

Revisiting the taxonomic position of *Aculamprotula polysticta* (Heude, 1877) (Bivalvia: Unionidae: Unioninae): confirming an earlier fortuitous conclusion drawn from misidentified materials

Zhong-Guang Chen^{1,5,*}, Hong-Fei Hu^{1,6}, Hui Zheng^{1,7}, Yu-Xin Ge²,
Yi-Jun Li³, Liang Guo⁴, Shan Ouyang^{1,8}, Xiao-Ping Wu^{1,9,*}

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

² Maryland Institute College of Art, Baltimore, Maryland, 21217, USA;

³ <https://orcid.org/0009-0003-5070-7119>

³ School of geoscience, faculty of science, the University of Sydney, Sydney, NSW 2006, Australia

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

⁵ <https://orcid.org/0000-0003-2689-3321>

⁶ <https://orcid.org/0009-0001-7088-6455>

⁷ <https://orcid.org/0009-0004-5222-3975>

⁸ <https://orcid.org/0009-0004-6973-4800>

⁹ <https://orcid.org/0000-0002-8037-5640>

Abstract. This study revisits the taxonomic position of *Aculamprotula polysticta* (Heude 1877), a species with a complex taxonomic history. Through phylogenetic analysis of verified specimens of *A. polysticta* and *A. scripta* (Heude 1875), it is found that the study reassigning *A. polysticta* to the family Unionidae was based on misidentified *A. scripta* specimens, and that the correct conclusion was inadvertently reached as a result. The phylogenetic results confirm that *A. polysticta* belongs to the unionid genus *Aculamprotula* and forms a sister group with *A. coreana* (von Martens, 1886), showing only minimal genetic divergence. Integrating molecular and morphological evidence, we propose synonymising *A. coreana* under *A. polysticta*.

Key words. Freshwater mussel, misidentified specimens, molecular phylogeny, taxonomic revision

Introduction

Freshwater mussels (Mollusca: Bivalvia: Unionida) represent one of the most threatened groups of benthic macroinvertebrates in freshwater ecosystems (Graf and Cummings 2007). In recent years, the application of molecular phylogenetics has significantly advanced our understanding of the diversity of these organisms. In China, more than 30 new freshwater mussel taxa have been identified over the past decade, primarily based on molecular phylogenetic studies, marking the second peak in species discovery since the late 19th century (Graf & Cummings, 2026; MolluscaBase eds, 2026).

Molecular approaches have also facilitated the correction of long-standing taxonomic inaccuracies. For instance, *Gibbosula rochechouartii* (Heude, 1875) was reclassified from the family Unionidae Rafinesque, 1820 to the family Margaritiferidae Henderson, 1929, more than 140 years after its original description (Huang *et al.*, 2018; Lopes-Lima *et al.*, 2018). A more complex case involves *Aculamprotula polysticta* (Heude, 1877). Lopes-Lima *et al.* (2018) reassigned this species to the genus *Gibbosula* Simpson, 1900, which belongs to the family Margaritiferidae, based on shell

*Corresponding authors: Z.-G. Chen: zgchen1002@foxmail.com; X.-P. Wu: xpwu@ncu.edu.cn
<http://zoobank.org/urn:lsid:zoobank.org:pub:821D16BC-8457-4FE2-892C-98B9FE7F7F0A>



FIGURE 1. Distributions of *Aculamprotula polysticta*. Solid stars: localities of sequenced and examined specimens; red hollow stars: localities of examined specimens; black hollow stars: localities of unexamined specimens.

morphology. Subsequently, Wu *et al.* (2020), incorporating both molecular phylogenetic data and shell characteristics, transferred it back to the genus *Aculamprotula* Wu, Liang, Wang & Ouyang, 1999 of the family Unionidae. However, the phylogenetic tree presented by Wu *et al.* (2020) indicated that *A. polysticta* could not be genetically distinguished from *A. scripta* (Heude, 1875), though the authors provided no explanation or discussion of this finding. Subsequent studies utilising the sequences of *A. polysticta* from Wu *et al.* (2020) have yielded similar results, showing no clear genetic differentiation between the two species (Wu *et al.*, 2022, 2023, 2024). This raises an important taxonomic question: can two species with such pronounced morphological differences be conspecific?

In this study, we performed sequencing and molecular phylogenetic analyses on previously collected specimens of *A. polysticta* and *A. scripta*. Our phylogenetic results reveal a paradoxical situation: the correct taxonomic conclusion in Wu *et al.* (2020) was reached serendipitously, based on genetic sequences derived from misidentified specimens. This case highlights the critical importance of using verifiable voucher specimens in studies involving molecular phylogenetics and taxonomic revision.

Materials and methods

Specimens were collected from China in 2019–2020 (Fig. 1). Specimens for molecular phylogenetic analysis were initially frozen at -20°C for 24 hours and subsequently thawed at room

TABLE 1. GenBank accession numbers and information of specimens used in this study.

Species	Accession / Specimen voucher numbers	Locations	References
<i>Aculamprotula polysticta</i>	PX631819 NCUMB B2511001	Fuhe River, Nanchang, Jiangxi, China	This study
	PX631820 NCUMB B2511002	Fuhe River, Nanchang, Jiangxi, China	This study
	PX631821 NCUMB B2511003	Fuhe River, Nanchang, Jiangxi, China	This study
<i>A. coreana</i> (= <i>A. polysticta</i>)	JX050180	Geum River, South Korea	Lopes-Lima <i>et al.</i> (2020)
	NC026035	Geum River, South Korea	Lopes-Lima <i>et al.</i> (2020)
	MT020521	Geum River, South Korea	Lopes-Lima <i>et al.</i> (2020)
<i>A. scripta</i>	PX631822 NCUMB B1912001	Fuhe River, Nanchang, Jiangxi, China	This study
	PX631823 NCUMB B1912004	Ganjiang River, Nanchang, Jiangxi, China	This study
	MG933689	Dongting Lake, Hunan, China	Wu <i>et al.</i> (2018)
	MG933688	Dongting Lake, Hunan, China	Wu <i>et al.</i> (2018)
	NC045529	Poyanghu Lake, Jiangxi, China	Wu <i>et al.</i> (2018)
	MG742235	Unknown	Wu <i>et al.</i> (2018)
	MG462911	Dongting Lake, Hunan, China	Huang <i>et al.</i> (2019)
	MG462912	Ganjiang River, Jiangxi, China	Huang <i>et al.</i> (2019)
“ <i>A. polysticta</i> ” (= <i>A. scripta</i>)	MK687418	Fuhe River, Jiangxi, China	Wu <i>et al.</i> (2020)
	MK687419	Fuhe River, Jiangxi, China	Wu <i>et al.</i> (2020)
	MK728823	Fuhe River, Jiangxi, China	Wu <i>et al.</i> (2020)
<i>A. fibrosa</i>	MG462909	Ganjiang River, Jiangxi, China	Huang <i>et al.</i> (2019)
	MG462910	Wanghu Lake, Hubei, China	Huang <i>et al.</i> (2019)
	MG742234	Unknown	Wu <i>et al.</i> (2018)
	MG933687	Poyanghu Lake, Jiangxi, China	Wu <i>et al.</i> (2018)
<i>A. tientsinensis</i>	MG462913	Ganjiang River, Jiangxi, China	Huang <i>et al.</i> (2019)
	MF072504	Unknown	Huang <i>et al.</i> (2019)
	NC029210	Ganjiang River, Jiangxi, China	Wu <i>et al.</i> (2016)
	MG742236	Unknown	Wu <i>et al.</i> (2018)
<i>A. tortuosa</i>	MG933690	Poyanghu Lake, Jiangxi, China	Wu <i>et al.</i> (2018)
	KX822631	Changjiang River, China	Lopes-Lima <i>et al.</i> (2017)
	MG933692	Poyanghu Lake, Jiangxi, China	Wu <i>et al.</i> (2018)
	MG933691	Poyanghu Lake, Jiangxi, China	Wu <i>et al.</i> (2018)
	MG933695	Ganjiang River, Jiangxi, China	Wu <i>et al.</i> (2018)
	MG933693	Ganjiang River, Jiangxi, China	Wu <i>et al.</i> (2018)
	MG933694	Ganjiang River, Jiangxi, China	Wu <i>et al.</i> (2018)
	MG462915	Qinglanghu Lake, Jiangxi, China	Huang <i>et al.</i> (2019)
	MG462916	Qinglanghu Lake, Jiangxi, China	Huang <i>et al.</i> (2019)
	MG462917	Poyanghu Lake, Jiangxi, China	Huang <i>et al.</i> (2019)
MG462914	Poyanghu Lake, Jiangxi, China	Huang <i>et al.</i> (2019)	
MG742237	Unknown	Wu <i>et al.</i> (2018)	
Outgroups			
<i>Huizhou xietianxiangi</i>	PX506473	Xinjiang River, Huangshan, Anhui, China	Chen <i>et al.</i> (2025b)
<i>Globunio mirificus</i>	PV368612	Ganjiang River, Nanchang, Jiangxi, China	Dai <i>et al.</i> (2025)
<i>Gibbosula laosensis</i>	OP749923	Laos	Unpublished
<i>G. sinensis</i>	PX067295	Lancangjiang River, Xishuangbanna, Yunnan, China	Chen <i>et al.</i> (2025a)
<i>G. rochechouartii</i>	KX378172	Ganjiang River, Jiangxi, China	Huang <i>et al.</i> (2018)
<i>G. crassa</i>	MH319826	Vietnam	Lopes-Lima <i>et al.</i> (2018)

TABLE 2. The inter- and intraspecific distances of *Aculamprotula* based on the *COI* dataset.

ID	Species	1	2	3	4	5	6
1	<i>Aculamprotula polysticta</i>	/					
2	<i>Aculamprotula coreana</i>	0.02	/				
3	<i>Aculamprotula scripta</i>	0.1	0.102	0.006			
4	<i>Aculamprotula fibrosa</i>	0.082	0.093	0.105	0.023		
5	<i>Aculamprotula tientsinensis</i>	0.073	0.084	0.103	0.061	/	
6	<i>Aculamprotula tortuosa</i>	0.129	0.141	0.138	0.117	0.102	0.005

temperature for 8 hours to allow the removal of the soft parts. The soft parts were then fixed in 95% ethanol. Empty shells were cleaned, dried, and preserved at room temperature. Photographs were taken by a Sony Alpha7CII and edited in Adobe Photoshop CC 2025 (Adobe, San Jose, USA). Maps were made in ArcGIS Pro (Esri, Redlands, USA).

Genomic DNA was extracted from the foot tissues preserved in 95% ethanol using a Qiagen Animals DNA Kit (Qiagen, Germany). The quality and concentration of the DNA were assessed using 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 *COI* sequences were aligned using MEGA v. 6.0 (Tamura *et al.*, 2013). The accession numbers of all sequences used in this study are provided in Table 1.

Phylogenies were reconstructed by the *COI* sequences using Maximum Likelihood (ML) and Bayesian Inference (BI). Four species of the family Margaritiferidae and two species of the tribe Globunionini Dai, Chen, Huang & Wu, 2025 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: one comprising partitions for the first and second codon positions of the *COI* gene, and the other comprising 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 HKY 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 (Adobe, San Jose, USA). The inter- and intra-specific distances of genus *Aculamprotula* based on the *COI* dataset were calculated in MEGA v. 6.0 using the uncorrected p-distance.

Abbreviations. NCUMB: Museum of Biology, Nanchang University (Nanchang, China); ASIZB: Institute of Zoology, Chinese Academy of Sciences (Beijing, China); BMNH: Natural History Museum (London, UK); SMF: Senckenberg Museum (Frankfurt, Germany); UMMZ: University of Michigan Museum of Zoology (Ann Arbor, USA); USNM: National Museum of Natural History (Washington, USA); ZMB: Museum für Naturkunde (Berlin, Germany); ZGCC: collection of Zhong-Guang Chen (Chengdu, China); GLC: collection of Liang Guo (Fuzhou, China); ZJLC: collection of Zheng-Jie Lou (Hangzhou, China); YCWC: collection of Yu-Chen Wang (Chengdu, China).

Results

Phylogenetic analyses and taxonomic revision

The dataset, comprising 43 *COI* sequences from six species plus six outgroup taxa, was used for phylogenetic analysis (Table 1). The alignment of the *COI* gene had a length of 656 characters. Within the alignment, 228 sites were variable, and 189 were parsimony informative. Phylogenetic analyses generated ML and BI trees with the same congruent topologies (Fig. 2). The phylogeny recovered the following relationship within *Aculamprotula*: *A. tortuosa* (Lea, 1865) + (*A. tientsinensis* (Crosse & Debeaux, 1863) + (*A. fibrosa* (Heude, 1877) + (*A. scripta* + (*A. polysticta* +

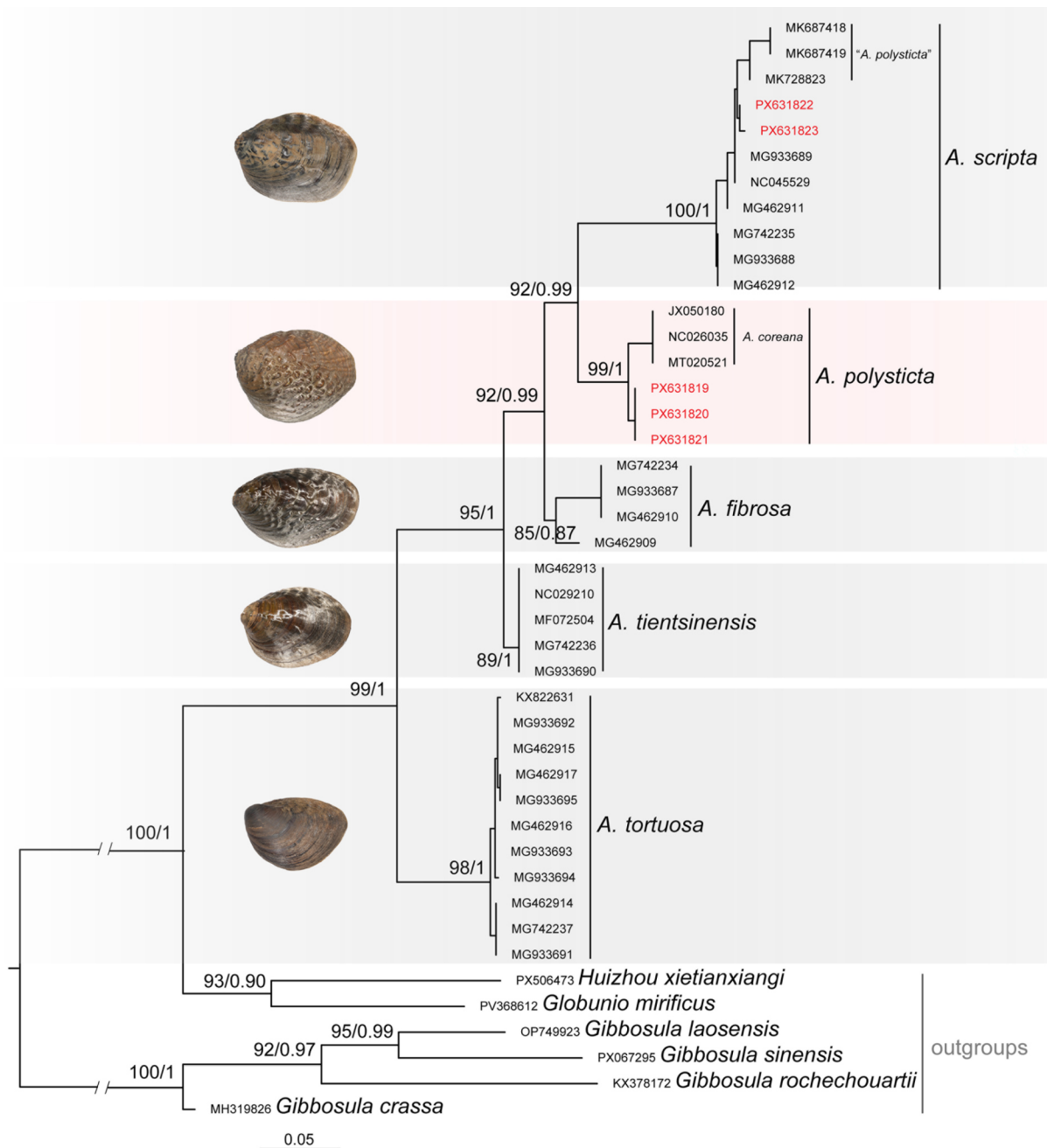


FIGURE 2. Maximum Likelihood and Bayesian inference trees inferred from *COI* gene sequences. Bootstrap supports/posterior probabilities are shown on the left/right of nodes.

A. coreana (von Martens, 1886))))). All three newly sequenced *A. polysticta* individuals formed a monophyletic group with other *Aculamprotula* species, to the exclusion of *Gibbosula*, thereby confirming the placement of *A. polysticta* within Unionidae. However, all three newly sequenced *A. polysticta* individuals exhibited a very close phylogenetic relationship with *A. coreana*. In contrast, all three “*A. polysticta*” sequences from Wu *et al.* (2020) were genetically indistinguishable from *A. scripta*, a finding supported by the two newly sequenced specimens attributed to this group. The pairwise uncorrected *COI* p-distance analysis demonstrated genetic distances ranging from 2.0% (between *A. polysticta* and *A. coreana*) to 14.1% (between *A. tortuosa* and *A. coreana*) (Table 2). The 2.0% genetic divergence between *A. polysticta* and *A. coreana* is smaller than the intraspecific distance within *A. fibrosa*. Given that *A. polysticta* is the most widely distributed species in the genus, a 2.0% genetic distance between geographically distant populations is considered insufficient to warrant species-level separation. If *A. coreana* is not recognised as a valid species, the interspecific genetic distance within the genus ranges from 6.1% to 14.1%. Furthermore, the shell morphology of *A. coreana* is highly similar to that of *A. polysticta* (Fig. 3). Therefore, we propose to treat *A. coreana* as a junior synonym of *A. polysticta*.

Systematics

Family **Unionidae** Rafinesque, 1820

Subfamily **Unioninae** Rafinesque, 1820

Genus *Aculamprotula* Wu, Liang, Wang & Ouyang, 1999

Type species. *Unio fibrosus* Heude, 1877, by original designation.

Remarks. While this manuscript was in press, Campbell & Lydeard (2026) treated *Aculamprotula* as a junior synonym of *Scriptolamprotula* Modell, 1964. Since this revision does not affect the conclusions of the present paper, the manuscript has not been revised. All occurrences of *Aculamprotula* in this paper refer to the genus *Scriptolamprotula*. To maintain the stability of the Chinese common names, we propose retaining the Chinese common name “尖丽蚌属” (Pinyin: jiān lì bàng shǔ).

Aculamprotula polysticta (Heude, 1877)

多瘤尖丽蚌 (Pinyin: duō liú jiān lì bàng)

(Figures 3A–O, 5B)

Unio affinis Heude, 1875: pl. 3, figs. 7, 7a. [junior homonym of *Unio affinis* Lea, 1852]

Unio polystictus Heude, 1877: pl. 12, fig. 25. [replacement name for *Unio affinis* Heude, 1875]

Unio polystico-scriptus Heude, 1877: pl. 13, fig. 26.

Quadrula (Lamprotula) similaris Simpson, 1900: 799. [replacement name for *Unio affinis* Heude, 1875]

Unio coreanus von Martens, 1886: 78. **new synonym.**

Type materials examined. Syntype of *Unio polystictus*: ASIZB 164, Hoai [= Huaihe River, 淮河], China. MCZ 167116, Siang River [= Xiangjiang River, 湘江], Hou-nan [= Hunan Province, 湖南省], China (photo examined). **Syntype of *Unio polystictoscriptus*:** ASIZB 163, Siang River [=

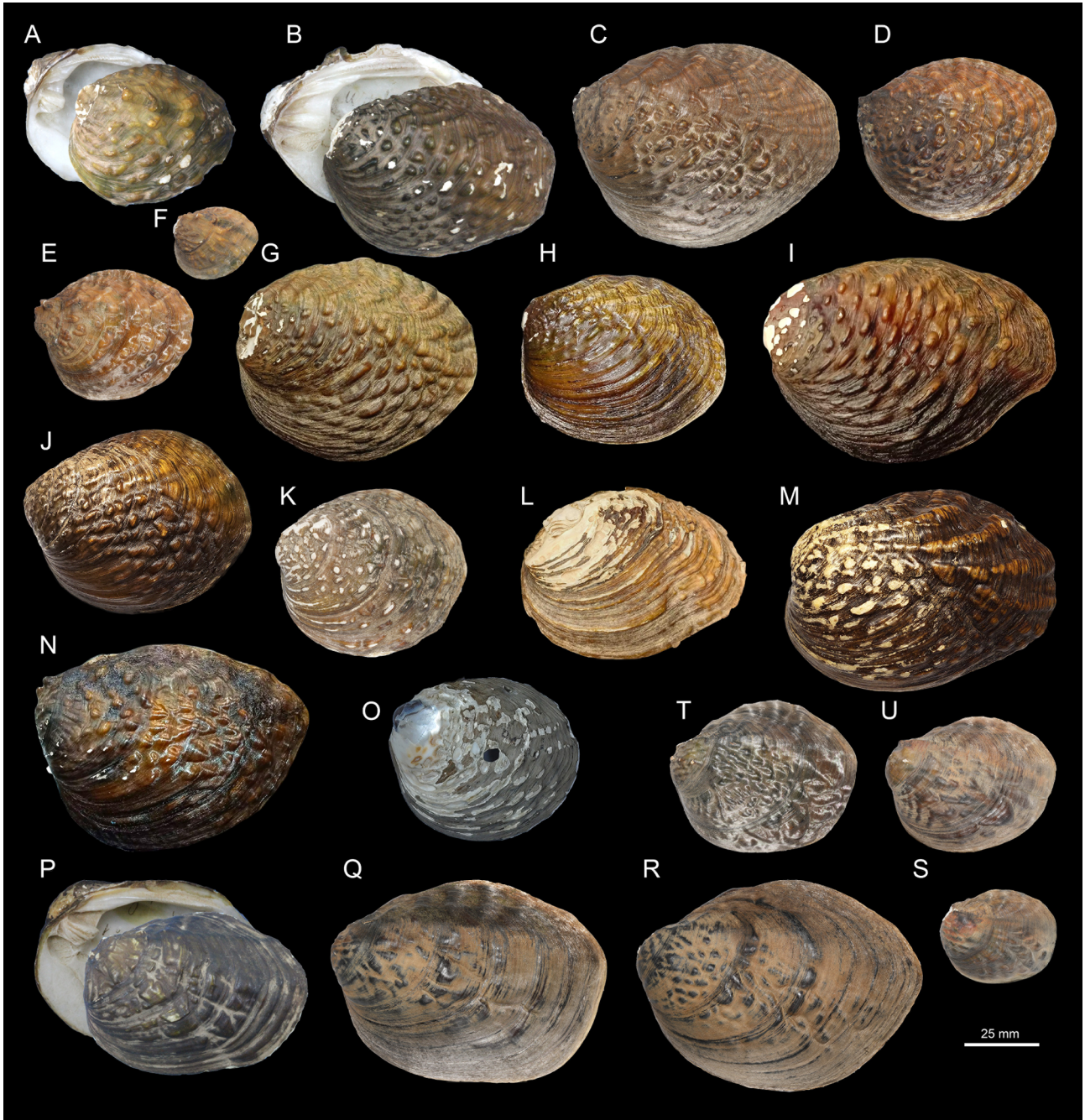


FIGURE 3. Shell variations of *Aculamprotula polysticta* and *A. scripta*. **A–O.** *A. polysticta*. **A.** Syntype of *A. polysticta*, ASIZB 164, Huaihe River. **B.** Syntype of *Unio polystictoscriptus*, ASIZB 163, Xiangjiang River. **C–F.** NCUMB B2511001–B2511004, Fuhe River, Nanchang. **G.** ZJLC 01, Xihe River, Dongzhi. **H.** ZJLC 02, Qingyijiang River, Wuhu. **I.** ZJLC 03, Zishui River, Shaoyang. **J–K.** NCUMB B2511011, YCWC 01, Qujiang River, Dazhou. **L.** ZJLC 04, Xinanjiang River, Huangshan. **M.** YCWC 02, Shuikouhe River, Longzhou. **N.** ZJLC 05, Huaihe River, Xinyang. **O.** GLC 20082801, Yalujiang River, Kuandian. **P–U.** *A. scripta*. **P.** Syntype of *A. scripta*, ASIZB 216. **Q.** NCUMB B1912001, Fuhe River, Nanchang. **R.** NCUMB B1912002, Xiuhe River, Jiujiang. **S–U.** NCUMB B1912003–B1912005, Ganjiang River, Nanchang.

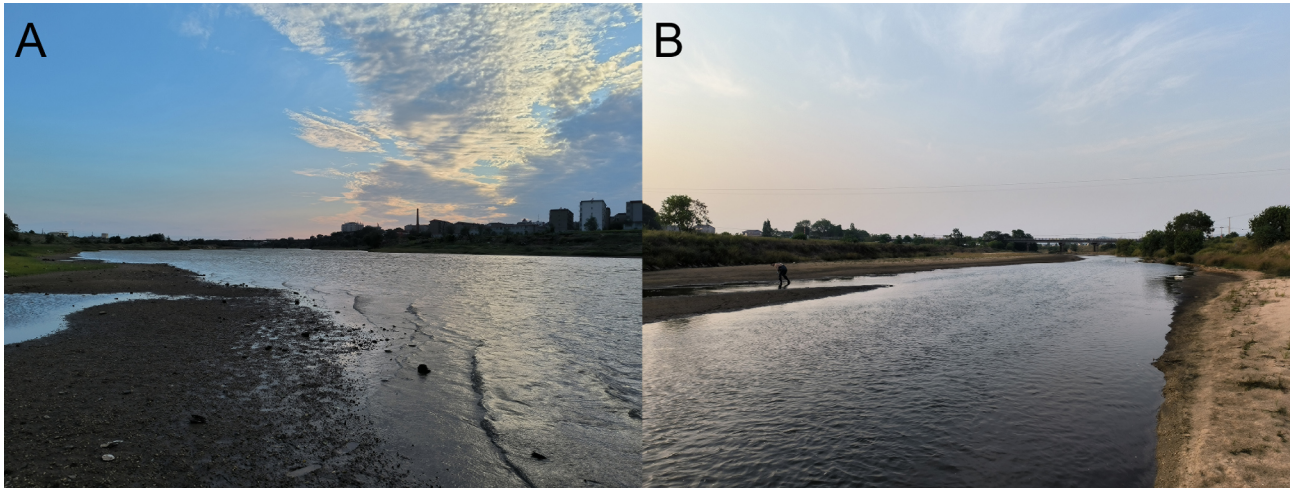


FIGURE 4. Habitats of *Aculamprotula polysticta*. **A.** Fuhe River at Nanchang. **B.** an unnamed tributary of the Fuhe River at Fuzhou.

Xiangjiang River, 湘江], China.

New materials. Specimens identified as *A. polysticta*: NCUMB B2511001–2511010, Fuhe River [抚河], Nanchang City [南昌市], Jiangxi Province [江西省], China, leg. Zhong-Guang Chen, December 2019. NCUMB B2511011, YCWC 01, Qujiang River [渠江], Dazhou City [达州市], Sichuan Province [四川省], China, leg. Yu-Chen Wang, May, December 2025. ZGCC03, Fujiang River [涪江], Jiangyou City [江油市], Sichuan Province [四川省], China, leg. Xin Liu, January 2020. GLC 20010501–20010510, ZJLC 03, Zishui River [资水], Shaoyang City [邵阳市], Hunan Province [湖南省], China, leg. local people, January 2020. ZJLC 01, Xihe River [西河], Dongzhi County [东至县], Chizhou City [池州市], Anhui Province [安徽省], China, leg. local people, 2020. ZJLC 02, Qingyijiang River [青弋江], Wuhu City [芜湖市], Anhui Province [安徽省], China, leg. local people, 2020. ZJLC 04, Xinanjiang River [新安江], Huangshan City [黄山市], Anhui Province [安徽省], China, leg. local people, 2020. ZJLC 05, Huaihe River [淮河], Xinyang City [信阳市], Henan Province [河南省], China, leg. local people, 2020. YCWC 02, Shuikouhe River [水口河], Longzhou City [龙州市], Guangxi Zhuang Autonomous Region [广西壮族自治区], China, leg. local people, 2020. 22 unnumbered specimens in NCUMB, Fuhe River [抚河], Fuzhou City [抚州市], Jiangxi Province [江西省], China, collector and date unknown. **Specimens identified as *A. coreana*:** GLC 20082801, Yalujiang River [鸭绿江], Kuandian [宽甸], Liaoning Province [辽宁省], China, leg. local people, August 2020. BMNH94-11-24, Korea (photo examined). SMF13747, Korea (photo examined). UMMZ76886, 43758, Korea (photo examined). USNM597448, Han R., 10 mi E of Seoul, So. Korea (photo examined). ZMB38359A, Seoul, Korea (photo examined).

Diagnosis. Shell symmetrical, medium-sized, very thick, flat to slightly inflated, rounded to oval, with dense and small tuberculate sculptures. Periostracum brown, with green ray patterns in juniors.

Re-description. Shell symmetrical, medium-sized, very thick, flat to slightly inflated, rounded to oval, sub-glossy, with dense tuberculate sculptures. The tuberculate sculptures on the upper part arranged to several ridges. Anterior small, rounded and short; posterior larger, expanded, rounded, extended in elders. Dorsal margin curved downwards. Ventral margin curved, posterior part retuse in elders. Umbo inflated, slightly higher than the hinge line, located at the beginning of the dorsal margin, with spina and tuberculate sculpture. Periostracum brown, with thin growth lines, with green ray patterns in juniors. Hinge short. Ligament short and strong. Beak cavities shallow, open. Without

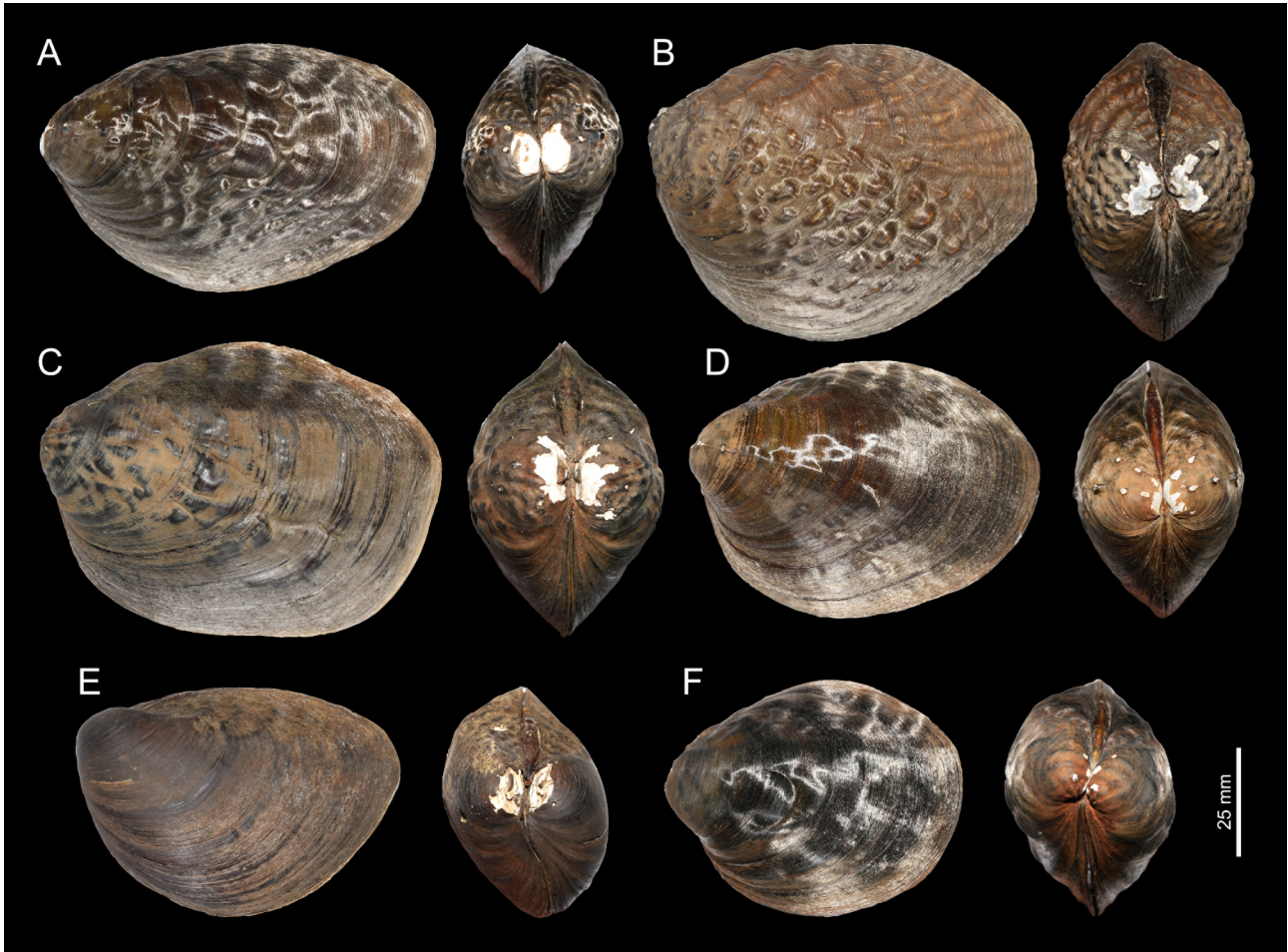


FIGURE 5. Shells of *Aculamprotula* distributed in the Changjiang River basin. **A.** *A. fibrosa*, NCUMB B1912101, Ganjiang River, Nanchang. **B.** *A. polysticta*, NCUMB B2511001, Fuhe River, Nanchang. **C.** *A. scripta*, NCUMB B1912001, Fuhe River, Nanchang. **D.** *A. tientsinensis*, NCUMB B1912102, Ganjiang River, Nanchang. **E.** *A. tortuosa*, NCUMB B1912104, Fuhe River, Nanchang. **F.** *A. zonata*, NCUMB B1912111, Ganjiang River, Nanchang.

mantle attachment scars. Anterior adductor muscle scars irregularly oval, deep and rough; posterior adductor muscle scars long oval, rather smooth. Left valve with two pseudocardinal teeth, very thick, irregular shaped. Right valve with two pseudocardinal teeth, the anterior one very thick and irregular shaped; the posterior one slender. Lateral teeth of both valves long and thick, with serrations. Nacre white.

Distribution and ecology. Distribution and ecology. Widely distributed across the middle and upper Changjiang River, the middle Huaihe River, the upper Pearl River, and the middle Yalujiang River extending to the southern part of the Korean Peninsula (Fig. 1). They prefer to inhabit the main stream of large rivers with sandy substrates and flowing water (Fig. 4A). Very few individuals were found downstream of the tributaries with sandy substrates (Fig. 4B). Although *A. polysticta*, *A. scripta*, and *A. tortuosa* often co-occur within the same river section, they typically exhibit microhabitat segregation. *Aculamprotula polysticta* shows a strong preference for sandy riverbeds in areas with higher flow velocity, whereas the other two species are predominantly found in muddy substrates with slower current speeds. Furthermore, among the six *Aculamprotula* species present in the Changjiang River basin, five of which are found in the downstream lake regions. However, *A. polysticta* appears to be a strict riverine specialist, confined solely to flowing water environments.

Key to the species of *Aculamprotula*

- 1 Shell symmetrical *A. polysticta*
- Shell asymmetrical 2
- 2 shell rather smooth, without tuberculate sculptures *A. tortuosa*
- shell with tuberculate sculptures 3
- 3 pseudocardinal teeth very large, accounting for one-third of the total length of the shell
..... *A. grandidens* (Lea, 1862)
- pseudocardinal teeth normal size 4
- 4 shells slender oval, with dense tuberculate sculptures *A. fibrosa*
- shell oval, with dense tuberculate sculptures *A. nodulosa* (Wood, 1815)
- shell oval, left shell higher than the right one, with sparse tuberculate sculptures
..... *A. tientsinensis*
- shell oval, right shell higher than the left one, with sparse tuberculate sculptures
..... *A. zonata* (Heude, 1883)
- shell irregular rectangle, with medium quantity of tuberculate sculptures *A. scripta*

Discussion

Phylogenetic analyses confirm that *A. polysticta* indeed belongs to the unionid genus *Aculamprotula*. However, our phylogenetic results differ fundamentally from those of Wu *et al.* (2020), despite both studies reaching the same taxonomic conclusion. The sequences identified as “*A. polysticta*” in Wu *et al.* (2020) were, in fact, derived from *A. scripta*. Consequently, their reassignment of *A. polysticta* to Unionidae was based on a phylogenetic analysis of misidentified specimens. Although Wu *et al.* (2020) included a figure of *A. polysticta*, the absence of a voucher number for the illustrated specimen prevents its unambiguous linkage to the sequenced material. Our attempts to locate the corresponding vouchers in the Museum of Biology at Nanchang University were unsuccessful. This lack of verifiable specimens makes it impossible to pinpoint the exact source of the misidentification. Field observations indicate differing breeding seasons for *A. polysticta* and *A. scripta*, and no intermediate morphological forms have been recorded, suggesting that natural hybridisation is unlikely. One plausible explanation is that Wu *et al.* (2020) misidentified *A. scripta* individuals with dense tuberculate sculptures (Fig. 3T) as *A. polysticta*, although the precise reason remains uncertain. This case underscores the critical importance of depositing and properly cataloguing voucher specimens in molecular phylogenetic and taxonomic revision studies.

The phylogenetic results indicate that *A. polysticta* and *A. coreana* form a sister group with minimal genetic differentiation. Morphologically, the two species are highly similar, both possessing brown, symmetrical, and relatively flat shells, which clearly distinguish them from other congeners characterised by dark, asymmetrical, and inflated shells (Fig. 5). As a species primarily inhabiting river mainstems, *A. polysticta* is widely distributed across China to Vietnam, and its occurrence in South Korea is therefore not unexpected. Given the negligible genetic divergence and high morphological similarity, we treat *A. coreana* as a junior synonym of *A. polysticta*.

Despite its broad distribution, the conservation status of *A. polysticta* is concerning, rendering it one of the most threatened freshwater mussels in China. The species has become extinct in the Pearl River, the Xinanjiang River and the Yalujiang River basins, where only unfresh empty shells can be found. Populations in the upper Changjiang River are also on the brink of extinction, with years of investigations yielding only dozens of unfresh shells and two living individuals. While populations

in the middle Changjiang River and the middle Huaihe River are in better condition, they have largely retreated to river sections located far from dams. *Aculamprotula polysticta* is highly dependent on flowing water habitats. As observed in the upper Pearl River and upper Changjiang River, populations rapidly decline when lotic environments are converted into lentic systems due to damming.

Although *A. polysticta* was designated as a second-class state-protected animal in China in 2021, illegal harvesting and trade continue. On the Chinese e-commerce platform Xianyu [闲鱼], wild living individuals are sold for less than 100 RMB each. There is an urgent need to strengthen attention and conservation efforts for this critically endangered species.

Acknowledgements

We thank Zheng-Jie Lou (Hangzhou), Yu-Chen Wang (Chengdu) and Xin Liu (McGill University) for providing specimens for examination. Thanks also go to Yue-Ming He and an anonymous reviewer for their comments on the manuscript. The specimen sampling and sequencing for this study were financially supported by the personal funds of Zhong-Guang Chen.

References

- Campbell, D. C. & Lydeard C. (2026) Three decades of mussel mitochondria. *Malacologia*, 68(1/2): 237–294.
- Chen, Z.-G., Dai, Y.-T., Ouyang, S., Huang, X.-C. & Wu, X.-P. (2023) Unveiling the identity of *Diaurora* Cockerell, 1903 (Bivalvia, Unionidae): morphology, molecular phylogenetics, and the description of a new species. *Zookeys*, 1173: 131–144.
- Chen, Z.-G., Dai, Y.-T., Chen, H., Hu, H.-F., Jiang, J., Guo, L., Ouyang, S., Zhao, X.-X. & Wu, X.-P. (2025a) *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). *Zoosystematics and Evolution*, 101(4): 1613–1620.
- Chen, H., Wang, W.-H., Chen, Z.-G., Xiang, H.-Q., He, Y.-M., Ouyang, S., Chu, K.-L. & Wu, X.-P. (2025b) A new genus and species of freshwater mussel (Bivalvia, Unionidae) from Anhui, China. *Zoosystematics and Evolution*, 101(4): 2243–2250.
- Crosse, H. & Debeaux, O. (1863) Note sur quelques espèces nouvelles ou peu connues du littoral de l'empire chinois. *Journal de Conchyliologie*, 11: 253–265.
- Dai, Y.-T., Chen, Z.-G., Ouyang, S., Huang, X.-C. & Wu, X.-P. (2025) A new tribe, genus, and species of freshwater mussel from the Changjiang River Basin in China (Bivalvia, Unionidae, Unioninae). *Zoosystematics and Evolution*, 101(2): 779–790.
- Graf, D. L. & Cummings, K. S. (2007) Review of the systematics and global diversity of freshwater mussel species (Bivalvia, Unionoida). *Journal of Molluscan Studies*, 73(3): 291–314.
- Graf, D. L. & Cummings, K. S. (2026) The MUSSEL Project. Available from: <https://musselpdb.org> (2026-02-15).
- Heude, P. M. (1875–1885) *Conchyliologie fluviatile de la province de Nanking [et de la Chine centrale]*. F. Savy, Paris, 72 + 8 pls, unnumbered pages of text. [(1): pls 1-8 (1875); (2): pls 9-16, (3): pls 17-24 (1877); (4): pls 25-32 (1878); (5): pls 33-40 (1879); (6): pls 41-48 (1880); (7): pls 49-56 (1881); (8): pls 57-64 (1883); (9): pls 65-72 (1885); (10): pls 1-8 (1880)]
- Henderson, J. (1929) Non-marine Mollusca of Oregon and Washington. *The University of Colorado Studies*, 17(2): 47–190.
- Huang, X.-C., Wu, R.-W., An, C.-T., Xie, G.-L., Su, J.-H., Ouyang, S., Zhou, C.-H. & Wu, X.-P. (2018) Reclassification of *Lamprotula rochechouartii* as *Margaritifera rochechouartii* comb. nov. (Bivalvia:

- Margaritiferidae) revealed by time-calibrated multilocus phylogenetic analyses and mitochondrial phylogenomics of Unionoida. *Molecular Phylogenetics and Evolution*, 120: 297–306.
- Huang, X.-C., Su, J.-H., Ouyang, J.-X., Ouyang, S., Zhou, C.-H. & Wu, X.-P. (2019) Towards a global phylogeny of freshwater mussels (Bivalvia, Unionida): Species delimitation of Chinese taxa, mitochondrial phylogenomics, and diversification patterns. *Molecular Phylogenetics and Evolution*, 130: 45–59.
- Lanfear, R., Frandsen, P.B., Wright, A.M., Senfeld, T. & Calcott, B. (2017) Partitionfinder 2: New methods for selecting partitioned models of evolution for molecular and morphological phylogenetic analyses. *Molecular Biology and Evolution*, 34: 772–773.
- Lea, I. (1862) Descriptions of ten new species of Unionidae of the United States. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 14: 168–169.
- Lea I. (1865) Descriptions of three new species of exotic uniones. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 17: 75–76.
- Lopes-Lima, M., Froufe, E., Do, V.T., Ghamizi, M., Mock, K.E., Kebapçı, Ü., Klishko, O., Kovitvadhi, S., Kovitvadhi, U., Paulo, O.S., Pfeiffer, III J.M., Raley, M., Riccardi, N., Şereflişan, H., Sousa, R., Teixeira, A., Varandas, S., Wu, X., Zanatta, D.T., Zieritz, A. & Bogan, A.E. (2017) Phylogeny of the most species-rich freshwater bivalve family (Bivalvia: Unionida: Unionidae): Defining modern subfamilies and tribes. *Molecular Phylogenetics and Evolution*, 106: 174–191.
- Lopes-Lima, M., Bolotov, I.N., Do, V.T., Aldridge, D.C., Fonseca, M.M., Ganh, H.M., Gofarov, M.Y., Kondakov, A.V., Prié, V., Sousa, R., Varandas, S., Vikhrev, I.V., Teixeira, A., Wu, R.-W., Wu, X.-P., Zieritz, A., Froufe, E. & Bogan, A.E. (2018) Expansion and systematics redefinition of the most threatened freshwater mussel family, the Margaritiferidae. *Molecular Phylogenetics and Evolution*, 127: 98–118.
- Lopes-Lima, M., Hattori, A., Kondo, T., Lee, J.H., Kim, S.K., Shirai, A., Hayashi, H., Usui, T., Sakuma, K., Toriya, T., Sunamura, Y., Ishikawa, H., Hoshino, N., Kusano, Y., Kumaki, H., Utsugi, Y., Yabe, S., Yoshinari, Y., Hiruma, H., Tanaka, A., Sao, K., Ueda, T., Sano, I., Miyazaki, J.I., Gonçalves, D.V., Klishko, O.K., Konopleva, E.S., Vikhrev, I.V., Kondakov, A.V., Gofarov, M.Y., Bolotov, I.N., Sayenko, E.M., Soroka, M., Zieritz, A., Bogan, A.E. & Froufe, E. (2020) Freshwater mussels (Bivalvia: Unionidae) from the rising sun (Far East Asia): phylogeny, systematics, and distribution. *Molecular Phylogenetics and Evolution*, 146: 106755.
- von Martens, E. (1886) Vorzeigungen einiger der von Dr. Gottsche in Japan und Korea gesammelten Land- und Süßwasser-Mollusken. *Sitzungs-Berichte der Gesellschaft Naturforschender Freunde zu Berlin*, 1886: 76–80.
- Minh, B.Q., Nguyen, M.A.T. & Haeseler, V.A. (2013) Ultrafast approximation for phylogenetic bootstrap. *Molecular Biology and Evolution*, 30: 1188–1195.
- Modell, H. (1964) Das natürliche System der Najaden. 3. *Archiv für Molluskenkunde*, 93: 71–126.
- MolluscaBase eds. (2026) MolluscaBase. Available from: <https://www.molluscabase.org> (2026-02-15).
- Rafinesque, C.S. (1820) Monographie des coquilles bivalves et fluviatiles de la Rivière Ohio, contenant douze genres et soixante-huit espèces. *Annales Générales des Sciences Physiques*, 5(5): 287–322, pls 80–82.
- Ronquist, F., Teslenko, M., van der Mark, P., Ayres, D.L., Darling, A., Höhna, S., Larget, B., Liu, L., Suchard, M.A. & Huelsenbeck, J. (2012) Mrbayes 3.2: Efficient bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology*, 61: 539–542.
- Simpson, C.T. (1900) Synopsis of the naiades, or pearly fresh-water mussels. *Proceedings of the United States National Museum*, 22(1205): 501–1044.
- Tamura, K., Stecher, G., Peterson, D., Filipowski, A. & Kumar, S. (2013) MEGA6: Molecular evolutionary genetics analysis version 6.0. *Molecular Biology and Evolution*, 30: 2725–2729.

- Wood, W. (1814–1815) *General conchology; or, a description of shells, arranged according to the Linnean system, and illustrated with plates, drawn and coloured from nature, Vol. 1.* [only one vol. issued]. John Booth, London, lxi + 7 + 246 pp., 60 pls.
- Wu R.-W., An C.-T., Wu X.-P., Zhou C.-H., Ouyang S. (2016) Complete maternal mitochondrial genome of freshwater mussel *Aculamprotula tientsinensis* (Bivalvia: Unionidae: Unioninae). *Mitochondrial DNA Part A*, 27(6): 1–2.
- Wu, R.-W., Liu, Y.-T., Wang, S., Liu, X.-J., Zanatta, D.-T., Roe, K.-J., Song, X.-L., An, C.-T. & Wu, X.-P. (2018) Testing the utility of DNA barcodes and a preliminary phylogenetic framework for Chinese freshwater mussels (Bivalvia: Unionidae) from the middle and lower Yangtze River. *PLOS One*, 13(8): e0200956.
- Wu, R.-W., Kim, K.-S., Xie, G.-L., Ouyang, S. & Wu, X.P. (2020) Phylogenetic position of *Aculamprotula polysticta*, comb. res. (Bivalvia : Unionidae) inferred from phylogenetic relationships in Unionida. *Invertebrate Systematics*, 34: 192–199.
- Wu, R., Liu, L., Zhang, L., Jin, D., Wu, X., Liu, X., Xie, Z. & Li, Z. (2023) Molecular phylogeny and comparative morphology reveal the species validity and systematic position of *Lepidodesma* (Bivalvia: Unionidae). *Organisms Diversity & Evolution*, 24(1): 51–66.
- Wu, R., Liu, L., Zhang, L., Liu, X., Hu, Z., Jin, D., Zhang, Z., Wu, X., Xie, Z., Li, Z. & Lopes-Lima, M. (2024) Diversity, morphology, and phylogeny of freshwater mussels of the genus *Nodularia* (Bivalvia: Unionidae) from China, with descriptions of four new species. *Zoologica Scripta*, 53(5): 594–613.
- Wu, X.-P., Dai, Y.-T., Yin, N., Shu, F.-Y., Chen, Z.-G., Guo, L., Zhou, C.-H., Ouyang, S. & Huang, X.-C. (2022) Mitogenomic phylogeny resolves *Cuneopsis* (Bivalvia, Unionidae) as polyphyletic: The description of two new genera and a new species. *Zoologica Scripta*, 51(2): 173–184.
- Wu, X.-P., Liang, Y.-L., Wang, H.-Z. & Ouyang, S. (1999) Morphological characters of glochidia of Unionidae and the taxonomic significance. *Acta Hydrobiologica Sinica*, 23 (supplement): 139–147.

多瘤尖丽蚌的分类学地位的再讨论 (双壳纲: 蚌科: 蚌亚科)

陈重光¹ 胡鸿飞¹ 郑辉¹ 葛雨馨² 李忆均³ 郭亮⁴ 欧阳珊¹ 吴小平¹

¹南昌大学生命科学学院 南昌 330031 中国

²马里兰艺术学院 巴尔的摩 21217 美国

³悉尼大学地球科学学院 悉尼 NSW 2006 澳大利亚

⁴福州虫林野趣 福州 353000 中国

摘 要

本研究重新审视了多瘤尖丽蚌 *Aculamprotula polysticta* (Heude, 1877) 这一具有复杂分类历史的物种的分类归属。通过对经验证的多瘤尖丽蚌及刻裂尖丽蚌 *A. scripta* (Heude, 1875) 标本开展分子系统发育分析, 我们发现, 先前将多瘤尖丽蚌重新归入蚌科的研究实际使用了误鉴定的刻裂尖丽蚌标本, 即该正确结论为偶然所得。分子系统发育结果表明, 多瘤尖丽蚌应归入蚌科尖丽蚌属, 并与鉴定为朝鲜尖丽蚌 *A. coreana* (von Martens, 1886) 的标本构成姐妹群, 二者之间仅存在极小的遗传分化。结合分子与形态学证据, 我们将朝鲜尖丽蚌处理为多瘤尖丽蚌的次异名。

关键词: 河蚌, 分类修订, 分子系统发育, 标本误定