

Molecular and morphological evidence reveals a hidden new taxon in the endemic genus *Pseudocuneopsis* (Bivalvia, Unionidae) from China

Lili Liu¹, Liping Zhang¹, Dandong Jin², Haotian Wang³, Xiongjun Liu⁴, Ruiwen Wu¹

¹ School of Life Science, Shanxi Normal University, Taiyuan 030031, China

² Datian High School, Linhai 317004, China

³ China Development Bank Guangxi Zhuang Autonomous Region Branch, Nanning 530025, China

⁴ School of Life Science, Jiaying University, Meizhou 514015, China

Corresponding author: Ruiwen Wu (wurw@sxnu.edu.cn, rwwu@qq.com)

Abstract

A new species of freshwater mussel belonging to the genus *Pseudocuneopsis*, namely *Pseudocuneopsis wuana* **sp. nov.**, is diagnosed and described from Guangxi Province, China. This paper provides a detailed shell morphological description, soft-body anatomical characteristics, and partial sequences of mitochondrial COI as DNA barcode data for the novel species. The new species can be distinguished from its congeners (*Pseudocuneopsis sichuanensis*, *P. yangshuoensis*, and *P. capitata*) by shell shape, beak position, and surface sculpture. Phylogenetic analyses based on the mitochondrial COI gene reveal that *Pseudocuneopsis wuana* **sp. nov.** forms a sister group with *P. yangshuoensis* and exhibits an interspecific genetic distance of 5.1%. Therefore, we provide robust morphological and molecular evidence to support the validity of this new species.

Key words: Bivalves, COI, freshwater mussel, morphology, taxonomy



Academic editor: Edmund Gittenberger

Received: 20 July 2023

Accepted: 25 August 2023

Published: 11 September 2023

ZooBank: <https://zoobank.org/76563AB8-9F81-4B91-BB6E-C4743C97E9E7>

Citation: Liu L, Zhang L, Jin D, Wang H, Liu X, Wu R (2023) Molecular and morphological evidence reveals a hidden new taxon in the endemic genus *Pseudocuneopsis* (Bivalvia, Unionidae) from China. ZooKeys 1179: 219–229. <https://doi.org/10.3897/zookeys.1179.109817>

Copyright: © Lili Liu et al.

This is an open access article distributed under terms of the Creative Commons Attribution License ([Attribution 4.0 International – CC BY 4.0](https://creativecommons.org/licenses/by/4.0/)).

Introduction

The Unionidae Gray, 1840 is a family of freshwater bivalves (Mollusca, Bivalvia, Unionida) commonly known as freshwater mussels (Lopes-Lima et al. 2014; Graf and Cummings 2021). These bivalves are important components of freshwater ecosystems, providing various ecosystem services such as nutrient cycling, water purification enhancement, bioturbation, and habitat creation (Vaughn 2018).

China is widely recognized as one of the major biodiversity hotspots for freshwater mussels owing to its abundant rivers and lakes which harbor a wealth of endemic species (Zieritz et al. 2018; Liu et al. 2022). However, field investigations of and research on unionids have been primarily focused on the middle and lower reaches of the Yangtze River (e.g. Wu et al. 2018; Huang et al. 2019; Liu et al. 2020, 2022), with less sampling in other river basins in southwest China, such as the river systems of Guangxi Province. These under-investigated areas severely limit our ability to discover new species and hinder a comprehensive understanding of phylogeny and evolution within this group.

The genus *Pseudocuneopsis* Huang, Dai, Chen & Wu, 2022 was recently established by Wu et al. (2022). Based on mitochondrial phylogenomic analyses, Wu et al. (2022) confirmed that the genus *Cuneopsis sensu lato* was polyphyletic and proposed two new genera: *Arcuneopsis* Wu et al., 2022 and *Pseudocuneopsis* Wu et al., 2022. However, *Arcuneopsis* was later considered a junior objective synonym of *Tchangsinaiia* Starobogatov, 1970 because these genera have the same type species, *Unio pisciculus* Heude, 1874 (Starobogatov 1970). Currently, comprehensive molecular systematics have stabilized the taxonomic status of *Pseudocuneopsis* as a member of the subfamily Unioninae in the Unionidae (Huang et al. 2019; Wu et al. 2019; Wu et al. 2022). The genus comprises three recognized species endemic to China (Graf and Cummings 2023; MolluscaBase eds 2023): *Pseudocuneopsis sichuanensis* Huang, Dai, Chen & Wu, 2022; *P. capitata* (Heude, 1874); and *P. yangshuoensis* Wu & Liu, 2023. While *P. sichuanensis* has a narrow distribution and is reported only from the Sichuan Province; *P. capitata* is widely distributed throughout the Yangtze river basin (Liu et al. 1979; Liu et al. 2022; Wu et al. 2022). *Pseudocuneopsis yangshuoensis* is the recently discovered and described addition to this group from Guangxi, as reported by us (Wu et al. 2023).

In this study, another new species of *Pseudocuneopsis* from Guangxi is diagnosed and described. In addition, we provide estimations of the intraspecific and interspecific genetic distances within *Pseudocuneopsis* based on the mitochondrial COI barcode fragment to examine this species' validity.

Materials and methods

Specimen collection, identification, and anatomical observations

In June 2023, six samples with tissues were collected from the Qingshui River, Nanning City, Guangxi Province, China (23.4075°N, 108.7557°E). All specimens are deposited as vouchers at the Museum of Zoology, Shanxi Normal University (SXNU), China (voucher numbers SXNU23062201–SXNU23062206). We performed dissections on all individuals to observe the soft-body characteristics through visual examination by eye and through a stereoscopic microscope.

DNA extraction and COI amplification

Total genomic DNA was extracted from dissected somatic tissues using TI-ANamp Marine Animals DNA Kit (Tiangen Biotech, Beijing, China) according to the manufacturer's instructions.

Polymerase chain reaction (PCR) amplification of the COI gene with a 680-base pair fragment was performed using a primer pair consisting of (LCO22me2 + HCO700dy2) (Walker et al. 2007). Thermal cycling conditions were 98 °C for 10 s, followed by 35 cycles of 94 °C for 1 min, 50 °C for 1 min, 72 °C for 1–2 min, and a final extension of 72 °C for 7 min, following the TaKaRa Ex manufacturer's protocol. The amplified PCR products were purified and sequenced by Sangon Biotech (Shanghai). The sequences obtained in this study have been uploaded to GenBank ([OR297986–OR297991](https://doi.org/10.26434/chemrxiv-2023-09-01)).

DNA barcode dataset construction

We compiled a mitochondrial COI dataset by incorporating newly obtained sequences from this study and available sequences of *Pseudocuneopsis sichuanensis*, *P. yangshuoensis*, and *P. capitata* from GenBank. Additionally, we downloaded GenBank COI sequences of 30 species of the subfamily Unioninae as the ingroup and two species of the subfamily Gonideinae as the outgroup to augment our dataset.

Finally, our study used a total of 38 COI sequences; detailed sequence information and GenBank accession numbers are provided in Table 1.

COI nucleotide sequences were aligned under the invertebrate mitochondrial code mode in MACSE (Ranwez et al. 2021) with default settings. We calculated and compared inter- and intraspecific distances with MEGA 7.0 (Kumar et al. 2016) using the uncorrected *p*-distance. Standard error was assessed using 1000 bootstrap replicates.

Phylogenetic analysis

Bayesian-inference (BI) analyses were inferred in MrBayes (Ronquist et al. 2012), using the GTR+I+G model of nucleotide substitution. Four chains were run simultaneously for 10 million generations and trees were sampled every 1000 generations. The first 25% of these trees were discarded as burn-in when computing the consensus tree (50% majority rule). Sufficient mixing of the chains was considered to have been reached when the average standard deviation of split frequencies was below 0.01. Additionally, IQ-TREE was run for maximum-likelihood (ML) tree reconstruction with 1000 ultrafast bootstrap replications (Minh et al. 2013).

Taxonomy

Pseudocuneopsis wuana Liu & Wu, sp. nov.

<https://zoobank.org/7D3D0EF8-1231-4610-AE5B-07E9A64E3F86>

Fig. 1

Type specimens. *Holotype*: CHINA • Guangxi Province, Nanning City (南宁市), Qingshui River (23.4075°N, 108.7557°E), 22 June 2023, Ruiwen Wu leg. (SXNU23062201). *Paratypes*: same data as holotype (voucher numbers SXNU23062202–SXNU23062206).

Diagnosis. *Pseudocuneopsis wuana* sp. nov. is morphologically distinct from the other three recognized species within the genus by shell shape, beak position and sculpture, and surface sculpture (Table 2). Diagnostic characteristics: shell ovaliform; ventral margin somewhat prominent at middle; umbo situated 1/3–1/4 of shell length and higher than dorsal margin; epidermis tawny to dark brown, shell surface sculptured with concentric ridges; nacre silvery-white, umbo pocket light yellow.

Description. Shell ovaliform, medium-thick; anterior margin rounded and inflated; ventral margin somewhat prominent in the middle; umbo located at 1/3–1/4 of shell length and higher than dorsal margin; umbo sculptured with nodes or nodulose wrinkles, or severely eroded; posterior slope formed by

Table 1. List of COI sequences used in this study.

Taxa	GenBank accession number
UNIONINAE Rafinesque, 1820	
<i>Lasmigona compressa</i> (Lea, 1829)	AF156503
<i>Pyganodon grandis</i> (Say, 1829)	AF231734
<i>Strophitus undulatus</i> (Say, 1817)	AF156505
<i>Pseudanodonta complanata</i> (Rossmässler, 1835)	KX822661
<i>Unio tumidus</i> (Philipsson, 1788)	KX822672
<i>Nodularia douglasiae</i> (Griffith & Pidgeon, 1833)	NC_026111
<i>Aculamprotula scripta</i> (Heude, 1875)	MF991456
<i>Aculamprotula tientsinensis</i> (Crosse & Debeaux, 1863)	NC_029210
<i>Acuticosta chinensis</i> (Lea, 1868)	MG462919
<i>Cuneopsis heudei</i> (Heude, 1874)	MG462974
<i>Cuneopsis rufescens</i> (Heude, 1874)	MG462982
<i>Inversiunio yanagawensis</i> (Kondo, 1982)	LC518988
<i>Pseudocuneopsis capitata</i> (Heude, 1874)	MZ540968
<i>Pseudocuneopsis capitata</i> (Heude, 1874)	MZ540969
<i>Pseudocuneopsis sichuanensis</i> Huang, Dai, Chen & Wu, 2022	MZ540966
<i>Pseudocuneopsis sichuanensis</i> Huang, Dai, Chen & Wu, 2022	MZ540967
<i>Pseudocuneopsis yangshuoensis</i> Wu & Liu, 2023	OQ696218
<i>Pseudocuneopsis yangshuoensis</i> Wu & Liu, 2023	OQ696219
<i>Pseudocuneopsis yangshuoensis</i> Wu & Liu, 2023	OQ696220
<i>Pseudocuneopsis yangshuoensis</i> Wu & Liu, 2023	OQ696221
<i>Pseudocuneopsis yangshuoensis</i> Wu & Liu, 2023	OQ696222
<i>Pseudocuneopsis wuana</i> sp. nov. 1*	OR297986
<i>Pseudocuneopsis wuana</i> sp. nov. 2*	OR297987
<i>Pseudocuneopsis wuana</i> sp. nov. 3*	OR297988
<i>Pseudocuneopsis wuana</i> sp. nov. 4*	OR297989
<i>Pseudocuneopsis wuana</i> sp. nov. 5*	OR297990
<i>Pseudocuneopsis wuana</i> sp. nov. 6*	OR297991
<i>Tchangsiniaia piscicula</i> (Heude, 1874)	KJ434496
<i>Tchangsiniaia piscicula</i> (Heude, 1874)	KJ434497
<i>Tchangsiniaia piscicula</i> (Heude, 1874)	KJ434498
<i>Tchangsiniaia piscicula</i> (Heude, 1874)	KJ434499
<i>Schistodesmus lampreyanus</i> (Baird & Adams, 1867)	MG463038
<i>Schistodesmus spinosus</i> (Simpson, 1900)	MG463045
<i>Lanceolaria gladiola</i> (Heude, 1877)	KY067441
<i>Lanceolaria grayii</i> (Griffith & Pidgeon, 1833)	NC_026686
<i>Lanceolaria lanceolata</i> (Lea, 1856)	NC_023955
GONIDEINAE Ortmann, 1916	
<i>Lamprotula leaii</i> (Gray, 1833)	NC_023346
<i>Sinosolenaia oleivora</i> (Heude, 1877)	KX822670

* Generated in this study.

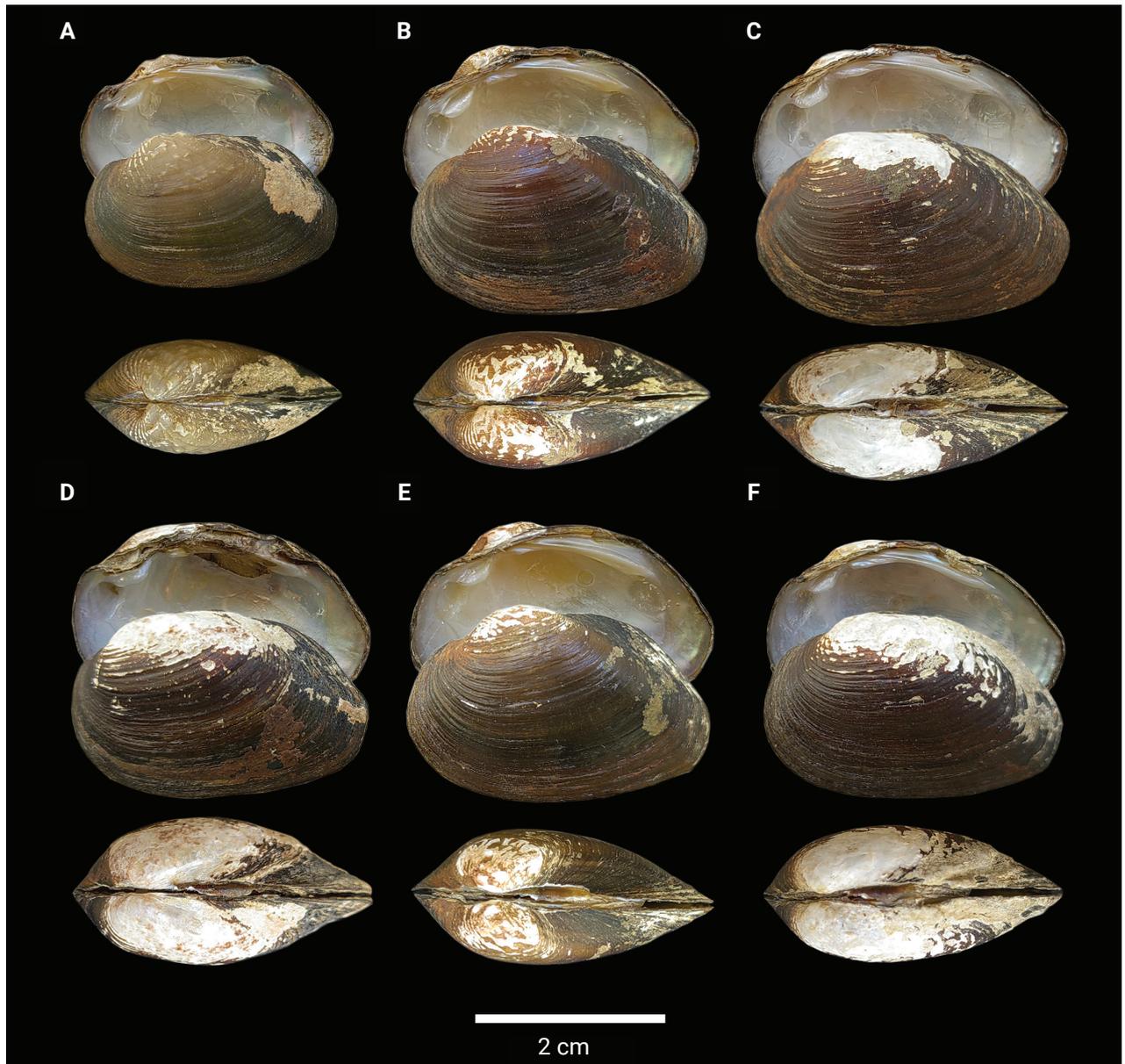


Figure 1. Photographs of *Pseudocuneopsis wuana* sp. nov. **A** holotype (SXNU23062201) **B–F** paratypes (SXNU23062202–SXNU23062206). All specimens shown at the same scale. Photographs by Lili Liu and Liping Zhang.

ventral margin and dorsal margin low, blunt, located at almost 1/3 of shell height; epidermis tawny to dark brown covered with concentric ridges; anterior adductor muscle scars elliptical, deep, and smooth; posterior adductor muscle scars round to elliptical, shallow and smooth; anterior and posterior retractor muscle scars noticeable, with anterior and posterior irregularly oval; mantle muscle scars obvious; left valve with two separate pseudocardinal teeth and two lateral teeth; outer and inner pseudocardinal teeth of different lengths and projecting outward at different levels, outer and inner pseudocardinal teeth roughly the same size; right valve with one well-developed pseudocardinal tooth and one lateral tooth; nacre silvery-white, umbo pocket light yellow.

Length 24.97–35.91 mm, height 15.49–21.95 mm.

Table 2. Conchological characters of *Pseudocuneopsis wuana* sp. nov., *P. yangshuoensis*, *P. capitata*, and *P. sichuanensis*. Characteristic descriptions of *P. capitata*, *P. sichuanensis*, and *P. yangshuoensis* are referenced from published works (Wu et al. 2022; Wu et al. 2023).

	<i>P. yangshuoensis</i>	<i>P. sichuanensis</i>	<i>P. capitata</i>	<i>P. wuana</i> sp. nov.
Length	41.39–50.51 (mm)	49.16–62.97 (mm)	101.68–121.32 (mm)	24.97–35.91 (mm)
Width	15.34–19.40 (mm)	15.01–22.42 (mm)	37.07–42.72 (mm)	10.72–15.74 (mm)
Height	27.25–28.99 (mm)	27.16–36.02 (mm)	49.23–61.02 (mm)	15.49–21.95 (mm)
Shell shape	Wedge-shaped	Oval	Elongate	ovaliform
Umbo position	1/3 of shell length; umbo obviously lower than the dorsal margin	1/4–1/5 of shell length; umbo slightly higher than the dorsal margin	1/6 of shell length; umbo obviously higher than the dorsal margin	1/3–1/4 of shell length; umbo higher than the dorsal margin
Surface sculpture	Epidermis brownish-black covered with concentric ridges	Epidermis dark brown with growth annuli with 1 or 2 sulci near posterior dorsal margin	Epidermis brownish with low ridges, which follow growth lines	Epidermis tawny to dark brown covered with concentric ridges
Nacre colour	Orange	White	Milk-white	Silvery-white, umbo pocket light yellow
Dorsal margin	Anterior margin oval, and inflated, with the dorsal margin curved downwards	Anterior margin oval, and inflated, with dorsal margin curved downwards	Anterior margin oval, highly inflated, dorsal margin sloped downwards	Anterior margin round, and inflated, with dorsal margin curved downwards
Posterior slope	Blunt	Blunt	Sharp	Blunt
Ventral margin	Nearly straight or slightly concave	Slightly concave inward at middle posterior	Rounded anteriorly, with sinus behind anterior inflation	Somewhat prominent at middle



Figure 2. The type locality of *Pseudocuneopsis wuana* sp. nov. in Qingshui River, Nanning City, China.

Etymology. This species' name is dedicated to Dr Ruiwen Wu, who collected these specimens. For the common name, we recommend “Wu ovaliform Mussel” (English) and “Wu Shi Wei Xie Bang” (武氏伪楔蚌) (Chinese).

Distribution. Qingshui River, Guangxi, China (Fig. 2).

Anatomical characteristics. Within the incurrent aperture, there are elongated papillae arranged in three or four rows; these have a slight swelling at their base; papillae of the excurrent aperture well developed, stubby, and arranged in two rows. The inner gills are larger than the outer gills. Labial palps are medium-thick and elongated (Fig. 3).

Molecular analyses. Pairwise COI sequence divergences from *Pseudocuneopsis wuana* sp. nov., *P. yangshuoensis*, *P. capitata*, and *P. sichuanensis* were calculated in MEGA 7.0 with the uncorrected *p*-distance model. The intraspecific divergence of the newly discovered species, *P. wuana* sp. nov., ranged from

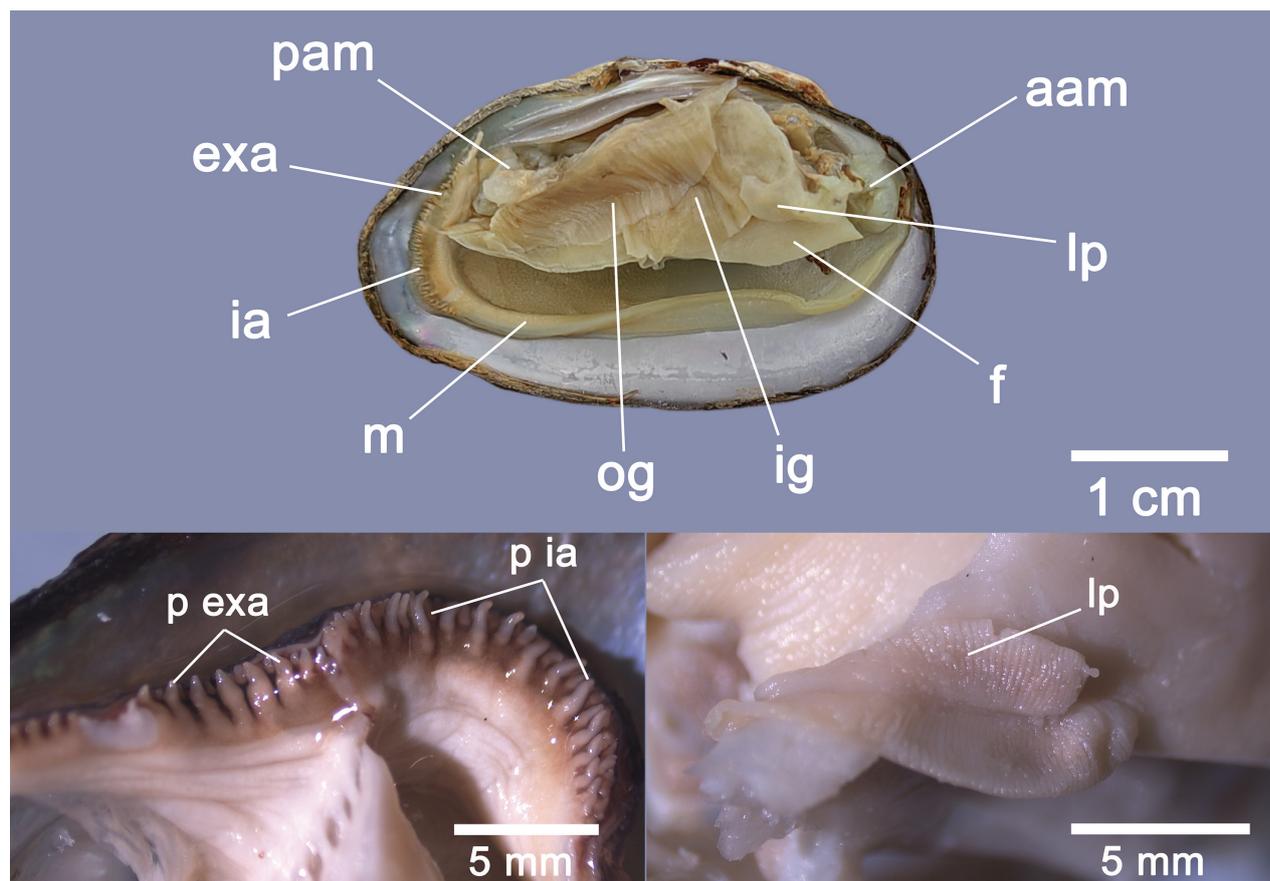


Figure 3. Anatomical features of *Pseudocuneopsis wuana* sp. nov. with right valve removed. Abbreviations: aam, anterior adductor muscle; pam, posterior adductor muscle; exa, excurrent aperture; ia, incurrent aperture; f, foot; ig, inner gill; og, outer gill; lp, labial palps; m, mantle; p ia, papillae in incurrent aperture; p exa, papillae in excurrent aperture.

0% to 0.5%. The genetic divergence between *P. wuana* and *P. yangshuoensis* was 5.1%, while that between *P. wuana* and the other two species, namely *P. sichuanensis* and *P. capitata*, was 8.2% and 10.2%, respectively.

The BI and ML trees based on the mitochondrial COI gene yielded incongruent topologies (Figs 4, 5). However, both phylogenetic trees consistently supported the sister-group relationship between *Pseudocuneopsis wuana* sp. nov. and *P. yangshuoensis* (BS = 100%; PP = 1.00, Figs 4, 5). The genus *Pseudocuneopsis* exhibited monophyly with robust bootstrap support (BS = 98%) and full Bayesian posterior probability (PP = 1.00) (Figs 4, 5).

Remarks. The placement of the new species in *Pseudocuneopsis* is supported by both morphological characteristics and phylogenetic analyses. *Pseudocuneopsis wuana* sp. nov. can readily be distinguished from congeneric species by its distinctive ovaliform shell, tawny to dark-brown epidermis covered with concentric ridges, and somewhat prominent at the middle of ventral margin. We conducted an analysis of interspecific divergence among *P. sichuanensis*, *P. capitata*, *P. yangshuoensis*, and the newly described species *P. wuana* using the COI gene. The results indicate that the genetic distances between *P. wuana* and its congeneric species, namely *P. yangshuoensis*, *P. sichuanensis*, and *P. capitata*, were 5.1%, 8.2%, and 10.2%, respectively, which are distinctly higher than intraspecific divergences. We conclude that the genetic analyses support the recognition of *P. wuana* sp.

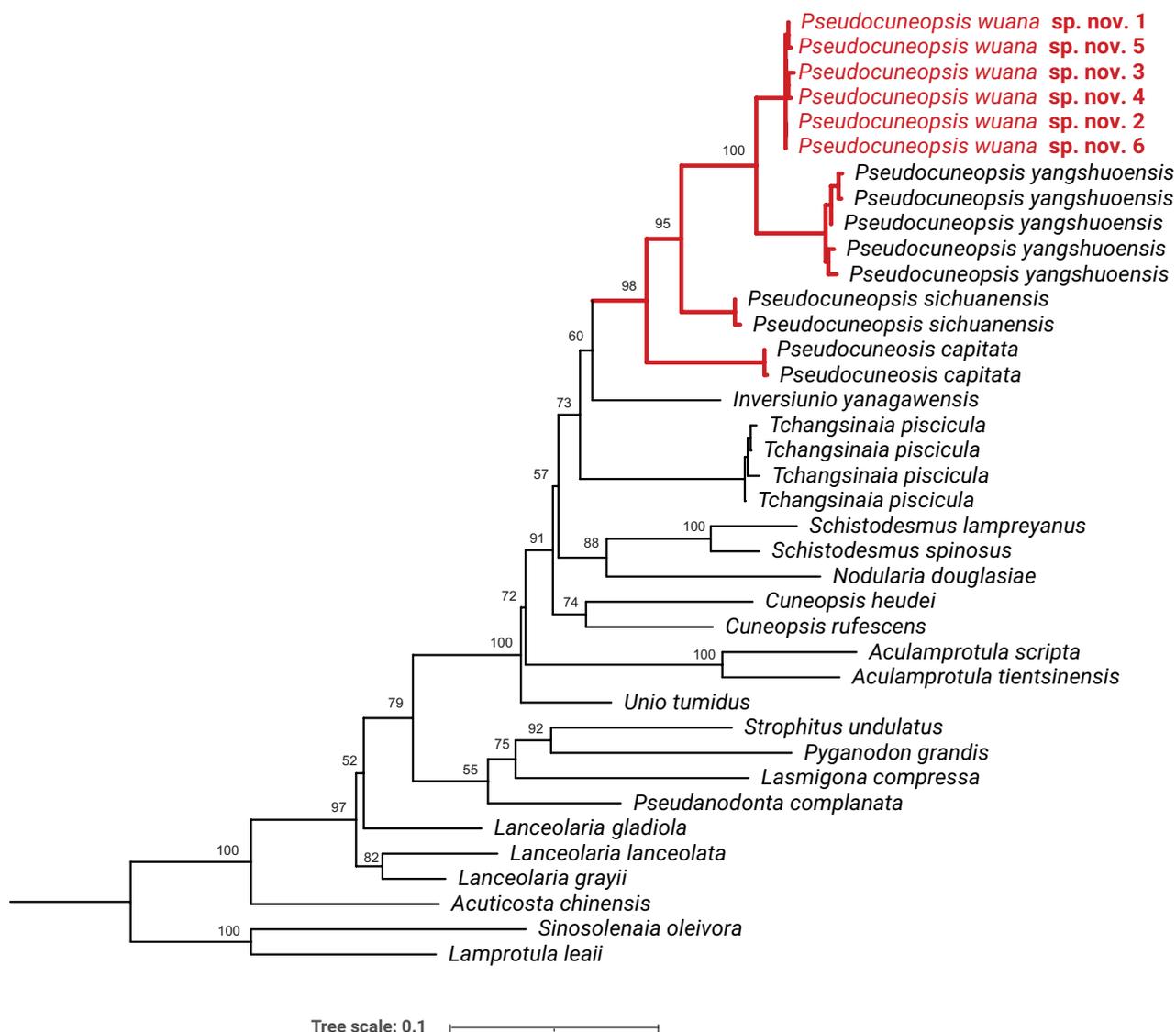


Figure 4. Phylogenetic tree of freshwater mussels inferred by maximum-likelihood (ML) analysis of the COI barcode fragment. Bootstrap-support (BS) values are shown at the nodes. The new species is indicated in red.

nov. as a valid new species, which can easily be distinguished by its unique COI barcode sequences.

In recent years, through more extensive investigations and field surveys, several new species of freshwater mussels, such as *Postolata guangxiensis* and *Pseudocuneopsis yangshuoensis*, have been discovered in Guangxi Province, China (Dai et al. 2023; Wu et al. 2023). As a major ecological barrier in southwest China, Guangxi is one of the significant watershed areas of the Pearl river basin. The province is noted for its distinctive karst landscape which harbors a rich diversity of species. However, due to the insufficient attention paid to freshwater mussels in the region, the mussel diversity in China is poorly understood. The lack of data regarding species' distributions, population trends, threats, and accurate taxonomic information has severely impeded conservation efforts for the unio-nids in this area. Our findings suggest that there is still much to be discovered regarding the diversity of freshwater mussels in Guangxi Province. Additional extensive exploration may reveal other species that have yet to be documented.

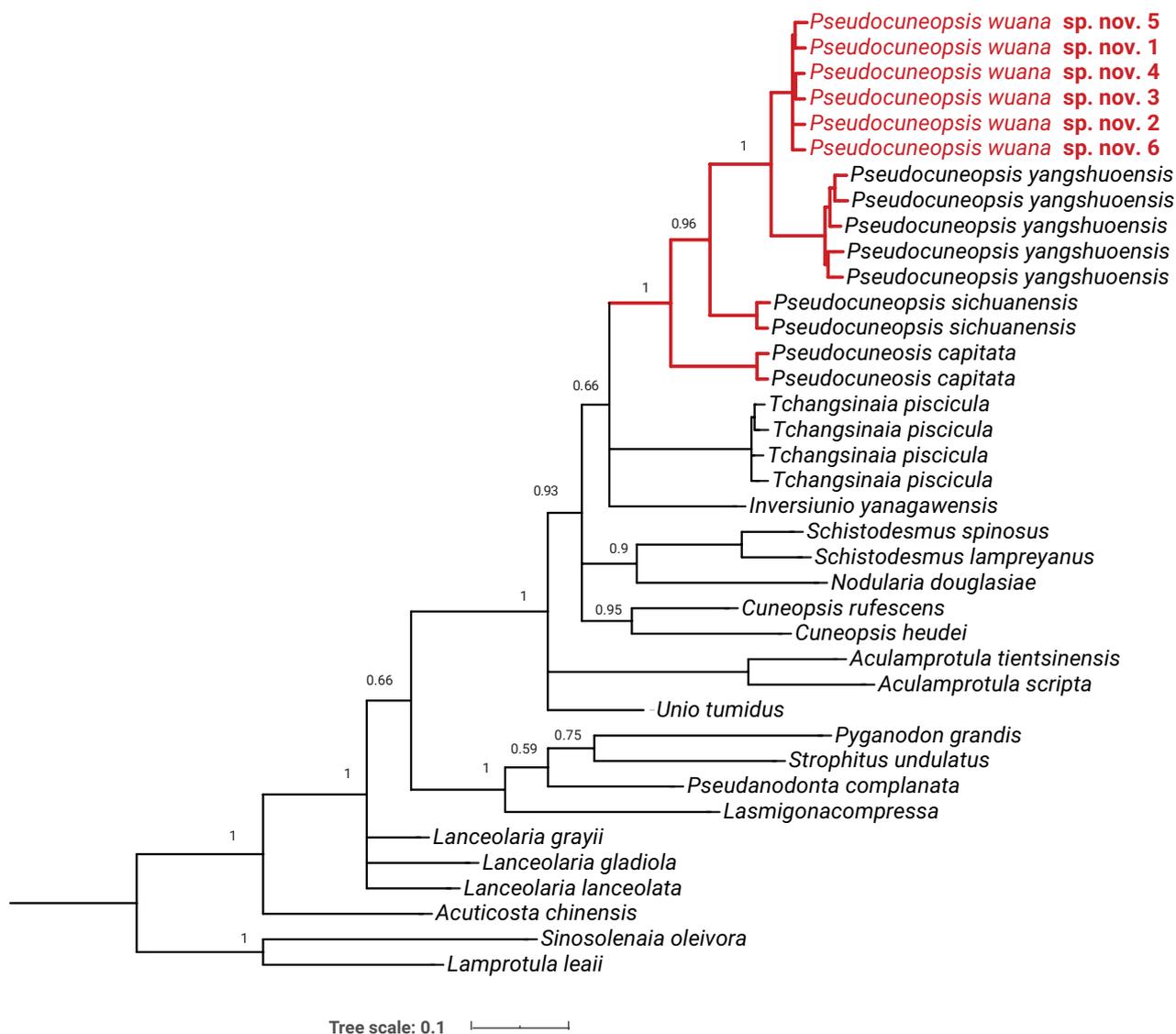


Figure 5. Phylogenetic tree of freshwater mussels inferred from Bayesian-inference (BI) analysis of the COI barcode fragment. Posterior probabilities (PP) are shown at the nodes. The new species is indicated in red.

Acknowledgements

We would like to express our sincere gratitude to the Editor Dr Edmund Gittenberger and the reviewer Dr Ivan N. Bolotov, for their helpful comments.

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Funding

This work was funded by the National Natural Science Foundation of China (no. 32200370), the Basic Research Program of Shanxi Province, China (no. 20210302124253).

Author contributions

Ruiwen Wu (RW-W) designed the study; RW-W, Lili Liu (LL-L), Liping Zhang (LP-Z), Haotian Wang (HT-W), Dandong Jin (DD-J) undertook field research and sampling, LL-L, Xiongjun Liu (XJ-L) and LP-Z conducted the data analysis, LL-L and RW-W wrote and edited the manuscript. All authors read and approved the final version of the manuscript.

Author ORCIDs

Lili Liu  <https://orcid.org/0009-0009-1164-7735>

Xiongjun Liu  <https://orcid.org/0000-0002-5333-6670>

Ruiwen Wu  <https://orcid.org/0000-0002-8936-6054>

Data availability

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

References

- Dai YT, Huang XC, Wu CHZ, Chen ZGL, Guo L, Shu FY, Ouyang S, Wu XP (2023) Multilocus and mitogenomic phylogenetic analyses reveal a new genus and species of freshwater mussel (Bivalvia: Unionidae) from Guangxi, China. *Invertebrate Systematics* 37(2): 152–166. <https://doi.org/10.1071/IS22048>
- Graf DL, Cummings KS (2021) A 'big data' approach to global freshwater mussel diversity (Bivalvia: Unionoida), with an updated checklist of genera and species. *Journal of Molluscan Studies* 87(2): eyab015. <https://doi.org/10.1093/mollus/eyab015>
- Graf DL, Cummings KS (2023) The MUSSEL project database. <http://www.mussel-project.net/>
- Huang XC, Su JH, Ouyang JX, Ouyang S, Zhou CH, Wu XP (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. <https://doi.org/10.1016/j.ympev.2018.09.019>
- Kumar S, Stecher G, Tamura K (2016) MEGA7: Molecular Evolutionary Genetics Analysis version 7.0 for bigger datasets. *Molecular Biology and Evolution* 33(7): 1870–1874. <https://doi.org/10.1093/molbev/msw054>
- Liu YY, Zhang WZ, Wang QX, Wang EY (1979) *Economic Fauna of China—Freshwater Mollusk*. Science Press, Beijing.
- Liu X, Yang X, Zanatta DT, Lopes-Lima M, Bogan AE, Zieritz A, Ouyang S, Wu XP (2020) Conservation status assessment and a new method for establishing conservation priorities for freshwater mussels (Bivalvia: Unionida) in the middle and lower reaches of the Yangtze river drainage. *Aquatic Conservation* 30(5): 1000–1011. <https://doi.org/10.1002/aqc.3298>
- Liu XJ, Liu YY, Wu RW, Zanatta DT, Lopes-Lima M, Gonçalves DV, Bogan AE, Ouyang S, Wu XP (2022) Systematics, distribution, biology, and conservation of freshwater mussels (Bivalvia: Unionida) in China. *Aquatic Conservation* 32(5): 859–895. <https://doi.org/10.1002/aqc.3799>
- Lopes-Lima M, Teixeira A, Froufe E, Lopes A, Varandas S, Sousa R (2014) Biology and conservation of freshwater bivalves: Past, present and future perspectives. *Hydrobiologia* 735(1): 1–13. <https://doi.org/10.1007/s10750-014-1902-9>
- Minh BQ, Nguyen MAT, von Haeseler A (2013) Ultrafast approximation for phylogenetic bootstrap. *Molecular Biology and Evolution* 30(5): 1188–1195. <https://doi.org/10.1093/molbev/mst024>

- MolluscaBase eds (2023) MolluscaBase. *Pseudocuneopsis* X.-C. Huang, Y.-T. Dai & X.-P. Wu, 2022. <https://www.molluscabase.org/aphia.php?p=taxdetails&id=1559799> [Accessed on: 2023-05-13]
- Ranwez V, Chantret N, Delsuc F (2021) Aligning protein-coding nucleotide sequences with MACSE. In: Katoh K (Ed.) Multiple Sequence Alignment. Methods in Molecular Biology, vol. 2231. Humana, New York, NY. https://doi.org/10.1007/978-1-0716-1036-7_4
- Ronquist F, Teslenko M, Mark PV, Ayres DL, Darling A, Höhna S, Larget B, Liu L, Marc A, Suchard MA, Huelsenbeck JP (2012) Mrbayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. Systematic Biology 61(3): 539–542. <https://doi.org/10.1093/sysbio/sys029>
- Starobogatov Y (1970) Fauna of Molluscs and Zoogeographic Division of Continental Waterbodies of the Globe. Nauka, Leningrad. [In Russian]
- Vaughn CC (2018) Ecosystem services provided by freshwater mussels. Hydrobiologia 810(1): 15–27. <https://doi.org/10.1007/s10750-017-3139-x>
- 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 amblesine freshwater mussels (Bivalvia: Unionoidea: Ambleminae). Molecular Ecology Notes 7(3): 489–491. <https://doi.org/10.1111/j.1471-8286.2006.01630.x>
- Wu RW, Liu YT, Wang S, Liu XJ, Zanatta DT, Roe KJ, Song XL, An CT, Wu XP (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. <https://doi.org/10.1371/journal.pone.0200956>
- Wu RW, Liu XJ, Wang S, Roe KJ, Ouyang S, Wu XP (2019) Analysis of mitochondrial genomes resolves the phylogenetic position of Chinese freshwater mussels (Bivalvia, Unionidae). ZooKeys 812: 23–46. <https://doi.org/10.3897/zookeys.812.29908>
- Wu XP, Dai YT, Yin N, Shu FY, Chen ZG, Guo L, Zhou CH, Ouyang S, Huang XC (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. <https://doi.org/10.1111/zsc.12527>
- Wu RW, Liu LL, Zhang LP, Jia JL, Jin DD, Wu XP, Liu XJ (2023) New species of the genus *Pseudocuneopsis* Huang, Dai, Chen & Wu, 2022 (Bivalvia, Unionidae) from Guangxi Province, China. ZooKeys 1166: 261–270. <https://doi.org/10.3897/zookeys.1166.104150>
- Zieritz A, Bogan AE, Froufe E, Klishko O, Kondo T, Kovitvadhi U, Kovitvadhi S, Lee JH, Lopes-Lima M, Pfeiffer JM, Sousa R, Van Do T, Vikhrev I, Zanatta DT (2018) Diversity, biogeography and conservation of freshwater mussels (Bivalvia: Unionida) in East and Southeast Asia. Hydrobiologia 810(1): 29–44. <https://doi.org/10.1007/s10750-017-3104-8>