ISSN 2755-3531

Vol. 45, no. 1 **Journal of Conchology** 4 April 2024

Published by the Conchological Society of Great Britain and Ireland, established 1874

Systematics and biogeography of the genera *Pseudiberus* Ancey, 1887 and *Platypetasus* Pilsbry, 1895 (Stylommatophora: Camaenidae), with the description of *Pseudiberus shanheicus* n. sp.

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Abstract. Phylogenetic analyses based on morphological character and molecular data indicate that *Platypetasus* Pilsbry, 1895 should not be synonymized with *Pseudiberus* Ancey, 1887. These genera occur in different geographical areas; *Pseudiberus* species are distributed in the Qinling, Taihang, Yimeng, and Taishan mountains, and *Platypetasus* species occur in the Daxueshan, Qionglaishan, Minshan, and Dabashan mountains. Here we describe a new species, *Pseudiberus shanheicus* n. sp., from Henan Province, China. Its shell is distinguished by its ribless surface and hollow peripheral keel. The phylogenetic relationship among *Pseudiberus sensu stricto* is discussed, based on an analysis of mitochondrial DNA (16S rRNA) and nuclear DNA (5.8S rRNA and ITS2), as well as shell morphology.

Key words. Bradybaeninae, China, cladistics, molecular phylogeny, Henan Province, new species, phylogenetics, Taihang Mountains, Taishan Mountains, Yimeng Mountains

ZooBank identifier. urn:lsid:zoobank.org:pub:473B366A-9073-43A1-9DE0-2C206BD4DA69

DOI. https://doi.org/10.61733/jconch/4510

Introduction

The modern genus *Pseudiberus* Ancey, 1887 presently contains nearly 30 species and subspecies and is mainly distributed in northern and north-western China (Wu 2002; Wu & Qi 2006; Ramakrishna & Dey 2010; Wu & Asami 2017; Zhang *et al.* 2021). Only two species occur outside of China in Central and South Asia (Wu & Qi 2006): *P. plectotropis* (E. von Martens, 1864) occurs in Kyrgyzstan and southern Kazakhstan, but it was transferred to *Fruticicola* Held, 1838 by Sysoev & Schileyko (2009), and *P. chitralensis* (Odhner, 1963) occurs in Pakistan (Odhner 1963). The type species of *Pseudiberus* Ancey, 1887 is *Helix tectumsinense* E. von Martens, 1873 from Shandong Province, China.

Malacologists have different taxonomic opinions of this widely distributed genus (Table 1), and there has been little focus on the phylogenetic relationships between *Pseudiberus* species (Zhang *et al.* 2021). Gude (1902) considered *Pseudiberus* to be a subgenus of *Cathaica* Möllendorff, 1884, while treating *Platypetasus* Pilsbry, 1895 as an independent genus. Theile (1931) endorsed Gude's (1902) taxonomic classification of *Pseudiberus* and included *Platypetasus* as a section within the nominotypical subgenus of *Pseudiberus*. Zilch (1959–1960), Richardson (1983), and Chen & Zhang (2004) considered *Pseudiberus* as genus instead of subgenus consisting of two subgenera, the nominotypical subgenus and *Platypetasus* Pilsbry, 1895. Schileyko (2004) and Zhang *et al.* (2024) classified *Platypetasus* as a separate genus, and Wu & Qi (2006) considered it to be a synonym based on the number of whorls, shell height, and shell width. Here, we use *Pseudiberus sensu lato* to refer to *Platypetasus* and *Pseudiberus* combined.

The distribution of species of *Pseudiberus sensu lato* is shown in Figure 1, which includes both type localities (Fig. 1A) and other occurrence records (Fig. 1B). *Pseud-*

Table 1. Historical taxonomy of *Pseudiberus sensu lato*. Subgenera are in parentheses.

Reference	*Pseudiberus*	*Platypetasus*
Gude 1902	*Cathaica* (*Pseudiberus*)	*Platypetasus*
Thiele 1931	*Cathaica* (*Pseudiberus*) section *Pseudiberus*	*Cathaica* (*Pseudiberus*) section *Platypetasus*
Zilch 1959–1960; Richardson 1983; Chen & Zhang 2004	*Pseudiberus* (*Pseudiberus*)	*Pseudiberus* (*Platypetasus*)
Schileyko 2004; Zhang *et al.* 2024	*Pseudiberus*	*Platypetasus*
Wu & Qi 2006	*Pseudiberus*	Synonymized with *Pseudiberus*

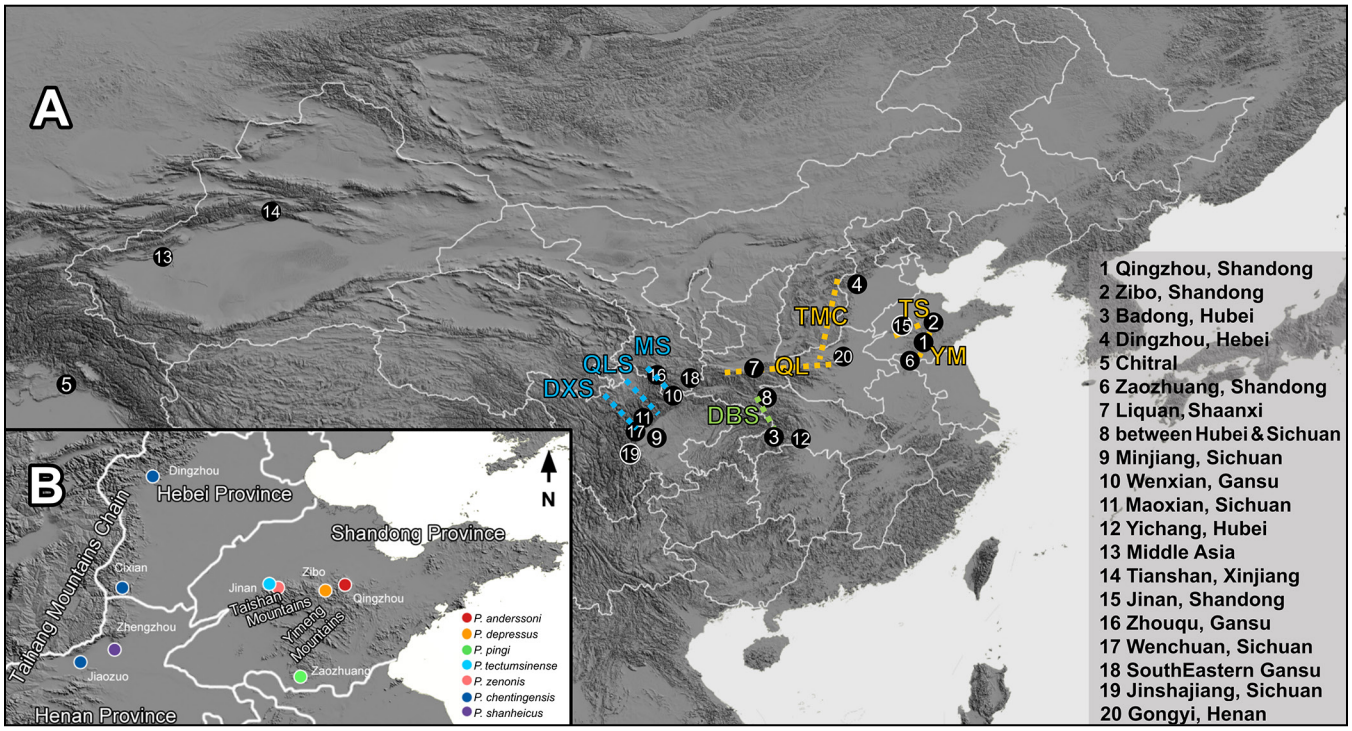

Figure 1. Distribution of *Pseudiberus sensu lato* in China. **A**, type localities of *Pseudiberus sensu lato* species. DXS = Daxueshan, QLS = Qionglaishan, MS = Minshan, DBS = Dabashan, QL = Qinling, TMC = Taihang Mountain Chain, TS = Taishan, YM = Yimeng. 1: Qingzhou, Weifang City, Shandong Province, type locality of *Pseudiberus anderssoni* (Odhner, 1925); 2: Zibo City, Shandong Province, type locality of *Ps. depressus* (Yen, 1935); 3: Badong City, Hubei Province type locality of *Platypetasus innominatus duplicatus* Möllendorff, 1899; 4: Dingzhou, Baoding City, Hebei Province, type locality of *Ps. chentingensis chentingensis* (Yen, 1935) and *Ps. chentingensis latispira* (Yen, 1935); 5: Chitral, type locality of *Platypetasus?* [not *Pseudiberus sensu lato*] *chitralensis* (Odhner, 1963); 6: Zaozhuang City, Shandong Province, type locality of *Ps. pingi* (Zhang & Wu, 2021); 7: Liquan, Xianyang City, Shaanxi Province, type locality of *Ps. futtereri* (Andreae, 1904); 8: Boarder of Hubei and Sichuan [now should Chongqing]: *Pl. castanopsis* Möllendorff, 1899; 9: Minjiang, Sichuan Province, type locality of *Pl. lancasteri* (Gude, 1919); 10: Wenxian, Gansu Province, type locality of *Platypetasus?* [not *Pseudiberus sensu lato*] *liuae* (Wu, 2017); 11: Maoxian, Ngawa Tibetan and Qiang Autonomous Prefecture, Sichuan Province, type locality of *Pl. maoensis* (Wu, 2002); 12: Yichang City, Hubei Province, type locality of *Pl. mariellus* (Adams, 1870); 13: Center Asia (prob Kargalik), type locality of *Platypetasus?* [= *Ponsadenia?*, not *Pseudiberus sensu lato*] *anisopleurus* (Ancey, 1897); 14: Tianshan, type locality of *Platypetasus?* [= *Ponsadenia?*, not *Pseudiberus sensu lato*] *plectotropis* (E. von Martens, 1864); 15: Jinan City, type locality of *Ps. tectumsinense* (E. von Martens, 1873) and *Ps. zenonis* (Gredler, 1882); 16: Zhouqu, Gannan Tibetan Autonomous Prefecture, Gansu Province: *Pl. encaustochilus* Möllendorff, 1899, *Pl. causius* Möllendorff, 1899; 17: Wenchuan, Ngawa Tibetan and Qiang Autonomous Prefecture, Sichuan Province type locality of *Pl. trochomorphus trochomorphus* Möllendorff, 1899, *Pl. trochomorpha wentschuanensis* (Blume, 1925); 18: Southeast Gansu, type locality of *Pl. wardi* (Preston, 1912), Gansu to Sichuan: *Pl. strophostomus* Möllendorff, 1899, Pei-shui-ho, Gaunsu Province: *Pl. obrutschewi* Sturany, 1899; 19 Jinshajiang, Sichuan Province: *Pl. innominatus innominatus* (Heude, 1885); 20: Gongyi, Zhengzhou City, Henan Province, type locality of *Ps. shanheicus* n. sp. **B**, inset map shows the distribution of *Pseudiberus sensu stricto,* besides *P. futtereri*.

iberus sensu lato is widely distributed and the species fall into two main groups (Zhang *et al.* 2021). West of the Taihang Mountain Chain (TMC), *Pseudiberus sensu lato* occurs in two regions; one region is the Dabashan Mountains (Adams 1870; Heude 1885; Möllendorff 1899), and the other is in the Minshan, Qionglaishan, and Daxueshan mountains (Möllendorff 1899; Preston 1912; Gude 1919; Blume 1925; Wu 2002; Wu & Asami 2017). The type species of *Platypetasus* occurs in this second region. *Pseudiberus sensu lato* species from east of the TMC (Zhang *et al.* 2021) are distributed in the Qinling, Taihangshan, Taishan, and Yimeng mountains (Provinces of Shandong, Henan, Hebei, and Shaanxi). Although the Qinling Mountains are west of the TMC, *Pseudiberus* found in the Qinling Mountains were also classified as belonging to the eastern group of *Pseudiberus* (Zhang *et al.* 2021). In Shandong Province, *Pseudiberus* species inhabit the Taishan and Yimeng mountains (Martens 1873; Gredler 1882a, 1882b; Odhner 1925; Yen 1935), and in Hebei and Henan provinces, they inhabit the TMC (Yen 1935; Chen & Zhang 2000; Wu & Qi 2006). Only one species, *Pseudiberus futtereri* (Andreae, 1904), is known from Shaanxi Province, where it lives in the Qinling Mountains (Andreae 1904). All occurrences, including the type locality of *Ps. tectumsinense*, the type species of *Pseudiberus*, are in the Taishan Mountains. Therefore, we consider *Pseudiberus* from east of the TMC and from the Qinling Mountains to belong to *Pseudiberus sensu stricto* and those west of the TMC (but excluding the Qinling Mountains) to belong to *Platypetasus*.

These two genera of *Pseudiberus sensu lato* species show differences in their genitalia. *Platypetasus* usually have an accessory sac at the base of the dart sac with two mucous glands inserted into it, and the penial pilasters are parallel instead of forming a network (Wu & Asami 2017). In *Pseudiberus sensu stricto*, subspecies of *Ps. tectumsinense* (E. von Martens, 1873) and *Ps. chentingensis* (Yen, 1935) have no accessory sac at the base of the dart sac but two proximal accessory sacs inserted near the atrium, and the penial pilasters are interlaced regularly and form a network (Wu 2004; Zhang *et al*. 2021).

Wu & Qi (2006) used only similarities of values of shells measurements, and no cladistic methods, for their synonymisation of *Platypetasus* with *Pseudiberus*. Here we tested the hypothesis that *Pseudiberus* and *Platypetasus* are synonyms (Wu & Qi 2006), and we propose a new hypotheis based on conchological-based and molecular-based phylogeny of *Pseudiberus sensu lato*. We also describe a new *Pseudiberus* species based on geometric morphometric methods and phylogenetics.

Materials and methods

Live adult specimens of the new *Pseudiberus* species were collected in Henan Province and relaxed in water for about 6 h and then preserved in 75% ethanol following the methods of Zhang & Xie (2021). Photographs of shells and genitalia were taken with a Canon EOS 650D camera with attached macro lens or Leica S6D stereomicroscope. Shells and genitalia were measured to the nearest 0.1 mm with vernier callipers or from photographs. Whorls were counted to the nearest ⅛ whorl, as described by Kerney & Cameron (1979). The measurements of soft tissue and descriptions of body colour were made on ethanol-fixed specimens.

Geometric morphometrics. We recorded semi-landmarks and landmarks of the shell in apertural view using tps series software, including tpsUtil (Rohlf 2004a) and tpsDig (Rohlf 2004b). MorphoJ v. 1.07a (Klingenberg 2011) was used for performing the principal component and canonical variate analyses. The landmarks and semi-landmarks used are as follows: LM1, the columellar insertion; LM2, the right edge of the keel on the penultimate whorl; LM3, the right edge of carina on the whorl preceding the penultimate whorl; LM4, shell apex (embryonic shell); LM5, the left edge of the carina on the whorl preceding the penultimate whorl; LM6, the left edge of the carina on the last whorl; LM7, the intersection of the peristome and the contour of the body whorl; LM8, the edge of the carina on the body whorl/peristome; LMs 9–36, semi-landmarks on the outline between LM6 and LM7 by length; LMs 37–72, semi-landmarks on the contour of the aperture by length from LM1 via LM 8 to LM2 (Fig. 2C).

Discrete numeric matrix preparation

Seventeen shell characters (Table 2) are listed below, and coding numbers begin at zero following the custom of TNT (Goloboff & Morales 2023). The terminology of shell characters mainly comes from Wu (2002), Zhang & Xie (2021), Zhang *et al.* (2021), and Zhang & Wade (2023). A single geographical character is also included as character 16.

The characters used in this matrix were obtained from Wu (2002, 2015), Zhang *et al.* (2021), and this study (Table 3). The size and shape of the shells of *Platypetasus liuae* (Wu, 2017) and *Pl. strophostomus* Möllendorff, 1899 are distinct from other *Pseudiberus sensu lato* species, and so the matrix (Table 1) does not include these two species. *Pseudiberus plectotropis* (E. von Martens, 1864) was used as the outgroup in the matrix, as this Central Asian species has been transferred to *Fruticicola* Held, 1838 (Sysoev & Schileyko 2009).

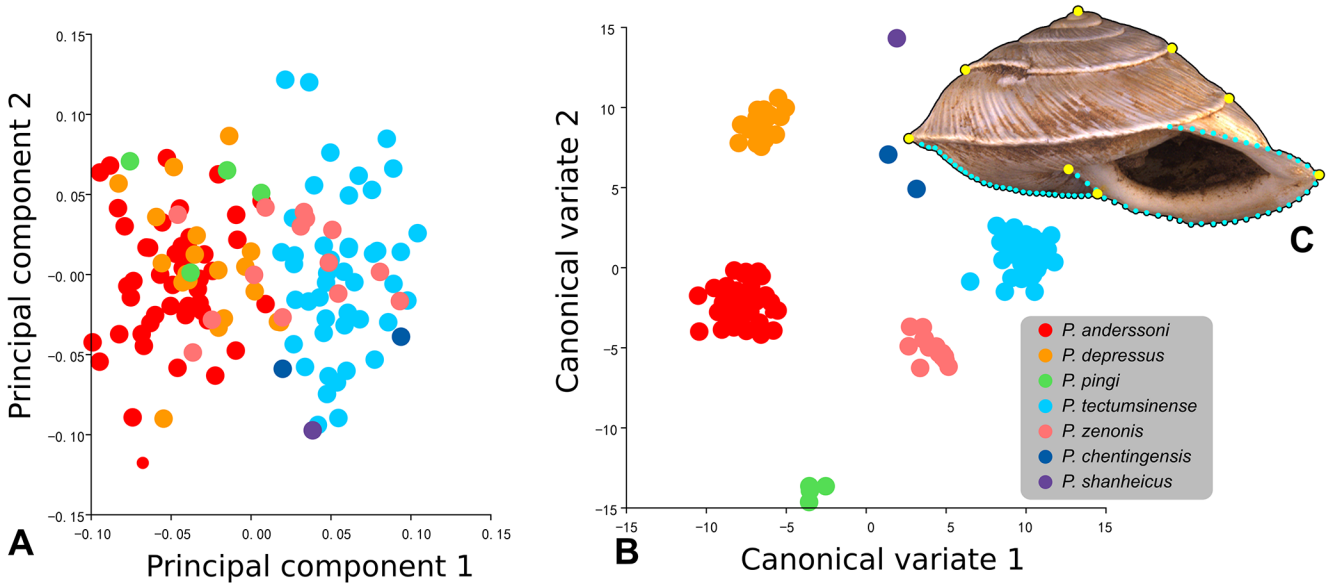

Figure 2. Scatter plots of (**A**) principal component analysis and (**B**) canonical variate analysis scores based on the data from apertural views of the *Pseudiberus* s.str. species from Taihang Mountains Chain, Yimeng and Taishan Mountains. PC1 explains 38.057% and PC2 explains 25.052% of the total shape variation of shells. CV1 explains 48.749% and CV2 explains 48.749% of the total shape variation of shells. **C**, the shell shows the landmarks (light yellow) and semi-landmarks (turquoise) plotting for morphometric geometric analyses.

Table 2. Characters and character states used in phylogeny based on morphological characters.

No.	Character	Character state
0	Shell shape	depressed, diameter c. 2× height (0); extremely depressed, diameter >2× height (1)
1	Shell whorl suture	covered by edge formed by adjacent upper whorl (0); superficial (1)
2	Umbilicus	broad, umbilicus diameter/shell diameter is greater than 1/7 (0); moderately wide, umbilicus diameter/shell diameter is smaller than 1/7 (1)
3	Ribs on shell surface	absent (0); present (1)
4	Adult shell surface	smooth (0); rough with periostracum derivatives (1)
5	Periphery shape	sawtoothed (0); smooth (1)
6	Carinate hollow or not	hollow (0); not hollow (1)
7	Aperture shape	strongly elliptical (0); rectangular (1)
8	Ring-like thickening within aperture	present (0); absent (1)
9	Aperture reflexed or not	reflexed on lower aperture (0); not reflexed (1)
10	Aperture lip double or single	single (0); double (1)
11	Aperture toothed or not	toothless (0); toothed (1)
12	Aperture expanded or not	expanded (0); unexpanded (1)
13	Peristome continuous or not/callus distinct or not	continuous/distinct (0); not continuous/indistinct (1)
14	Base with several obscure spiral bands or not	surface without spiral band(s) (0); with one thin continuous band (1)
15	Upper surface with several obscure spiral bands or not	without continuous band(s) (0); with one thin continuous band (1)
16	Distribution	Qinling, Taihangshan, Tiashan, and Yimeng mountains (0); Dabashan Mountains (1); Minshan, Qionglaishan, and Daxueshan mountains (2); other regions (3)

Table 3. Morphological characters used in the phylogeny of *Pseudiberus sensu lato*.

Species	Characters																
	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Fruticicola plectotropis	0	1	1	0	0	1	1	0	1	0	0	0	0	0	0	0	3
Pseudiberus tectumsinense	0	0	1	1	1	0	0	0	0	0	0	0	0	1	1	1	0
Pseudiberus zenonis	0	1	1	0	1	1	1	0	0	0	0	0	0	1	1	1	0
Pseudiberus anderssoni	0	1	1	0	1	1	1	0	0	0	0	0	0	1	1	1	0
Pseudiberus depressus	0	1	1	1	1	1	1	0	0	0	0	0	0	1	1	1	0
Pseudiberus pingi	0	1	1	0	0	1	1	0	0	0	0	0	0	1	0	0	0
Pseudiberus shanheicus n. sp.	0	0	1	0	1	0	0	0	0	0	1	0	0	1	0	0	0
Pseudiberus chentingensis	0	1	1	0	1	1	1	0	0	0	0/1	0	0	1	0	0	0
Pseudiberus futtereri	0	2	1	0	1	1	1	0	0	0	0	1	0	1	1	1	0
Platypetasus castanopsis	1	1	1	0	0	1	1	0	1	0	0	0	0	0	0	0	1
Platypetasus innominatus duplicatus	1	1	1	0	0	1	1	0	1	0	0	0	0	0	0	0	1
Platypetasus innominatus innominatus	1	1	1	0	0	1	1	0	1	0	0	0	0	0	0	0	2
Platypetasus mariellus	1	1	1	0	0	1	1	0	1	1	0	0	1	0	0	0	1
Platypetasus lancasteri	1	1	0	0	0	1	1	1	1	1	0	0	1	0	0	0	2
Platypetasus maoensis	1	1	0	0	0	1	1	1	1	1	0	0	1	0	0	0	2
Platypetasus trochomorphus	1	1	0	0	0	1	1	1	1	1	0	0	1	0	1	1	2
Platypetasus t. wentschuanensis	1	1	0	0	0	1	1	1	1	1	0	0	1	0	0	0	2
Platypetasus wardi	1	1	0	1	0	1	1	1	1	1	0	0	0	0	0	0	2
Platypetasus encaustochilus	1	1	0	0	0	1	1	1	?	1	0	0	1	0	0	0	2

DNA extraction and polymerase chain reactions

Whole DNA was extracted from a piece of the ethanol-preserved foot muscle, following instructions from the manufacturer of the TIANamp Micro DNA Kit (DP316; TIANgen Biotech Co., Beijing). The primers used in the polymerase chain reactions (PCR) are listed in Table 1. Each 25 μL PCR mixture consisted of 12.5 μL cwbio 2× Es Taq MasterMix Dye, 9.5 μL ddH_2O, 1 μL template DNA, 1 μL forward primer (10μL/L), and 1 μL reverse primer (10 μL/L). The primers and PCR cycles are the same as used by Zhang *et al*. (2021).

Phylogenetic analysis based on molecular and morphological characters

The phylogenetics of *Pseudiberus* species from east of the TMC based on 16S and 5.8S and ITS2 was performed under Arch Linux with BioArchLinux repository (Zhang *et al.* 2022). The chromatographs and sequences were initially assembled in pregap4 1.6 and gap4 4.11.2 (Staden *et al.* 2003) with visualization by trev 1.9 (Bonfield *et al.* 2002). Sequence alignment was performed by MAFFT 7.520 (Nakamura *et al.* 2018). The dataset was trimmed by Gblocks 0.91b (Castresana 2000) before performing the analysis: 488 positions of 16S and 284 positions of ITS were retained, hence only 57 × 640 bp sequences were obtained. Substitution models were selected based on BIC by Modeltest-NG 0.1.7 (Darriba *et al.* 2020). GTR+I+G was used for 16S and HKY+I was used for 5.8S+ITS2. SequenceMatrix 1.9 (Vaidya *et al.* 2011) was used for concatenating different gene sections. A maximum-likelihood (ML) phylogenetic analysis was performed by RAxML-NG 1.2.0 (Kozlov *et al.* 2019), using an ML search from 10 random starting trees and 10 parsimonystarting trees and the bootstrap method with 1000 receptions and majority rule consensus. The Bayesian-inference (BI) phylogeny was generated by MrBayes3.2.7 (Ronquist *et al.* 2012), with two runs of 4 million generations sampling every 2,000 generations. The consensus tree and posterior probabilities were estimated by the last 50% of trees (burn-in = 0.5).

The maximum-parsimony (MP) method was used for the morphological dataset and trimmed molecular dataset. It was performed by TNT1.6 (Goloboff & Morales 2023) and running the script guoyi.run v. 0.6 provided by Zhang (2023) with some modification. Therefore, the parsimony analysis was performed with implied weighting, and the K value setting was 12, following the recommendations of Goloboff *et al.* (2017). It hit the best score of 1,000 times and stopped. For each hit, the search initially was with 20

replications with 10 cycles of drift, ratchet and tree fusing, followed by strict consensus. Jackknifing was replicated 1,000 times. The character mapping for the phylogenetic tree was performed by WinClada 2.0 with unambiguous optimizations method (Nixon 2021) with conversion via TNT2WinClada (Zhang 2023).

All molecular data were from Zhang *et al.* (2021, 2023) and Wu *et al.* (2023). The sequences are same as in the supplementary file of Zhang *et al.* (2023), with *Pseudiberus liuae* added from Wu *et al.* (2023). Newly added sequences of new species were registered in GenBank (16S: PP555183; ITS: PP555182).

Here, PP = 1.00, ML = 100%, and JK=100% is considered as full support, PP > 0.90, ML > 70%, and JK > 70% is considered as strong support, and PP > 0.80, ML > 60%, and JK >50% is considered as moderately support; lower values are considered as weak support.

Abbreviations

BS = bootstrap for maximum likelihood; BI = Bayesian inference; HBUMM = Mollusc Collection of the Museum of Hebei University, Baoding, China; JK = jackknifing for maximum parsimony; PP = posterior probabilities for Bayesian inference; ML = maximum likelihood; MP = maximum parsimony; SDNU = Zoological Collection of the Shandong Normal University, Jinan, China; THZ = prefix of the museum catalogue number for Zoological Collections of Tianjin Natural History Museum.

Results

Geometric morphometrics

Examination of the shell (Fig. 2) showed that species of *Pseudiberus sensu stricto* from the TMC, Yimeng and Taishan Mountains could not be distinguished with statistical significance in the principal component analysis (Fig. 2A), but they could be distinguished from each other by canonical variate analysis (Fig. 2B).

Phylogenetic tree based on morphological characters

The phylogenetic tree based on morphological and geographical characters (Fig. 3) shows two groups of *Pseudiberus sensu lato* species. One represents *Pseudiberus sensu stricto*, including the type species of *Pseudiberus*, and the other is the sister group of *Pseudiberus sensu stricto*, namely *Platypetasus*, including the type species of *Platypetasus*. The relationship of the sister groups is fully supported (JK = 100). For the *Pseudiberus sensu stricto* lineage, *Ps. pingi* falls to the base with strong support (JK = 86). The remaining *Pseudiberus* species are sister to *Ps. pingi*, with moderate support (JK = 64). For the *Platypetasus* lineage, the JK score (64) moderately supports *Platypetasus* as a monophyletic group. *Platypetasus castanopsis*, *Pl. mariellus*, and two subspecies of *Pl. innominatus* fall to the base of this lineage. The remaining *Platypetasus* species have moderate support (JK = 59). *Platypetasus wardi* is sister to other *Platypetasus* species inhabiting the Minshan, Qionglaishan, and Daxueshan mountains, together with *Pl. innominatus innominatus*.

Phylogenetic tree based on molecular genetics

In the phylogenetic tree based on molecular genetics (Fig. 4), *Camaena* was used as the outgroup. All species not tested against the type species of designated genera are indicated by a question mark after the genus name.

There are two main lineages in the phylogenetic tree. The first lineage embraces *Pliocathaica? ottoi*, *Pliocathaica? buvigneri*, *Bradybaena*, and *Cathaica sensu stricto* with moderate support (PP = 0.66, BS = 55; JK does not support the topology). *Bradybaena* is sister to *Pliocathaica? buvigneri* + *Cathaica sensu stricto* with moderate support from BI and ML (PP = 0.89, BS = 65). The sister-group relationship between *Pliocathaica? buvigneri* and *Cathaica sensu stricto* is strongly supported (PP = 1.00, BS = 99, and JK = 90).

The second lineage is strongly supported (PP = 0.99, ML = 77) and can be divided into two groups, although the groups are not supported by all three methods. One group embraces *Pliocathaica? gansuica*, *Pliocathaica? ochthephiloides*, *Platypetasus? liuae*, and *Platypetasus? strophostomus*. Two *Platypetasus?* species are sister groups with strong support on ML and MP (BS = 92, JK = 86). *Pliocathaica? ochthephiloides* is sister to *Platypetasus?* spp. with strong BI and ML support (PP = 1.00, ML = 92). The other group embraces *Stilpnodiscus stictotaenia*, *Pliocathaica? pulveratricula*, and *Pseudiberus sensu stricto. Stilpnodiscus stictotaenia* is basal in this group, and *Pliocathaica? pulveratricula* is strongly supported as sister to *Pseudiberus sensu stricto* species (PP = 1.00, BS = 90, JK = 80). Although *Pseudiberus sensu lato* is polyphyletic, *Pseudiberus sensu stricto* is monophyletic, with full support (PP = 1.00, BS = 100, JK = 100). Among *Pseudiberus sensu stricto* species, *Pseudiberus shanheicus* n. sp. is basal in the lineage. *Pseudiberus sensu stricto* species from Shandong province cluster together, with strong BI and MP support (PP = 1.00, JK = 78).

Character mapping

In the phylogenetic tree based on morphology (Fig. 3), *Pseudiberus sensu stricto* is supported as monophyletic group

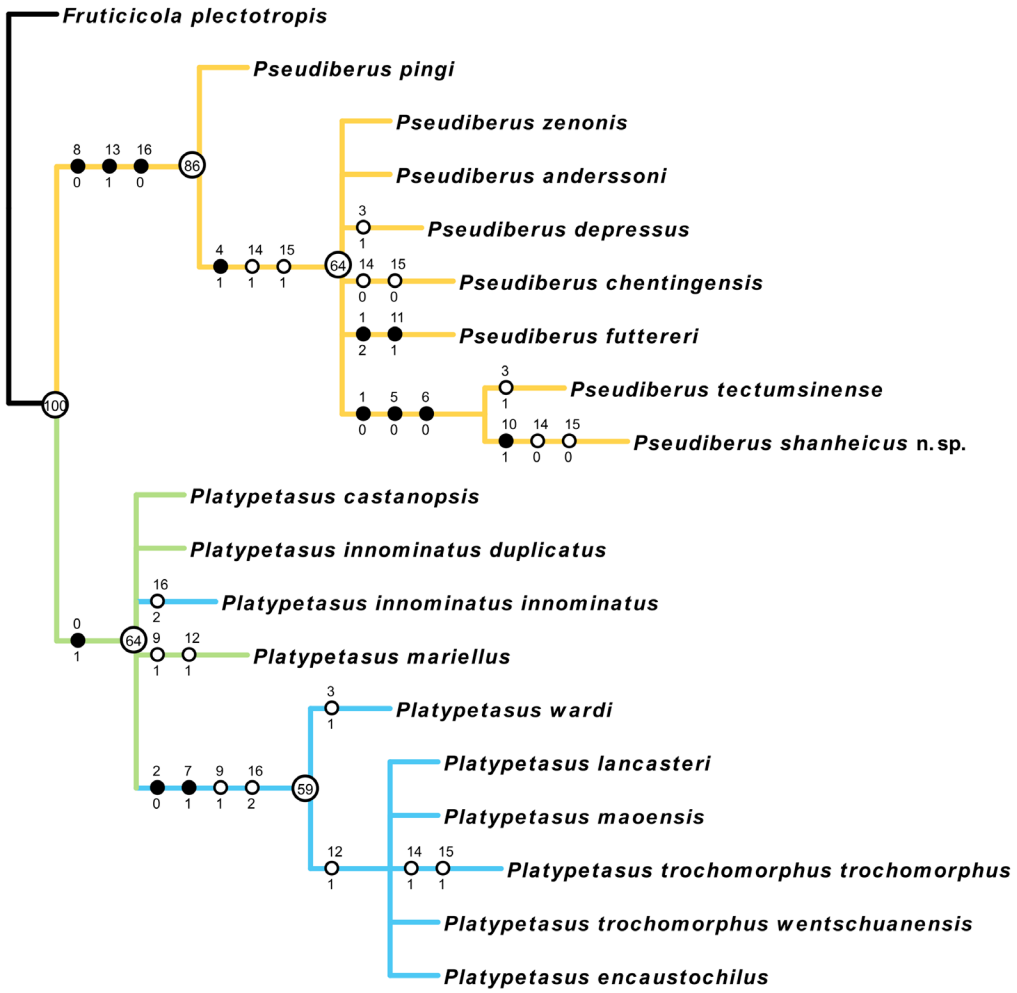

Figure 3. Phylogeny based on morphological character was performed by TNT. Characters mapping was generated by WinClada. Jackknifing is marked at the nodes and scores lower than 50 is omitted. The upper number on each branch is the morphological character. The lower number on each branch is the status of that character. Black dots on branch indicate unambiguous apomorphic characters and white dots on branch indicate homoplastic characters. Blue Branch indicates species from Daxueshan, Qionglaishan, Minshan mountains. Green branch indicates species from Dabashan mountains. Yellow branch indicates species from east-to-TMC. CI = 0.667, RI = 0.861, TL = 30.

by the ring-like thickening within the aperture, the non-continuous peristome with indistinct callus, and a geographic distribution within the Qinling, Taihangshan, Tiashan, and Yimeng mountains. The more depressed shell shape is apomorphic in *Platypetasus*, and a rectangular aperture and broad umbilicus are apomorphies of *Platypetasus* from the Minshan, Qionglaishan, and Daxueshan mountains.

Systematics

Superfamily Helicoidea Rafinesque, 1815

Family Camaenidae Pilsbry, 1895

Genus *Pseudiberus* Ancey, 1887

Type species. *Helix tectumsinense* E. von Martens, 1873, by subsequent designation (Pilsbry 1895).

***Pseudiberus shanheicus* n. sp.**

Figures 1–7

ZooBank identifier. urn:lsid:zoobank.org:act:8FB5E253-745F-45D3-B172-4B3D804303DF

Type locality. Ciyunsi Temple, Gongyi, Zhengzhou City, Henan Province, China, 34.67°N 103.32°E, 530 m above sea level.

Type material. Holotype: SDNU.Gas.0400.01.01, leg. Z. Liu, 17 August 2019, mature animal, dissected. Paratypes:

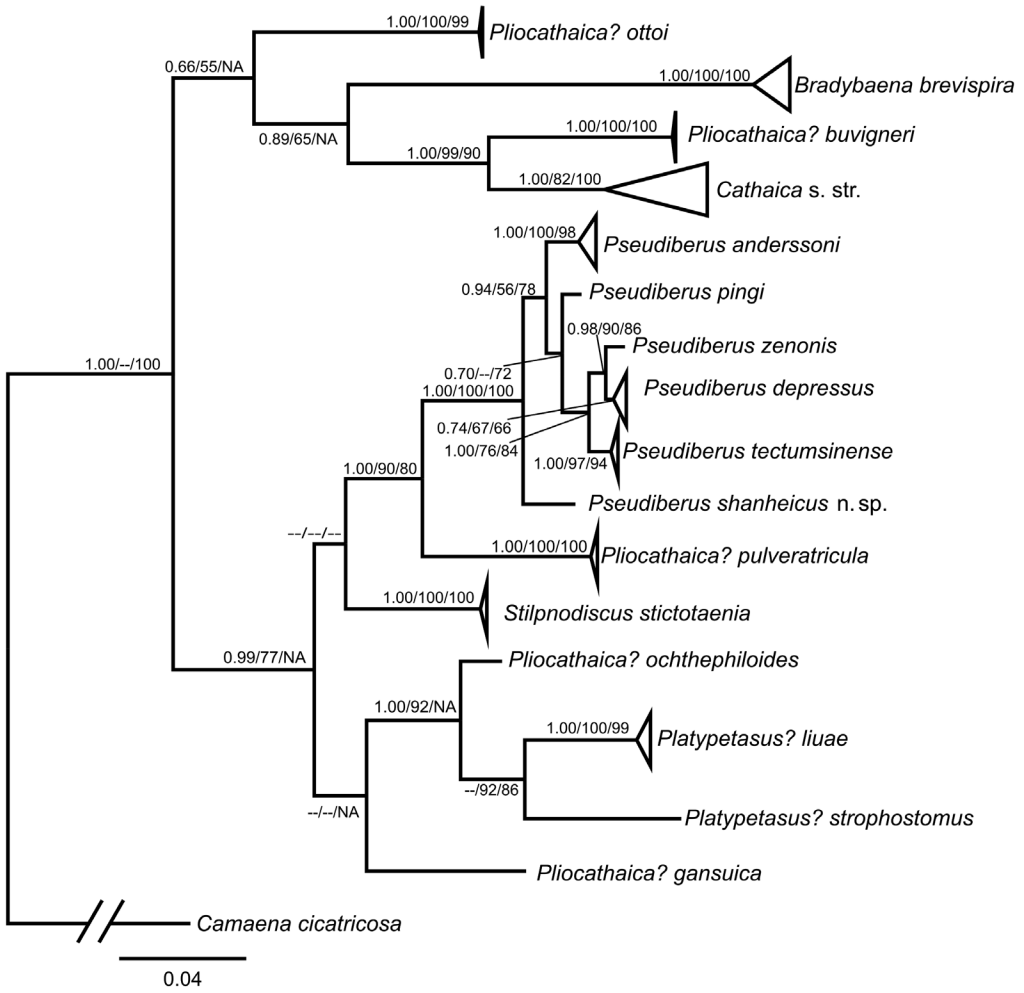

Figure 4. Bayesian inference phylogenetic tree of *Pseudiberus sensu lato* together with *Stilpnodiscus*, *Bradybaena*, *Pliocathaica*?, and *Cathaica sensu stricto.* The tree is rooted on the outgroup *Camaena cicatricosa*. Bayesian posterior probabilities and bootstrap values are given in the following order: BI(posterior probabilities)/ML(bootstrap)/MP(jackknifing). BI posterior probabilities lower than 0.70 and ML bootstrap and MP jackknifing values lower than 50% are not shown. C = 0.613, RI = 0.888, TL = 571.

SDNU.Gas.0400.01.02, locality data, collector, and date same as holotype; mature animal; SDNU.Gas.0400.01.03, Weihui, Xinxiang City, Henan Province, China, 35.48° N 113.97° E, 500 m above sea level, leg. Q. Zhang, 31 July 2023; mature animal; SDNU.Gas.0400.01.04, Qinglongshan, Gongyi, Zhengzhou City, Henan Province, China, 35.48° N, 113.97° E; 500 m above sea level, leg. Q. Zhang, 24 August 2023, shell.

The description of the shell is based on all type specimens. The description of genitalia is only based on the holotype.

Diagnosis. Shell lens-shaped, depressed, without bands or ribs, strongly carinate at periphery, growth lines distinct. Carina saw-toothed, hollow. Proximal accessory sacs two, equally developed, inserted on proximal dart sac; each proximal accessory sac with an opening into dart-sac chamber. Penis internally with interlaced pilasters that form a network (not parallel).

Description. Shell (Fig. 5A). Dextral, depressed, lens-shaped, thin. Whorls flattish, without bands. Suture shallow. Last whorl flattish. Base convex. Base–umbilicus transition rather abrupt. Umbilicus narrow. Columella dilated, partially covering umbilicus. Protoconch finely granulate (Fig. 5B). Teleoconch sculpture: spiral lirae present on last whorl; surface ribless; growth lines distinct, not accompanied with irregular thickenings. Whorls sharply carinate at periphery in both young and adult shells. Peripheral carina saw-toothed, hollow (Fig. 5C). Aperture strongly elliptical (= "peach-shaped" of Zhang *et al.* 2021), toothless, with inner ring-like callus thickening. Lip expanded, double (in holotype), thin, with lower lip very narrowly reflexed. Peristome

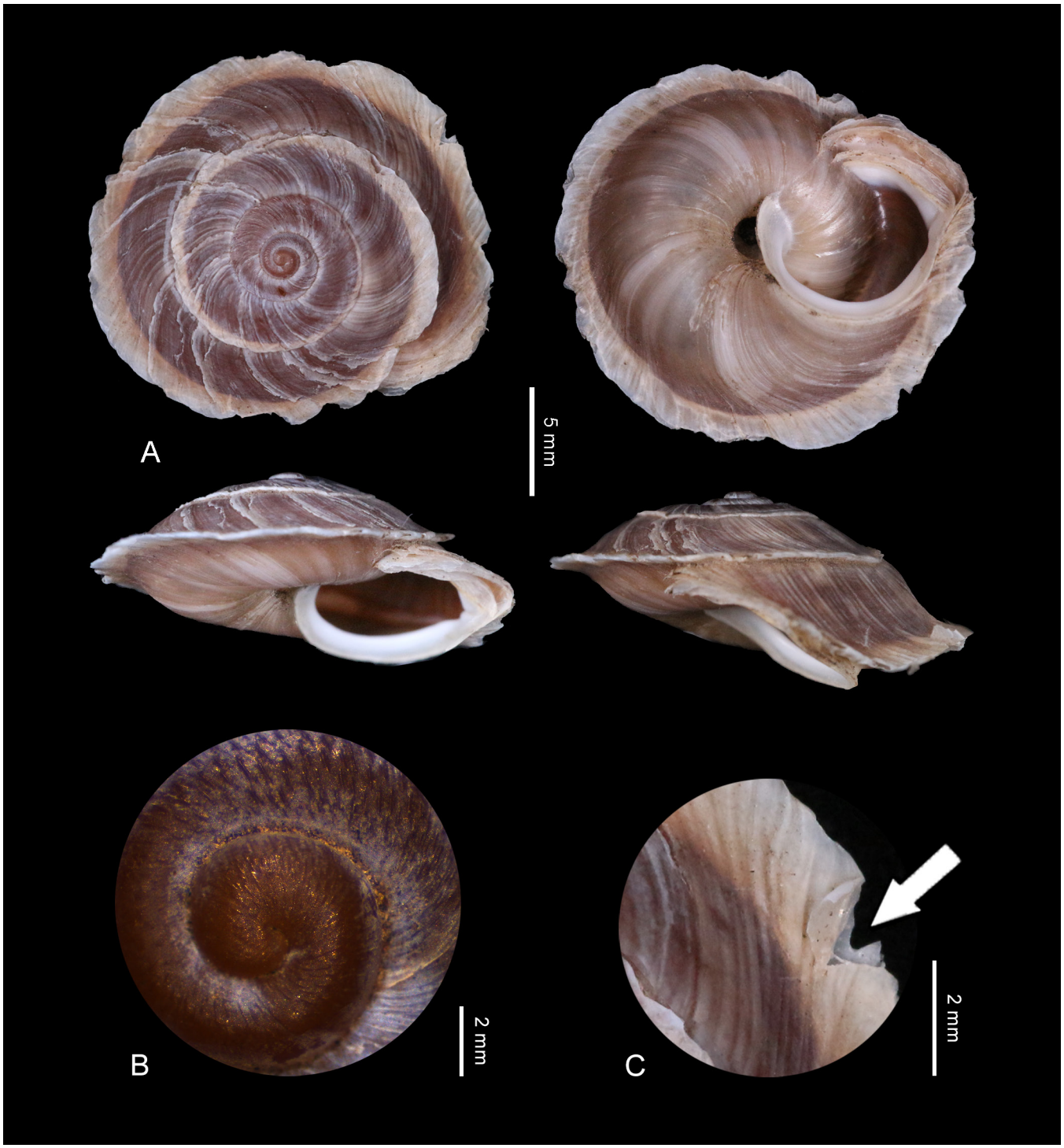

Figure 5. *Pseudiberus shanheicus* n. sp.; shell of holotype (SDNU.Gas.0400.01.01). **A,** apical, apertural and umbilical views of fully mature shells. **B**, protoconch of holotype, with fine ribs. **C**, arrow points to hollow keel.

not continuous. Parietal callus somewhat distinct. Shell dull, reddish brown.

Animal (Fig. 6A–C). Wart present between tentacle insertions (Fig. 6C). No leaf-shaped appendage present on left and right sides of mantle edge (Fig. 6A, B).

Genitalia (Figs 6D, 7). Membranous sac surrounding terminal genitalia absent. Penis sheath short. Penis short, thick, slightly expanded medially, externally simple (Fig. 7E).

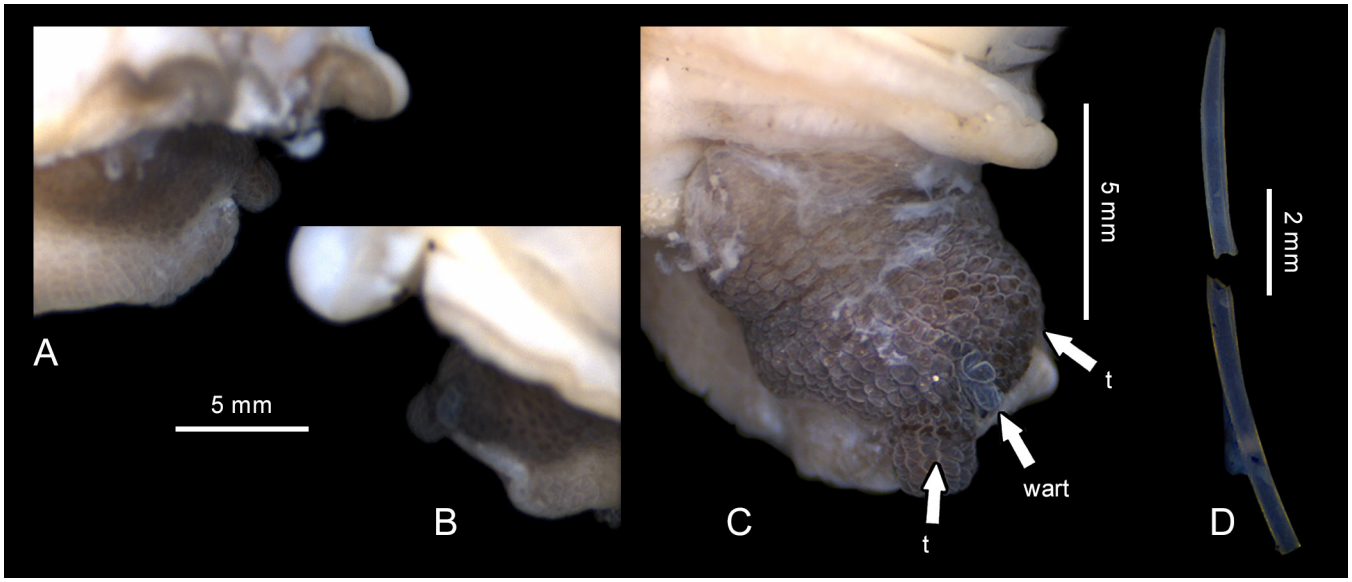

Figure 6. *Pseudiberus shanheicus* n. sp.; animal of holotype (SDNU.Gas.0400.01.01). **A**, **B**, left and right sides of mantle edge with no leaf-shaped appendage present. **C**, wart between the tentacles (t). **D**, love dart.

Penial pilasters split into numerous fine pilasters that regularly interlace to form a network (Fig. 7C). Penis–epiphallus chamber absent. Epiphallic papilla absent. Flagellum lacking. Vas deferens not thickened near penial retractor. Mucous glands four, each with a distinct peduncle, one longer than others, complicatedly branched; shorter glands approximately equal in length to dart sac (Fig. 7D). Vaginal region between dart sac and atrium very short. Proximal part of dart sac without neck-structure. Dart sac contains one dart. Dart c. 9 mm long, curved, basally expanded, three-bladed at its apex (Fig. 7D). Accessory sac not visible from outside dart sac. Mucous-gland-insertion papilla absent. Proximal accessory sacs two, unequally developed, inserted on proximal dart sac; each proximal accessory sac opening into dart-sac chamber, internally without pilasters (Figs 7F, H). Poly-layered structure in dart apparatus absent.

Measurements (SDNU.Gas.0400.01.01). Genitalia: DS = 9.4 mm long, 3.9 mm wide; MG = 3.7 (shorter) or 9.5 (longer) mm long; Va = 27.5 mm long; BC plus BCD = 20.7 mm long; VD = 21.0 mm long; PS = 3.0 mm long; P = 11.3 mm long; PR = 2.6 mm long. Shell: protoconch 1.75, whorls 4.875, shell breadth 18.7 mm, shell height 8.0 mm. Abbreviations are explained in the legend of Figure 3.

Ecology. Similar to *Pseudiberus* species from Shandong (Zhang *et al*. 2021), the new species prefers rocky habitats and occurs with *Cathaica* species. However, the new species especially prefers the upper part of the mountain, where it occurs under rocks.

Distribution. Gongyi, Zhengzhou City, and Huxian, Xinxiang City, Henan Province, China (Fig. 1).

Etymology. The species is named after Shanhe University, which was established by Chinese internet users to advocate for educational fairness in China, particularly for students from Shandong, Shanxi, Henan, and Hebei provinces. The admission rate for students from these provinces to top universities is only one-seventh to one-third of that for Beijing students. Here we use this name to call on the government to break down the wall of regional protection in the university entrance examination and fulfil the commitment to educational equality.

Chinese name. 山河蛇蜗牛 (Pinyin: shān hé shé wō niú).

Remarks. *Pseudiberus chentingensis* (Yen, 1935), which lives in Zhengding (= Dingzhou), Heibei Province (Fig. 1B), is the only other *Pseudiberus* species known to occur near this new species (Fig. 1B: Zhengzhou) (Chen & Zhang 2000; Wu & Qi 2006). In addition, *Ps. chentingensis* has been recorded from Cixian City (Chen & Zhang 2000) and Jiaozuo City (Wu & Qi 2006). Compared with the new species, the holotype (THZ015006) and paratypes (THZ015007, THZ015008, and THZ015171) of *P. chentingensis* have neither the hollow peripheral carina nor spiral furrows, and the penial pilasters are parallel near the atrium (Wu 2004). In the phylogenetic tree based on morphological characters (Fig. 3), *Ps. shanheicus* shares with *Ps. tectumsinense* a similar peripheral carina, but it lacks ribs on the shell surface and parallel penial pilasters. This species is larger than other

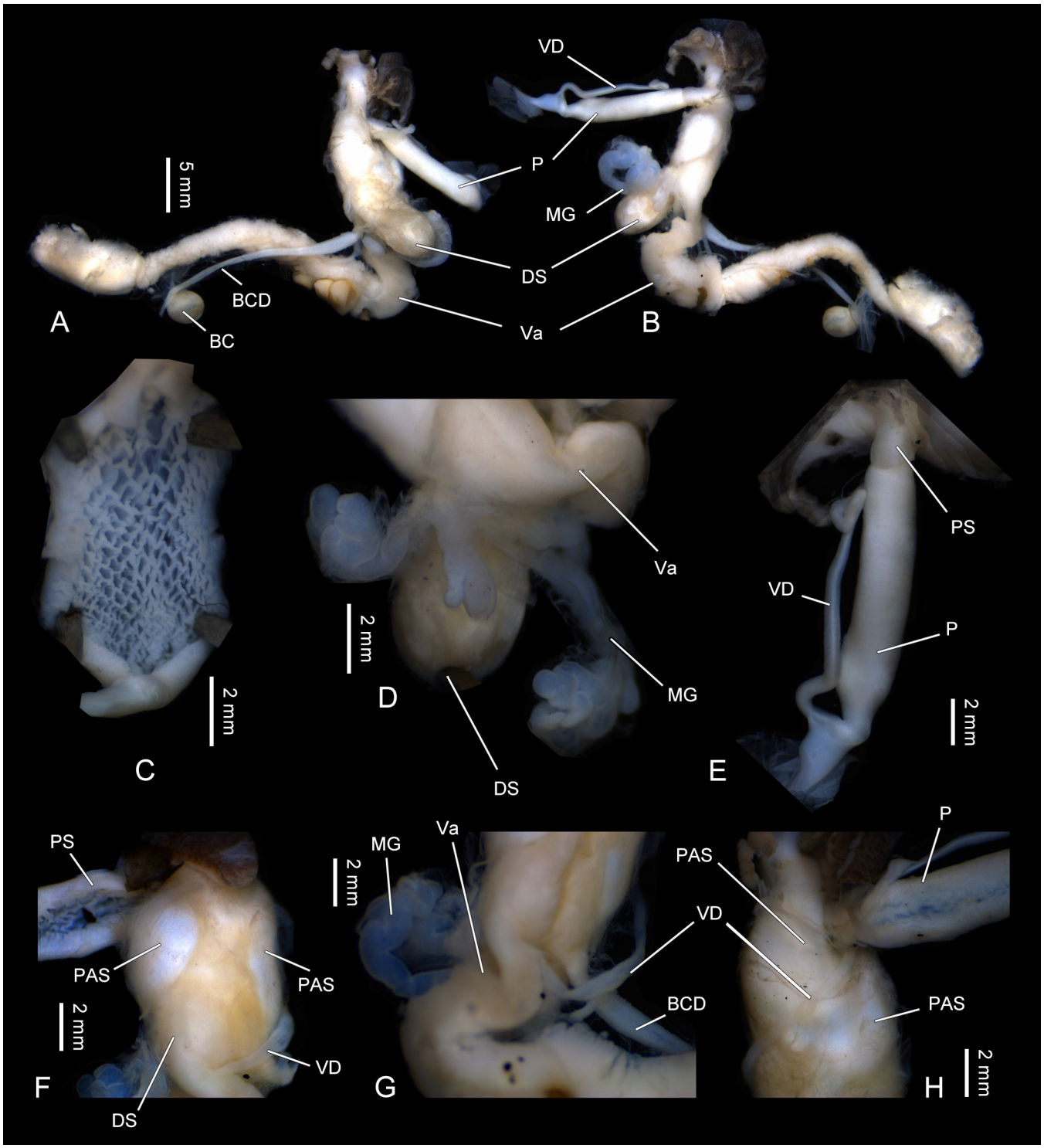

Figure 7. *Pseudiberus shanheicus* n. sp. Genitalia of holotype (SDNU.Gas.0400.01.01). **A**, **B**, both sides of genitalia. **C**, inner structure of penis with numerous fine, regularly interlaced pilasters that form a network. **D**, view of mucous glands. **E**, penis and penial sheath. **F**, **H**, dart sac; **G** vagina. Abbreviations: At = atrium, BC = bursa copulatrix, BCD = bursa copulatrix duct, DS = dart sac, MG = mucous glands, P = penis, PAS = proximal accessory sac, PR = penial retractor muscle, PS = penis sheath, Va = vagina, VD = vas deferens.

species of *Pseudiberus sensu stricto* from Shandong (Gredler 1882a, 1882b; Martens 1873; Odhner 1925; Yen 1935). A double lip is present in both the new species and *P. chentingensis* (Wu & Qi, 2006), but absent in *Pseudiberus sensu stricto* from Shandong (Gredler 1882a, 1882b; Martens 1873; Odhner 1925; Yen 1935).

Cai *et al.* (1992) recorded *Ps. tectumsinense* at Huixian, Xinxiang City, but this appears to be mistakenly identified: they did not provide an adequate description or photograph, and we could not find this species there, although we explored the same localities as those authors

Discussion

Phenetic (or numerical taxonomic) methods, such as geometric morphometrics, failed to distinguish the species. *Pseudiberus chentingensis latispira* is considered a synonym of *Ps. chentingensis chentingensis* because shell shape is highly variable in this genus (Fig 2A, B) and the localities are identical (Zhang *et al.* 2020). In contrast, the phylogenetic method worked well for species differentiation.

The phylogeny based on morphological characters (Fig. 3) suggests that the genus *Pseudiberus sensu stricto* is monophyletic and that subspecies-level taxa in *Pseudiberus sensu stricto* from Shandong Province should be considered as full species considering the apomorphic characters. Thus, *Pseudiberus sensu stricto* now embraces eight species: *Ps. pingi*, *Ps. zenonis*, *Ps. anderssoni*, *Ps. depressus*, *Ps. chentingensis*, *Ps. futtereri*, *Ps. tectumsinense*, and *Ps. shanheicus* n. sp. *Pseudiberus sensu stricto* is also fully supported by molecular phylogeny (Fig. 4). The cladistic species concept (Ridley 1989) allows geographical characters to be included as well as morphological and molecular characters, and this is particularly beneficial in the systematic analysis of these slow-moving animals. Species of *Pseudiberus sensu stricto* have restricted distributions in the Qinling, Taihangshan, Taishan, and Yimeng mountains. This character should be considered as an apomorphy of *Pseudiberus sensu stricto*.

Fruticicola plectotropis and *Ps. chitralensis* are distant from the main area of distribution of *Platypetasus* and *Pseudiberus sensu stricto*, and these species should be removed from that genus and possibly transferred to *Ponsadenia sensu lato*, as defined by Schileyko (2004). *Platypetasus liuae* differs in size from other *Pseudiberus sensu lato* species, and this species should also be removed from *Pseudiberus sensu lato.* The shell of *Pl. strophostomus* differs in shape from those of *Pseudiberus sensu lato*, and this species should also be removed. In the molecular phylogenetic tree (Fig. 4), *Pl.*? *liuae* and *Pl.*? *strophostomus* are sister groups and cluster together with *Pliocathaica? ochthephiloides*. Other *Pseudiberus sensu lato* species recognized by Wu & Qi (2006) should be temporally moved to *Platypetasus*. However, the apomorphy which supports this lineage as monophyletic (Fig. 3) is quite weak because it is defined using a fixed number. Phenetic methods already fail to distinguish these two genera due to homoplasy caused by environmental pressure (Hull 1989; Felsenstein 2004; Wu & Qi 2006; Rieppel 2008).

To summarize, *Pseudiberus sensu stricto* is polyphyletic. *Pseudiberus sensu stricto* includes only those *Pseudiberus* species occurring in the Qinling, Taihangshan, Taishan, and Yimeng mountains. *Platypetasus* includes those species with lens-shaped shells distributed in the Minshan, Qionglaishan, Daxueshan, and Dabashan mountains, forming a monophyletic group. Central Asian species previously were thought to be probably *Ponsadenia sensu lato*.

Acknowledgements

This study is supported by the National Students' innovation and entrepreneurship training program (201910445019) and the Tony Whitten Award 2020. Thanks go to the Willi Hennig Society for providing TNT software. We are grateful to Peter S. Andrus, Robert G. Forsyth, and the two reviewers for their comments and helpful suggestions. We also thank Larisa A. Prozorova for her help with checking the distribution of species.

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