

Gibbosula sinensis, a new species on the verge of extinction of the world's most threatened freshwater mussel family Margaritiferidae Henderson, 1929 from China (Bivalvia, Palaeoheterodonta, Unionida)

Zhong-Guang Chen^{1*}, Yu-Ting Dai^{2*}, Hui Chen¹, Hong-Fei Hu¹, Jiao Jiang³, Liang Guo⁴, Shan Ouyang¹, Xing-Xing Zhao³, Xiao-Ping Wu¹

1 School of Life Sciences, Nanchang University, Nanchang 330031, China

2 College of Animal Science and Technology, Jiangxi Agricultural University, Nanchang, Jiangxi 330045, China

3 Zhejiang Museum of Natural History, Hangzhou, Zhejiang 310012, China

4 Fuzhou Wilds of Insects Cultural Creativity, Fuzhou, Fujian 353000, China

<https://zoobank.org/8489E84F-4A50-441F-B3E5-9904D0BAC6A9>

Corresponding authors: Xiao-Ping Wu (xpwu@ncu.edu.cn); Xing-Xing Zhao (zhaoxx@zmnh.com)

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Abstract

A new species of freshwater mussel, *Gibbosula sinensis* Z.-G. Chen, Y.-T. Dai, H. Chen & X.-P. Wu, **sp. nov.**, is described from the lower Lancangjiang River Basin in Yunnan, China based on comparative morphology and molecular phylogeny. The new species can be distinguished from congeners by the oblong, slender, very curved, relatively thin, fragile, and rather smooth shell, the front end of the shell higher than the posterior end, and the special habitat selection. The new species is on the verge of extinction and urgently requires attention and protection.

Key Words

Biodiversity, molluscs, phylogeny, taxonomy

Introduction

Margaritiferidae Henderson, 1929, is a group of medium to large freshwater mussels widely distributed across North America, Europe, North Africa and Asia (Bolotov et al. 2016; Araujo et al. 2017; Lopes-Lima et al. 2018; Graf and Cummings 2025; MolluscaBase 2025). Compared to its wide distribution, the species diversity of the family is relatively limited, encompassing only four genera and 15 extant species (Bogan and Do 2016; Lopes-Lima et al. 2018; Wu et al. 2020; Graf and Cummings 2025; MolluscaBase 2025). The family is the most threatened freshwater mussel worldwide, with all species assessed with sufficient data presenting a near threatened or threatened conservation status (Lopes-Lima et al. 2018). In China,

only five extant species of the family have been recorded: *Margaritifera dahurica* (Middendorff, 1850), *Gibbosula confragosa* Frierson, 1928, *G. crassa* (Wood, 1815), *G. laosensis* (Lea, 1863), and *G. rochechouartii* (Heude, 1875) (He and Zhuang 2013; Wu et al. 2020; Guo 2022; Graf and Cummings 2025; MolluscaBase 2025). The distribution of these species encompasses the substantial expanse of the eastern Chinese mainland, extending from the Heilongjiang River Basin at the northernmost reaches to the Pearl River and Lancangjiang River Basins at the southernmost limits (He and Zhuang 2013; Guo 2022).

Based on the specimens collected from the Lancangjiang River Basin (Mekong) in Xishuangbanna, Yunnan, China in 2023–2025, we describe a new species of *Gibbosula* Simpson, 1900. The discovery enhances the

* These authors contributed equally to this work.

diversity of freshwater mussels in China and underscores the imperative for the conservation of the extremely threatened family Margaritiferidae.

Materials and methods

Specimens were collected from Yunnan of China in 2023–2025. Specimens for molecular phylogenetic analysis were initially frozen at -20°C for 24 hours and subsequently thawed at room temperature for 8 hours to take out the soft parts. The soft parts were then fixed in 95% ethanol. Empty shells were cleaned, dried, and preserved at room temperature. Eight specimens were fixed in 8% formalin to observe the morphology of the soft part. Photographs were taken by camera and edited in Adobe Photoshop CC 2015 (Adobe, San Jose, USA). Maps were made in ArcGIS Pro (Esri, Redlands, USA).

Genomic DNA was extracted from foot tissues preserved in 95% ethanol using a TIANamp Marine Animals DNA Kit (Tiangen Biotech, China). The quality and concentration of the DNA were checked on 1% agarose gel electrophoresis and NanoDrop 2000 (Thermo Scientific, USA). Partial cytochrome c oxidase subunit 1 (*COI*) was amplified and sequenced for molecular phylogenetic analyses. Polymerase chain reaction (PCR) systems, conditions and primer pairs were followed Chen et al. (2023). The *COI* sequences were

aligned using MEGA v. 6.0 (Tamura et al. 2013). The accession numbers of all sequences used in this study are given in Table 1.

Phylogenies reconstructed by the *COI* sequences using Maximum Likelihood (ML) and Bayesian Inference (BI). Family Trgoniidae Lamarck, 1819 of order Trgoniida and five families of order Unionida, Unionidae Rafinesque, 1820, Mulleriidae Deshayes, 1832, Etheriidae Deshayes, 1832, Iridinidae Swainson, 1840, and Hyriidae Swainson, 1840 were used as the outgroups for rooting the trees. The best-fit model for each gene and gene partition was calculated by PartitionFinder2 v. 1.1 (Lanfear et al. 2017), based on the corrected Akaike Information Criterion (AICc) and using a heuristic search algorithm. The program proposed the division of the concatenated dataset into two partitions, comprising partitions for the first and second codon positions of the *COI* gene and the third codon positions of the *COI* gene. The best-fit model was determined to be GTR+I+G for the first and second codon positions of *COI*, while GTR+G was selected for the third position of *COI*. ML analyses were performed in IQ-TREE v. 1.6.12 (Minh et al. 2013) using the Ultrafast bootstrap approach (Minh et al. 2013) with 10,000 iterations. Bayesian inference (BI) analysis was conducted in MrBayes v. 3.2.6 (Ronquist et al. 2012). Four simultaneous runs with four independent Markov Chain Monte Carlo (MCMC) were implemented for 10 million generations, and trees were sampled every 10,000 generations

Table 1. Genbank accession numbers of sequences used in this study.

Species	Accession number	Locality
Margaritiferidae		
<i>Gibbosula sinensis</i> sp. nov. 1	PX067295	Nanbanhe River, Xishuangbanna, Yunnan, China
<i>Gibbosula sinensis</i> sp. nov. 2	PX067296	Nanbanhe River, Xishuangbanna, Yunnan, China
<i>Gibbosula sinensis</i> sp. nov. 3	PX067297	Nanbanhe River, Xishuangbanna, Yunnan, China
<i>Gibbosula sinensis</i> sp. nov. 4	PX067298	Nanbanhe River, Xishuangbanna, Yunnan, China
<i>Gibbosula sinensis</i> sp. nov. 5	PX067299	Nanbanhe River, Xishuangbanna, Yunnan, China
<i>Gibbosula sinensis</i> sp. nov. 6	PX067300	Nanbanhe River, Xishuangbanna, Yunnan, China
<i>Gibbosula laosensis</i> 1	KR006698	Nam Pe River, Nam Ou River Basin, Phongsali Province, Northern Laos
<i>Gibbosula laosensis</i> 2	KR006699	Nam Pe River, Nam Ou River Basin, Phongsali Province, Northern Laos
<i>Gibbosula laosensis</i> 3	KP843087	Nam Pe River, Nam Ou River Basin, Phongsali Province, Northern Laos
<i>Gibbosula laosensis</i> 4	JX497731	Nam Long River, Nam Ou River Basin, Phongsali Province, Northern Laos
<i>Gibbosula laosensis</i> 5	JX497732	Nam Long River, Nam Ou River Basin, Phongsali Province, Northern Laos
<i>Gibbosula laosensis</i> 6	JX497733	Nam Long River, Nam Ou River Basin, Phongsali Province, Northern Laos
<i>Gibbosula laosensis</i> 7	KJ943551	Nam Long River, Nam Ou River Basin, Phongsali Province, Northern Laos
<i>Gibbosula laosensis</i> 8	KJ943552	Nam Pe River, Nam Ou River Basin, Phongsali Province, Northern Laos
<i>Gibbosula laosensis</i> 9	KJ161531	Nam Pe River, Nam Ou River Basin, Phongsali Province, Northern Laos
<i>Gibbosula laosensis</i> 10	KJ161532	Nam Pe River, Nam Ou River Basin, Phongsali Province, Northern Laos
<i>Gibbosula laosensis</i> 11	KJ161533	Nam Pe River, Nam Ou River Basin, Phongsali Province, Northern Laos
<i>Gibbosula laosensis</i> 12	KJ943553	Nam Pe River, Nam Ou River Basin, Phongsali Province, Northern Laos
<i>Gibbosula laosensis</i> 13	KJ943554	Nam Pe River, Nam Ou River Basin, Phongsali Province, Northern Laos
<i>Gibbosula laosensis</i> 14	KJ943555	Nam Pe River, Nam Ou River Basin, Phongsali Province, Northern Laos
<i>Gibbosula laosensis</i> 15	KU763224	Mun River, Thailand
<i>Gibbosula laosensis</i> 16	KU763225	Luang Prabang, Laos
<i>Gibbosula laosensis</i> 17	KU763226	Luang Prabang, Laos
<i>Gibbosula laosensis</i> 18	JX497734	Nam Pe River, Nam Ou River Basin, Phongsali Province, Northern Laos
<i>Gibbosula laosensis</i> 19	JX497735	Nam Pe River, Nam Ou River Basin, Phongsali Province, Northern Laos

Species	Accession number	Locality
<i>Gibbosula crassa</i> 1	MH293546	Bang River, Cao Bang, Vietnam
<i>Gibbosula crassa</i> 2	MH293547	Bang River, Cao Bang, Vietnam
<i>Gibbosula rochechouartii</i> 1	MF072498	Poyang Lake, Yangtze, China
<i>Gibbosula rochechouartii</i> 2	MF072502	Poyang Lake, Yangtze, China
<i>Cumberlandia monodonta</i> 1	AY579131	Missouri, USA
<i>Cumberlandia monodonta</i> 2	MH293545	Meramec River, Missouri, USA
<i>Margaritifera dahurica</i> 1	KJ161516	Ilistaya River, Primorye, Russia
<i>Margaritifera dahurica</i> 2	KJ161520	Ilistaya River, Primorye, Russia
<i>Margaritifera falcata</i> 1	AY579128	Idaho, USA
<i>Margaritifera falcata</i> 2	AY579127	North Umpqua River, Oregon, USA
<i>Margaritifera hembeli</i> 1	KU763218	Valentine Creek, Louisiana, USA
<i>Margaritifera hembeli</i> 2	KU763219	Brown Creek, Louisiana, USA
<i>Margaritifera laevis</i>	KU763222	Iwaizumi, Honshu, Japan
<i>Margaritifera margaritifera</i> 1	KU763227	Locust Creek, Pennsylvania, USA
<i>Margaritifera margaritifera</i> 2	AF303342	Nore River, Ireland
<i>Margaritifera marrianae</i>	KU763243	Hunter Creek, Alabama, USA
<i>Margaritifera middendorffi</i> 1	AY579124	Iturup, Kuril Islands, Russia
<i>Margaritifera middendorffi</i> 2	KJ161547	Nachilova River, Kamchatka, Russia
<i>Pseudunio auricularius</i> 1	AY579125	Ebro River, Tarragona, Spain
<i>Pseudunio auricularius</i> 2	AF303309	Canal Imperial, Zaragoza, Spain
<i>Pseudunio homsensis</i>	KX550090	Karasu River, Turkey
<i>Pseudunio marocanus</i> 1	EU429678	Oum Er Rbia River, Morocco
<i>Pseudunio marocanus</i> 2	EU429679	Laabid River, Morocco
Unionidae		
<i>Lampsilis cardium</i>	KX713472	Illinois, USA
<i>Potomida littoralis</i>	KP217871	Cadiz, Spain
Hyriidae		
<i>Hyridella australis</i>	KX713467	New South Wales, Australia
<i>Triplodon corrugatus</i>	KX713505	Peru
Mulleriidae		
<i>Anodontites elongata</i>	KX713444	Peru
<i>Lamproscapha ensiformis</i>	KX713471	Peru
Etheriidae		
<i>Etheria elliptica</i>	KX713462	Zambia
Iridinidae		
<i>Aspatharia pfeiffieriana</i>	KC429107	Chambeshi River, Zambia
<i>Chambardia wahlbergi</i>	KX713448	Zambia
Trigoniidae		
<i>Neotrigonia lamarckii</i>	KC429105	North Stradbroke Island, Australia
<i>Neotrigonia margaritacea</i>	U56850	Tasmania, Australia

with a burn-in of 25%. The convergence was checked with the average standard deviation of split frequencies <0.01 and the potential scale reduction factor (PSRF) ~ 1. Trees were visualized in FigTree v.1.4.3 (<http://tree.bio.ed.ac.uk/software/figtree/>).

Abbreviations. NCUMB: Museum of Biology, Nanchang University (Nanchang, Jiangxi, China); ZMNH: Zhejiang Museum of Natural History (Hangzhou, Zhejiang, China); USNM: National Museum of Natural History, USA (Washington, D.C., USA); aam: anterior adductor muscle; pam: posterior adductor muscle; ea: excurrent aperture; ia: incurrent aperture; pia: papillae of the incurrent aperture; pea: papillae of the excurrent aperture; ig: inner gills; og: outer gills; m: mantle; lp: labial palps; vm: visceral mass; f: foot.

Results

Phylogenetic analyses

The sequence dataset consisting of 59 *COI* sequences from 26 species, including with 11 outgroup taxa, was employed for phylogenetic analyses (Table 1). The alignments of *COI* genes had a length of 656 characters. Within the alignment, 315 sites were variable, and 283 sites were parsimony informative. The Bayesian and Maximum Likelihood analyses produced almost same phylogenies (Fig. 1). The new species represents a sister but divergent lineage to *Gibbosula laosensis*, although with moderate support (BS/PP = 83/0.83). The p-distances of *COI* sequences between the new species and its congeners is 12.1%–14.8%.

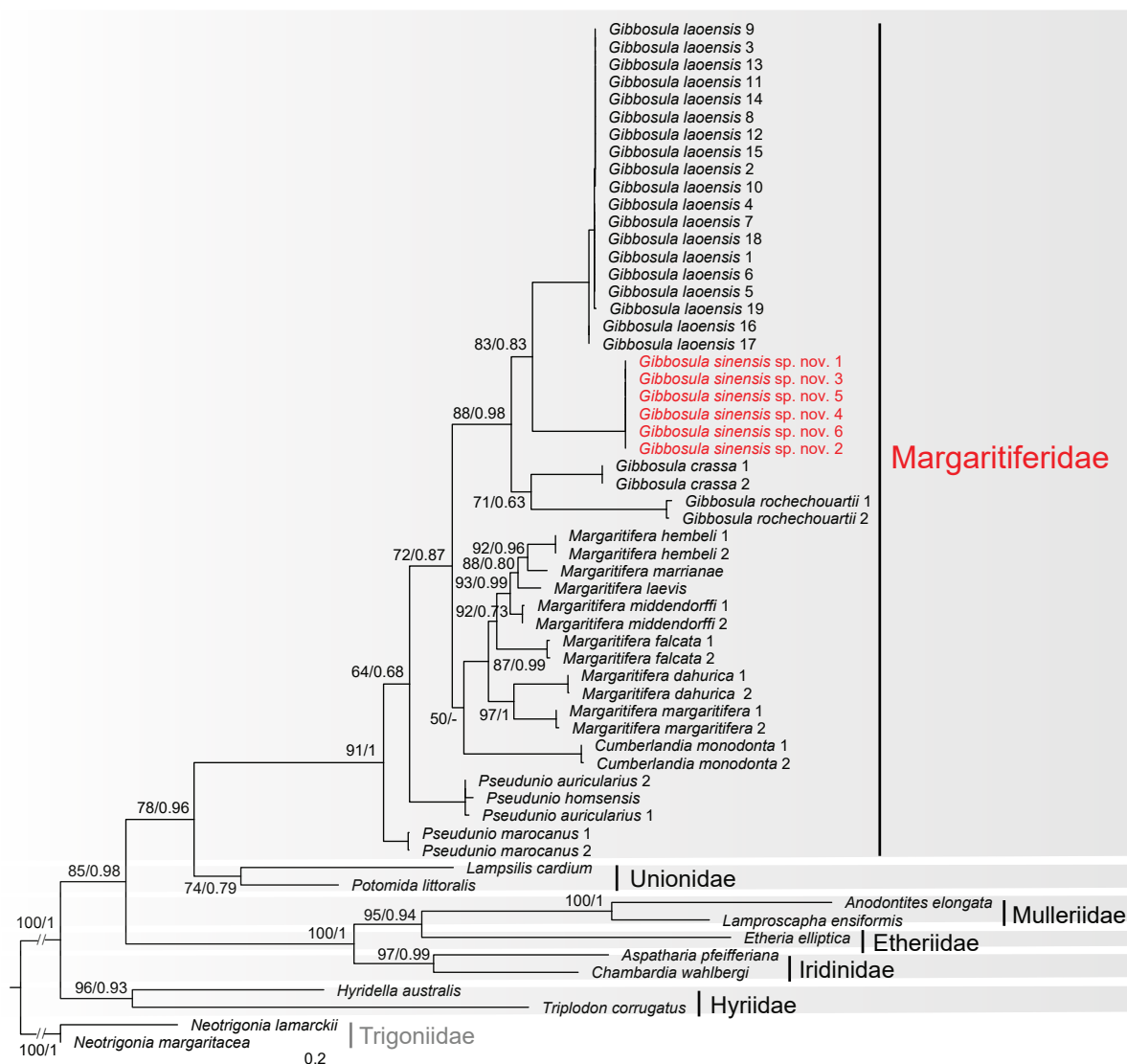


Figure 1. Maximum Likelihood tree and Bayesian inference tree inferred from *COI* gene sequences. Bootstrap supports/posterior probabilities are shown on the left/right of nodes on the tree if greater than 50%.

Systematics

Family Margaritiferidae Henderson, 1929

Subfamily Gibbosulinae Bogan, Bolotov, Froufe & Lopes-Lima, 2018

Genus *Gibbosula* Simpson, 1900

Type species. *Mya crassa* Wood, 1815, by original designation.

Gibbosula sinensis Z.-G. Chen, Y.-T. Dai, H. Chen & X.-P. Wu, sp. nov.

<https://zoobank.org/A482FBB5-3619-45BC-B949-E37651EA97A4>

Figs 2, 3, 5D

Gibbosula laosensis – Guo 2022: 42 (southern Yunnan).

Type material. Holotype: • NCUMB B2507001, Nanbanhe River, a large tributary of the Lancangjiang River [澜沧

江支流南班河], upstream of Menglun Town [勐仑镇上游], Xishuangbanna Dai Autonomous Prefecture [西双版纳傣族自治州], Yunnan Province [云南省], China, leg. Z.-G. Chen, Y.-T. Dai, H.-F. Hu, Y.-Y. Zhang, March 2023.

Paratypes: • 18 shells with soft part, 27 paired dead empty shells, 62 single piece dead empty shells. NCUMB B2507002–011 (soft part stored in alcohol separately), leg. Z.-G. Chen, March 2024, other information same as holotype; NCUMB B2507012–019 (soft part kept in shell and stored in formalin), NCUMB B2507020–045 (paired dead empty shells), ZMNH RS202501 (paired dead empty shell), NCUMB B2507047–104 (single piece dead empty shells), ZMNH RS202502–05 (single piece dead empty shells), other information same as holotype.

Diagnosis. Shell oblong, slender, very curved, relatively thin, fragile, rather smooth. Front end of the shell higher than the posterior end. Inhabiting the deep torrent of the wide section of the lower Lancangjiang River (upper Mekong River).

Description. Shell large, symmetric, flat, relatively thin, fragile, sub-glossy, oblong, slender, very curved,

rather smooth, dark brown to black. Anterior, dorsal and posterior margin rounded; ventral margin concave. Umbo smooth, inflated, slightly under hinge line, located at 1/4 of the dorsal margin, and often eroded. Umbo cavity shallow. Growth lines arranged in irregular concentric circles. Hinge long and strong. Mantle attachment scars small, deep and sparse. Mantle muscle scars obvious. Anterior adductor muscle scars irregular oval, deep and coarse; posterior adductor muscle scars oval, smooth. Left valve with two pseudocardinal teeth, anterior one reduced, posterior one strong and connected to lateral teeth; right valve with two pseudocardinal teeth, anterior one strong and high, posterior one reduced, connected to lateral teeth. Lateral teeth of both valves relatively strong, rough, long and thick. Nacre white, with irregular yellow halo in partial individuals.

Mantle light brown. aperture margins black, papillae of the excurrent aperture highly degraded, papillae of the incurrent aperture strong and forked. Gills light brown, inner gills slightly longer and wider than outer gills. Labial palps brown, irregular triangle, distally pointed. Visceral mass grayish white. Foot black, fades to brown in formalin.

Measurements. Holotype: shell length 116.4 mm, height 45.3 mm, width 30.4 mm. Paratypes: shell length 101.9–130.2 mm, height 40.3–49.1 mm, width 27.2–36.0 mm.

Etymology. The species is made from Latin *Sino* for China, referring to its type locality. The Chinese vernacular name is 中华弓背蚌 (pīnyīn: zhōng huá gōng bèi bàng) and the English vernacular name is Chinese freshwater pearl mussel.

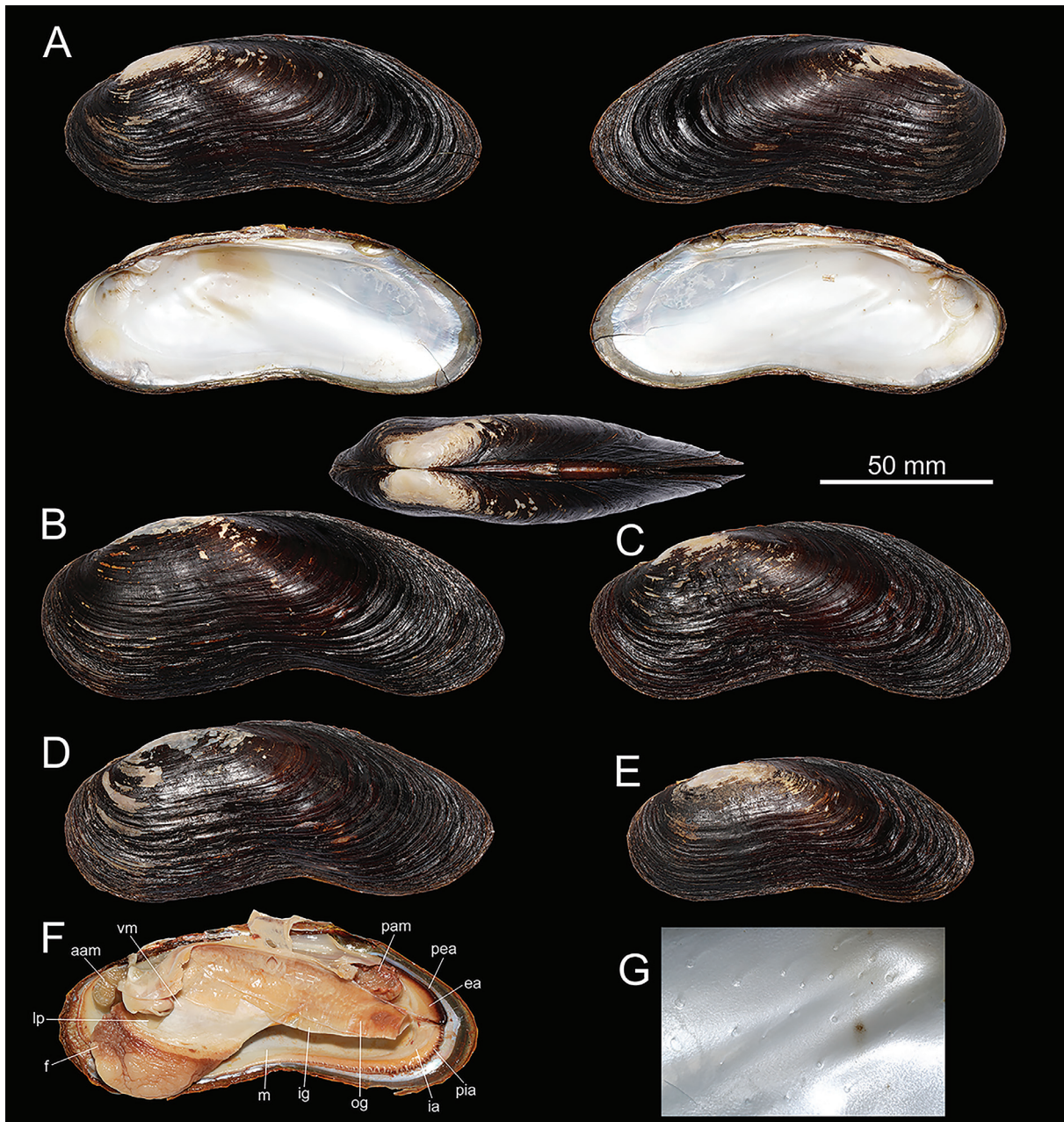


Figure 2. *Gibbosula sinensis* sp. nov. **A.** Holotype, NCUMB B2507001; **B–E.** Partial paratypes, NCUMB B2507002–05; **F.** Paratype, NCUMB B2507012, shows the soft anatomy; **G.** Shows mantle attachment scars.

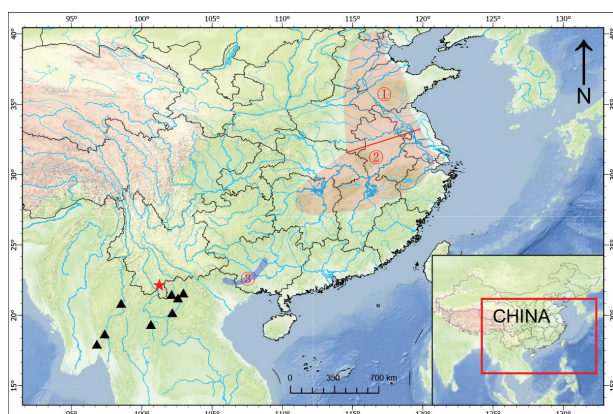


Figure 3. Distribution of genus *Gibbosula*. **1.** Historical distribution of *G. confragosa* and *G. rochechouartii*; **2.** Current distribution of *G. rochechouartii*; **3.** *G. crassa*; **star.** *Gibbosula sinensis* sp. nov.; **triangle.** *G. laosensis*.

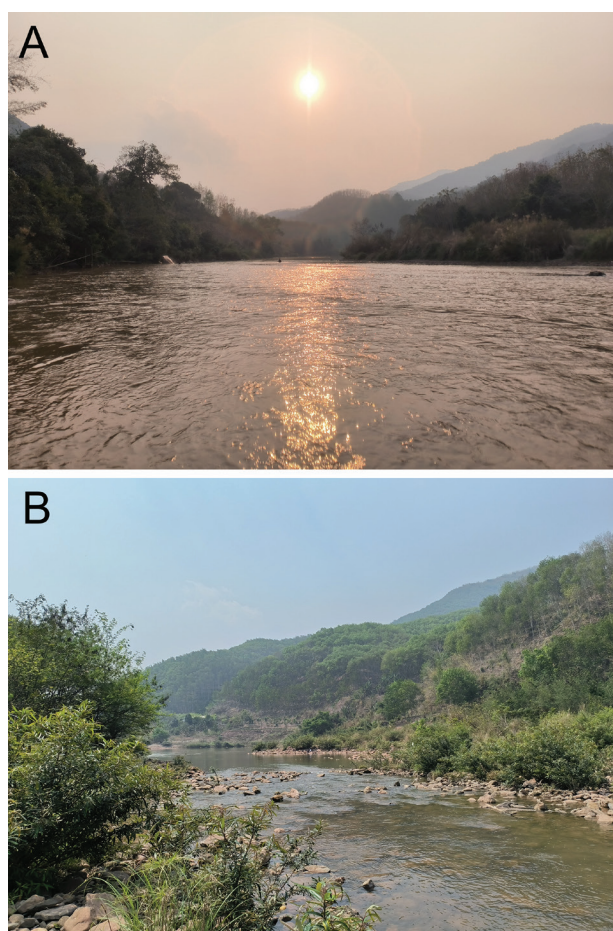


Figure 4. The environment of the Nanbanhe River. **A.** Habitat of *Gibbosula sinensis* sp. nov.; **B.** The environment of river sections without *Gibbosula sinensis* sp. nov. habitat.

Distribution and ecology. Known from several kilometers of the Nanbanhe River upstream of Menglun Town (Fig. 3). Living under huge stone in the deep torrent of the wide river section (Fig. 4). The habitat will not be exposed out of the water even during the season with the lowest water level. Usually found together with *Lens comptus* (Deshayes, 1876), *Unionetta fabagina* (Deshayes, 1876), and

Bineurus mouhotii (Lea, 1863). The population is extremely small, with fewer than 100 living animals found in a 3-year survey. The reproduction of the new species has encountered serious problems, the population is almost entirely composed of elderly individuals and with no juveniles. It will soon become extinct without protective measures.

Remarks. The new species was misidentified as *G. laosensis* by Guo (2022). Guo (2022) vaguely recorded the distribution of “*G. laosensis*” in China as southern Yunnan, which is actually the type locality of the new species.

Discussion

The placement of the new species within *Gibbosula* is supported by both its morphology and molecular phylogeny. Within the genus, the new species can be easily distinguished from *G. confragosa*, *G. crassa*, and *G. rochechouartii* by the oblong, slender, thin, fragile, and rather smooth shell (vs. irregular oval, fat, very thick and carved shell) (Fig. 5). The new species resembles *G. laosensis* on account of the similar shell shape, but differs by the more slender and more curved shell, the front end of the shell higher than the posterior end (vs. lower or equal), and the different habitat selection (deep torrent of the wide river section vs. shallow stream) (Bolotov et al. 2014). The molecular phylogenetic results also provide strong support for the independence of the new species. The new species exhibited significant genetic differentiation (12.1%) with *G. laosensis* from three localities in Laos and Thailand, indicating that it is an independent species rather than an upstream population of *G. laosensis*. The differentiation between these two species may be attributable to divergent habitat selection strategies.

A grave problem was identified concerning the reproductive capacity of the new species during the course of field surveys. The population was found to be predominantly composed of elderly individuals, with a complete absence of juveniles. In view of the fact that the population size is small and extremely threatened, and the economic value of the new species is high, the precise type locality will not be disclosed in this article until such time as further protective measures have been implemented. We take the congener also distributed in southern China, *G. crassa*, as an example. It has been subject to severe illegal fishing in recent years, with all living animals and even every empty shell in the Shuikouhe River being caught and sold. Despite the fact that *G. crassa* is classified as a national second-class protected animal in China, its shells are still being illegally traded on Chinese e-commerce platforms, such as Xianyu [闲鱼] (Suppl. material 1). The Chinese population of *G. crassa* is facing an imminent threat of extinction. Another congener, *G. confragosa*, which is distributed in northern China, is likely to have gone extinct earlier. This species has never been observed alive in the wild since its initial description. It is evident that the vast majority of the substantial rivers in the northern China have either desiccated or been transformed into reservoirs. This phenomenon renders

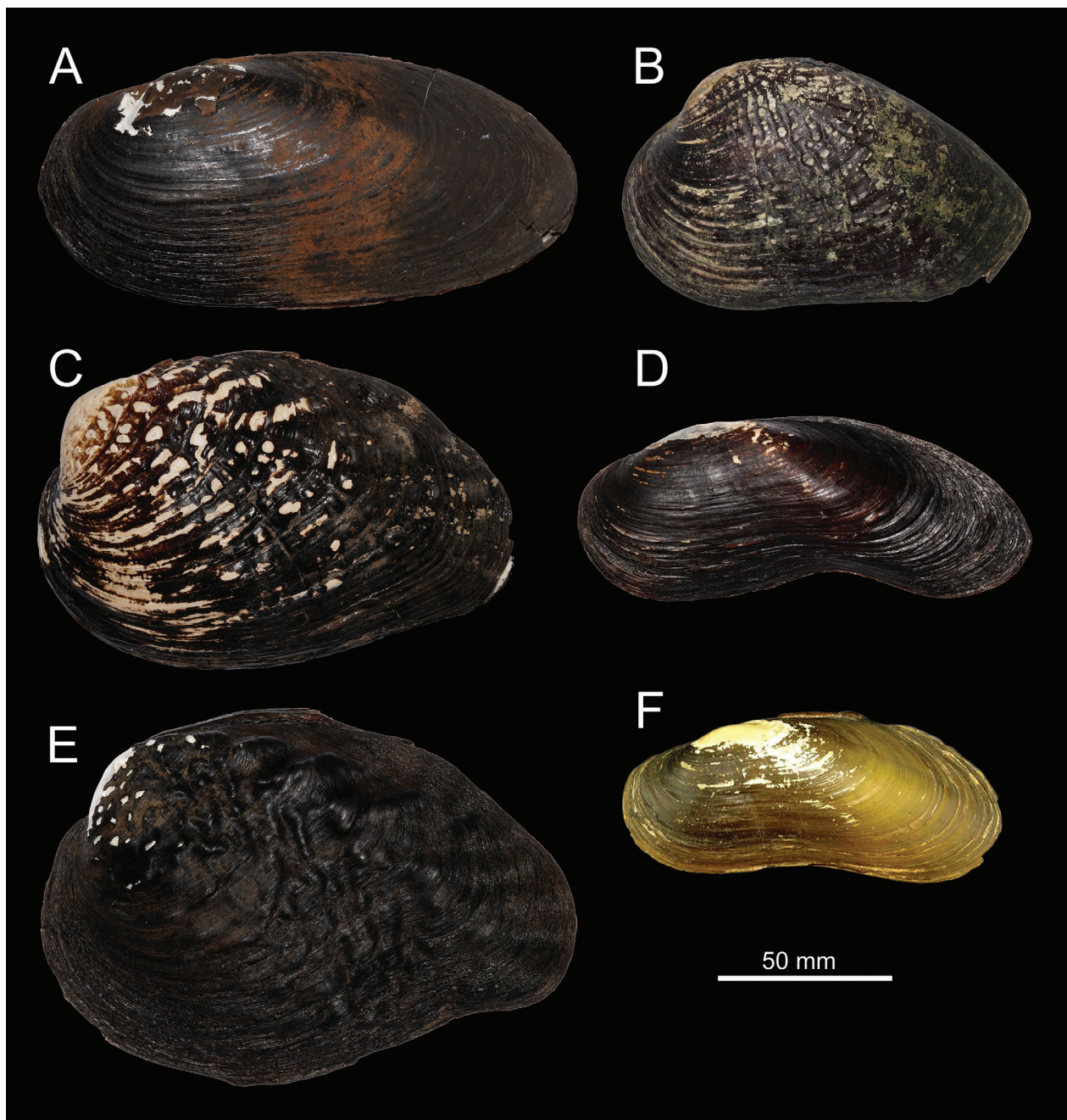


Figure 5. Morphological comparison of family Margaritiferidae distributed in China and *G. laosensis*. **A.** *Margaritifera dahurica*, Heihe, Heilongjiang, China; **B.** *Gibbosula crassa*, Shuikou, Chongzuo, Guangxi, China; **C.** *G. confragosa*, Baigou, Baoding, Hebei, China; **D.** *Gibbosula sinensis* sp. nov., Menglun, Xishuangbanna, Yunnan, China; **E.** *G. rochechouartii*, Wucheng, Jiangxi, China; **F.** *G. laosensis*, holotype, USNM 86160, Laos Mountains, Graf and Cummings (2025).

it improbable for *Gibbosula* to subsist within the region, given its reliance on the flowing waters of these substantial rivers. Even *G. rochechouartii*, which exhibits the widest distribution and largest population in the genus, has experienced severe decline in its distribution range. The species became extinct in northern China along with *G. confragosa*, and the remaining population retreated to the middle and lower Changjiang River (Yangtze). As the most threatened freshwater mussel group of the world, the new species and its congeners require urgent attention and protection.

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Supplementary material 1

Illegal trade of *Gibbosula crassa* on Xianyu

Authors: Zhong-Guang Chen, Yu-Ting Dai, Hui Chen, Hong-Fei Hu, Jiao Jiang, Liang Guo, Shan Ouyang, Xing-Xing Zhao, Xiao-Ping Wu

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