed no valid information about this species. Therefore, this study concludes that *A. lateriplana* is invalid. Regarding *M. jiaoyue* **sp. nov.**, its shell shape is the most rounded among the Unionidae species endemic to the ancient lakes of Yunnan, and it features a very inflated shell compared to *Sinanodonta* species, making it easy to distinguish from them. As for *M. guoliangi* **sp. nov.**, it has a very flattened shell, which facilitates its distinction from *Sinanodonta* species. Upon examining the shell anatomy, *M. guoliangi* **sp. nov.** has a relatively smooth excurrent aperture with few small round papillae, a feature absent in *Sinanodonta* species, and mature *Sinanodonta* and other *Mimo* **gen. nov.** species do not exhibit weak pseudocardinal teeth. For *M. guoliangi* **sp. nov.** and *M. fenouilii* **comb. nov.**, although the shell shapes of the two species show some similarities, the shell of *M. fenouilii* **comb. nov.** is more inflated, making it relatively easy to distinguish from *M. guoliangi* **sp. nov.** However, it is unfortunate that no shells or shell fragments of *M. fenouilii* **comb. nov.** were found during the survey of Lake Dianchi. It is possible that *M. fenouilii* **comb. nov.** became extinct long ago, along with *R. fultoni* from Lake Dianchi, which makes further research on *M. fenouilii* **comb. nov.** difficult. However, the mature shells of species in the genus *Mimo* **gen. nov.** can be clearly distinguished in terms of morphology. The scatter plot shows distinct differences between the three species. Even the largest shell of *M. guoliangi* **sp. nov.** does not exhibit the same expansion as *M. Fenouilii* **comb. nov.** (Fig. 8), and their distribution ranges do not overlap. Therefore, this study considers these three species to be valid. Due to the isolating effect of the ancient plateau lakes (Xiang *et al.* 2024, Zhang *et al.* 2015), the species of the newly discovered genus *Mimo* **gen. nov.** are all found exclusively in ancient highland lakes, similar to those of the genus *Rhombuniopsis*, which are also specialized species of ancient highland lakes.

The survival status of freshwater mussels in the highland ancient lakes of Yunnan Province is concerning, and the lake-specific genus *Rhombuniopsis* may have already become extinct (Du *et al.* 2011; Xiang *et al.* 2024). As for *Mimo fenouilii* **comb. nov.** and *M. jiaoyue* **sp. nov.**, no living specimens have been found in Lake Dianchi, Lake Fuxian or surrounding water bodies. Its shells are often found alongside the extinct *Rhombuniopsis linan* (Xiang, He & Zhang 2024). Despite Lake Fuxian having a large surface area and considerable depth, the low oxygen content in the highland lakes, similar to the situation that led to the disappearance of *R. linan*, means that the majority of freshwater mussels are found in shallow waters. The modern pollution and destruction of the shoreline have caused them to lose their essential habitat (Xiang et al. 2024). Furthermore, due to increased pollution, the dissolved oxygen levels in Lake Fuxian have decreased even further (Zhang *et al.* 2023), making it highly unlikely that any surviving populations remain in the deeper parts of the lake. This view is further supported by previous trawl surveys of Lake Fuxian, which failed to find any specimens of this species in the deeper waters (Cui *et al.* 2008). The loss of host fish species is also a reason for the extinction of these Unionidae species endemic to the ancient plateau lakes (Du *et al.* 2011; Xiang *et al.* 2024). In addition, invasive species may also contribute to its extinction. In surveys of the Lake Fuxian shoreline, researchers discovered a number of *Sinanodonta woodiana* (Lea, 1834), and since no shell fragments of this species were found in the Quaternary sediment layers around Lake Fuxian, this study concludes that it is an invasive species in Lake Fuxian, further displacing native bivalve species. Notably, the Quaternary sediment layers sometimes contain fragments of Qing Dynasty porcelain bowls alongside *M. jiaoyue* **sp. nov.**, indicating that these species still had living populations between one hundred and three hundred years ago. This suggests that these species declined due to modern damage to the lake, rather than natural extinction. In addition, this study also discovered a small number of shell fragments of *M. jiaoyue* **sp. nov.** in the shell mounds near Lake Xingyun, but no traces of the species were found within the lake area. Fossil evidence of this species was also found in the Neogene Ciying Formation strata near Lake Lulianghai, its inflated round shell shape (Fig. 5F) rules out the possibility of it being *M. Fenouilii* **comb. nov.** or *M. guoliangi* **sp. nov.**, further suggesting a very ancient history for this species. Therefore, it is necessary to establish a unique genus for the distinct shells of these ancient highland lakes. Further investigation into the species' current status is necessary. As for *M. guoliangi* **sp. nov.**, records of the species have also been found in Lake Yangzonghai (Zhang 1949). The species was initially identified as *M. fenouilii* **comb. nov.** However, due to its relatively low degree of shell expansion, this study proposes that the species should be classified as *M. guoliangi* **sp. nov.** Furthermore, this study's researchers discovered empty shells of this species in Lake Jialize and three live individuals in a remnant water body of Lake Lulianghai. Both live individuals had severely corroded shells, and no juvenile empty shells or live specimens were found in this water body. This suggests that these three individuals are likely of considerable age, and the population of this species is in a critically endangered state. No evidence of this species was found in surveys of Lake Yangzonghai. Trawling, apart from a large number of *Sinanodonta woodiana* (Lea, 1834), yielded no other Unionidae species. A small number of fragments from *Rhombuniopsis* species were found in the sediment layers around Lake Yangzonghai (previously, no *Rhombuniopsis* species had been recorded in Lake Yangzonghai), these shell fragments were too worn to identify the specific species. Given the severe pollution in Lake Yangzonghai and Lakes Dianchi(Gong *et al.* 2009; Zhao 2009), this study concludes that *Mimo* **gen. nov.** species has likely disappeared from both lakes. Unfortunately, except for *M. guoliangi* **sp. nov.**, all other species have only left behind empty shells. It is noteworthy that although some species appear in multiple lakes, no shells of these species have been found in the rivers or other water systems connecting these lakes. How these species have spread between the lakes remains a topic for further research.

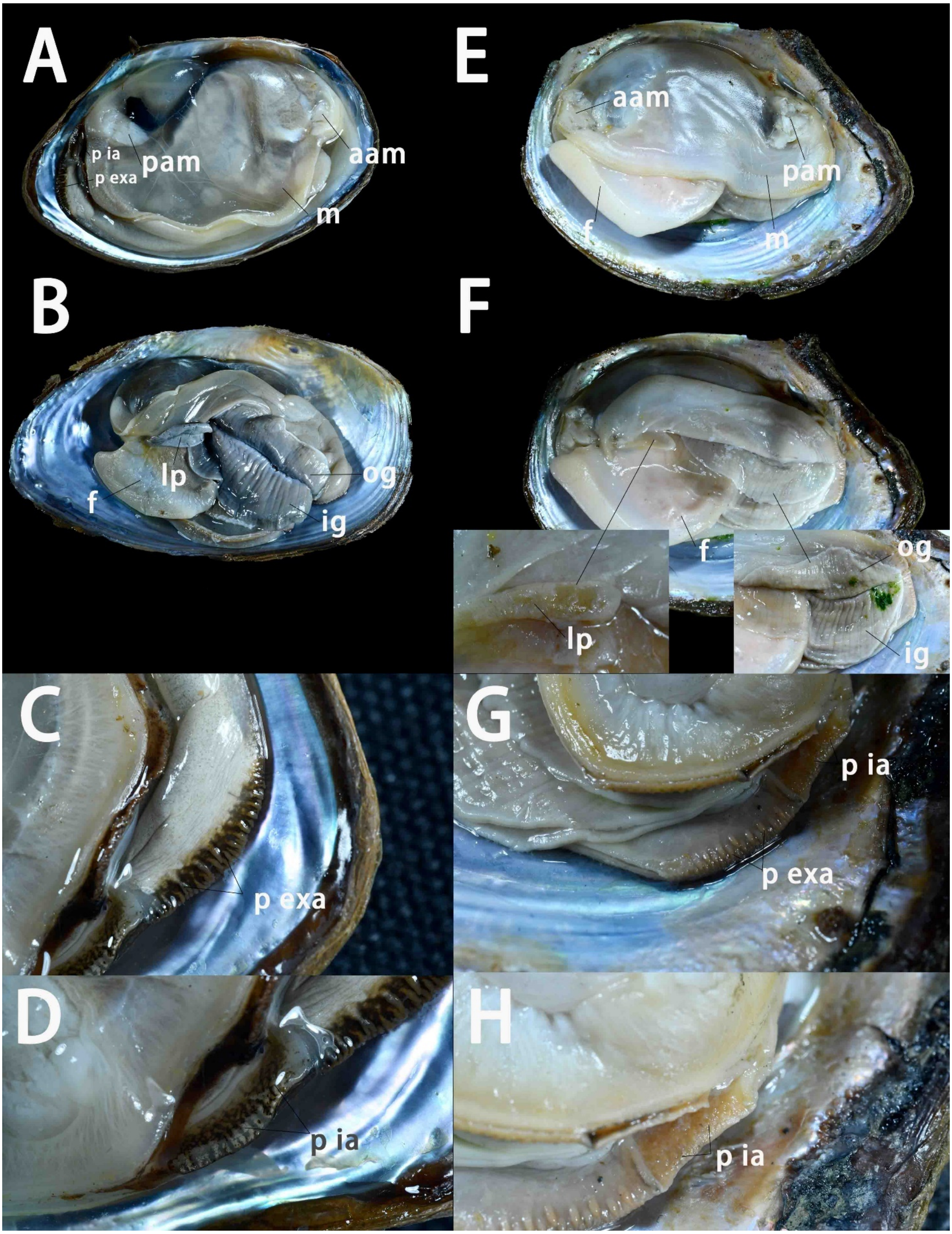

FIGURE 4. Anatomy: **A**–**D** *Sinanodonta woodiana,* Lake Fuxian **E**–**H** *Mimo guoliangi* **gen. nov. sp. nov.**, Lake Lulianghai. **aam** (anterior adductor muscle) **pam** (posterior adductor muscle) **f** (foot) **ig** (inner gill) **og** (outer gill) **lp** (labial palps) **m** (mantle) **p ia** (papillae in incurrent aperture) **p exa** (papillae in excurrent aperture).

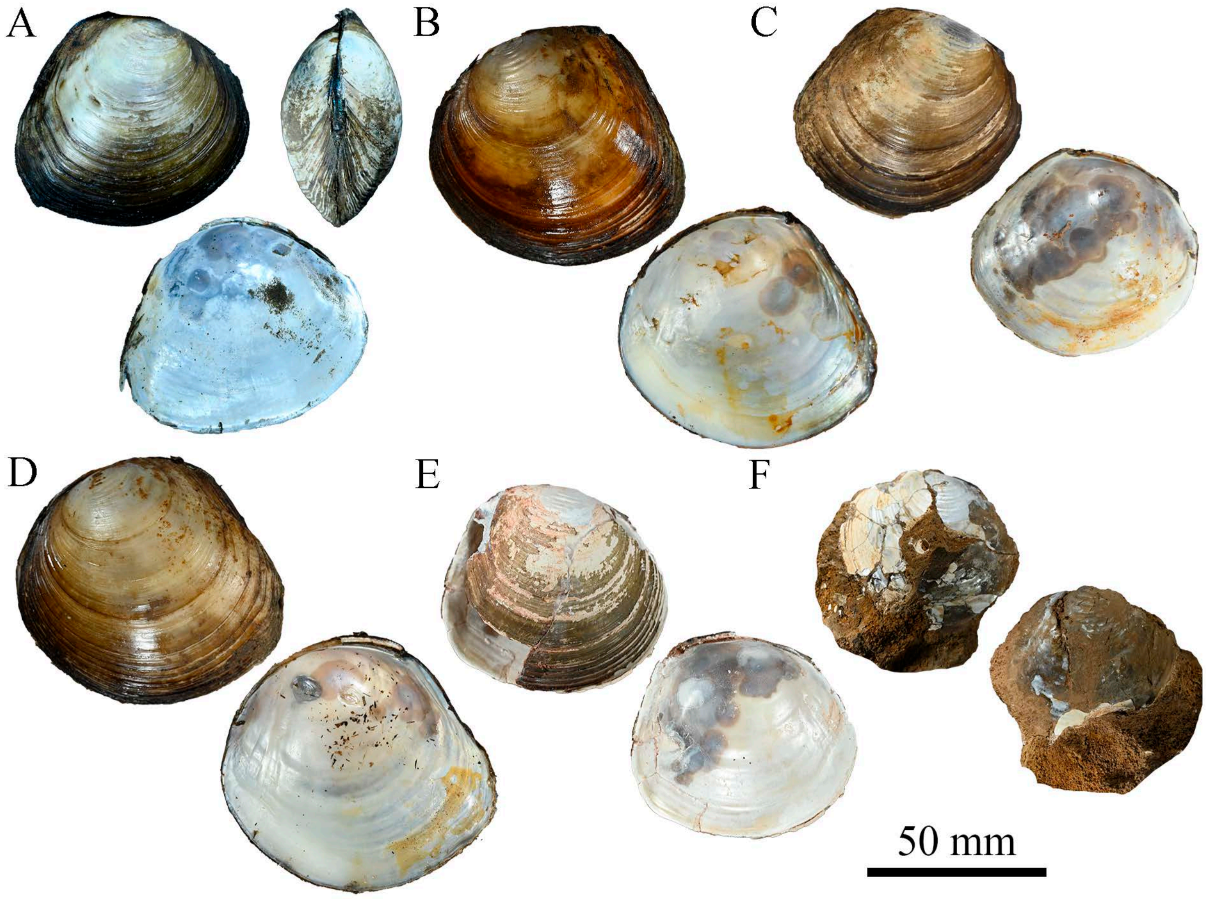

FIGURE 5. Shell of *Mimo jiaoyue* **gen. nov. sp. nov.**: **A** Holotype collected from Lake Fuxian, shell length 68 mm **B**–**E** Specimens collected from Lake Fuxian, shell length 75 mm, 65 mm, 74 mm and 64mm **E** Specimen fossil collected from Lake Luliang, shell length 60 mm. Scale bars = 50 mm.

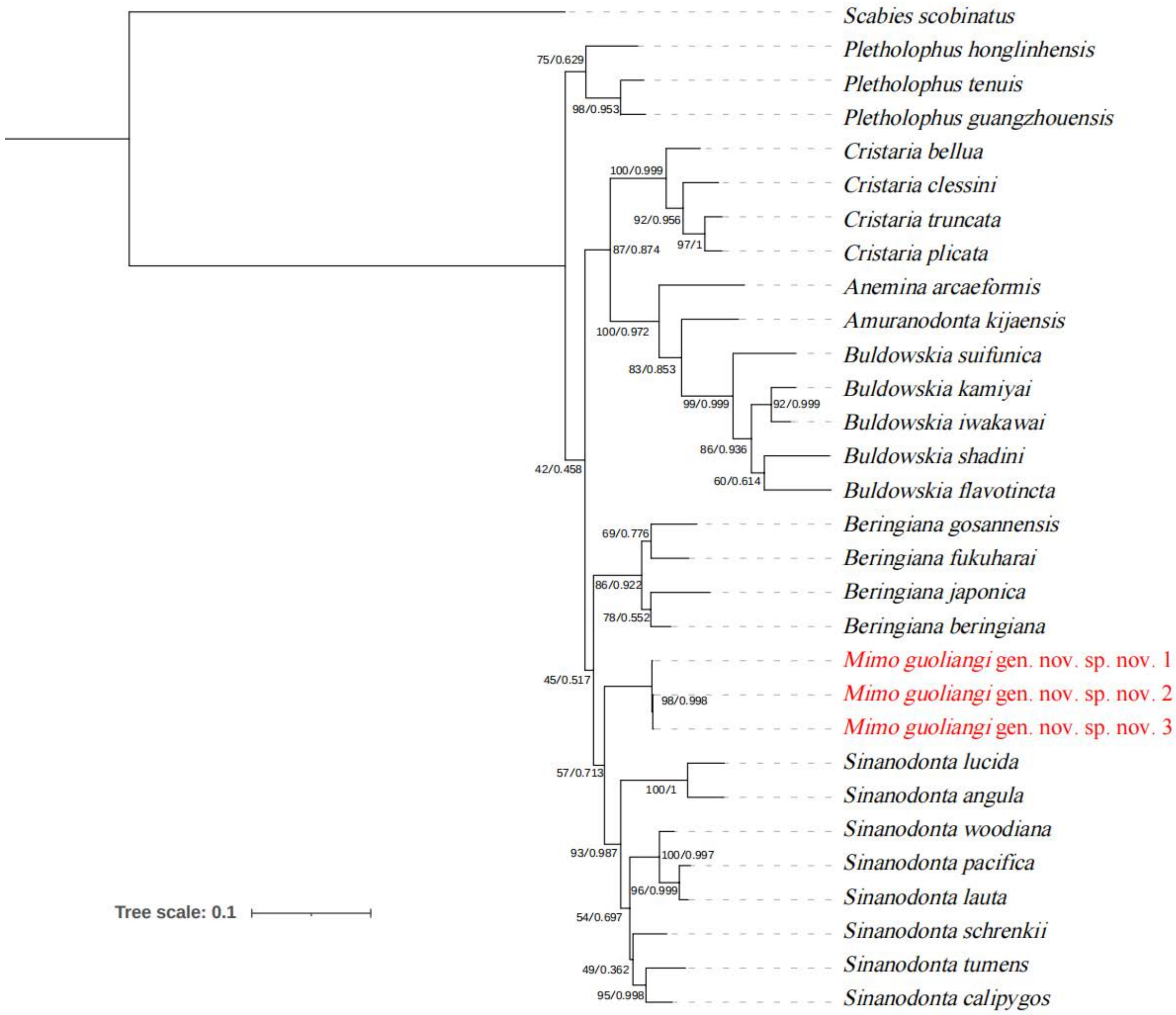

FIGURE 6. A Maximum-likelihood (ML) and Bayesian inference (BI) tree for the new species and other Unionidae species based on the COI and 28S rDNA. Values (BPP/BS) at nodes represent Bayesian posterior probabilities and Bootstrap values. Red indicates the new specie.

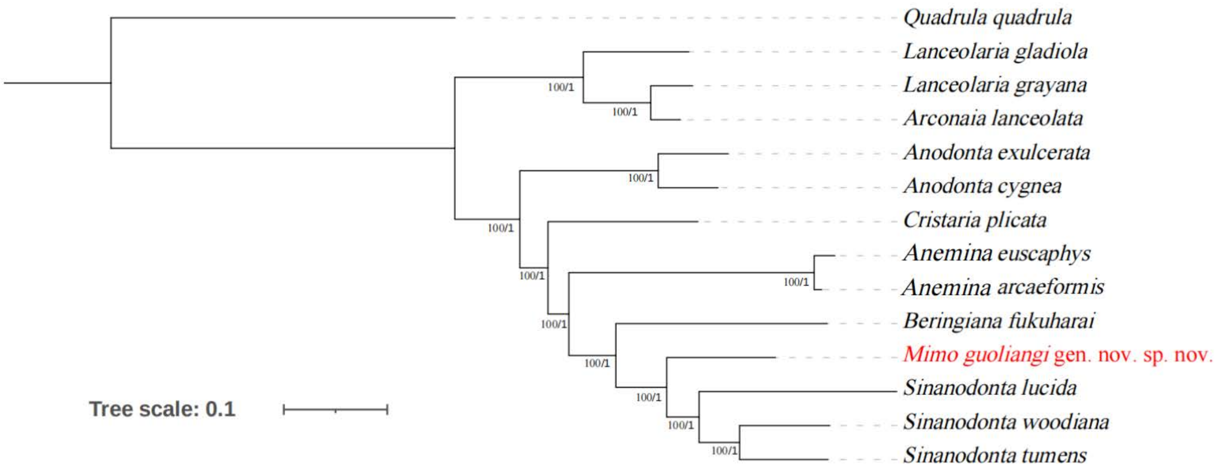

FIGURE 7. A Maximum-likelihood (ML) and Bayesian inference (BI) tree for the new species and other Unionidae species based on the mitochondrial data. Values (BPP/BS) at nodes represent Bayesian posterior probabilities and Bootstrap values. Red indicates the new specie.

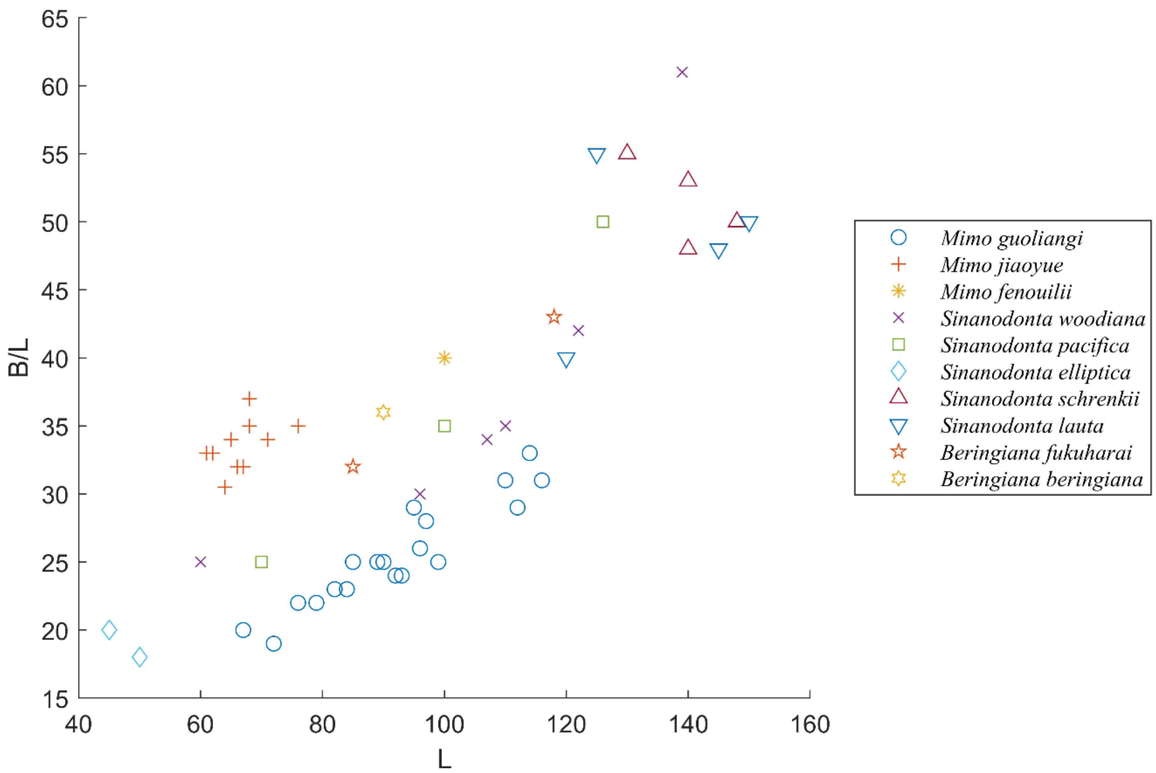

FIGURE 8. Comparison of the Unionidae species with respect to parameters L, B/L.

Acknowledgements

We acknowledge Ge Guo, Xian-Ming Zhang, Li Gang, Le-Jia Zhang, Jian-Hao Su, Ji-Zhou Yang and Yu-Tong Yao for their help in obtaining samples for this study.

References

Bernt M, Donath A, Jühling F, Externbrink F, Florentz C, Fritzsch G, Pütz J, Middendorf M & Stadler PF 2013: MITOS: improved de novo metazoan mitochondrial genome annotation. *Molecular Phylogenetics and Evolution*, 69 (2): 313–319. https://doi.org/10.1016/j.ympev.2012.08.023

Cui Y-D, Liu X-Q & Wang H-Z 2008: Macrozoobenthic community of Fuxian Lake, the deepest lake of southwest China. *Limnologica*, 38: 116–125. https://doi.org/10.1016/j.limno.2007.10.003

Du L-N, Li Y, Chen X-Y & Yang J-X 2011: Effect of eutrophication on molluscan community composition in the Lake Dianchi (China, Yunnan). *Limnologica*, 41 (3): 213–219. https://doi.org/10.1016/j.limno.2010.09.006

Gong Z-J, Li Y-L, Shen J & Xie P 2009: Diatom community succession in the recent history of a eutrophic Yunnan Plateau lake, Lake Dianchi, in subtropical China. *Limnology*, 10: 247–253. https://doi.org/10.1007/s10201-009-0282-8

Huang B-Y & Zhang L 1984: Freshwater Unionidae fauna of Erhai Lake and Cibi Lake in Yunnan Province, China. *Journal of Nanjing Institute of Geography. Chinese Academy of Sciences*, 1984: 2.

Huang B-Y & Zhang L 1986: Freshwater Lamellibranchia from Dianchi, Yunnan, Chinese. *Transactions of the Chinese Society of Malacology*, 2: 171.

Kalyaanamoorthy S, Minh BQ, Wong TK, Haeseler A & Jermiin LS 2017: Model Finder: fast model selection for accurate phylogenetic estimates. *Nature methods*, 14: 587–589. https://doi.org/10.1038/nmeth.4285

Kumar S, Stecher G, Li M, Knyaz C & Tamura K 2018: MEGA X: molecular evolutionary genetics analysis across computing platforms. *Molecular Biology and Evolution*, 35: 1547–1579. https://doi.org/10.1186/1471-2148-11-118

Katoh K & Toh H 2008: Recent developments in the MAFFT multiple sequence alignment program. *Briefings in Bioinformatics*, 9: 286–298. https://doi.org/10.1093/bib/bbn013

Kearse M, Moir R, Wilson A, Stones-Havas S, Cheung M, Sturrock S, Buxton S, Cooper A, Markowitz S, Duran C, Thierer T, Ashton B, Meintjes P & Drummond A 2012: Geneious Basic: an integrated and extendable desktop software platform for the organization and analysis of sequence data. *Bioinformatics*, 28 (12): 1647–1649. https://doi.org/10.1093/bioinformatics/bts199

Laslett D & Canbäck B 2008: ARWEN: a program to detect tRNA genes in metazoan mitochondrial nucleotide sequences. *Bioinformatics*, 24 (2): 172–175. https://doi.org/10.1093/bioinformatics/btm573

Minh BQ, Schmidt HA, Chernomor O, Schrempf D, Woodhams MD, Haeseler A, Lanfear R 2020: IQ-TREE 2: new models and efficient methods for phylogenetic inference in the genomic era. *Molecular Biology and Evolution*, 37: 1530–1534. https://doi.org/10.1093/molbev/msaa015

Park JK & Ó Foighil D 2000: Sphaeriid and corbiculid clams represent separate heterodont bivalve radiations into freshwater environments. Molecular *Phylogenetics and Evolution*, 14 (1): 75–88. https://doi.org/10.1006/mpev.1999.0691

Ronquist F, Teslenko M, Mark P, Ayres DL & Darling A 2012: MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology*, 61: 539–542. https://doi.org/10.1093/sysbio/sys029

Walker JM, Bogan AE, Bonfiglio EA, Campbell DC, Christian AD, Curole JP, Harris JL, Wojtecki RJ & Hoeh WR 2007: Primers for amplifying the hypervariable, male-transmitted COII-COI junction region in amblemine freshwater mussels (Bivalvia: Unionoidea: Ambleminae). *Molecular Ecology Notes*, 7 (3): 489–491. https://doi.org/10.1111/j.1471-8286.2006.01630.x

Xiang H-Q, He Y-M, Zhang L-J, Gao H, Guo L, Lu Y-Z, Fan S-Y & Chen H 2024: A revision of *Rhombuniopsis* Haas, 1920 (Unionida, Unionidae) endemic to the ancient lakes of Yunnan, China, with descriptions of two new species. *Zootaxa*, 5481 (2): 273–289. https://doi.org/10.11646/zootaxa.5481.2.6

Zhang X 1949: Liste Des Mollusoues d'eau douce recueillispendant les annees 1938-1946 au YUNNAN etdescription D'especes nouvelles. *Peking Academy of Sciences*, 1949 5 (5): 763–779.

Zhang N-G, Hao T-X, Wu C-Y, Chen Y-X, Zhang W, Li J-F & Zhang Y 1997: Primary investigation of freshwater Gastropoda in Yunnan Province. *Studia Marina Sinica*, 39: 15–26. [In Chinese]

Zhang L-J, Chen S-C, Yang L-T, Jin L & Frank Köhler 2015: Systematic revision of the freshwater snail *Margarya* Nevill, 1877 (Mollusca: viviparidae) endemic to the ancient lakes of Yunnan, China, with description of new taxa. *Zoological Journal of the Linnean Society*, 174 (4): 760–800. https://doi.org/10.1111/zoj.12260

Zhang Y-D, Fu H, Chen H-H & Liu Z-W 2023: Climate-driven intensification of hypolimnetic deoxygenation in Lake Fuxian, a monomictic lake in south-western China, since the 1990s. *Ecological Indicators*, 154 (3–4): 110567. https://doi.org/10.1016/j.ecolind.2023.110567

Zhao X 2009: Comparative Study on Pollution in Yangzonghai Lake and Dianchi Lake. *Legal System And Society*, 2009 (5): 219–220. [in Chinese] https://doi.org/10.19387/j.cnki.1009-0592.2009.13.143

Additional information

Author contributions: Resources: H-Q Xiang, Y-M He & C-Y Li. Writing: H-Q Xiang & Y-Z Lu. All authors have read and agreed to the published version ofthe manuscript.

Conflict of interest: The author has declared that no competing interests exist.

Data availability: All of the data that support the findings of this study are available in the main text.

Ethical statement: No ethical statement was reported.

Funding: This project was funded by Y-Z Lu.