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Polyphyly in a morphologically defined genus: phylogeny and morphology of *Pseudobuliminus* (Eupulmonata: Camaenidae) from eastern and northern China, with a checklist of species from mainland China

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ABSTRACT

Pseudobuliminus (Eupulmonata: Camaenidae) has traditionally been delimited to exclusively contain species with conoidal shells, but questions regarding its monophyly have remained. Extensive morphometric analyses conducted on almost all *Pseudobuliminus* species from China indicate that possessing a conoidal shell alone is not a sufficient character to establish genus membership. It was previously shown that *Pseudobuliminus* species from Shandong Province lack a dart sac and possess a flagellum. We found the same reproductive characteristics in additional species from eastern and northern China, such as *P. buliminoides* from Nanjing, Jiangsu Province, and *P. beijingensis* n. sp., described herein from Fangshan, Beijing Province. In contrast, species from western China differ from this configuration by having a dart sac but lacking a flagellum. Based on partial sequences of the mitochondrial 16S rRNA and the nuclear spacer ITS2, our molecular phylogeny demonstrates that the species from eastern and northern China form a clade. We conclude that the combination of lack of a dart sac and presence of a flagellum is a morphological synapomorphy shared by the members of this taxonomic lineage.

Abbreviations: SDNU: Shandong Normal University; UNSM: United States National Museum

ZooBank registration: https://zoobank.org/NomenclaturalActs/D0972FF3-F730-4291-A019-2A53B5FC1F82

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Beijing; Bradybaeninae; cladistics; Yanshan Mountains; synapomorphy

Introduction

In mainland China, the genus *Pseudobuliminus* Gredler, 1886 has usually been divided into five subgenera: *Pseudobuliminus*, *Buliminidius* Heude, 1890, *Rudens* Heude, 1890, *Secusana* Gredler, 1894 and *Stenogyropsis* Möllendorff, 1899 (Thiele 1931; Schileyko 2004). The type species of *Pseudobuliminus* is *Helix pseudobuliminus* Heude, 1882, originally described from Chaohu, Anhui Province, a location geographically close to Nanjing, Jiangsu Province. Nanjing is the type locality of the type species of *Buliminidius*, *Helix squamosella* Heude, 1882. The type species of *Secusana*, *Buliminopsis cerasinus* Gredler, 1892, is believed to inhabit Hubei (Yü et al. 1982). *Rudens* is a monotypic subgenus with the type species *Funiculus rudens* Heude, 1888 from Dali, Yunnan. *Stenogyropsis*, known from Gansu Province, has recently been elevated to full genus rank by Páll-Gergely and Hunyadi (2016) for its distinctively turreted shell and the lack of a penial sheath. The type species is *Buliminopsis potanini* Möllendorff, 1899 by monotypy.

The above-mentioned genus-level taxa comprise 37 nominal species altogether in mainland China (Table 2). These species occupy a combined range that extends through large parts of the country, including western (e.g., Sichuan, Chongqing, Gansu, and Hubei), northern and eastern (e.g., Shandong, Jiangsu), and south-western China (Yunnan). The genus is also found in Taiwan, on the Ryukyu Islands, in Korea, and in mainland Japan (Hayase and Habe 1998; Chang and Hwang 2000; Hsieh et al. 2013; Hirano et al. 2014; Qian and Zhou 2015; Choi and Park 2020). Reports from Southeast Asia by Thach (2017) are due to misidentifications, as shown by Sutcharit et al. (2019). The current taxonomic classification is not supported by molecular phylogenetic studies, which revealed that *Pseudobuliminus* is a polyphyletic group (Hirano et al. 2014; Wu et al. 2023).

In earlier taxonomic treatments, land snail classifications relied predominantly on shell characteristics. The taxonomic significance of shell characters is questionable because they may be particularly sensitive to

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environmental pressures (e.g., Goodfriend 1986). More recently, however, the genital system had been recognised as taxonomically informative in land snails (Tiller 1989). Hirano et al. (2014) demonstrated that many morphological traits, such as the elongated turret shell, evolved multiple times independently due to parallel evolution. Molecular analyses revealed a substantial incongruence between morphology-based taxonomy and genetic relationships. While genital anatomy tends to be more conserved, even these characters (e.g., dart sac and associated organs) showed independent losses in several lineages of Bradybaeninae (Hirano et al. 2014). Indeed, *Pseudobuliminus* represents this morphological parallel evolution issue in a nutshell.

A major unresolved issue concerning *Pseudobuliminus* is the disagreement over its distinguishing characters, particularly anatomical characters. Initially, Thiele (1931) noticed that species exhibited differences in their reproductive anatomy. Subsequently, studies of species from different geographical regions also reported inconsistent anatomies (Wu 2002; Wu 2004; Chang and Hwang 2000; Hayase and Habe 1998; Schileyko 2004; Zhang et al. 2025a). *Pseudobuliminus* species from Taiwan and Japan usually lack a dart sac and possess a flagellum (Chang and Hwang 2000; Hayase and Habe 1998). However, species from north-west China exhibit a different pattern, possessing a dart sac while lacking a flagellum (Wu 2002, 2004). The recently described *Pseudobuliminus dongyiicus* Zhang, 2024 from eastern China lacks a dart sac but possess a flagellum, therefore aligning more closely with the Japanese and Taiwanese species rather than those from north-west China (Zhang et al. 2025a). In summary, the regional discrepancies in the anatomical features of *Pseudobuliminus* highlight the need for further scrutiny of the whole group, including an in-depth analysis of its synapomorphies.

In this study, we examine the shell variation using morphometric methods, reconstruct the phylogenetic tree based on 16S and ITS2, summarise synapomorphies based on the phylogeny and describe a new species of *Pseudobuliminus* based on a comparative analysis of shell morphology and molecular phylogenetic analyses. Additionally, we provide an updated checklist of *Pseudobuliminus* species in mainland China, adding to a more comprehensive understanding of this taxonomically challenging genus.

Materials and methods

Living adult specimens were relaxed in water for approximately 6 h before being preserved in 75% ethanol. Shells and genitalia were photographed using a Leica S6D stereo microscope with camera. Shells were measured to the nearest 0.1 mm using vernier callipers. Whorls were counted with an accuracy of 0.125 whorls following the method described by Kerney and

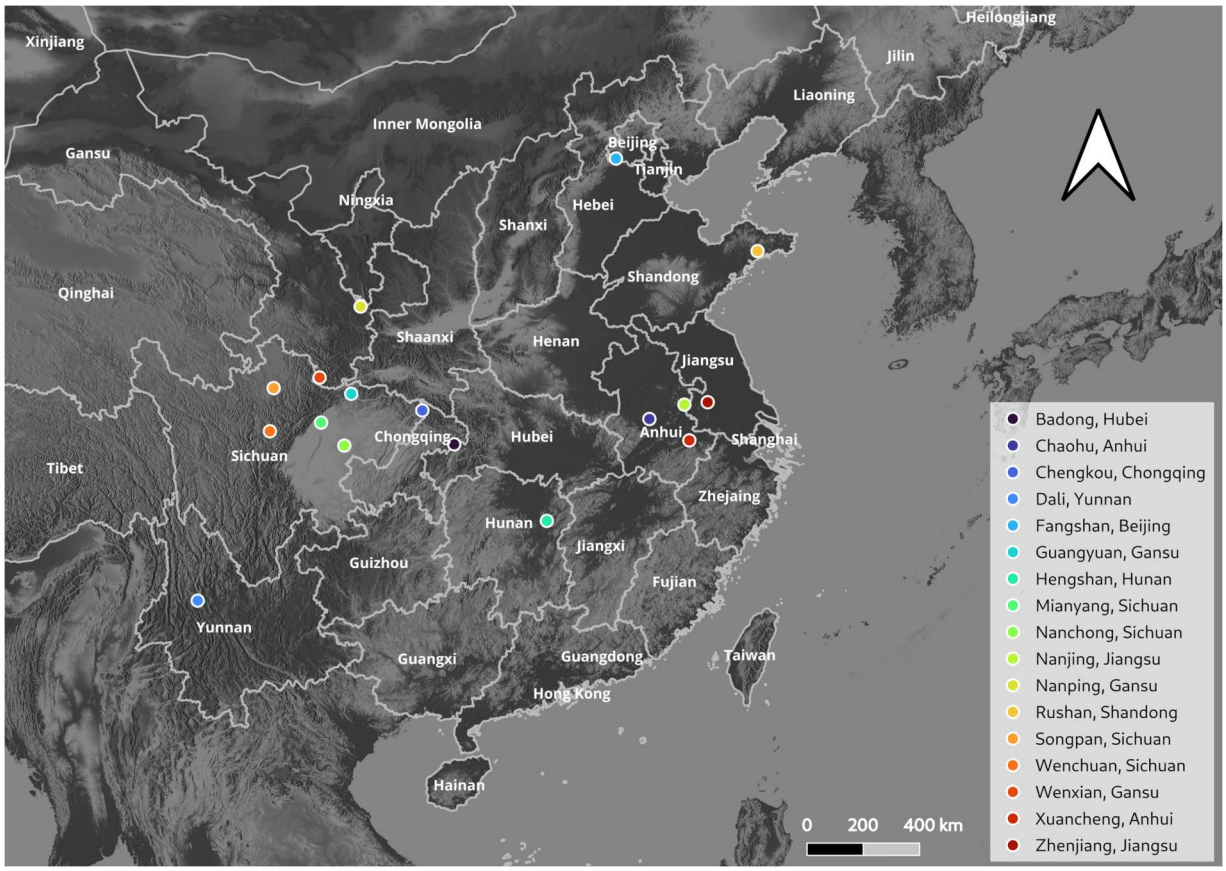

Figure 1. Type localities of *Pseudobuliminus* nominal species from mainland China.

Table 1. Checklist of *Pseudobuliminus* in mainland China including shell measurements, type locality and original literature information (one species lacks literature information). * Indicates type species of subgenera. *Pseudobuliminus* from western China (PWC), the group from northern and eastern China (PNEC), the group from Taiwan (PT) and the group from Yunnan (PY).

Genus	Subgenus	Group	Species	Authorship and year	Page and plates	Original combination	Type locality	Diam.	Height	Whorl	Note
Pseudobuliminus	?	PWC	*alveolus*	(Heude, 1890)	146, pl. 37, fig. 23	*Helix alveolus*	Tchen-k'eou [Chengkou, Chongqing City]	5	5	?	
Pseudobuliminus	?	PWC	*cristatellus*	(Moellendorff, 1902)	79, pl. 17, figs. 23–25	*Buliminus* (*Lophauchen*) *cristatellus*	Ga-nsu: Nanping [Nanping, Gansu Province]	3.5	11.5	10.5	
Pseudobuliminus	?	PWC	*cylindrus*	(Moellendorff, 1899)	92, pl. 8, fig. 8	*Buliminopsis* (*Buliminopsis*) *cylindra*	Gansu: Zwischen Wen-hsien und Yü-lin-guan [between Wenxian and Yü-lin-guan, Gansu Province]	5.5	18	12	
Pseudobuliminus	?		*macroceramiformis*	(Deshayes, 1870)	25 (pl. 1, figs. 17–18 in Deshayes, 1874)	*Bulimus macroceramiformis*	?	5	6	12	
Pseudobuliminus	?	PWC	*ortmanni*	(Blume, 1925)	17	*Funiculus ortmanni*	Wentschuan [Wenchuan, Sichuan Province]	3–3.1	12.1–12.7	10	
Pseudobuliminus	?	PWC	*soleniscus*	(Moellendorff, 1902)	78, pl. 17, figs. 21–22	*Buliminus* (*Pupopsis*) *soleniscus*	Gan-su Wen-hisen [Wenxian, Gansu Province]	3.75	9	10	
Pseudobuliminus	*Buliminidius*	PWC	*achatininus*	(Moellendorff, 1899)	93, pl. 8, fig. 11	*Buliminopsis* (*Funiculus*) *achatinina*	Gansu: Nanping [Nanping, Gansu Province]	7	20.5	12	
Pseudobuliminus	*Buliminidius*	PWC	*hirsutus*	(Moellendorff, 1899)	92, pl. 8, fig. 6	*Buliminopsis* (*Funiculus*) *hirsuta*	Gansu: Nanping [Nanping, Gansu Province]	6.25	19	12	
Pseudobuliminus	*Buliminidius*	PT	*larvatus*	(Heude, 1890)	146, pl. 35, figs. 22–22a	*Buliminus larvatus*	Ta-li fou [Dali, Yunan Province]	4	13	11	
Pseudobuliminus	*Buliminidius*	PT	*pupatus*	(Heude, 1890)	146, pl. 35, figs. 23–23a	*Buliminus pupatus*	Ta-li fou [Dali, Yunan Province]	5	11	10	
Pseudobuliminus	*Buliminidius*		*schaeferi*	(Yen, 1938)	1938b, 456, fig.14	*Funiculus schaeferi*	Waszekou [Waze, Kangding?], Sichuan	2.8	9	10.5	
Pseudobuliminus	*Buliminidius*	PNEC	*squamosellus squamosellus**	(Heude, 1882)	36, pl. 15, figs. 9–9a	*Helix squamosella*	Nanking [Nanjing, Jiangsu Province]	11	8	6.5	
Pseudobuliminus	*Buliminidius*	PNEC	*squamosellus depressus*	Hsu, 1936	14, pl. 1, figs. 5–10	*Ganesella squamosellus depressus*	Chenkiang [Zhenjiang, Jiangsu Province]	?	?	?	
Pseudobuliminus	NA	PNEC	*beijingensis*	Wang n. sp.	This paper		Beijing, China				
Pseudobuliminus	NA	PNEC	*dongyiicus*	Zhang, 2024	Supplementary material S3		Rushan [misspelling of Lushan], Shandong Province	5.6	5	5.75	
Pseudobuliminus	*Pseudobuliminus*	PNEC	*buliminoides buliminoides*	(Heude, 1882)	47, pl. 17, figs. 6, 30	*Helix buliminoides*	Nanking [Nanjing, Jiangsu Province]	6–7	10–13	7–9	
Pseudobuliminus	*Pseudobuliminus*	PNEC	*buliminoides tropidophorus*	(Ancey, 1885)	121	*Buliminus buliminoides tropidophorus*	?	7	13	9	Synonym of *P. buliminoides*
Pseudobuliminus	*Pseudobuliminus*	PWC	*buliminus buliminus*	(Heude, 1882)	48, pl. 20, fig. 20	*Helix buliminus*	Se Tchouan [Sichuan Province]	6.5	16	8	

(*Continued*)

Table 1. Continued.

Genus	Subgenus	Group	Species	Authorship and year	Page and plates	Original combination	Type locality	Diam.	Height	Whorl	Note
Pseudobuliminus	*Pseudobuliminus*	PWC	*buliminus strigatus*	(Moellendorff, 1899)	89	*Buliminopsis* (*Buliminopsis*) *buliminus strigatus*	Sytshuan: Guang-yüan-hsien [Guangyuan, Sichuan Province]	6.5–7.75	12	?	
Pseudobuliminus	*Pseudobuliminus*	PWC	*conoidius*	(Heude, 1890)	147, pl. 37, fig. 25	*Buliminopsis conoidius*	Tchen-k'eou [Chengkou, Chongqing City]	5	7	7	
Pseudobuliminus	*Pseudobuliminus*	PWC	*gracilispirus*	(Moellendorff, 1899)	90, pl. 8, fig.10	*Buliminopsis* (*Buliminopsis*) *gracilispira*	Sytshuan: Sung-Pan [Songpan, Sichuan Province]	5.33–5.5	14–15	9	
Pseudobuliminus	*Pseudobuliminus*	PWC	*helicopsis*	(Ancey, 1885)	121	*Buliminus helicopsis*	?	?	?	?	Synonym of *P. buliminus*
Pseudobuliminus	*Pseudobuliminus*	PNEC	*macrogonus*	(Ancey, 1885)	121	*Buliminus macrogonus*	?	?	?	?	Synonym of *P. pseduobuliminus*
Pseudobuliminus	*Pseudobuliminus*	PWC	*nanchongensis*	Wu, 2002	46, figs.1–7	*Pseudobuliminus nanchongensis*	Nanchong, Sichuan	5.83–7.59	11.72–16.42	8.00–9.25	
Pseudobuliminus	*Pseudobuliminus*		*paradoliolus*	Zilch, 1951	6 in Gredler, 1887 (86 in Zilch, 1951)		Batung [Badong, Hubei]	6	13–16	11.5–12	
Pseudobuliminus	*Pseudobuliminus*	PWC	*piligerus*	(Moellendorff, 1899)	90, pl. 8, fig. 14	*Buliminopsis* (*Buliminopsis*) *piligera*	Gansu: Nanping [Nanping, Zhuanglang County, Gansu Province]	10–11.5	17.5–20.5	9.5	
Pseudobuliminus	*Pseudobuliminus*	PNEC	*pseudobuliminus**	(Heude, 1882)	48, pl. 17, figs. 29–29a	*Helix pseudobuliminus*	Tch'ao [Chaohu, Anhui Province]	8	12	9	
Pseudobuliminus	*Pseudobuliminus*		*quaternarius*	(Heude, 1890)	147, pl. 37, fig. 24	*Buliminopsis quaternarius*	Yu-Ho, province de Chen-Si [Weihe, Shaanxi Province]	9	13	8	
Pseudobuliminus	*Pseudobuliminus*	PWC	*subcylindricus*	(Moellendorff, 1899)	91, pl. 8, fig. 12	*Buliminopsis* (*Buliminopsis*) *subcylindrica*	Guang-ting [Gansu Province]	6	14.5	8.5	
Pseudobuliminus	*Pseudobuliminus*		*subdoliolus*	(Haas, 1935)	192, fig. 8	*Buliminopsis* (*Buliminopsis*) *subdoliolum*	Badung, Hubei [Badong, Hubei Province]	4.5–5	11–12.5	12	
Pseudobuliminus	*Rudens*	PT	*rudens**	(Heude, 1888)	242	*Funiculus rudens*	Ta-li fou [Dali, Yunnan Province]	8	18	12	
Pseudobuliminus	*Secusanus*		*cerasinus**	(Gredler, 1892)	6 (421, figs. 5–6 in Gredler, 1984)	*Buliminopsis cerasinus*	Se cu san [Hubei Province]	9	30–38	8.5–10	
Pseudobuliminus	*Secusanus*		*ravia*	Yü et al. 1982	20, pl. 4, figs. 20–21		Xuancheng, Anhui	2.7-2.8	8.5-9.5	?	
Pseudobuliminus	*Secusanus*		*superbus*	(Moellendorff, 1888)	44	*Stenogyra superbus*	Heng-shan-hsien provinciae Hunan [Hengshan, Hunan Province]	11.5	40	9	
Stenogyropsis	NA	*Stenogyropsis*	*cocoa*	Páll-Gergely & Hunyadi, 2016	388, figs. 1A–B, 2A, 3, 4A–I		Wenxian, Gansu	4.6–5.3	22.6–24.9	12.75–13.25	
Stenogyropsis	NA	*Stenogyropsis*	*chorismenostoma*	Chen et al. 2022	3, fig. 2A–E		Mianyang, Sichuan Province	3.88	11.4	10.5–11	
Stenogyropsis	NA	*Stenogyropsis*	*potanini**	Moellendorff, 1899	94, pl. 8, fig. 9		Hsi-gu-tsheng	7.25–7.75	21–21.5	11.5	

Table 2. The GenBank registered sequences used in this study.

Sequence name	16S	ITS2
Bradybaena brevispira (H. Adams, 1870) SDNU.M5104.2	OR039869	OR061122
Bradybaena brevispira (H. Adams, 1870) SDNU.M5112.2	OR039870	OR061125
Camaena cicatricosa (O. F. Müller, 1774)	KU586483	KU958542
Cathaica pyrrhozona (R. A. Philippi, 1845) SDNU.0270.1.1	OR039838	OR061090
Cathaica pyrrhozona (R. A. Philippi, 1845) SDNU.0270.1.3	OR039871	OR061091
'*Euhadra*' *stictotaenia* Möllendorff, 1899 SDNU.M5406.2	OR039865	OR061118
'*Euhadra*' *stictotaenia* Möllendorff, 1899 SDNU.M5406.3	OR039868	OR061121
Pliocathaica buvigneri (Deshayes, 1874) SDNU.M8140.1	OR039861	OR061114
Pliocathaica buvigneri (Deshayes, 1874) SDNU.M8140.3	OR039862	OR061115
Pliocathaica gansuica (Möllendorff, 1899) SDNU.M5655.3	OR039864	OR061117
Pliocathaica pulveratricula (E. von Martens, 1882) SDNU.M8208.1	OR039874	OR061126
'*Pseudiberus*' *liuae* M. Wu, 2017 HBUMM6758	PP668891	PP725912
Pseudiberus tectumsinense (E. von Martens, 1874) SDNU.0195.01.03	MK775727	MK778464
Pseudobuliminus achatininus (Möllendorff, 1899) HBUMM06678	ON261758	ON261848
Pseudobuliminus beijingensis n. sp. SDNU.0397.2	PV470884	PV470864
Pseudobuliminus beijingensis n. sp. SDNU.0397.3	PV470883	PV470865
Pseudobuliminus buliminoides (Heude, 1882) SDNU.0421.1	PV470885	PV470866
Pseudobuliminus buliminus strigatus (Möllendorff, 1899) HBUMM5450.2	PP668799	PP725846
Pseudobuliminus certus (Zilch, 1938) Kameda.2953	NA	AB852974
Pseudobuliminus dongyiicus G. Zhang, 2024 SDNU.0324.1.2	PV470890	PV470861
Pseudobuliminus dongyiicus G. Zhang, 2024 SDNU.0333.1.2	PV470888	PV470862
Pseudobuliminus dongyiicus G. Zhang, 2024 SDNU.0333.1.3	PV470889	PV470863
Pseudobuliminus dongyiicus G. Zhang, 2024 SDNU.0364.1.2	PV470886	PV470859
Pseudobuliminus dongyiicus G. Zhang, 2024 SDNU.0364.1.3	PV470887	PV470860
Pseudobuliminus hirsutus (Möllendorff, 1899) HBUMM06676	ON261759	ON261849
Pseudobuliminus meiacoshimensis (Adams & Reeve, 1850) Kameda.3211	NA	AB852977
Pseudobuliminus piligerus (Möllendorff, 1899) HBUMM5412.2	PP668783	PP725838
Pseudobuliminus piligerus (Möllendorff, 1899) HBUMM54122	ON261760	ON261850
Pseudobuliminus subcylindricus (Möllendorff, 1899) HBUMM06720	ON261761	ON261851
Pseudobuliminus turrita (Gude, 1900) Hirano.H0780	NA	AB852980

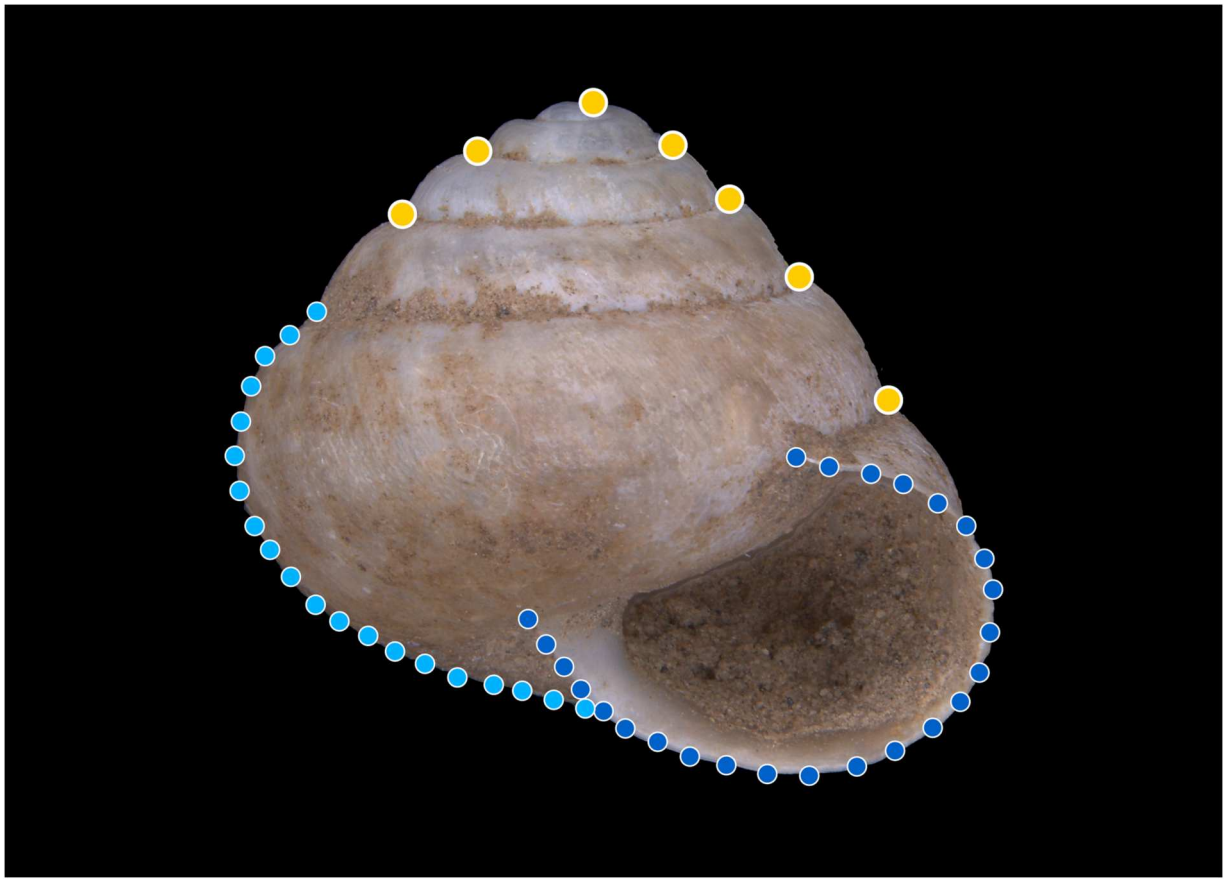

Figure 2. Shell diagram showing the plotting of landmarks (light yellow) and semi-landmarks (blue and dark blue) for morphometric geometric analyses.

Cameron (1979). In anatomical descriptions, 'proximal' indicates a direction towards the genital atrium, whereas 'distal' denotes the opposite direction. All newly collected specimens are deposited in the Zoological Collection of Shandong Normal University (SDNU).

Where known, the type localities of species were plotted on a distribution map (Figure 1) based on information gathered from the original descriptions and using QGIS 3.40.3 (Table 1).

We used morphometric analyses to compare shell shapes, based on our own shell photographs as well as photographs published by Hiseh et al. (2013), Qian and Zhou (2015), Wu (2015) and Páll-Gergely and Hunyadi (2016). Landmarks and semi-landmarks were collected from shells photographed in apertural view using tpsDig (Rohlf 2021). The landmark configuration is illustrated in Figure 2. We treated landmarks and semi-landmarks equally in the analysis. A total of 31 shells from 18 species and subspecies were included in the geometric morphometric analysis. We performed a Procrustes fit, generated a covariance matrix and conducted a principal component analysis (PCA). Group average shape variation was visualised using thin-plate spline deformation in MorphoJ version 1.08.02 (Klingenberg 2011). To test the a priori hypothesis that species occupying the same bioregion exhibit more similar shells than species from different bioregions, we classified the examined species into five groups based on their distribution: species from Sichuan, Chongqing, Gansu, Hubei, and Hunan represent the group from western China (PWC). Species from Beijing, Shandong, Anhui, and Jiangsu were assigned to the group from northern and eastern China (PNEC). Species from Taiwan and Yunnan were treated as distinct, namely the group from Taiwan (PT) and the group from Yunnan (PY). *Stenogyropsis* is considered another separate group.

Reproductive anatomy was studied with the use of a binocular microscope with an attached camera. Genomic DNA was extracted from foot muscle tissue using the Tiangen DP316 kit, following the manufacturer's protocol. Each 25 µL PCR reaction contained 12.5 µL of CWBio 2 × Es Taq MasterMix Dye, 9.5 µL of ddH_2O, 1 µL of template DNA, and 1 µL each of forward and reverse primers (10 µM). We performed PCR amplification on a SimpliAmp™ Thermal Cycler under the following conditions: an initial denaturation at 94°C for 2 min, followed by 30 cycles of 94°C for 30 s, 50°C for 30 s, and 72°C for 90 s, with a final extension at 72°C for 2 min. We examined amplicons on a 1% agarose gel to assess quality and fragment size before purification

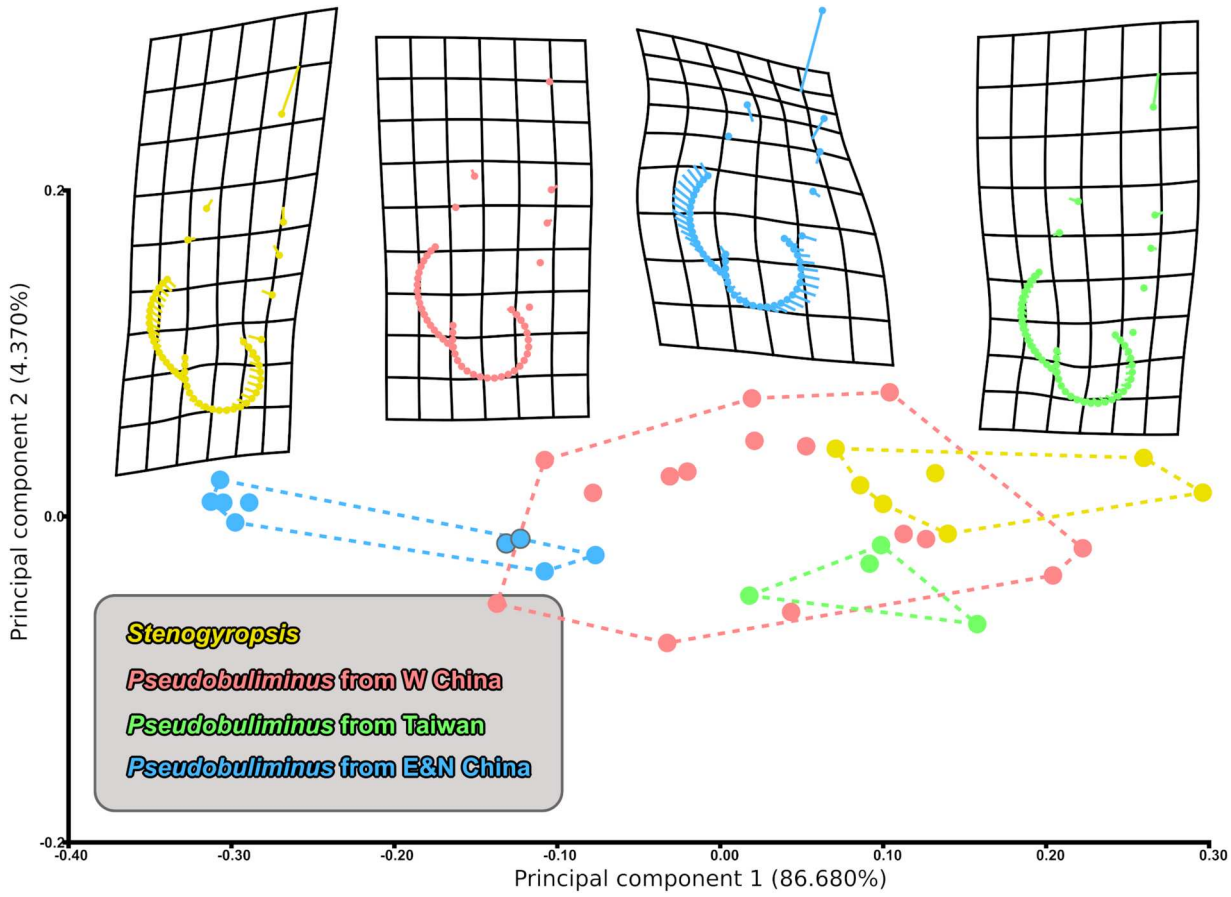

Figure 3. Scatter plots of principal component analysis and thin-plate spine of group average variation. W China is an abbreviation of Western China; E&N China is an abbreviation of Eastern and Northern China. The grey-outlined blue dots are *Pseudobuliminus beijingensis* Wang n. sp.

and sequencing. ITS2 was amplified and sequenced using the primers ITS-4 (Innis et al. 1990) and 18d (Hillis and Dixon 1991). The primers 16Sar and 16Sbr (Palumbi et al. 1991) were used for 16S amplification and sequencing.

We examined chromatograms and assembled them into contigs using STADEN (Staden et al. 2003). Sequences were aligned using MAFFT 7.526 (Katoh and Standley 2013) and then trimmed using trimAl v. 1.5.rev0 (Capella-Gutiérrez et al. 2009). After that, we concatenated sequences from the two subsets of 16S and ITS into a single sequence dataset using catsequences. We identified the best-fit substitution model using ModelTest-NG 0.1.7

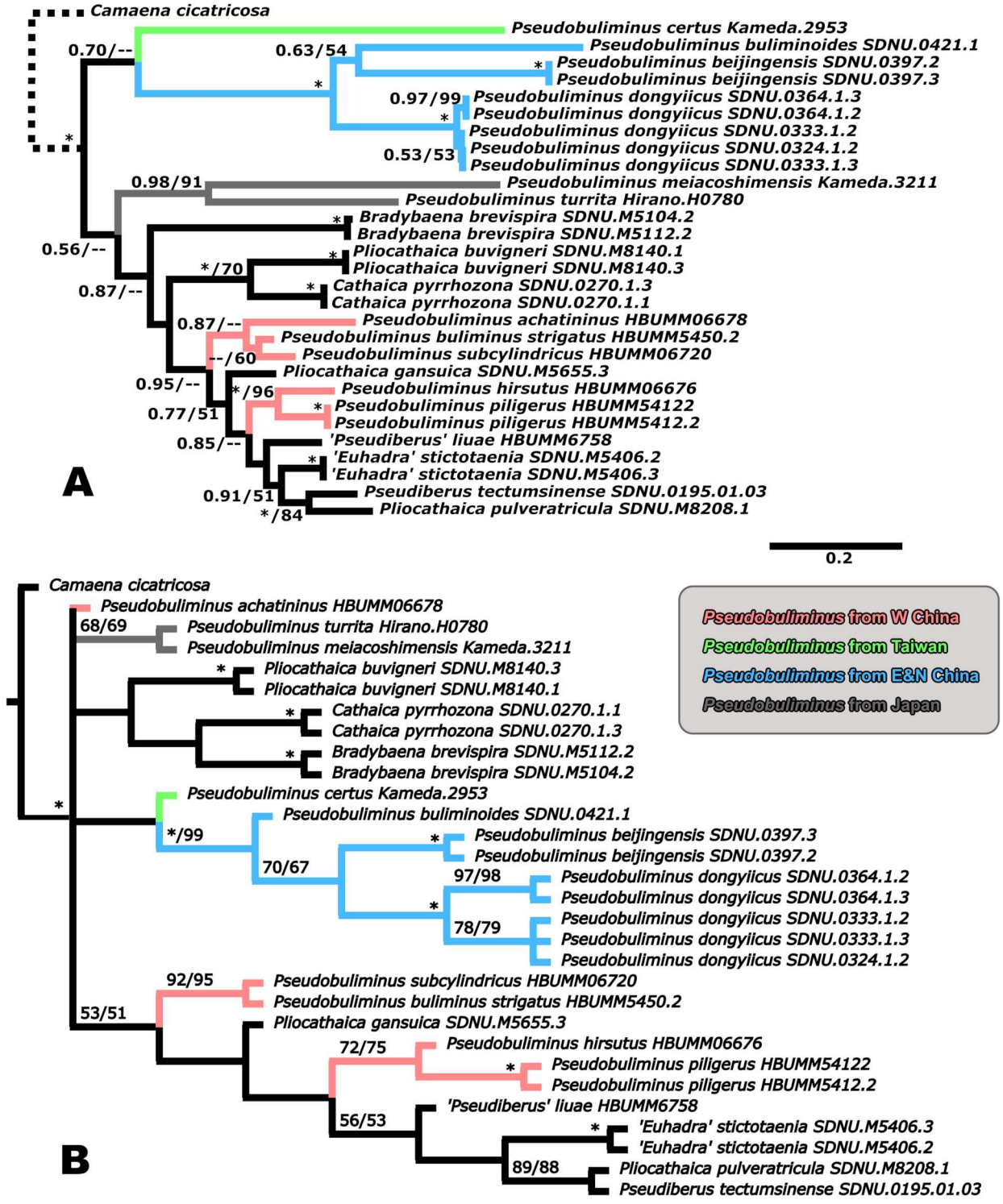

Figure 4. Phylogeny based on 16S and ITS genes. **A.** Bayesian inference phylogeny. Node support values are indicated as Bayesian posterior probabilities (PP) and maximum likelihood bootstrap values (BS); nodes with PP < 0.7 and BS < 50 are omitted. Dashed lines indicate shortened branch lengths. **B.** Equal-weighted strict consensus maximum parsimony tree. The consistency index (CI) is 0.524, the retention index (RI) is 0.686, and the tree length (TL) is 1226. A star symbol (*) indicates full support. W China denotes Western China, and E&N China represents Eastern and Northern China.

(Darriba et al. 2019) based on the Bayesian information criterion (BIC) for each data partition. We reconstructed a maximum likelihood (ML) phylogeny using RAxML-NG 1.2.2 (Kozlov et al. 2019). We used heuristic search to obtain the best ML tree, initiated with 10 random starting trees and 10 parsimony trees, followed by tree refinement using the subtree pruning and regrafting (SPR) algorithm. Bootstrap support values were estimated by performing 1000 replicates. A Bayesian inference (BI) phylogenetic analysis was performed using MrBayes v. 3.2.7 (Ronquist et al. 2012). We conducted two independent Markov chain Monte Carlo (MCMC) runs, each comprising four chains, which ran for 3,000,000 generations. The final consensus tree was generated after discarding 50% of all trees as burn-in. We reconstructed a maximum parsimony (MP) tree using TNT v. 1.6 (Goloboff and Morales 2023) under equal weighting. The most parsimonious trees (MPTs) were obtained through 1000 iterations of tree bisection and reconnection (TBR) searches. A strict consensus tree was subsequently constructed from the MPTs. We used the jackknife and symmetric resampling to evaluate group support. The GenBank accession codes for the sequences used in this study are listed in Table 2. All analyses were conducted in the BioArchLinux environment (Zhang et al., 2025b)

Results

Morphological analyses

Pseudobuliminus species from the northern and eastern China (PNEC) group include *Pseudobuliminus buliminoides* (Heude, 1882), *P. dongyiicus*, and *P. beijingensis* n. sp., all of which exhibit a similar genital anatomy, each possessing a flagellum and penial sheath.

The landmark-based PCA of the shell in aperture view captured 91% of the total shell variation (Figure 3). Principal component 1 (PC1) accounted for 86.7% of the variation while Principal component 2 (PC2) accounted for 4.4%. *Pseudobuliminus* species from western China (PWC) displayed a wide range of variation in the PCA scatter plots. Within the PSEC group, two distinct clusters emerged: one cluster contained a single species, *P. dongyiicus*. This cluster was clearly separated from another cluster comprising

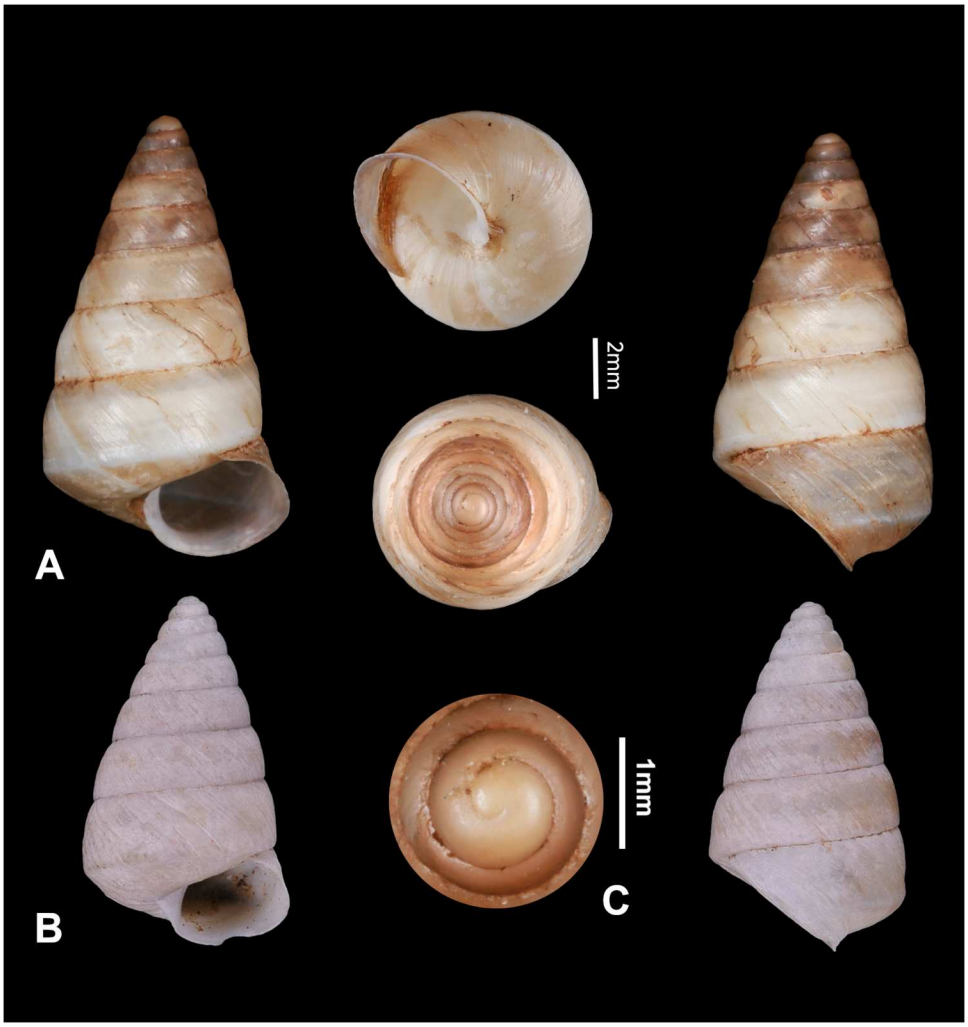

Figure 5. Shells of *Pseudobuliminus buliminoides*. **A** Four views of SDNU.Gas.042.01.01; **B T**wo views of paratype UNSM 472141; **C** Protoconch of SDNU.Gas.042.01.01.

P. beijingensis n. sp. and *P. buliminoides*, both of which are morphologically similar to some PWC members (including *P. conoidius* [Heude, 1890], *P. piligerus* [Möllendorff, 1899] and *P. buliminus buliminus* [Heude, 1882]). Nearly all specimens of *Pseudobuliminus* from Taiwan (PT) fell within the range of the PWC group, as did *Stenogyropsis potanini* (Möllendorff, 1899) from the *Stenogyropsis* group.

Molecular phylogenetic analyses

The HKY model with 16 gamma categories was selected as the most suitable substitution model and used separately for the 16S and ITS2 sequences. Phylogenetic analyses based on BI and ML show identical topologies, whereas the MP analysis shows a different topology. MP analysis reveals a polytomy of Bradybaeninae, whereas both the BI and ML analyses indicate that Bradybaeninae is composed of two distinct sister groups rather than a polytomy (Figure 4). Although all species are recovered as monophyletic, support values at the genus level are generally low, as indicated by Bayesian posterior probabilities (PP) and ML bootstrap (BS) values. These statistically poorly supported relationships are consistently resolved as polytomies in the equal-weighting MP phylogeny.

The phylogeny shows that *Pseudobuliminus* and *Pliocathaica* Andraea, 1900 are polyphyletic. The phylogeny supports our hypothesis that the PNEC group forms a clade, which is strongly supported across all

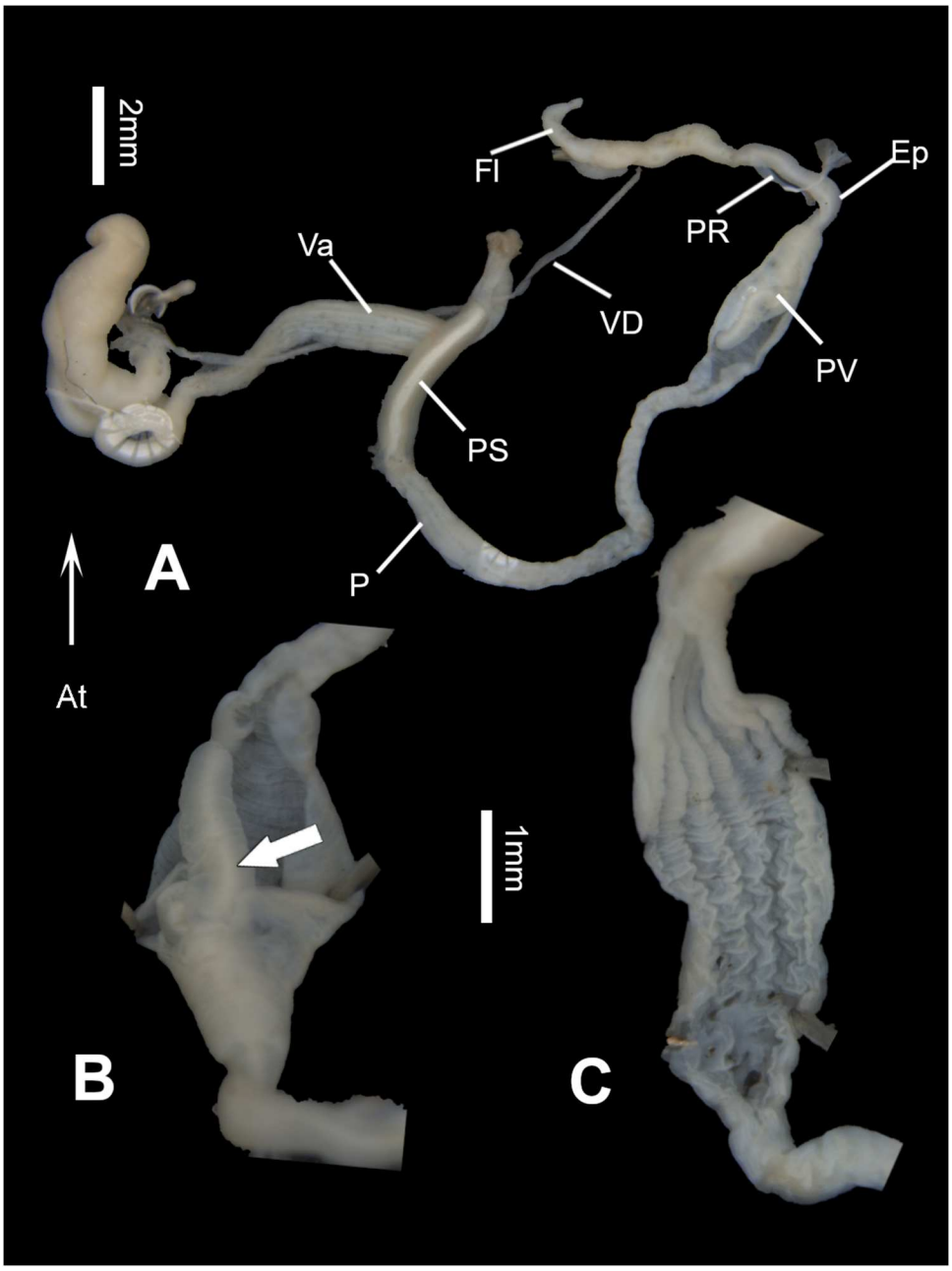

Figure 6. Genital system of *Pseudobuliminus buliminoides* (Heude, 1882). **A** full view of genital system of SDNU.Gas.042.01.01; **B** details of penial verge; **C** details of inner penial pilasters. At – atrium; AG – albumen gland; Fl – flagellum; P – penis; PR – penial retractor muscle; PS – penis sheath; PV – penial verge; Va – vagina.

three analyses (PP = 1.00; BS = 99; jackknifing, JK = 98, symmetric resampling, SR = 97). Within this clade, the relationship between *P. beijingensis* n. sp. and *P. dongyiicus* has weak support in the MP analysis (JK = 70, SR = 67), whereas BI and ML analyses inferred *P. buliminoides* as the sister group to *P. beijingensis* n. sp. with weak support (PP = 0.63; BS = 54). Additionally, *Pseudobuliminus certus* Zilch, 1949 (a species from Taiwan) is weakly supported as the sister group of the PNEC clade (PP = 0.70).

The PWC group is not monophyletic. *Pseudobuliminus subcylindricus* (Möllendorff, 1899) and *P. buliminus strigatus* (Möllendorff, 1899) are sister taxa with strong support in both BI (PP = 0.87) and MP (JK = 92, SR = 95). The relationship between *P. hirsutus* and *P. piligerus* is also well supported by BI and ML (PP = 1.00; BS = 96) but only moderately by MP (JK = 72, SR = 75).

Additionally, we found that the Japanese species *Pseudobuliminus turrita* (Gude, 1900) and *P. meiacoshimensis* (Adams & Reeve, 1850) exhibit a well-supported sister-group relationship in BI and ML (PP = 0.98; BS = 91), although support was weaker in the MP analysis (JK = 68, SR = 69).

Discussion

The morphometric results highlight the fact that species with similar shell shapes from different geographic areas are not necessarily closely related. Hence, shell shape alone is not a dependable indicator for reliable subgeneric classification (Zhang and Wade 2023). Traditionally, some malacologists have assumed that the limited mobility of land snails implies that populations from different regions should represent distinct species or even genera (Zhang et al. 2024). The *Pseudobuliminus* species from northern and eastern China all share several morphological characteristics, such as lack of a dart sac, a smooth protoconch, a conical shell

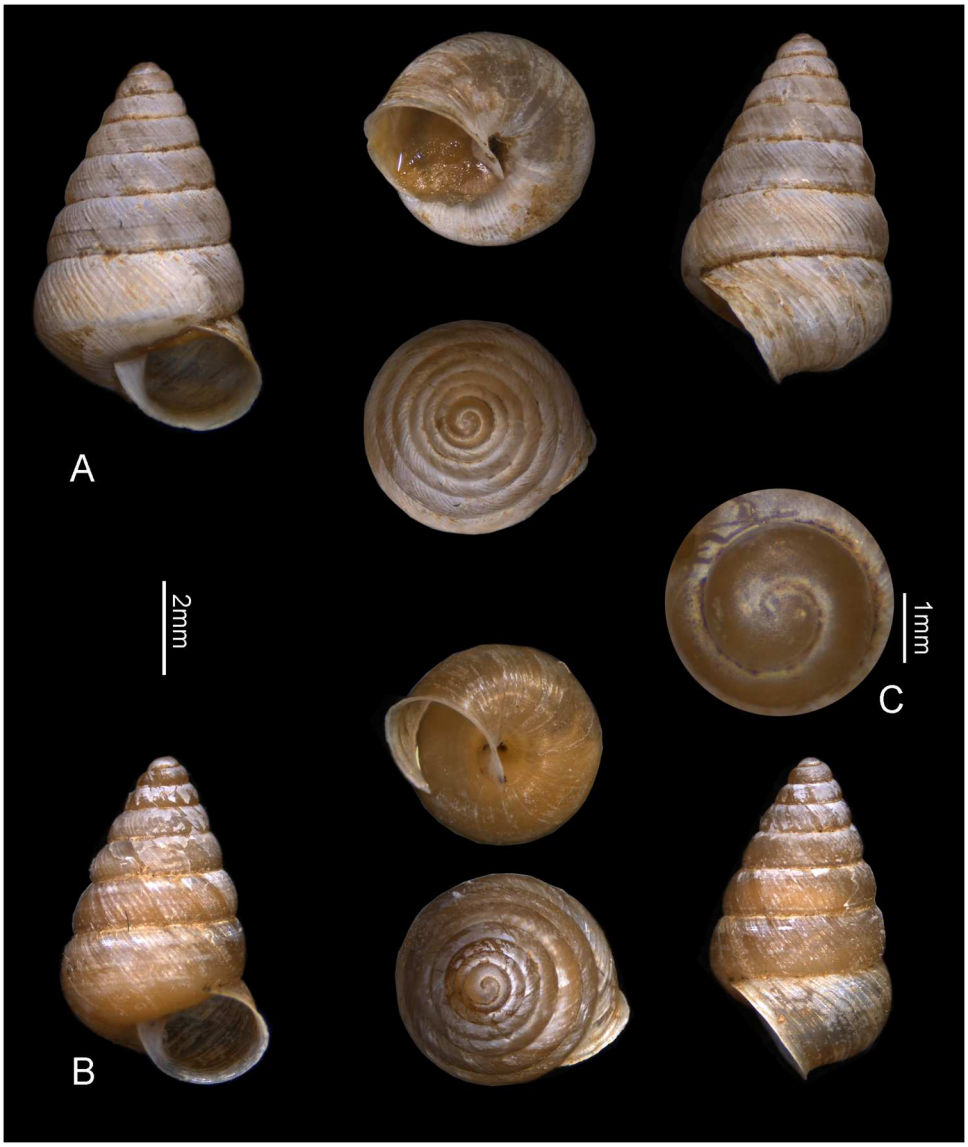

Figure 7. Shells of *Pseudobuliminus beijingensis* n. sp. type specimens. **A** Aperture, umbilicus and apex views of holotype. **B** Aperture, umbilicus and apex views of paratype SDNU.Gas.0397.01.02. **C** View of protoconch, smooth.

shape, and a flagellum. We consider these shared characteristics synapomorphies, which establish the monophyly of the PNEC group. One the other hand, we also found that species with a similar shell shape may not be closely related even when they inhabit the same general region, as in the case of *Pseudobuliminus piligerus*, *P. buliminus*, and *P. beijingensis* n. sp. According to the molecular phylogeny they belong to three different lineages, even though both *P. piligerus* and *P. buliminus* are from western China. These findings underscore the need for comprehensive documentation of morphological characters and further research to identify reliable synapomorphies, rather than relying on a single morphological trait. As Nixon and Carpenter (2002) noted, homoplasy is mistakenly interpreted as homology; therefore, systematics must be revisited with comprehensive evidence to test characters' homology.

Systematic taxonomy

Family Camaenidae Pilsbry, 1895

Subfamily Bradybaeninae Pilsbry, 1934

***Pseudobuliminus* Gredler, 1886**

Type species: *Helix pseudobuliminus* Heude, 1882, by absolute tautonymy.

***Pseudobuliminus buliminoides* (Heude, 1882)**

Helix buliminoides Heude 1882: 47, pl. 17, figs. 6, 30; Tryon 1887: 52, figs. 18–19; Tryon 1888 in Tryon & Pilsbry, 1888–1889: 31.

Buliminus buliminoides var. *tropidophorus* Ancey 1885: 121.

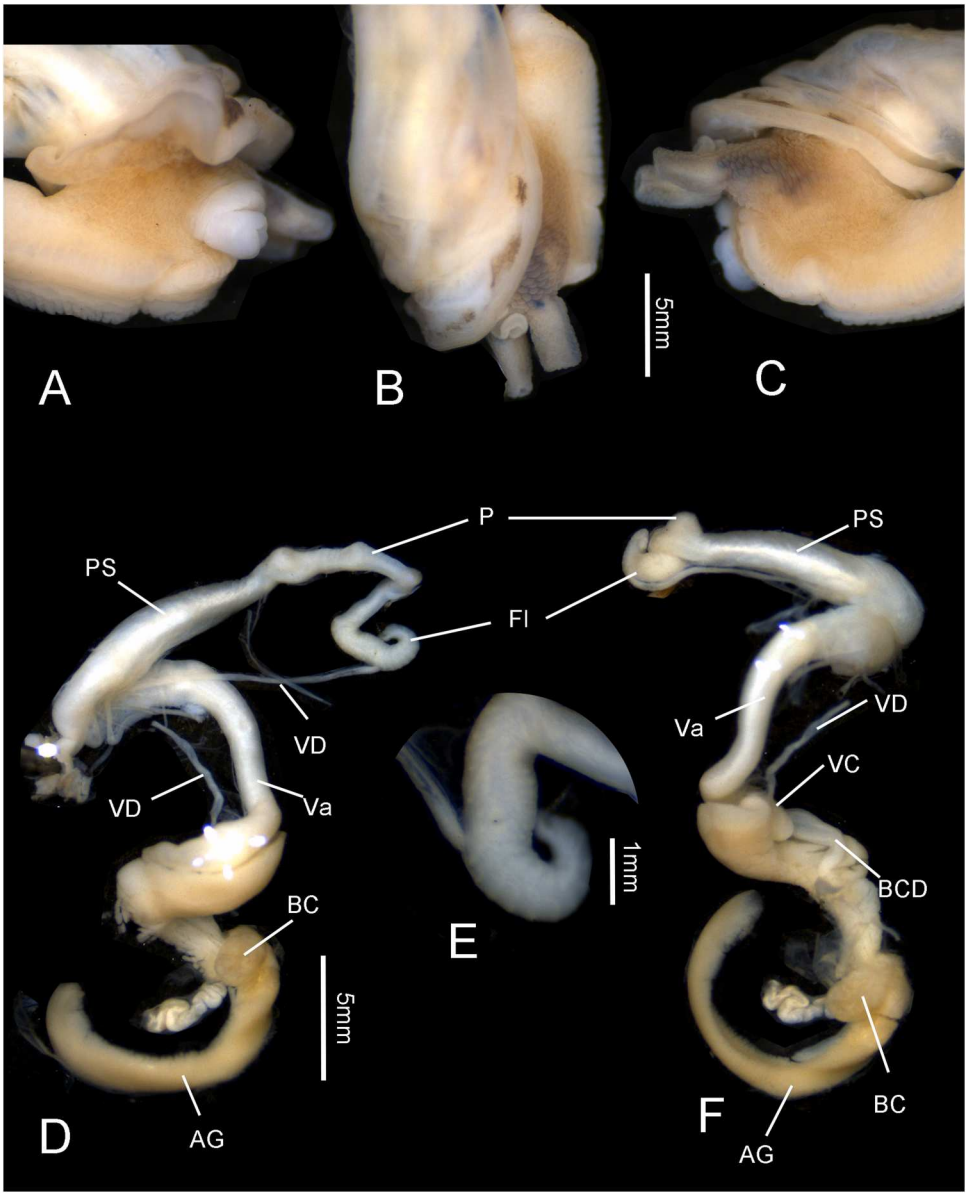

Figure 8. Animal and genital views of *Pseudobuliminus beijingensis* n. sp. **A** – **C** Head wart between ommatophores present and on both sides of mantle edge, leaf-shaped appendage absent, paratype SDNU.Gas.0397.01.02. **D, F** Both sides of genitals of holotype. **E** Detail view of flagellum. AG – albumen gland; BC – bursa copulatrix; BCD – bursa copulatrix duct; Fl – flagellum; P – penis; PS – penis sheath; VC – vaginal chamber; VD – vas deferens.

Buliminopsis (*Buliminopsis*) *buliminoides* – Pilsbry 1894: 171; Gude 1902: 5.

Buliminopsis buliminoides. – Yen 1939: 444: 151, pl. 15, fig. 49; Taki 1940: 118.

Pseudobuliminus (*Pseudobuliminus*) *buliminoides*. – Richardson 1983: 91.

Pseudobuliminus (*Pseudobuliminus*) *buliminoides*. – Zilch 1960: 639–640; Zilch 1968: 176.

Pseudobuliminus buliminoides. – Wu 2015: 216–271, fig. 4.

Figures 1–6, Tables 1–2.

Material examined

Paratype, UNSM (United States National Museum) 472141, Nanjing City; other material, SDNU.Gas.042.01.01–03, 30 Sep 2023, Mufu Mountain, Nanjing City, Jiangsu Province, China, coll. J. Du, dissected.

Diagnosis

Shell conoidal and smooth; periphery keeled. Penial sheath short, penial pilasters present. Penial verge tube-shaped.

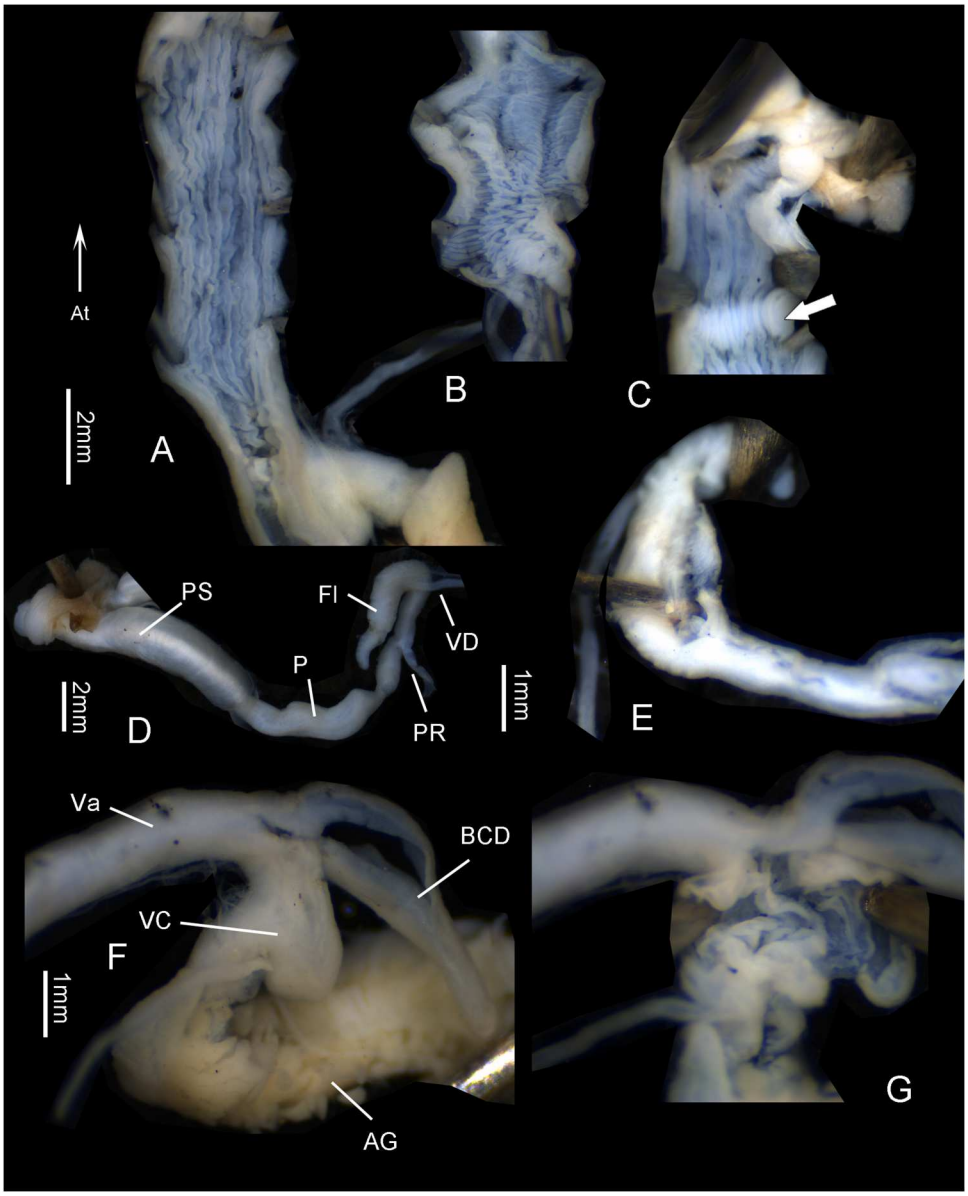

Figure 9. Detail view of genitals. **A** Pilasters of vagina, arrow shows the direction of atrium. **B** Pilasters of penis. **C** Pilasters of atrium, arrow shows the thickening position. **D** Penial sheath present. **E** Flagellum inner view. **F** Surface of vaginal chamber, pilasters of bursa copulatrix duct absent. **G** Pilasters of vaginal chamber. At – atrium; AG – albumen gland; BCD – bursa copulatrix duct; Fl – flagellum; P – penis; PR – penial retractor muscle; PS – penis sheath; PV – penial verge; Va – vagina; VC – vaginal chamber.

Description

Shell (Figure 5) conoidal, thin, dextral, dull in colour, without spiral bands. Whorls convex, separated by deep suture, without super- or suprasutural depression. Body whorl keeled. Umbilicus narrowly open. Columellar lip dilated, partially covering umbilicus. Protoconch smooth. Sculpture smooth with distinct axial growth lines. Shell not perforated, not accompanied by irregular thickenings. Aperture lunate. Ring-like thickening within aperture absent. Peristome thin, not continuous. Callus indistinct.

Genitalia (Figure 6). Penial sheath present, short, covering less than half of penis (Figure 6A). Penis thin, long. Epiphallic flagellum present. Seven penial pilasters present extending from near end of penial sheath to near atrium, regularly interlaced forming

Figure 10. Photographs of live specimens of *Pseudobuliminus beijingensis* n. sp and its habitat. **A** The mountain habitat where the species is found. **B**–**C** Living individuals on the tree. **D** The mating. **E** The probable host.

four or five z-shaped pilasters (Figure 6C). Penial verge (= epiphallus papilla) present, tube-shaped (Figure 6B). Epiphallus not thicker than penis. Vas deferens thin. Dart sac and related organs (Figure 2A).

Remarks

This species is closely related to *P. beijingensis* n. sp. and *P. dongyiicus* in the phylogeny. All members of this lineage lack a dart sac and related stimulatory structures (Figure 4). This species can be distinguished from two other species by having a more conical shell (Figure 3), a keel on body whorl (Figure 5), and a tube-shaped penial verge (Figure 6B).

***Pseudobuliminus beijingensis* Wang n. sp.**
Figures 1–4, 7–10, Tables 1–2.

Type material

Holotype, SDNU.Gas.0397.01.01, 2 May, 2019, Shangfang Mountain, Beijing, China, 200 m a.s.l., coll. X.-X. Wang, dissected; 9 paratypes, SDNU.Gas.0397.01.02–06, other information same as holotype, dissected, SDNU.Gas.0410.01.01–05, 13 Sep, 2019, Shangfang Mountain, Beijing, China, 115.8 N, 39.7° E, 189 m a.s.l., coll. X.-X. Wang.

Measurements

Holotype SDNU.Gas.0397.01.01, width 4.7 mm, height 8.0 mm. Paratypes SDNU.Gas.0397.01.02, width 4.4 mm, height 7.9 mm.

Diagnosis

Shell conoidal and smooth, body whorl without keel; penial sheath covers nearly half of the penis, penial verge absent, vaginal chamber present.

Description

Shell (Figure 7) conoidal, thin, dextral, dull without spiral bands. Whorls convex, separated by deep suture, without super- or suprasutural depression. Body whorl without keel. Umbilicus narrowly open. Columellar lip dilated, partially covering umbilicus. Protoconch smooth. Shell surface ribless. Growth lines distinct. Shell not perforated, not accompanied with irregular thickenings. Teleoconch without other microscopic structure. Adult shell smooth, with bottom convex. Aperture lunate. Ring-like thickening within aperture absent. Peristome thin, not continuous. Callus indistinct.

Animal (Figure 8A–C). Head wart between ommatophores present. On both sides of mantle edge, leaf-shaped appendage absent. Foot creamy white, head grey-brown.

Genitals (Figure 8D–F, 9). Penial sheath present, short, covering half of penis, with three narrow regions (Figure 9D). Penis thick, short. Epiphallus flagellum present, short (Figure 8E). Penial pilasters differentiated near the end of penial sheath, three near atrium, interlaced regularly and forming four or five z-shaped pilasters (Figure 9B). Penial verge (= epiphallus papilla) absent (Figure 9B). Epiphallus not thicker than penis. Vas deference undifferentiated, thin. Dart sac and related organs absent (Figure 8D, 8F). Boundary of atrium and vagina ticked (Figure 9C). Four parallel atrium pilasters present in the atrium, forming 11 parallel and wavy vaginal pilasters (Figure 9A). Bursa copulatrix duct without pilasters, base not expanded (Figure 9F). Vaginal chamber present, with three or four inner pilasters (Figure 9G).

Ecology

Arboreal (Figure 10B–C) or terrestrial (in leaf litter). Mating pattern is simple tube connected (Figure 10D). Found under a tree, *Pteroceltis tatarinowii* Maxim, 1873 (Figure 10E).

Distribution

Only known from the type locality, Bejing.

Etymology

The name is after Beijing, capital of the P.R. China.

Remarks

This species resembles *Pseudobuliminus piligerus*, *P. buliminus buliminus* and *P. conoidius* from western China. *P. piligerus*, *P. buliminus* and *P. beijingensis* n. sp. do not cluster together in molecular phylogeny, highlighting the homoplasy in shell shapes.

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Disclosure statement

No potential conflict of interest was reported by the author(s).

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