

Unionetta xishuangbannaensis n. sp. is the only representative of Parreysiinae Henderson, 1935 (Bivalvia: Unionidae) in China: evidence from molecular phylogeny and morphology

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Abstract. A new species of freshwater mussel, *Unionetta xishuangbannaensis* n. sp., is described from a tributary of the Lancangjiang River (Mekong) basin in Yunnan, China. It can be distinguished from congener by an irregularly elongated triangle shell with an elongated, narrow and relatively pointed posterior, a weak ridge near the posterior dorsal margin, and a smooth transition between dorsal and posterior margins. The validity of the new species is further supported by the molecular phylogenetic results based on *COI* sequences. Molecular phylogenetic results reveal that the genera of Indochinellini are generally non-monophyletic and await a comprehensive systematic revision.

Key words. Freshwater biodiversity, molluscs, new species, phylogeny, taxonomy

Introduction

The unionid subfamily Parreysiinae Henderson, 1935 is widely distributed across the tropical regions of Africa and Asia (Graf & Cummings, 2026; MolluscaBase eds, 2026). It can be distinguished from other subfamilies of Unionidae Rafinesque, 1820 by the presence of unhooked glochidia, tetragenous brooding, and the complete fusion of the ascending lamella of the inner demibranch to the visceral mass (Bolotov *et al.*, 2018; Pfeiffer *et al.*, 2018). China lies at the periphery of its distribution. To date, only one validated species, *Unionetta fabagina* (Deshayes in Deshayes & Jullien, 1876), has been recorded in China (Guo, 2022; Ning *et al.*, 2023; Dai *et al.*, 2024). Based on molecular phylogenetic analysis and morphological comparisons of the “*U. fabagina*” populations in China, we hereby describe it as a species new to science.

Materials and methods

Living specimens were initially frozen at -20 °C for 2 hours and subsequently thawed at room temperature for 1 hour to facilitate the extraction of soft tissues. The soft tissues were then fixed in 95% ethanol. Empty shells were cleaned, dried, and preserved at room temperature. Photographs

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<http://zoobank.org/urn:lsid:zoobank.org:pub:7D3A0E30-30B3-4308-AF2D-152A15F350D1>

TABLE 1. GenBank accession numbers of sequences used in this paper.

Species	Accession numbers	References
<i>Unionetta xishuangbannaensis</i> n. sp. 1	PZ178068	This study
<i>Unionetta xishuangbannaensis</i> n. sp. 2	PZ178069	This study
<i>Unionetta xishuangbannaensis</i> n. sp. 3	PZ178070	This study
<i>Unionetta xishuangbannaensis</i> n. sp. 4	PZ178071	This study
<i>Unionetta xishuangbannaensis</i> n. sp. 5	PZ178072	This study
<i>Unionetta xishuangbannaensis</i> n. sp. 6	PZ178073	This study
<i>Unionetta xishuangbannaensis</i> n. sp. 7	PZ178074	This study
<i>Unionetta xishuangbannaensis</i> n. sp. 8	PZ178075	This study
<i>Unionetta fabagina</i> 1	MH350930	Pfeiffer <i>et al.</i> (2018)
<i>Unionetta fabagina</i> 2	MH350931	Pfeiffer <i>et al.</i> (2018)
<i>Unionetta fabagina</i> 3	MH350932	Pfeiffer <i>et al.</i> (2018)
<i>Unionetta fabagina</i> 4	MH350933	Pfeiffer <i>et al.</i> (2018)
<i>Unionetta fabagina</i> 5	MH350934	Pfeiffer <i>et al.</i> (2018)
<i>Unionetta fabagina</i> 6	MH350935	Pfeiffer <i>et al.</i> (2018)
<i>Unionetta fabagina</i> 7	PP697624	Pfeiffer <i>et al.</i> (2018)
<i>Unionetta cf. fabagina</i>	MH350962	Pfeiffer <i>et al.</i> (2018)
<i>Coelatura aegyptiaca</i>	JN243894	Whelan <i>et al.</i> (2011)
<i>Gibbosula rochechouartii</i>	MF072498	Chen <i>et al.</i> (2025)
<i>Gibbosula sinensis</i>	PX067295	Chen <i>et al.</i> (2025)
<i>Harmandia somboriensis</i>	MH350952	Pfeiffer <i>et al.</i> (2018)
<i>Indochinella khadakvaslaensis</i>	JQ861244	Unpublished
<i>Indochinella pugio</i> 1	JN243899	Whelan <i>et al.</i> (2011)
<i>Indochinella pugio</i> 2	KX865852	Bolotov <i>et al.</i> (2017)
<i>Lamellidens corrianus</i>	JN243903_	Whelan <i>et al.</i> (2011)
<i>Lamellidens generosus</i>	JN243902_	Whelan <i>et al.</i> (2011)
<i>Leoparreysia mandelayensis</i>	JN243900	Whelan <i>et al.</i> (2011)
<i>Leoparreysia olivacea</i>	KP795022	Pfeiffer & Graf (2015)
<i>Leoparreysia tavoyensis</i>	JN243901	Whelan <i>et al.</i> (2011)
<i>Nitia teretiuscula</i>	JN243897	Whelan <i>et al.</i> (2011)
<i>Parreysia corrugata</i> 1	JQ861229	Unpublished
<i>Parreysia corrugata</i> 2	KJ872809	Unpublished
<i>Parreysia favidens</i>	JQ861238	Unpublished
<i>Prisodontopsis aviculaeformis</i>	KJ081180	Graf <i>et al.</i> (2014)
<i>Radiatula bonneaudii</i>	JN243898	Pfeiffer <i>et al.</i> (2018)
<i>Radiatula humilis</i>	MH350923	Pfeiffer <i>et al.</i> (2018)
<i>Radiatula pilata</i>	MH350945	Pfeiffer <i>et al.</i> (2018)
<i>Scabiellus songkramensi</i>	MH350926	Pfeiffer <i>et al.</i> (2018)
<i>Scabies anceps</i>	MH350928	Pfeiffer <i>et al.</i> (2018)
<i>Scabies crispata</i>	MH350921	Pfeiffer <i>et al.</i> (2018)
<i>Scabies mandarinus</i>	MH350937	Pfeiffer <i>et al.</i> (2018)
<i>Scabies nucleus</i>	MH350943	Pfeiffer <i>et al.</i> (2018)
<i>Scabies phaselus</i>	MH350938	Pfeiffer <i>et al.</i> (2018)
<i>Scabies scobinatus</i>	MH350951	Pfeiffer <i>et al.</i> (2018)

were taken using a Sony® A7C II and processed in Adobe Photoshop® CC 2025. The distribution map was generated using ArcGIS® Pro.

Genomic DNA was extracted from muscle tissues preserved in 95% ethanol using a QIAamp DNA Blood Mini kit (Qiagen, Germany). 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 followed Chen *et al.*

(2023). The 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 were reconstructed using the dataset of the *COI* gene using Maximum Likelihood (ML) and Bayesian Inference (BI). Two species of Margaritiferidae Henderson, 1929 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 position 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 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 visualised in FigTree v.1.4.3 (<http://tree.bio.ed.ac.uk/software/figtree/>) and Adobe Illustrator® 2025.

Abbreviations. NCUMB: Museum of Biology, Nanchang University (Nanchang, China); SNHM: Shanghai Natural History Museum (Shanghai, China); ZGCC: Collection of Zhong-Guang Chen (Chengdu, China).

Results

Phylogenetic analyses

The sequence dataset consisting of 46 *COI* sequences from 28 species, including two outgroup taxa, was employed for phylogenetic analyses (Table 1). The alignments of the *COI* gene had a length of 655 characters. Within the alignment, 257 sites were variable, and 218 sites were parsimony informative. The Bayesian and Maximum Likelihood analyses produced largely consistent topologies (Fig. 1). The subfamily Parreysiinae comprises five tribes, as the similar topology recovered by Pfeiffer *et al.* (2018). The new species is assigned to the tribe Indochinellini Bolotov, Pfeiffer, Vikhrev & Konopleva in Bolotov *et al.* 2018. It forms a sister group with *Unionetta* cf. *fabagina* with a moderate support rate (BS/PP = 84/0.81).

Systematics

Family **Unionidae** Rafinesque, 1820

Subfamily **Parreysiinae** Henderson, 1935

Tribe **Indochinellini** Bolotov, Pfeiffer, Vikhrev & Konopleva in Bolotov *et al.*, 2018

Genus *Unionetta* Haas, 1955

Type species. *Unionetta fabagina* (Deshayes in Deshayes & Jullien, 1876), type by typification of replaced name.

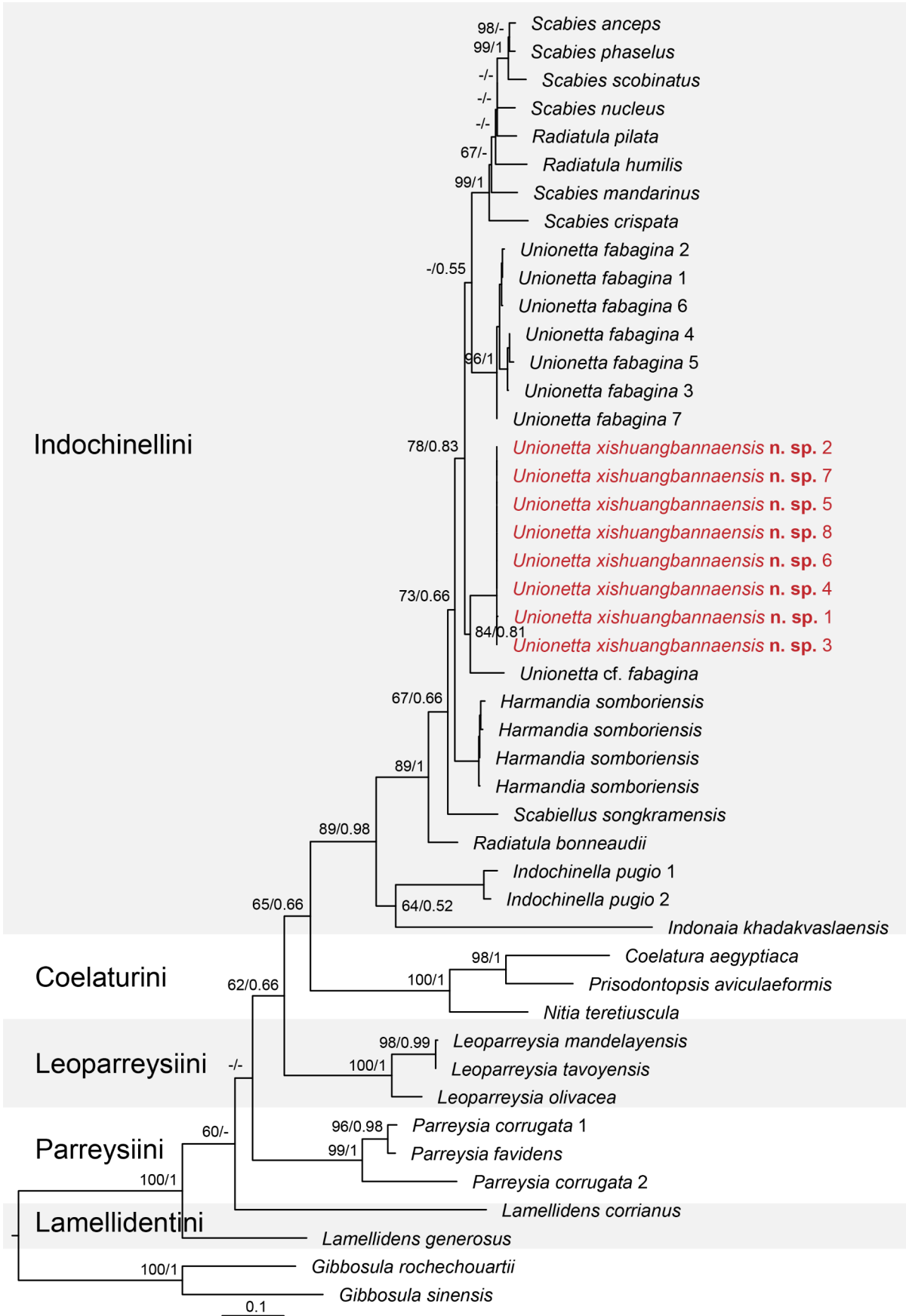


FIGURE 1. Maximum Likelihood tree and Bayesian inference tree inferred from the *COI* gene sequences. BS below 50 and BPP below 0.5 are hidden.

***Unionetta xishuangbannaensis* n. sp.**

版纳小珠蚌 (Pinyin: bǎn nà xiǎo zhū bàng)

(Figure 2)

Unionetta fabagina – Guo, 2022: 218–219 (Xishuangbanna, Yunnan).*Unionetta fabagina* – Ning *et al.*, 2023: 137–138, fig. 2 (Menglun, Xishuangbanna, Yunnan).

Type materials. *Holotype*. NCUMB B2603001, Luosuojiang River [罗梭江], Menglun Town [勐仑镇], Xishuangbanna Dai Autonomous Prefecture [西双版纳傣族自治州], Yunnan Province [云南省], China, 101.28856°E, 21.92421°N, leg. Zhong-Guang Chen, May 2020. *Paratypes*. ZGCC/30, other information same as holotype; SNHM 17582, other information same as holotype.

Diagnosis. A *Unionetta* species characterised by an irregularly elongated triangle shell with an elongated, narrow and relatively pointed posterior, a weak ridge near the posterior dorsal margin, and a smooth transition between dorsal and posterior margins.

Description. Shell irregularly elongated triangle, medium-sized, thick, inflated, short, sub-glossy, with distinct growth lines. Anterior small, rounded and short; posterior elongate, narrow and relatively pointed. Dorsal margin curved downwards; ventral margin straight to slightly curved. The dorsal and posterior margins transition smoothly. The posterior dorsal margin with a weak ridge. Umbo higher than the hinge line, located at 1/4–1/5 of the dorsal margin, with weak sculpture. Periostracum dark green to brownish black. Ligament short and weak. Beak cavities deep, open. Anterior adductor muscle scars rounded, shallow, smooth; posterior adductor muscle scars oval,

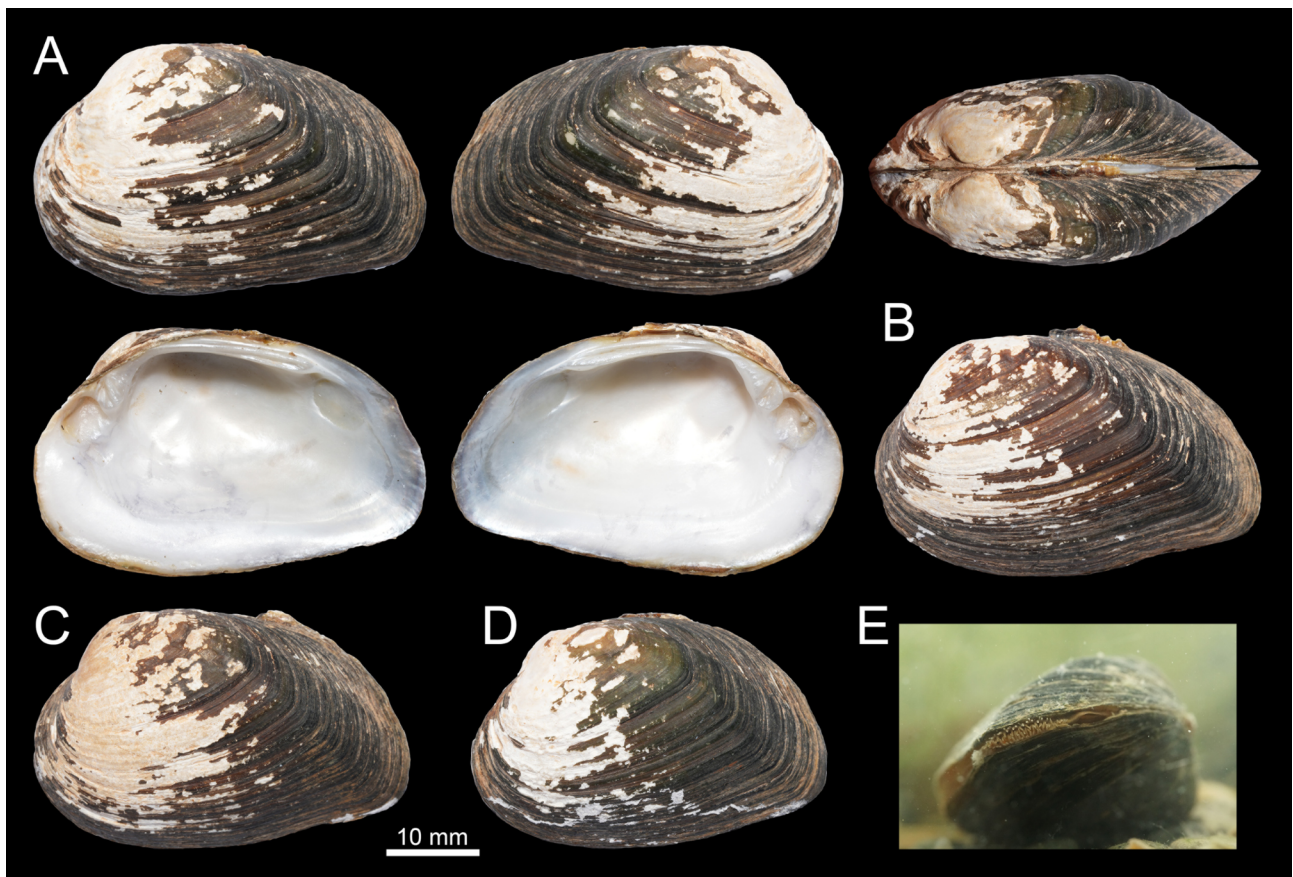


FIGURE 2. *Unionetta xishuangbannaensis* n. sp. A. holotype. B–D. partial paratypes. E. a live animal, non-type.



FIGURE 3. Distribution of *Unionetta xishuangbannaensis* n. sp. Star shows the type locality.

smooth. Left valve with two pseudocardinal teeth, anterior one thin, posterior one strong and triangle shaped; right valve with one pseudocardinal tooth, strong and triangle shaped. Lateral teeth of both valves relatively strong, rough, long and thick. Nacre white.

Measurements. Holotype: shell length 42.1 mm, height 27.0 mm, width 19.7mm. Paratypes: shell length 34.0–45.2 mm, height 23.5–27.8 mm, width 16.1–20.6 mm.

Etymology. The species is named after its type locality.

Distribution and ecology. The new species is restricted to the Menglun Town section of the Luosuojiang River, a major tributary of the Lancangjiang River, with no specimens found in either the upstream or downstream reaches during field surveys conducted over a distance of more than one hundred kilometres. It typically co-occurs sympatrically with large populations of *Lens comptus* (Deshayes in Deshayes & Jullien, 1876), and smaller numbers of *Bineurus mouhotii* (Lea, 1863) and *Gibbosula sinensis* Chen, Dai, Chen & Wu in Chen *et al.* (2025). Several freshwater mussel species in the Luosuojiang River exhibit distinct microhabitat segregation. The new species is primarily found in relatively shallow, slow-flowing waters with a muddy mixed pebble substrate; *B. mouhotii* is mainly found in deep, fast-flowing waters with a pebble substrate; *G. sinensis* occurs beneath large stones in deep, fast-flowing waters; and *L. comptus* is distributed across all microhabitat types.

Remarks. Pfeiffer *et al.* (2018) demonstrated that *U. fabagina*, from the same locality in Cambodia (type locality), was divided into two distantly related clades in the phylogenetic tree. However, the two clades could not be fully distinguished based on shell morphology, and it remained unclear which clade represents the true *U. fabagina*. The molecular phylogenetic results of the present study also failed to recover the monophyly of the genus *Unionetta*. The new species forms a sister group to *U. cf. fabagina* from Cambodia, while *U. fabagina* from the same locality constitutes

a separate clade. These molecular phylogenetic results are highly congruent with those of Pfeiffer *et al.* (2018), suggesting that *Unionetta* either requires further subdivision or that several closely related genera should be merged. Given the complex phylogenetic relationships within Indochinellini and the widespread non-monophyly of its constituent genera, no taxonomic revision at the generic level is proposed in the present study. Although the true clade of *U. fabagina* remains uncertain in the phylogenetic tree, the new species is placed within *Unionetta* due to its morphological similarities. Within Indochinellini, the morphology of the new species is similar only to *Unionetta*, while it differs significantly from other genera. Compared to *U. fabagina*, the new species can be distinguished by its more elongated shell with a narrow, elongated, and relatively pointed posterior (vs. a short, wide, and pointed posterior), a weak ridge near the posterior dorsal margin (vs. a strong ridge), and a smooth transition between the dorsal and posterior margins (vs. an obtuse angle). Both Chen *et al.* (2025) and the present study reveal significant genetic differentiation between closely related freshwater mussels distributed in the Chinese and Indochinese tributaries of the Lancangjiang River (Mekong), indicating distinct species. This may reflect that freshwater mussels in the tributaries of the Lancangjiang River have been isolated by the mainstem, leading to divergence into distinct species.

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版纳小珠蚌是雕刻蚌亚科（双壳纲：蚌科）在中国的唯一代表： 基于分子系统发育与形态学的证据

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摘 要

本文描述了产自云南澜沧江流域的河蚌新种：版纳小珠蚌 *Unionetta xishuangbannaensis* n. sp.。该种可依据以下特征与同属其他种区分：贝壳延长，不规则的三角形，具延长、狭窄且相对较尖的后部，背缘后部具一弱脊，且背缘与后缘平滑过渡。其有效性也被基于COI序列的分子系统发育结果所证实。分子系统发育结果表明，印支蚌族各属普遍非单系群，有待开展全面的系统修订。

关键词：水生生物多样性，软体动物，新物种，系统发育，分类学