European Journal of Taxonomy 1005: 1–64
https://doi.org/10.5852/ejt.2025.1005.2985

europeanjournaloftaxonomy.eu
ISSN 2118-9773
2025 · Zhang L.-J. *et al.*

Received: 29 July 2024 • *Accepted: 7 April 2025* • *Published: 31 July 2025*

Topic editor: Magalie Castelin • *Section editor: Thierry Backeljau* • *Desk editor: Pepe Fernández*

Monograph

urn:lsid:zoobank.org:pub:BAD3B10F-13AB-43E3-8B52-0B613A992602

A new genus of river snails, *Bakyietaia* (Mollusca, Viviparidae), from South China and the Indochinese Peninsula

Le-Jia ZHANG [1+], Yu-Hsiu YEN [2,*+], Zhe-Yu CHEN [3], Li-Na DU [4], Ting Hui NG [5] & Thomas von RINTELEN [6,*]

[1] Kunming Institute of Zoology, Chinese Academy of Sciences, Kunming 650023, China.
[1] Museum für Naturkunde, Leibniz Institut für Evolutions und Biodiversitätsforschung, Berlin 10115, Germany.
[1] Southeast Asia Biodiversity Research Institute, Chinese Academy of Sciences, Yezin, Nay Pyi Taw, 05282, Myanmar.
[2] Department of Marine Biotechnology and Resources, National Sun Yat-sen University, Kaohsiung 80424, Taiwan.
[3] Parasitology Research Group, Department of Veterinary Biosciences, Faculty of Science, The University of Melbourne, Parkville VIC 3010, Australia.
[3] Department of Life Sciences, Natural History Museum, London SW7 5BD, UK.
[4] Key Laboratory of Ecology of Rare and Endangered Species and Environmental Protection, Guangxi Normal University, Ministry of Education, Guilin, Guangxi 541004, China.
[5] Institute for Tropical Biology and Conservation, Universiti Malaysia Sabah, Jalan UMS, 88400 Kota, Malaysia.
[5] Lee Kong Chian Natural History Museum, National University of Singapore, 2 Conservatory Drive, Singapore 117377, Republic of Singapore.
[6] Museum für Naturkunde, Leibniz Institut für Evolutions- und Biodiversitätsforschung, Berlin 10115, Germany.

[*] Corresponding authors: yhyenann@gmail.com – Thomas.vonRintelen@mfn.berlin
[1] Email: zhanglejia@mail.kiz.ac.cn
[3] Email: chenzheyu1998@163.com
[4] Email: dulina@mailbox.gxnu.edu.cn
[5] Email: ngtinghui@ums.edu.my

[+] These two authors contributed equally to the manuscript

Abstract. A new genus of the river snail family Viviparidae, *Bakyietaia* Zhang, Yen & von Rintelen gen. nov., is described based on a comprehensive study of its morphology, anatomy, mtDNA (COI), ecology and distribution. This genus is widely distributed in South China and the Indochinese Peninsula. It can be distinguished from all other viviparid genera, especially *Angulyagra*, *Sinotaia* and *Anulotaia*, by characters of the columellar lip of the shell, the operculum and the marginal teeth of radula. Based on an integrative taxonomic approach, 17 species are assigned to this new genus and described here, including 7 new combinations and 10 new species: *Bakyietaia subcostata* gen. et comb. nov., *B. polyzonata* gen. et

comb. nov., *B. boettgeri* gen. et comb. nov., *B. duchieri* gen. et comb. nov., *B. guangdungensis* gen. et comb. nov., *B. mutica* gen. et comb. nov., *B. wilhelmi* gen. et comb. nov., *B. chenghuang* Zhang, Yen & von Rintelen gen. et sp. nov., *B. jingweiae* Yen, Zhang & von Rintelen gen. et sp. nov., *B. liusanjieae* Zhang, Yen & von Rintelen gen. et sp. nov., *B. avisvenatoris* Yen, Zhang & von Rintelen gen. et sp. nov., *B. liangzhuorum* Yen, Zhang & von Rintelen gen. et sp. nov., *B. luikongi* Yen, Zhang & von Rintelen gen. et sp. nov., *B. fontinalis* Zhang, Yen & von Rintelen gen. et sp. nov., *B. naiadica* Zhang, Yen & von Rintelen gen. et sp. nov., *B. luuemxlong* Zhang, Yen & von Rintelen gen. et sp. nov. and *B. indrapura* Zhang, Yen & von Rintelen gen. et sp. nov. The monophyly of all morphospecies is supported by the COI phylogeny. Radular characters, especially the number of cusps of the outer marginal teeth, are considered valuable in the classification of species of *Bakyietaia* with similar shells.

Keywords. *Angulyagra*, biogeography, gastropod, systematics, taxonomy.

Zhang L.-J., Yen Y.-H., Chen Z.-Y., Du L.-N., Ng T.H. & von Rintelen T. 2025. A new genus of river snails, *Bakyietaia* (Mollusca, Viviparidae), from South China and the Indochinese Peninsula. *European Journal of Taxonomy* 1005: 1–64. https://doi.org/10.5852/ejt.2025.1005.2985

Introduction

Viviparidae J.E. Gray, 1847 (river snails) is a family of freshwater snails comprising 125 to 150 valid described extant species with a worldwide native distribution except for South America and Antarctica (Strong *et al.* 2008). The Viviparidae have a rich fossil record (Prashad 1928), and many extinct species are found outside the current geographic range of this family, such as in the Middle East (Sivan *et al.* 2006) and South America (Ghilardi *et al.* 2011). The oldest fossils can be traced back to the Early to Middle Jurassic: *Viviparus sangongheensis* Zhu, 1994 from Xinjiang, China (Early Jurassic; Zhu 1994) and *Bathonella scotica* (Tate, 1873) from England, UK (Middle Jurassic; Tracey *et al.* 1993). The early origin, abundant fossil record and (almost) worldwide distribution of the Viviparidae has drawn many researchers' attention to the systematics, evolutionary history and biogeography of this family (Sengupta *et al.* 2009; Schultheiß *et al.* 2014; Zhang *et al.* 2015; Hirano *et al.* 2019a, 3019b, 2023; Stelbrink *et al.* 2020; Ye *et al.* 2020).

South China and Southeast Asia harbour the highest biodiversity of Viviparidae (Strong *et al.* 2008; Zhang *et al.* 2015; Stelbrink *et al.* 2020). Yunnan Province in Southwestern China harbours ten genera, including four endemic ones (*Anularya* Zhang & Chen, 2015; *Dalipaludina* Zhang, 2023; *Margarya* Nevill, 1877; *Tchangmargarya* He, 2013) and at least 15 endemic species (Zhang *et al.* 2023). Southeast Asia harbours 12 genera, including four endemic to the Indochinese Peninsula (*Anulotaia* Brandt, 1968; *Eyriesia* Fischer, 1885; *Taia* Annandale, 1918; *Trochotaia* Brandt, 1974) and two endemic to insular Southeast Asia (*Celetaia* Clench, 1966; *Torotaia* F. Haas, 1939) (Molluscabase 2023). However, Viviparidae from this region are understudied, with only a few recent studies focussing on this hotspot of viviparid diversity (Zhang *et al.* 2015; Stelbrink *et al.* 2019, 2020; Zhang *et al.* 2023).

Rao (1925) established a new genus in the Viviparidae, *Dactylochlamys*, for a single species with many smooth, strong keels on the shell, endemic to the Manipur Valley of India, *Paludina oxytropis* Benson, 1836. However, Rao (1931) later identified *Dactylochlamys* Rao, 1925 as a junior homonym of the ciliate *Dactylochlamys* Lauterborn, 1901; therefore, *Angulyagra* Rao, 1931 was established as a replacement name for this genus. *Angulyagra* soon became a 'wastebasket taxon' for species from Asia possessing a shell with many smooth, strong keels (Prashad 1928; Yen 1939, 1943; Starobogatov 1970; Liu *et al*. 1995). However, most of these species are distinct from the type species of *Angulyagra* based on characters of the shell, radula, operculum, and anatomy. Therefore, a systematic revision of *Angulyagra* is needed.

Here, we revise the species of *Angulyagra* from South China and the Indochinese Peninsula based on their morphology (shell, operculum, radula), ecology, distribution and variation in the mitochondrial

COI gene. Our integrative study has revealed that there are at least 17 species within this group, and all of these species of *Angulyagra* should actually be assigned to a new genus described here: *Bakyietaia* Zhang, Yen & von Rintelen gen. nov.

Material and methods

Material

Type specimens of ten viviparid species from five institutions (Natural History Museum, London (NHMUK); Gymnasium der Franziskaner, Bozen (GFBI); Naturhistorisches Museum, Vienna (NHMW); Naturmuseum Senckenberg, Frankfurt (SMF); Muséum national d'Histoire naturelle, Paris (MNHN)) have been examined. The type specimens of nine new species described here have been deposited in the Kunming Institute of Zoology, Chinese Academy of Sciences, Kunming (KIZ) and the Museum für Naturkunde, Berlin (ZMB), non-types are also in the collections of Le-Jia Zhang (ZLJ) and Yu-Hsiu Yen (YHY). In addition, comparative non-type material held in ZMB, KIZ and and the BORNEENSIS Collection, Institute for Tropical Biology and Conservation, Universiti Malaysia Sabah (BOR) have also been examined. The specimens used for the morphological and molecular analysis were collected during 2006–2022. A two-month expedition for collecting species of Viviparidae from rivers, springs, lakes and wetlands of Southern China was conducted in early 2022. Altogether 73 sites were sampled and are illustrated in the map (Fig. 1).

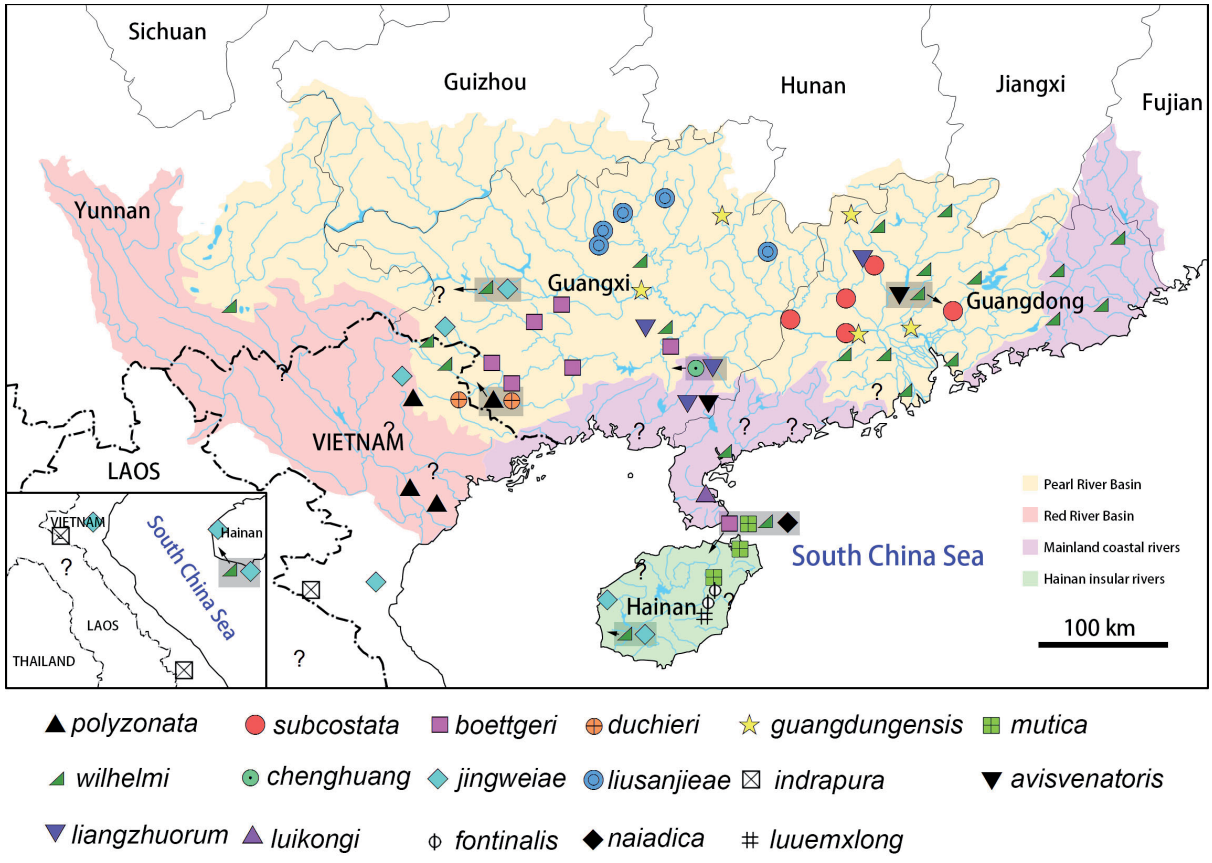


Fig. 1. Map of the main river basins in South China and the Indochinese Peninsula with the collecting sites of species of *Bakyietaia* Zhang, Yen & von Rintelen gen. nov. Sites with more than one species are indicated by an arrow and multiple species symbols on a grey background. The symbol "?" indicates sites with species of *Bakyietaia* only identified to genus level.

Examination of morphology

The height (H) and width (W) of shells of mature and complete specimens were measured with an electronic calliper to a precision of 0.1 mm. The mass (M) of several selected shell specimens was measured by an electronic scale to a precision of 0.01 g. Selected shells comprised nine specimens of *Angulyagra oxytropis* (Benson, 1836) and 44 specimens of species of *Bakyietaia* gen. nov. The shells were completely dry and the mass was constant. All specimens were photographed in a consistent orientation using a Sony alpha 7R 4 camera. Radulae were extracted by dissection, cleaned by boiling in 1% NaOH solution for half an hour and rinsed with distilled water. Radulae were coated with gold and imaged with a Zeiss EVO LS10 scanning electron microscope. Terms used for describing the operculum follow Zhang & von Rintelen (2021).

Abbreviations for features of the radula:

ct = central teeth
imt = inner marginal teeth
lt = lateral teeth
omt = outer marginal teeth.

Molecular methods

DNA was extracted from 10–20 mg foot tissue from each snail, using a mollusc-specific CTAB/chloroform extraction protocol (Winnepenninckx *et al*.1993). A fragment (570 bp) of the mitochondrial cytochrome c oxidase subunit I (COI) gene was amplified through polymerase chain reaction (PCR) with the following primer pair: LCO1490, 5′-GGTCAACAAATCATAAAGATATTGG-3′ and COX-B7R, 5′-ACCACCAGCTGGATCAAAAA-3′. (Schultheiß *et al*. 2011) PCR amplifications were conducted in 25 µl volumes under the following cycling conditions: initial denaturing step at 94°C for 10 min, followed by 30 cycles of 94°C for 1 min, 50°C for 1 min, and 72°C for 1 min, with a final extension step of 10 min at 72°C. The purification and sequencing were conducted by Macrogen Europe, Amsterdam, Netherlands.

Sequence and phylogenetic analyses

140 new COI sequences of species of Viviparidae and 16 sequences of 13 genera of the subfamily Bellamyinae Rohrbach, 1937, mostly from Stelbrink *et al*. (2020), were included in the present study (Supp. file 1). *Viviparus contectus* (Millet, 1813) of the subfamily Viviparinae J.E. Gray, 1847 was selected as outgroup based on Stelbrink *et al*. (2020).

Sequences were aligned using MUSCLE as implemented in Geneious Prime 2020 (https://www.geneious.com). Genetic distances were calculated using MEGA X (Kumar *et al*. 2018). TN93+G+I was suggested as the best-fit model of sequence evolution for our dataset by means of the Akaike and Bayesian information criteria in MEGA X. A Bayesian inference (BI) analysis was performed with MrBayes ver. 3.2.6 (Ronquist *et al*. 2012) as implemented in Geneious Prime 2020 with four independent chains for 5 000 000 generations, sample freq = 1000, burnin = 25%, and we confirmed that convergence was reached based on the trace plots generated in Geneious Prime 2020. A maximum likelihood (ML) analysis was conducted with RAxML as implemented in Geneious Prime 2020, with nodal support estimated by 1000 bootstrap replicates (Kozlov *et al.* 2019).

Species delimitation

Assemble Species by Automatic Partitioning (ASAP) (Puillandre *et al*. 2020) was performed on the ASAP web platform (https://bioinfo.mnhn.fr/abi/public/asap/) using the Jukes Cantor (JC69) model and simple genetic distance calculated with default settings: probability .01, seed value −1, genetic distances between 0.005 and 0.05.

Fig. 2. Bayesian inference phylogram of the species of *Bakyietaia* Zhang, Yen & von Rintelen gen. nov. and some related viviparid genera based on cytochrome c oxidase subunit I (COI) with operational taxonomic unit (OTU) assignments. Numbers at nodes indicate Bayesian posterior probabilities (left) and maximum likelihood bootstrap support values (right). Supporting values lower than 0.5/50 are not presented and are shown as '-'. Background in colours indicate new combinations (blue) and new species (orange). ASAP: Assemble Species by Automatic Partitioning. Scale bar = 0.04 substitutions per site.

Table 1. Shell measurements of species of *Angulyagra* Rao, 1931 and *Bakyietaia* Zhang, Yen & von Rintelen gen. nov. Abbreviations: H = height; M = mass; N = measured specimens; n = measured completely dry shells; W = width.

Species	*N*	*n*	H (mm)	W (mm)	W/H	M (g)
Angulyagra oxytropis	9	9	34.60±3.77	27.15±3.79	0.78±0.03	1.01±0.28
Bakyietaia polyzonata	3		26.60±1.91	19.19±1.30	0.72±0.01	–
Bakyietaia subcostata	10		27.17±3.64	20.25±1.75	0.75±0.05	2.52±0.36
Bakyietaia boettgeri	9	7	26.76±6.67	18.87±5.12	0.70±0.04	2.16±2.78
Bakyietaia duchieri	2		32.88±1.00	24.46±1.77	0.74±0.03	–
Bakyietaia guangdungensis	7	3	20.87±0.93	14.57±0.61	0.70±0.03	0.78±0.18
Bakyietaia mutica	11	2	22.14±1.74	15.49±1.06	0.70±0.04	0.84±0.16
Bakyietaia wilhelmi	10	10	25.53±3.72	17.28±2.11	0.68±0.04	1.63±0.97
Bakyietaia chenghuang	3	2	23.70±5.37	17.67±3.42	0.74±0.03	1.19±0.02
Bakyietaia jingweiae	9	9	26.79±5.37	17.67±3.42	0.66±0.04	1.94±1.90
Bakyietaia liusanjieae	12	1	25.69±3.35	18.98±2.31	0.74±0.04	3.00
Bakyietaia avisvenatoris	6		19.78±1.67	14.50±1.48	0.73±0.03	–
Bakyietaia liangzhuorum	8	4	25.25±3.07	18.13±2.33	0.72±0.04	0.77±0.22
Bakyietaia luikongi	3		20.66±0.70	15.44±0.62	0.75±0.02	–
Bakyietaia fontinalis	8	1	24.25±2.59	17.44±1.84	0.72±0.03	0.40
Bakyietaia naiadica	3		25.73±0.62	18.02±0.31	0.70±0.01	–
Bakyietaia luuemxlong	4		23.56±2.58	16.49±1.29	0.70±0.02	–
Bakyietaia indrapura	3	3	26.92±2.45	17.67±1.40	0.66±0.01	1.07±0.41

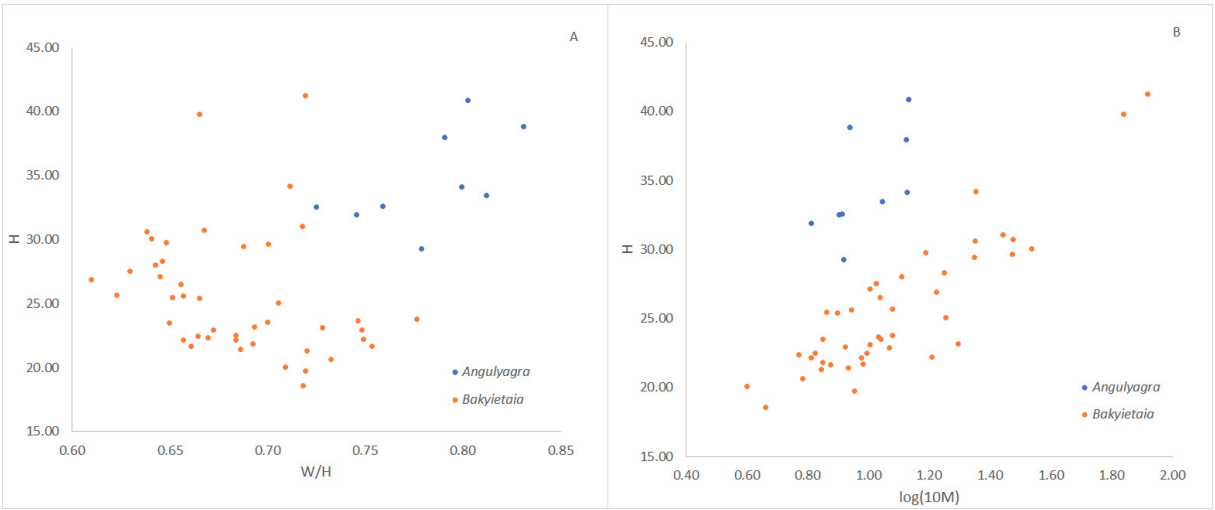


Fig. 3. Comparison of *Bakyietaia* Zhang, Yen & von Rintelen gen. nov. and *Angulyagra* Rao, 1931 with respect to parameters H and W/H (A), and with respect to parameters H and log (10M) (B).

Results

Genetic differentiation, phylogeny and species delimitation

The COI p-distances within species of *Bakyietaia* gen. nov. are 0–1.42% and between species of *Bakyietaia* are 1.68%–7.53%; the COI p-distances between *Bakyietaia* and other genera of Viviparidae are 8.45%–15.65%.

The phylogenetic trees reconstructed by BI and ML based on COI are congruent, but the ML tree (Supp. file 2) contains several substaintial polytomies and, therefore, only the BI tree is displayed (Fig. 2). The new genus *Bakyietaia* gen. nov. is monophyletic with high and low support in the BI and ML trees, respectively, and it is distinct from all other genera of Viviparidae included in the analysis. The type species of *Angulyagra* (*Angulyagra oxytropis*) is not included in the current tree. *Angulyagra costata* (Quoy & Gaimard, 1834) clusters with *Torotaia* cf. *mainitensis* (Bartsch, 1907) with a high degree of support and is not closely related to any species of *Bakyietaia*. *Filopaludina* Habe, 1964 (including type species *F. bengalensis* (Lamarck, 1822), *F. doliaris* (A. Gould, 1844), *F. javanica* (von dem Busch, 1844), *F. decipiens* (Tapparone Canefri, 1883)) is monophyletic with moderate to high support and in the BI analysis, and is recovered as the tentative sister clade of *Bakyietaia* with low support. The 17 morphologically identified species of *Bakyietaia* are each recovered as monophyletic, mostly with high support values, although the support for some species such as *B. liangzhuorum* gen. et sp. nov. and *B. wilhelmi* is weak to moderate.

The 17 groups/operational taxonomic units (OTUs) given by the ASAP analysis were the best partition from the lowest ASAP-score under all default settings. The two ASAP results are consistent with the phylogeny and morphological identifications.

Statistics of shell characters

The shell measurements reveal that *Angulyagra oxytropis* has a larger, more compact but lighter shell compared to species of *Bakyietaia* gen. nov. The shell height of *Angulyagra oxytropis* is larger than that of any species of *Bakyietaia*, and the larger W/H of *Angulyagra oxytropis* shows that it has a relatively more compact shell regardless of size (Table 1, Fig. 3A). *Angulyagra oxytropis* always has a larger shell than species of *Bakyietaia* when the mass of both is the same; correspondingly, *Angulyagra oxytropis* always has a much lighter shell than species of *Bakyietaia* when the height of both is the same (Fig. 3B).

Values are arithmetic means and standard deviations of height (H) and width (W) of *N* measured specimens and mass (M) of *n* measured completely dry shells.

Systematics

Class Gastropoda Cuvier, 1795
Order Architaenioglossa Haller, 1892
Family Viviparidae J.E. Gray, 1847
Subfamily Bellamyinae Rohrbach, 1937

Genus ***Angulyagra*** Rao, 1931

Dactylochlamys Rao, 1925: 132 [non *Dactylochlamys* Lauterborn, 1901 (Ciliophora), junior homonym]. *Angulyagra* Rao, 1931: 301.

Type species

Paludina oxytropis Benson, 1836, by original designation.

Diagnosis

"The shell is of large size, conical, thin but ornamented with prominent smooth spiral ridges which are concave on the internal surface. The base is somewhat flattened. The umbilicus is broadly rimate with a broad channel descending downwards from it. The mantle has enlarged and highly vascular finger-shaped processes on the margin" (Rao 1925).

Remarks

The shell of *Angulyagra* is most similar to that of *Torotaia* or *Dalipaludina*, all of them possessing a large thin shell with strong keels, acute apex, and simple columellar lip. It can be distinguished from the latter two genera based on the following combination of characters: teleoconch whorls with strong keels obviously darker than the rest of the shell surface in colour, open umbilicus bordered by a strong keel; operculum with growth lamellae on exterior surface and radial striae on interior surface; radula with narrow marginal teeth, the width of both inner and outer marginal teeth is only half that of the lateral teeth, and outer marginal teeth with 15 tiny cusps; highly vascular finger-shaped processes on the mantle margin.

Angulyagra oxytropis (Benson, 1836)
Fig. 4

Paludina oxytropis Benson, 1836: 745 (type locality not stated in the original description).
Paludina pyramidata von dem Busch, 1844 in Philippi 1842–1850: 113, pl. 1 figs 3–4.

Vivipara oxytropis – Preston 1915: 84. — Annandale & Seymour Sewell 1920: 113. — Annandale 1921: 544–552, figs 2–5.
Dactylochlamys oxytropis – Rao 1925: 132.
Angulyagra oxytropis – Rao 1931: 301. — Subba Rao 1989: 51, fig. 70. — Preece *et al.* 2022: 94, fig. 38a.

Diagnosis

Shell large, fragile and lightweight. Each teleoconch whorl with three strong keels, open umbilicus bordered by one strong keel. Operculum with growth lamellae on exterior surface and radial striae on interior surface. Inner and outer marginal teeth of radula both nearly half of lateral tooth in width. Mantle edge with a number of finger-shaped processes.

Material examined

Holotype
BENGAL • dry preserved specimen; NHMUK.1879.12.26.120.

Other material
INDIA • 8 specs (preserved dry, 6 adults and 2 juveniles); Manipur, Loktak "Logtak Lake"; NHMUK.1974.03.7.1 to NHMUK.1974.03.8 • 2 specs (preserved dry); Assam, Manipur, Loktak Lake; NHMUK.2019.04.31.

Description

Shell (Fig. 4A–F) large, broadly conical, thin, lightweight, fragile, olive to greenish brown; up to six whorls at adulthood, including one relatively smooth protoconch whorl, apex acute; each teleoconch whorl with three strong primary keels of darker colour, the strongest keel above suture, one to two weaker smooth secondary keels located between primary keels; base of shell with three to four spiral keels of darker colour, one to two weaker secondary keel located between strong primary keels; aperture

ovate, inner shell surface bluish white, with obvious grooves corresponding to the position of the three strong keels, outer lip thin, three strong keels extending to margin of outer lip, columellar lip thin and simple; umbilicus broadly open, bordered by a strong keel.

Operculum (Fig. 4G–H) corneous, transparent pale brown, rather thin; nucleus sub-central, close to inner margin; exterior surface with regularly distributed growth lamellae; interior surface with large inner opercular region and radial striae starting from nucleus; nuclear region relatively large, smooth and glossy, with veins at margin.

Radular central tooth with one broad central denticle and five small sharp cusps on either side; lateral tooth with one broad central denticle, three small sharp cusps on inner side and six small sharp cusps on outer side; inner and outer marginal teeth narrow, both nearly half of lateral tooth in width; inner marginal tooth with one broad central denticle and three small sharp cusps on either side; outer marginal tooth with 15 tiny sharp cusps (summarized based on the figure and description from Annandale 1921).

Mantle edge with a number of finger-shaped processes, three of these processes larger, each large process corresponding to a groove of the inner shell surface; gill lamella with a broad base and a long finger-shaped part; about ten embryos and ten eggs in the uterus of a pregnant female (summarized based on the figure and description from Rao (1925) and Annandale (1921)).

Remarks

This species can be easily distinguished from the other viviparid species according to the remarks for the genus. As the type species of *Angulyagra*, *A. oxytropis* shows large morphological and anatomical

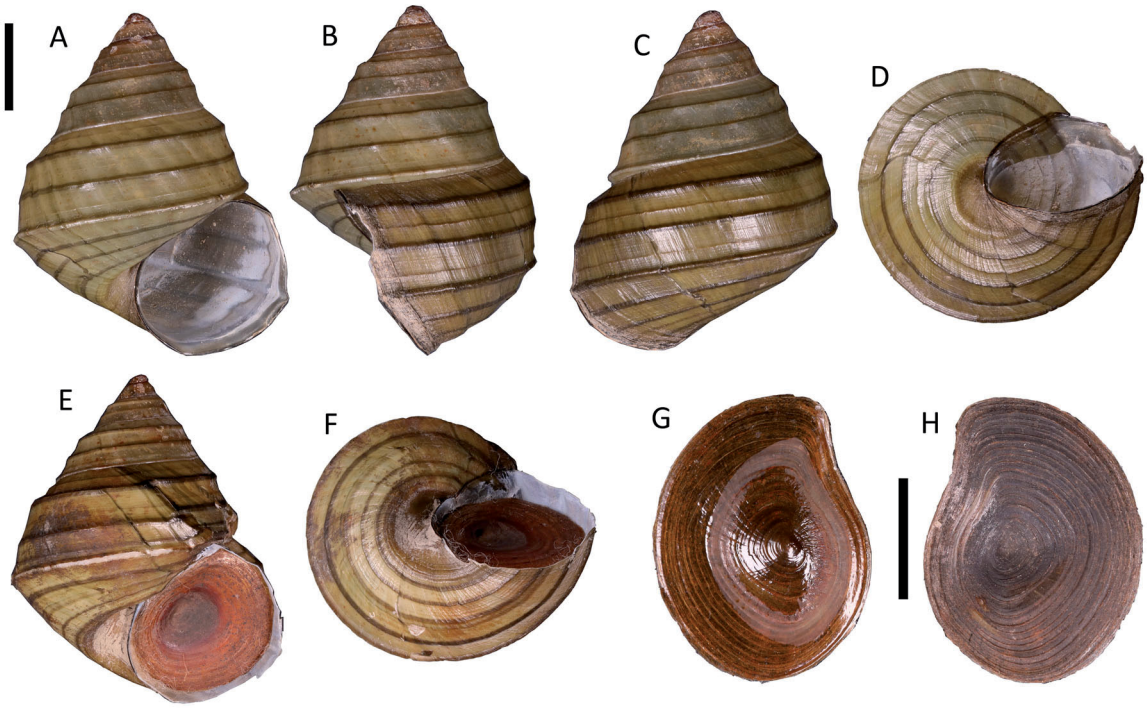


Fig. 4. Shells and operculum of *Angulyagra oxytropis* (Benson, 1836). **A–D**. NHMUK.2019.04.31.1, Loktak Lake, India. **E–F**. NHMUK.2019.04.31.2, Loktak Lake, India. **G–H**. Operculum of NHMUK.2019.04.31.1. Scale bars = 1 cm, top left bar applies to all shells, separate bar for operculum G–H.

differences to many species nominally assigned to *Angulyagra*, especially in the large, thin, light and fragile shell with an open umbilicus and simple columellar lip, the distinctive operculum, and marginal teeth of the radula.

Habitat and distribution

Loktak Lake and nearby wetland ponds in the Manipur Valley of India.

Identification key to genera *Bakyietaia* gen. nov., *Taia*, *Angulyagra, *Sinotaia*, *Anulotaia*, *Filopaludina***

1. Columellar lip recurved, forming callus covering umbilicus completely or partially 2
– Columellar lip simple, not recurved, umbilicus open 3

2. Primary keels smooth, operculum with small nuclear region (around 1/4 to 1/5 of inner opercular region) with shiny grains or veins ..... ***Bakyietaia*** Zhang, Yen & von Rintelen gen. nov.
– Keel absent, or with obvious spines or nodules on primary keel, inner opercular region completely or partly covered by a rough sandpaper-like layer ..... ***Taia*** Annandale, 1918

3. Umbilicus widely open, with a strong keel around, primary keels strong 4
– Umbilicus narrowly open, without obvious keel around, primary keel weak or absent 5

4. Shell large, ~35 mm in height, thin and fragile, operculum with growth lamellae on exterior surface and radial striae on interior surface, with large smooth nuclear region (around 1/3 of inner opercular region) ..... ***Angulyagra*** Rao, 1931
– Shell small to medium, always 20 to 30 mm in height, thick and solid, operculum with small nuclear region (around 1/5 of inner opercular region) with shiny grains or veins ..... ***Anulotaia*** Brandt, 1968

5. Operculum with small nuclear region with shiny grains or veins ..... ***Sinotaia*** Haas, 1939
– Operculum with inner opercular region (including nuclear region) completely or partly covered by a rough sandpaper-like layer ..... ***Filopaludina*** Habe, 1964

*Only characters of the type species of *Angulyagra* have been included when building the key.

Genus ***Bakyietaia*** Zhang, Yen & von Rintelen gen. nov.
urn:lsid:zoobank.org:act:0CAF30C4-7358-447E-864B-D3AE06F19240

Type species

Vivipara polyzonata Frauenfeld, 1862.

Diagnosis

Adult shell mostly medium in size for the family (20~30 mm in height), sturdy. Each teleoconch whorl with three to five (mostly three) strong smooth keels. Umbilicus covered by crescent-shaped callus formed from columellar lip. Operculum with small nuclear region (around 1/4 to 1/5 of inner opercular region) with shiny grains or veins. Inner marginal teeth of radula nearly half of outer marginal teeth in width. Mantle margin simple and smooth.

Etymology

'Bakyie' is derived from 'Bakyied' in the Zhuang Language (百越 in Chinese), referring to various ethnic groups living in South China and northern Vietnam; 'taia' refers to its similarity to the viviparid genus *Taia* Annandale, 1918. The recommended Chinese name is 越田螺.

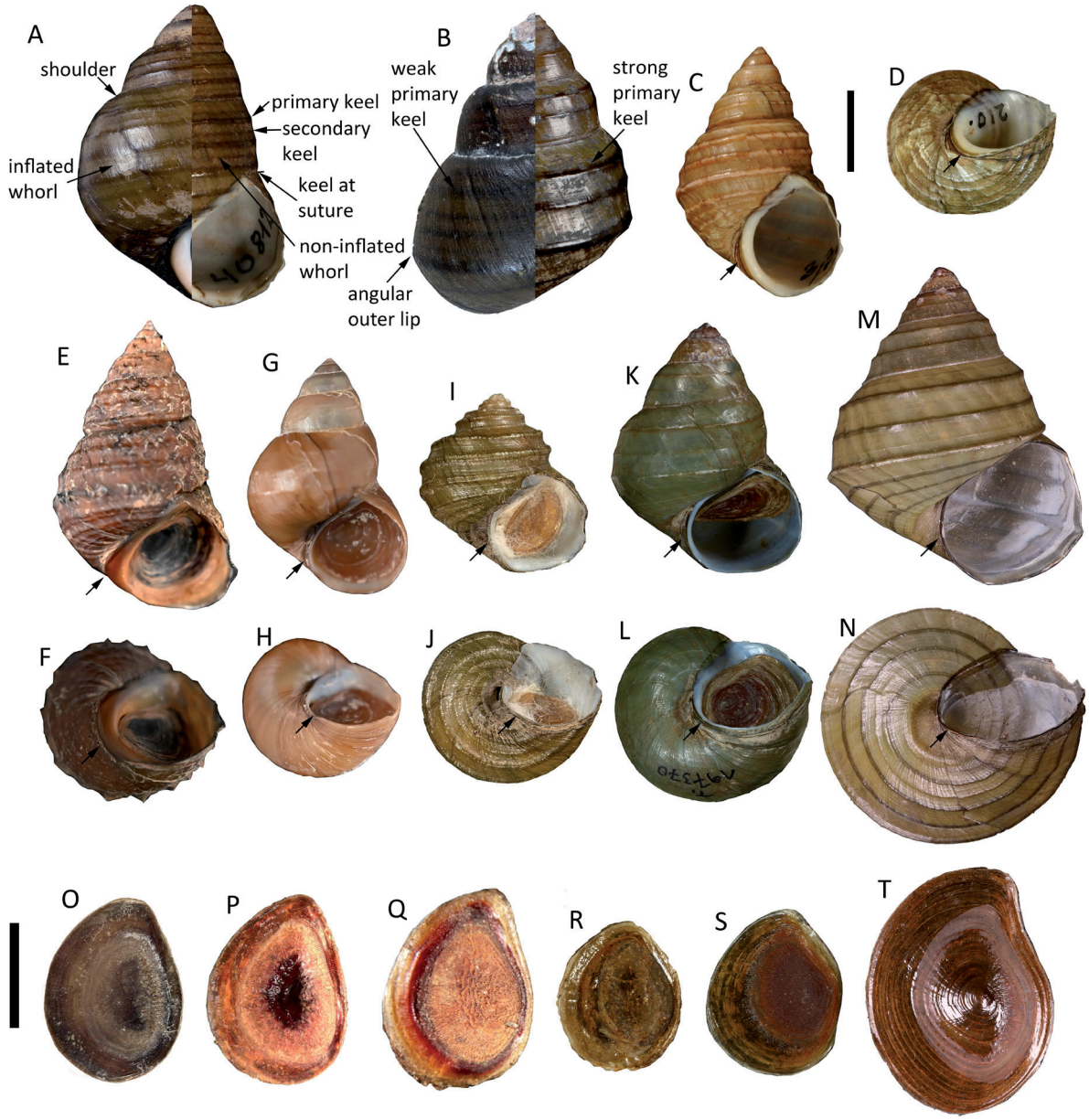


Fig. 5. Shell and opercula of *Bakyietaia* Zhang, Yen & von Rintelen gen. nov. and morphologically similar viviparid genera for comparison. **A–N**. Shells. **A–B**. Chimeras of species of *Bakyietaia* showing diagnostic characters of the shell. **C–D**. *Bakyietaia polyzonata* (Frauenfeld, 1862) gen. et comb. nov., NHMW 68037. **E–F**. *Taia* sp., Inle Lake, Myanmar. **G–H**. *Sinotaia* sp., Weishan Lake, Shandong, China. **I–J**. *Anulotaia forcarti* Brandt, 1968, SMF.197369, Maenam Mun, Thailand. **K–L**. *Filopaludina maekoki* Brandt, 1968, SMF.197370, Ban Mae Chai, Thailand. **M–N**. *Angulyagra oxytropis*. **O–T**. Opercula. **O**. *Bakyietaia boettgeri* (Möllendorff, 1890) gen. et comb. nov. **P**. *Sinotaia angularis* (O.F. Müller, 1774). **Q**. *Taia shanensis* (Kobelt, 1909). **R**. *Anulotaia forcarti* Brandt, 1968, SMF.193416. **S**. *Filopaludina maekoki* (Brandt, 1968), SMF.197370. **T**. *Angulyagra oxytropis* (Benson, 1836). Scale bars: shells (C–N) = 1 cm; operculum (O–T) = 0.5 cm. The columellar lip of the shell is indicated by arrows (C–N).

Description

Shell mostly medium in size for the family (20~30 mm in height), thin to thick, solid, conical; apex acute, teleoconch whorls with three to four smooth primary keels, with one to two weaker smooth secondary keels located between suture and first keel, base of shell with one to six keels, keels usually darker than rest of shell surface; recurved columellar lip from different growing periods sometimes forming a crescent-shaped callus, normally covering umbilicus; operculum with smooth exterior surface and a relatively small nuclear region (around 1/4 to 1/5 of inner opercular region) with shiny grains or veins; radula with narrow inner marginal teeth (narrower than lateral teeth) and wide outer marginal teeth (almost same as lateral teeth in width), outer marginal teeth with 15 to 43 tiny cusps; mantle margin simple and smooth.

Remarks

Previously described species in this genus have hitherto mostly been assigned to the genus *Angulyagra*, while a few have been assigned to the genera *Taia* or *Sinotaia*. Species of *Bakyietaia* gen. nov. can be

Fig. 6. Habitat (A–F) and living animals (G–I) of species of *Bakyietaia* Zhang, Yen & von Rintelen gen. nov. **A**. Xi River near Xiaoxiang Town, Guangdong, China. **B**. Spring pool near Longpo Temple, Hainan, China. **C**. Yangshan Reservoir, Hainan, China. **D**. Yangshan Wetland, Hainan, China. **E**. Baishou River, Guangxi, China. **F**. Concrete canal in Zhadian Village, Yunnan, China. **G**. *Bakyietaia guangdungensis* (Kobelt, 1906) gen. et comb. nov. from Yangshuo, Guangxi, China. **H**. *Bakyietaia chenghuang* Zhang, Yen & von Rintelen gen. et sp. nov. from Chenghuang Town, Guangxi, China. **I**. *Bakyietaia liangzhuorum* Yen, Zhang & von Rintelen gen. et sp. nov. from Chenghuang Town, Guangxi, China.

easily distinguished from species of *Angulyagra* based on their smaller, more solid and heavier shell with a crescent-shaped callus-like structure formed from the columellar lip covering the umbilicus; the characters of the operculum and the radula of *Bakyietaia* are obviously distinct from those of *Angulyagra*; the mantle margin of species of *Bakyietaia* is smooth and does not bear the 'finger-shaped processes on the margin' of the mantle as observed in *Angulyagra*. *Taia*, *Sinotaia*, *Anulotaia* and some species of *Filopaludina* have a similar medium-sized and solid conical shell (Fig. 5).

Bakyietaia gen. nov. can be distinguished from these genera based on the following combination of characters: teleoconch whorls with three smooth primary keels and one to two weaker secondary keels, mostly darker in colour than the other part of shell surface; recurved columellar lip from different growing periods usually completely covering umbilicus; inner marginal teeth narrow, outer marginal teeth wide and with 15 to 30 tiny cusps. The COI tree supports the notion that *Bakyietaia* is a lineage distinct from *Taia*, *Sinotaia*, *Anulotaia*, *Filopaludina* and *Angulyagra costata*.

We have checked the type specimens of *Angulyagra thersites* (Reeve, 1864) from Hongkong, China, and we are confident that it should be assigned to the genus *Sinotaia*. A future taxonomic revision of this species should be based on a systematic study of *Sinotaia*. In addition, *Bakyietaia* gen. nov. is usually dominant and the only viviparid group in its habitat. Species of *Bakyietaia* are found to co-occur with widely-distributed species of *Sinotaia* in some localities, but seldom found to co-occur with species of other genera of Viviparidae.

Habitat and distribution

Found in many kinds of lentic and lotic freshwater habitats (Fig. 6). Native to southern China, northern to central Vietnam and Laos.

Identification key to species of *Bakyietaia* gen. nov.

1. Shell rounded, primary keels weak, height and width isometric 2
– Shell conical, shell height obviously larger than width 3

2. 29–43 cusps in outer marginal teeth .....***B. subcostata*** (Gray, 1833) gen. et comb. nov.
– 14–15 cusps in outer marginal teeth .... ***B. chenghuang*** Zhang, Yen & von Rintelen gen. et sp. nov.

3. Three to five weak primary keels on body whorl, sometimes as smooth as spiral lines 4
– Three to five strong primary keels on body whorl 8

4. Shell height usually less than 20 mm, spiral whorls lower, shoulder angular .....
..... ***B. luikongi*** Yen, Zhang & von Rintelen gen. et sp. nov.
– Shell height greater than 20 mm, spiral whorls higher, shoulder rounded 5

5. Whorls nearly cylindrical, weak keel above suture, outer lip not angular .....
..... ***B. naiadica*** Zhang, Yen & von Rintelen gen. et sp. nov.
– Whorls nearly trapezoidal, prominent keel above suture, outer lip angular 6

6. Whorls not inflated, shoulder rounded, 26–29 cusps in outer marginal teeth .....
..... ***B. fontinalis*** Zhang, Yen & von Rintelen gen. et sp. nov.
– Whorls inflated, shoulder angular, 19–24 cusps in outer marginal teeth 7

7. Prominent keel above suture, distributed in northern Hainan Island, China .....
..... ***B. mutica*** (Kobelt, 1909) gen. et comb. nov.
– Moderate keel above suture, distributed in southern Hainan Island, China .....
..... ***B. luuemxlong*** Zhang, Yen & von Rintelen gen. et sp. nov.

8. Shell height greater than 30 mm, solid and thick, whorls inflated, shoulder angular ..... ***B. duchieri*** (Fischer, 1898) gen. et comb. nov.
– Shell height usually smaller than 30 mm 9

9. Shell height usually less than 20 mm, whorls inflated, prominent keel above suture, 28–30 cusps in outer marginal teeth .....***B. guangdungensis*** (Kobelt, 1906) gen. et comb. nov.
– Shell height between 20 and 30 mm 10

10. Shell thin, shoulder more angular, whorls inflated 11
– Shell thick, shoulder more rounded, whorls not inflated 13

11. Moderate keel above suture, outer lip more rounded, distributed in northern Vietnam and across the border in SW Guangxi, China .....***B. polyzonata*** (Frauenfeld, 1862) gen. et comb. nov.
– Prominent keel above suture, outer lip more angular 12

12. More inflated whorls and more prominent keel at suture, distributed in central Vietnam ....***B. indrapura*** Zhang, Yen & von Rintelen gen. et sp. nov.
– Less inflated whorls and less prominent keel at suture, distributed in Guangdong and across the border in SE Guangxi, China ..... ***B. avisvenatoris*** Yen, Zhang & von Rintelen gen. et sp. nov.

13. Spire low, W/H 0.72~0.74 14
– Spire high, W/H 0.68~0.70 15

14. Primary keels less prominent, outer lip thin, 26–27 cusps in outer marginal teeth, distributed in nothern Guangxi, China .....***B. liusanjieae*** Zhang, Yen & von Rintelen gen. et sp. nov.
– Primary keels more prominent, outer lip thick, 24–27 cusps in outer marginal teeth, distributed in eastern Guangxi and central Guangdong, China .... ***B. liangzhuorum*** Yen, Zhang & von Rintelen gen. et sp. nov.

15. Moderate keel above suture, 18–25 cusps in outer marginal teeth, mostly distributed in Guangdong, China ..... ***B. wilhelmi**** (Yen, 1939) gen. et comb. nov.
– Prominent keel above suture, 23–28 cusps in outer marginal teeth, not occurring in Guangdong, China 16

16. 23–24 cusps in outer marginal teeth, distributed in southern Guangxi and northern Hainan Island, China .....***B. boettgeri*** (Möllendorff, 1890) gen. et comb. nov.
– 26–28 cusps in outer marginal teeth, distributed in Vietnam, across the border in western Guangxi and western Hainan Island, China .....***B. jingweiae*** Yen, Zhang & von Rintelen gen. et sp. nov.

***** In light of the high phenotypic plasticity in *B. wilhelmi*, incorporates only the morphological traits of the holotype. DNA barcoding may be required to confirm the species identity of other morphological variations of this species.

Bakyietaia polyzonata (Frauenfeld, 1862) gen. et comb. nov.
Figs 7–8

Vivipara polyzonata Frauenfeld, 1862: 1165–1166 (type locality not stated in the original description).

Paludina polyzonata – Fischer & Dautzenberg 1904: 92. — Dautzenberg & Fischer 1908: 199.
Angulyagra polyzonata – Thanh *et al.* 2004: 3–4, fig. 4. — Richter 2015: 127–128, fig. 3.5.
Angulyagra boettgeri – Madsen & Hung 2014: 109, fig. 2 (10 right) [non *Paludina boettgeri* Möllendorff, 1890].

Diagnosis

Shell medium (26.60 ± 1.91 mm), thin and conical, whorls inflated, primary keels smooth, moderate keel above suture, outer lip rounded; columellar lip recurved, umbilicus completely or partly calloused; operculum with small nuclear region (around 1/4 of inner opercular region) with shiny grains or veins.

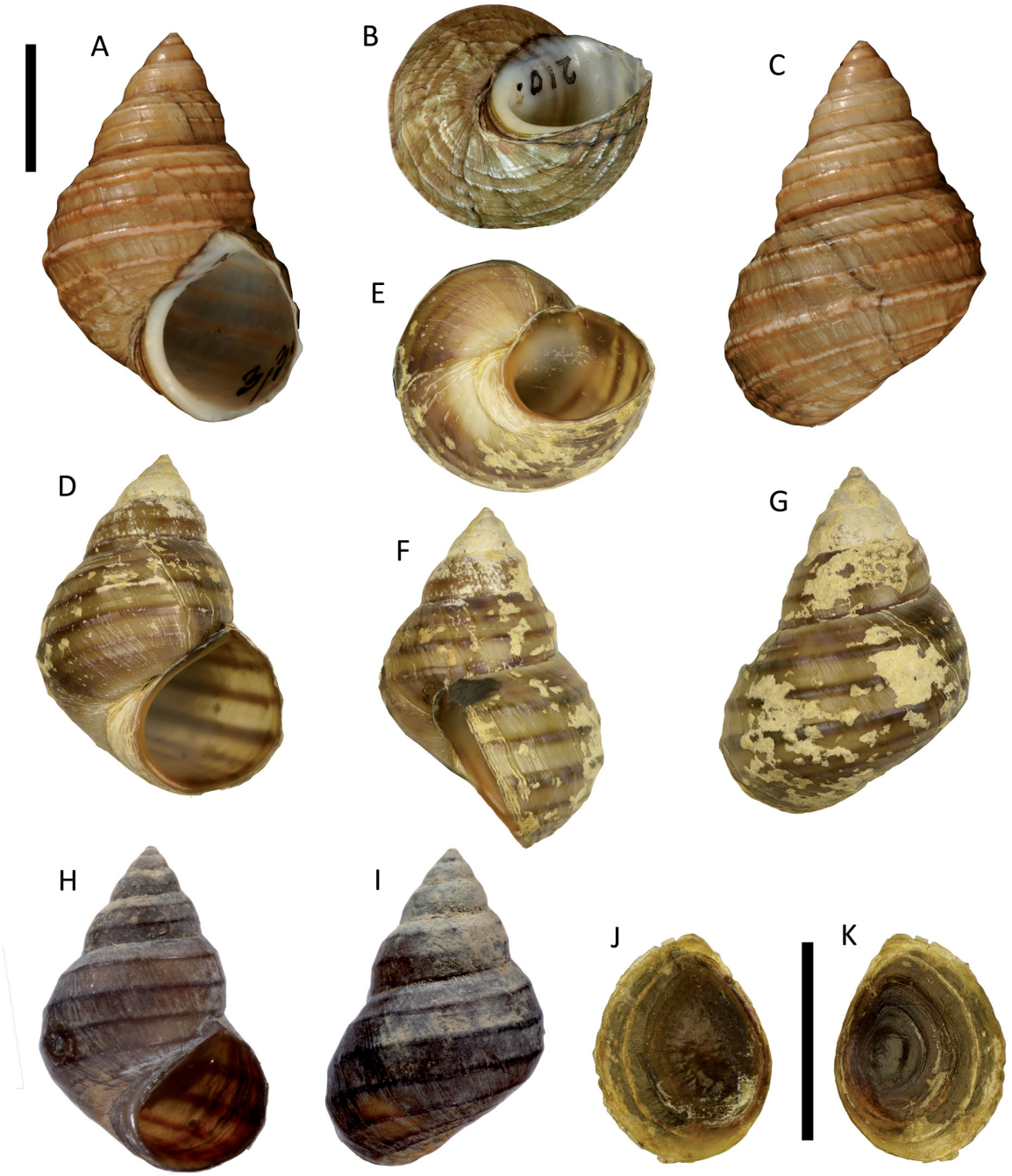


Fig. 7. Shells and operculum of *Bakyietaia polyzonata* (Frauenfeld, 1862) gen. et comb. nov. **A–C**. Lectotype, NHMW 68037, photos by A. Schumacher and I. Gallmetzer. **D–G**. KIZ.240051, Longzhou, Guangxi, China. **H–I**. ZMB.114171, Deng Dang, Vietnam. **J–K**. Operculum of KIZ.240051. Scale bars = 1 cm, top left bar applies to all shells, separate bar for operculum J–K.

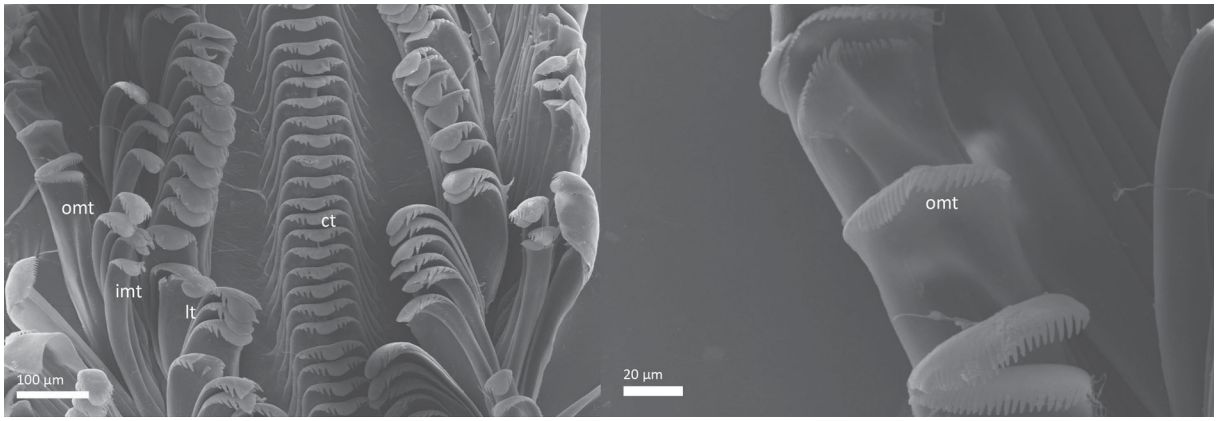


Fig. 8. SEM photo of the radula of *Bakyietaia polyzonata* (Frauenfeld, 1862) gen. et comb. nov., ZMB.114171.

Material examined

Lectotype

CHINA? • dry preserved specimen; designated by Yen (1939); NHMW68037.

Paralectotype

CHINA? • 1 spec. (preserved dry); NHMW68038.

Other material

CHINA • 3 specs (preserved in ethanol); Guangxi, Chongzuo City, Longzhou County, Shuikou Town, Poliu Village, outlet of an underground river in a cave; 4 Mar. 2023; KIZ.240051 to KIZ.240053.

VIETNAM • 11 specs (preserved in ethanol); Ninh Binh, Reservoir near Dang, Cuc Phuong N.P.; ZMB.114132 • 1 spec. (preserved in ethanol); Hoa Binh, Tan Lac district, Ngoc Ly; ZMB.114150 • 3 specs (preserved in ethanol); Bac Kan, Phu Luong, Yen Ninh, Dong Dang; ZMB.114171.

Description

Adult shell (Fig. 7A–J) medium in size (26.60 ± 1.91 mm), thin but sturdy, conical, olive to greenish brown, with five to six whorls, apex acute; teleoconch whorls slightly inflated especially on body whorl. Shoulder angular, with three smooth primary keels and one to two weaker smooth secondary keels between suture and first keel. Sometimes, one additional weak keel located between first and second/second and third keels. Shell base with three to five weak keels, and usually darker than other parts of shell surface; aperture ovate, less than half of shell in height, inner shell surface bluish white, outer lip thin, smooth and rounded. Inner layers of adult columellar lip thickened, white or orange, recurved columellar lip partially or wholly covering umbilicus, sometimes forming a callus.

Operculum (Fig. 7J–K) corneous, ovate, thin, yellow to orange; exterior surface smooth; interior surface with smal nuclear region (around 1/4 of inner opercular region), with shiny grains or veins.

Radular (Fig. 8) (n = 4) central tooth with one broad central denticle and five small sharp cusps on either side; lateral tooth with one broad central denticle and five small sharp cusps on either side; inner marginal tooth narrow, about half of lateral tooth in width, with one broad central denticle and five to six small sharp cusps on either side; outer marginal tooth wide, almost same as lateral tooth in width, with 21 to 26 small sharp cusps.

Remarks

The newly collected specimens from Longzhou, China have a shell that is very similar to that of the lectotype. The type locality of this species was not clear from the original description, and it was considered simply as China (Yen 1939). *Bakyietaia polyzonata* can be distinguished from most congeners, especially *Bakyietaia indrapura* gen. et sp. nov., by its medium-sized, thin conical shell with inflated whorls, more rounded outer lip and distribution. The recommended Chinese name is 多棱越田螺.

Habitat and distribution

Rivers and lakes of Western Guangxi of China and Northern Vietnam.

Bakyietaia subcostata (Gray, 1833) gen. et comb. nov.
Figs 7–8

Paludina subcostata Gray, 1833 in Griffith & Pidgeon 1833–1834: 599, pl. 36 fig. 3 ("China").
Paludomus futaii Gredler, 1889: 159 ("Peho, Kuang-tung", refers to Bei River, Guangdong Province, China). **Syn. nov.**

Sinotaia? *futaii* – Zilch 1974: 64, pl. 7 fig. 9.
Angulyagra subcostata – Liu *et al.* 1995: 14.

Diagnosis

Adult shell medium to large (27.17 ± 3.64 mm), rounded and thin, primary keels weak, teleoconch with weak primary keels; columellar lip recurved, forming callus covering umbilicus completely; operculum with small nuclear region (around 1/5 of inner opercular region) with shiny grains or veins; outer marginal tooth of radula with 29 to 43 small sharp cusps.

Material examined

Holotype of *Paludina subcostata*
CHINA • dry preserved specimen; NHMUK.2007.01.7.1.

Holotype of *Paludomus futaii*
CHINA • dry preserved specimen; Guangdong Province, Bei River; GFBI.22.

Other material
CHINA – **Guangdong Province** • 4 specs (preserved in ethanol); Guangzhou City, Zhengguo Town, Zeng River, 0.7 m deep under rock; 25 Sep. 2019; Da-Ming Shi leg.; ZMB.122694 • 3 specs (preserved dry); Guangzhou City, Zhengguo Town, Zeng River, 0.7 m deep under rock; 25 Sep. 2019; Da-Ming Shi leg.; YHY-BAKSUB-ZG-1, YHY-BAKSUB-ZG-18, YHY-BAKSUB-ZG-28 • 3 specs (preserved dry); Zhaoqing City, Xiaoxiang Town, Xi River, under rock; Aug. 2021; Ji-Lin Jiang leg.; KIZ.240084 • 2 specs (preserved in ethanol); Qingyuan City, Shitan Town, Bin River, 0.6 m deep on rock; 24 Sep. 2022; Mr Chen leg.; ZMB.122767 • 2 specs (preserved dry); Qingyuan City, Shitan Town, Bin River, 0.6 m deep on rock; 24 Sep. 2022; Mr Chen leg.; YHY-BAKSUB-ST-1, YHY-BAKSUB-ST-4 • 2 specs (preserved in ethanol); Zhaoqing City, Huaiji County, Sui River; 15 Sep. 2022; ZMB.122766 • 1 spec. (preserved in ethanol); Qingyuan City, Jintan Town, Bin River; 10 Oct. 2022; KIZ.240085 • 4 specs (preserved in ethanol); Zhaoqing City, Fengkai County, Xi River; 19 Jan. 2024; Lejia Zhang leg.; KIZ.240086.

Description

Adult shell (Fig. 9A–Q) medium to large (27.17 ± 3.64 mm), thin but sturdy, rounded, olive to dark brown; with five to six whorls, apex acute; teleoconch whorls inflated, sometimes forming shoulder, with three smooth weak primary keels, with one to two weaker smooth secondary keels located between

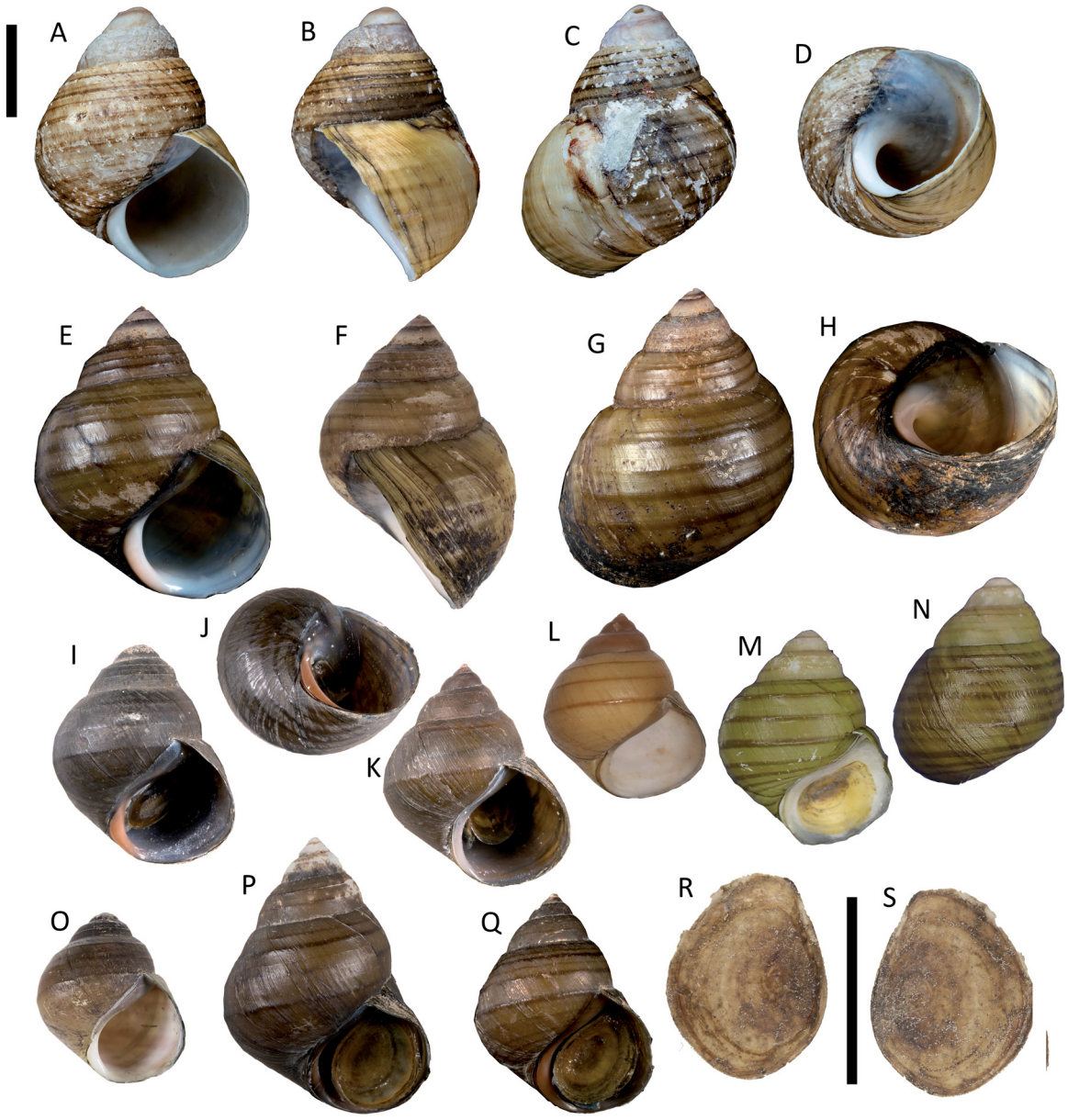


Fig. 9. Shells and operculum of *Bakyietaia subcostata* (Gray, 1833) gen. et comb. nov. **A–D**. Holotype, NHMUK.2007.01.7.1, China, photo by Jonathan Ablett. **E–H**. KIZ.240084, Xiaoxiang Town, Guangdong, China. **I–J**. ZMB.122766, Huaiji County, Guangdong, China. **K**. KIZ.240085, Jintan Town, Guangdong, China. **L**. Holotype of *Paludomus futaii*, GFBI.22, Bei River, Guangdong, China. **M–O**. YHY-BAKSUB-ZG-18 (M), YHY-BAKSUB-ZG-28 (N), ZMB.122694 (O), Zhengguo, Guangdong, China. **P–Q**. ZMB.122767, Shitan Town, Guangdong, China. **R–S**. Operculum of KIZ.240086; scale bars = 1 cm, top left bar applies to all shells, separate bar for operculum R–S.

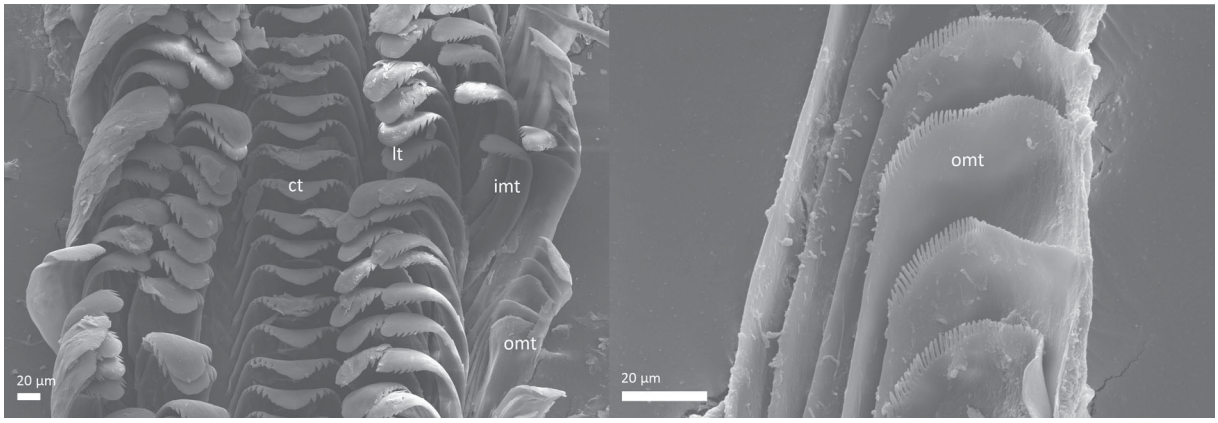


Fig. 10. SEM photo of the radula of *Bakyietaia subcostata* (Gray, 1833) gen. et comb. nov., ZMB.122766.

suture and first keel, sometimes one additional weak keel located between first and second/second and third keels, base of shell with three to five weak keels; aperture ovate, large, around half of shell in height, inner shell surface bluish white to purple, outer lip thin, always with a relatively rounded periphery, columellar lip covered with thick inner shell layers, always whitish orange or pink, adult columellar lip recurved, forming a very narrow crescent-shaped callus or without this structure, columellar lip or this structure completely covering umbilicus.

Operculum (Fig. 9R–S) corneous, ovate, thin, yellow; exterior surface smooth; interior surface with nuclear region small, around 1/5 of inner opercular region, with shiny grains or veins.

Radular (Fig. 10) (n = 4) central tooth with one broad central denticle and five to six small sharp cusps on either side; lateral tooth with one broad central denticle and five small sharp cusps on either side; inner marginal tooth narrow, about half of lateral tooth in width, with one broad central denticle and four small sharp cusps on either side; outer marginal tooth wide, almost same as lateral tooth in width, with 29 to 43 small sharp cusps.

Remarks

Bakyietaia subcostata can be easily distinguished from most congeners based on the rounded thin shell with weak primary keels. It can be differentiated from the morphologically similar species *Bakyietaia chenghuang* gen. et sp. nov. based on the larger number of small cusps on the outer marginal teeth of the radula (29–43 vs 15–16). *Paludomus futaii* was described based on a juvenile shell of this species, and it is here placed in synonymy of *B. subcostata*. The recommended Chinese name is 次肋越田螺.

Habitat and distribution

Rock substrate in the shallow water of rivers of Guangdong Province, China.

Bakyietaia boettgeri (Möllendorff, 1890) gen. et comb. nov.
Figs 11–12

Paludina boettgeri Möllendorff, 1890 in Heude 1882–1890: 177, pl. 10 fig. 6 (“Hai-nan”, Hainan Province, China).

Viviparus (*Taia*) *boettgeri* – Zilch 1938: 131.
Angulyagra boettgeri – Yen 1939: 38, pl. 3 fig. 17. — Liu *et al.* 1995: 14.

Diagnosis

Adult shell medium to large (26.76 ± 6.67 mm), sturdy, conical, whorls not inflated, prominent keel above suture; columellar lip recurved, forming callus covering umbilicus completely; operculum with small nuclear region (around 1/5 of inner opercular region) with shiny grains or veins; outer marginal tooth of radula with 23 to 24 small sharp cusps.

Material examined

Paratypes

CHINA • 5 specs (preserved dry); Hainan Island; O. Böttger leg.; SMF.7651 • 2 specs (preserved dry); Hainan Island; O.v. Möllendorff leg.; SMF.7653.

Other material

CHINA – **Guangxi** • 1 spec. (preserved in ethanol); Nanning City, Dawangtan Reservoir; Aug. 2019; KIZ.240087 • 5 specs (preserved in ethanol); Baise City, Youjiang District, Wula Village, Sanglu, 0.5 m deep on rocks of creeks; 17 Oct. 2019; Jian-Zhuo Li leg.; ZMB.122687 • 3 specs (preserved dry); same data as for preceding; YHY-BAKBOE-SL-1, YHY-BAKBOE-SL-2, YHY-BAKBOE-SL-18 • 5 specs (preserved in ethanol); Guigang City, Gangnan District, Batang Village, a pond near Yapengling, 0.7 m deep on rocks; 31 Oct. 2020; Xia-Ming Li leg., ZMB.122759 • 1 spec. (preserved dry); same data as for preceding; YHY-BAKBOE-BT-1 • 1 spec. (preserved dry); Chongzuo City, Daxin County, Leiping Town, Heishui River, 1 m deep on rocks; 27 Mar. 2021; Yi-Wen Liang leg.; ZMB.122690 • 4 specs (preserved dry); same data as for preceding; YHY-BAKBOE-HSH-21, YHY-BAKBOE-HSH-15, YHY-BAKBOE-HSH-9, YHY-BAKBOE-HSH-3 • 4 specs (preserved in ethanol); Chongzuo City, Jiangzhou District, Tuozao Village, Zuo River, 0.5 to 1.5 m deep on rocks; 27 Mar. 2021; Yi-Wen Liang leg.; ZMB.122758 • 3 specs (preserved dry); same data as for preceding; YHY-BAKBOE-JZ-15, YHY-BAKBOE-JZ-14, YHY-BAKBOE-JZ-1 • 2 specs (preserved in ethanol); Nanning City, Mashan County, Shitang Village, 0.3 m deep on sand/mud substrate in the wetland; 19 Mar. 2022; Le-Jia Zhang leg.; ZMB.122734 • 3 specs (preserved in ethanol); Pingguo City, Yihao Village, Bujian River, 0.5 to 1 m deep on mud substrate; 19 Mar. 2022; Le-Jia Zhang leg.; ZMB.122720. – **Hainan Province** • 2 specs (preserved dry); Hainan Island, Jetschin leg.; SMF.88400 • 5 specs (preserved in ethanol); Haikou, wetlands near Yangshan Reservoir; 20 Oct. 2019; bought by Sheng-Zhuo Huang on local market; ZMB.122710.

Description

Adult shell (Fig. 11A–R) medium to large (26.76 ± 6.67 mm), thin to thick, sturdy, conical, olive brown to dark brown, with five to six whorls, apex acute; teleoconch whorls not inflated, with three smooth primary keels, with one to two weaker smooth secondary keels located between suture and first keel, sometimes one additional weak keel located between first and second/second and third keels, base of shell with one to five weak keels, all keels usually darker than rest of shell surface, prominent keel above suture; aperture ovate, less than half of shell in height, inner shell surface bluish white, orange-red or dark purple, outer lip thin, always with an obvious angular periphery, columellar lip covered with thick inner shell layers, white or orange-red, adult columellar lip recurved, forming a relatively wide crescent-shaped callus, completely covering umbilicus.

Operculum (Fig. 11S–T) corneous, ovate, relatively thick, dark red; exterior surface smooth; interior surface with small nuclear region, around 1/5 of inner opercular region, with shiny grains or veins or smooth glossy surface.

Radular (Fig. 12) (n = 3) central tooth with one broad central denticle and five to six small sharp cusps on either side; lateral tooth with one broad central denticle and four to five small sharp cusps on either side; inner marginal tooth narrow, about half of lateral tooth in width, with one broad central denticle and

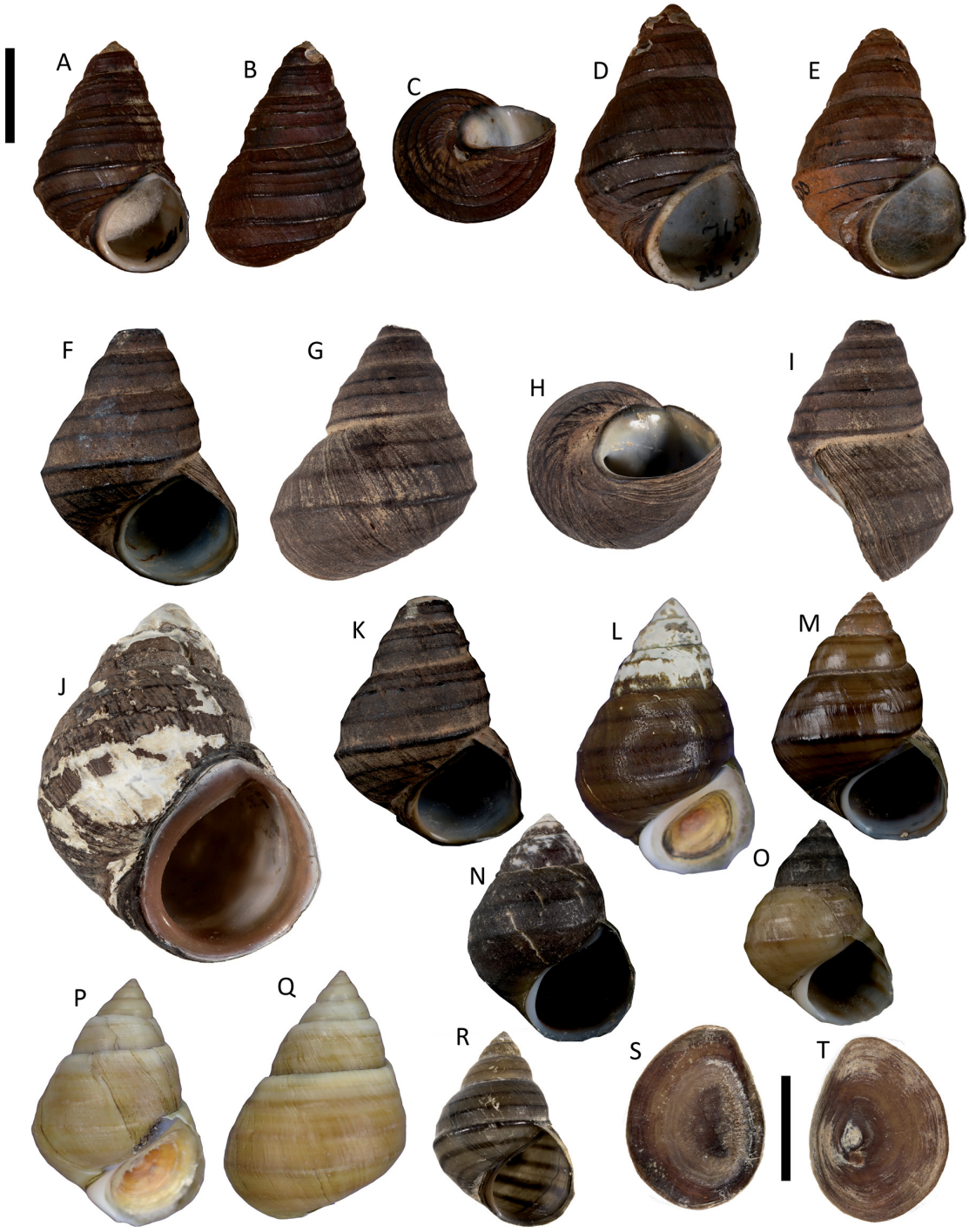


Fig. 11. Shells and operculum of *Bakyietaia boettgeri* (Möllendorff, 1890) gen. et comb. nov. **A–C**. Paratype, SMF.7651, Hainan, China. **D**. Paratype, SMF7653, Hainan, China. **E**. SMF.88400, Hainan, China. **F–I**. ZMB.122710, Haikou, Hainan, China. **J**. KIZ.240087, Nanning, Guangxi, China. **K**. ZMB.122687, Sanglu, Guangxi, China. **L**. YHY-BAKBOE-JZ-1, Jiangzhou, Guangxi, China. **M**. ZMB.122720, Pingguo, Guangxi, China. **N**. ZMB.122758, Jiangzhou, Guangxi, China. **O–Q**. ZMB.122690 (O), YHY-BAKBOE-HSH-9 (P–Q), Leiping, Guangxi, China. **R**. ZMB.122734, Mashan County, Guangxi, China. **S–T**. Operculum of KIZ.240087. Scale bars = 1 cm, top left bar applies to all shells, separate bar for operculum K–L.

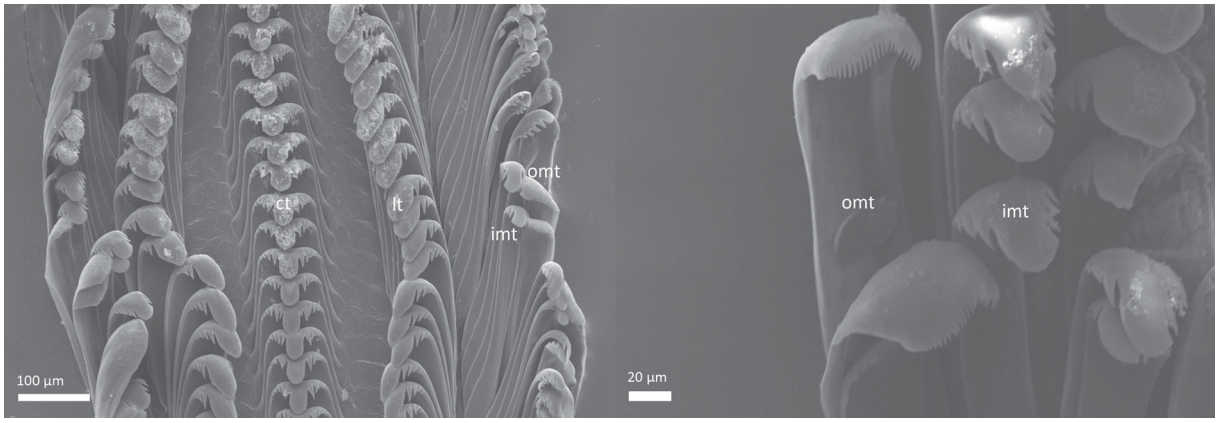


Fig. 12. SEM photo of the radula of *Bakyietaia boettgeri* (Möllendorff, 1890) gen. et comb. nov., ZMB.122710.

four small sharp cusps on either side; outer marginal tooth wide, almost same as lateral tooth in width, with 23 to 24 small sharp cusps.

Remarks

The newly collected specimens from Haikou City of Hainan have a shell that is very similar to that of the type specimens. *Bakyietaia boettgeri* can be distinguished from most congeners based on its medium-sized to large conical shell with non-inflated whorls, and strongly keeled suture. Some small individuals of this species may be confused with *Bakyietaia jingweiae* Yen, Zhang & von Rintelen gen. et sp. nov. based on shell morphology, but differ by possessing fewer cusps on the outer marginal tooth (23–24 vs 26–28). The COI tree supports *B. boettgeri* and *B. jingweiae* as distinct species, and the two species are allopatric (Fig. 1). The recommended Chinese name is 伯氏越田螺.

Habitat and distribution

Mud, sand and rock substrate in the shallow water of rivers, lakes and wetlands of northern Hainan and southern Guangxi, China.

Bakyietaia duchieri (Fischer, 1898) gen. et comb. nov.
Fig. 13

Paludina duchieri Fischer, 1898: 330–331, pl. 18 figs 48–49 ("Riv. Song-KI-Kong, à Déo-Cat", Kỳ Cùng River, at Đèo Khách, Lạng Sơn, Vietnam).

Angulyagra duchieri – Starobogatov 1970: 202. — Thanh *et al.* 2004: 3–4, fig. 5.
Angulyagra boettgeri – Madsen & Hung 2014: 109, figs 2 (10 left), (10 middle) [non *Paludina duchieri* Fischer, 1898].

Diagnosis

Shell large (32.88 ± 1.00 mm), thick and sturdy, whorls inflated, with narrow angular shoulder; columellar lip recurved, forming callus covering umbilicus completely; operculum with small nuclear region (around 1/5 of inner opercular region) with shiny grains or veins.

Material examined

Holotype

VIETNAM • dry preserved spec.; Lạng Sơn, Đèo Khách, Kỳ Cùng River; Juillet Billet leg.; MNHN-IM-2000-4486.

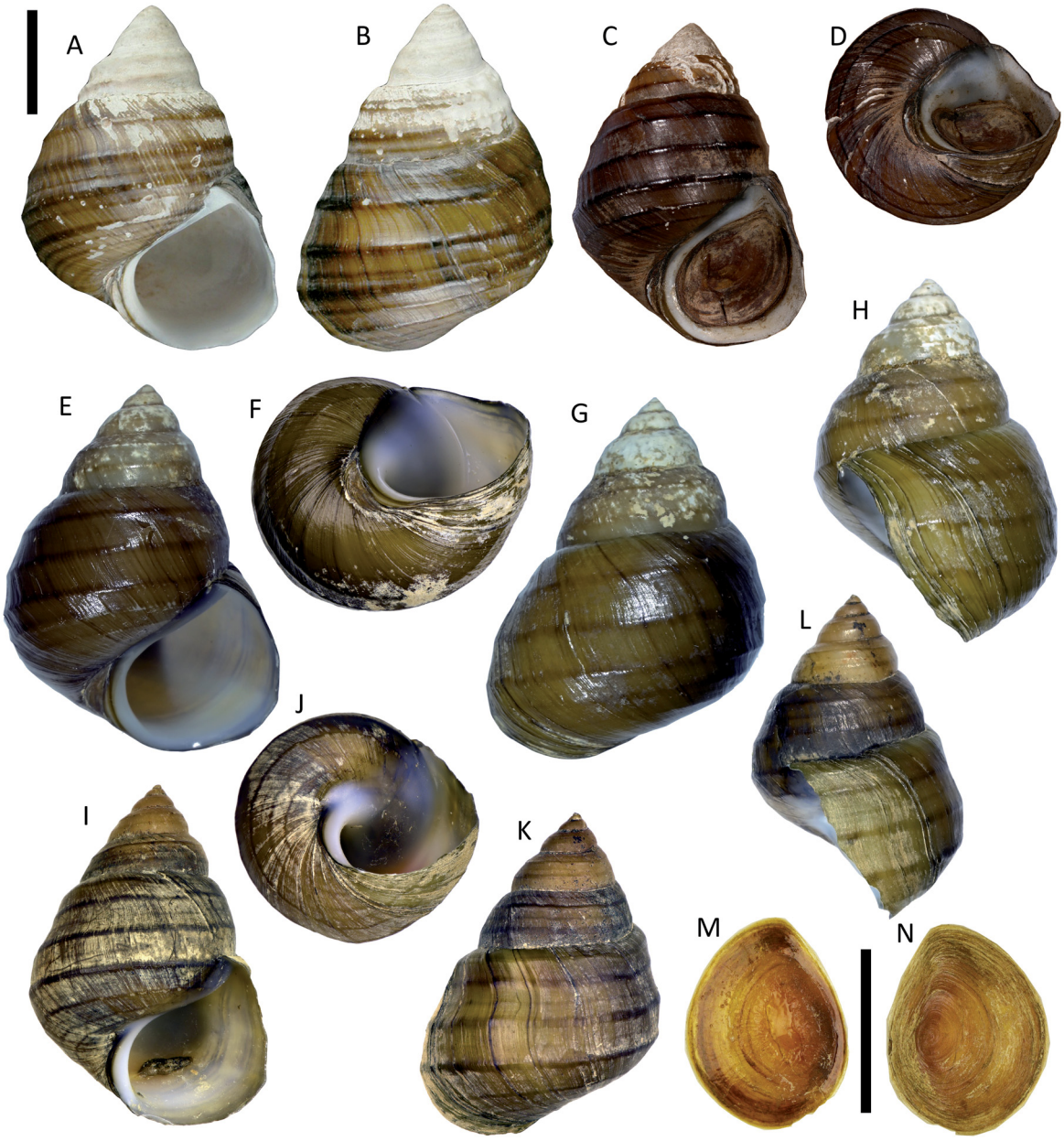


Fig. 13. Shells and operculum of *Bakyietaia duchieri* (Fischer, 1898) gen. et comb. nov. **A–B**. Holotype, MNHN-IM-2000-4486 (http://coldb.mnhn.fr/catalognumber/mnhn/im/2000-4486, credit: MNHN-Brabant D.-2005), Đèo Khách, Lạng Sơn, Vietnam. **C–D**. SMF.48146, Tonkin, Vietnam. **E–L**. KIZ.240049–240050, Longzhou, Guangxi, China. **M–N**. Operculum of KIZ.240049. Scale bars = 1 cm, top left bar applies to all shells, separate bar for operculum M–N.

Other material

CHINA • 2 specs (preserved in ethanol); Guangxi, Chongzuo City, Longzhou County, Shuikou Town, Poliu Village, Shuikou River, 0.5 m deep on mud substrate; 4 Mar. 2023; KIZ.240049, KIZ.240050.

VIETNAM • 1 spec. (preserved dry); "Tonkin" (Hanoi); O.v. Möllendorff leg.; SMF.48146

Description

Adult shell (Fig. 13A–K) large (32.88 ± 1.00 mm), thick, sturdy, conical, olive to olive brown, with six whorls, apex acute; teleoconch whorls slightly inflated, with three smooth primary keels, with one to two weaker smooth secondary keels located between suture and first keel, sometimes one additional weak keel located between first and second/second and third keels, base of shell with one to three weak keels, all keels usually darker than rest of shell surface; aperture ovate, less than half of shell in height, inner shell surface bluish white, outer lip thin, always with an obvious angular periphery, columellar lip covered with thick inner shell layers, white or orange red, adult columellar lip recurved, sometimes forming a narrow to wide crescent-shaped callus, this structure or columellar lip completely covering umbilicus.

Operculum (Fig. 13M–N) corneous, ovate, relatively thick, dark red; exterior surface smooth; interior surface with small nuclear region, around 1/5 of inner opercular region, with shiny grains or veins or smooth glossy surface.

Radula currently unknown.

Remarks

The newly collected specimens in Longzhou of China have a shell that is very similar to that of the holotype, and the collecting site is close to the type locality on the same river basin. *Bakyietaia duchieri* can be easily distinguished from the other species of *Bakyietaia* gen. nov. based on its large sturdy shell and inflated body whorl with shoulder. The recommended Chinese name is 杜氏越田螺.

Habitat and distribution

Sand substrate and rocks in the shallow water of rivers and lakes of Western Guangxi, China and Northern Vietnam.

Bakyietaia guangdungensis (Kobelt, 1906) gen. et comb. nov.
Figs 14–15

Vivipara heudei var. *guangdungensis* Kobelt, 1906 in Kobelt 1906–1909: 124–125, pl. 21 figs 12, 14 ("Provinz Guang-dung", Guangdong Province, China).

Dactylochalamys guangdungensis – Prashad 1928: 169.
Vivipara polyzonata – Yen 1939: 37, pl. 3 figs 14–15 [non *Vivipara polyzonata* Frauenfeld, 1862].
Angulyagra guangdungensis – Yen 1943: 128.
Sinotaia polyzonata – Zilch 1955: 77, fig. 52. — Qian *et al.* 2014 [non *Vivipara polyzonata* Frauenfeld, 1862].
Taia polyzonata – Johnson 1973: 120, 122. — Palmieri *et al.* 1980: 40. — Ng 1992: 125. — Chan 1996: 184–185, fig. 2. — Maassen 2001: 44. — Clements *et al.* 2006: 144. — Tan & Woo 2010: 26. — Yeo & Chia 2010: 32. — Tan *et al.* 2012: 133 [non Frauenfeld 1862].
Viviparus polyzonata – Ng *et al.* 1993: 20 [non *Vivipara polyzonata* Frauenfeld, 1862].
Bellamya heudei guangdungensis – Shea 1994: 3–11.
Sinotaia guangdungensis – Ng *et al.* 2014: 401–408

Angulyagra polyzonata – Madsen & Hung 2014: 110, fig. 2(11) [non *Vivipara polyzonata* Frauenfeld, 1862].

Diagnosis

Shell relatively small (20.87 ± 0.93 mm), whorls inflated; columellar lip recurved, forming callus covering umbilicus completely; operculum with small nuclear region (around 1/5 of inner opercular region) with shiny grains or veins; outer marginal tooth of radula with 28 to 29 small sharp cusps.

Material examined

Lectotype

CHINA • dry preserved spec.; Guangdong Province; O.v. Möllendorff leg.; designated by Yen (1939); SMF.38890.

Paralectotypes

CHINA • 4 specs (preserved dry); Guangdong Province; O.v. Möllendorff leg.; SMF.38822.

Other material

CHINA – **Guangdong Province** • 1 spec. (preserved dry); Guangzhou City, Baiyun Mountain, creeks in Taohuajian Valley, mud substrate, on bank; 25 Feb. 2022; Le-Jia Zhang leg.; KIZ.240054 • 1 spec. (preserved in ethanol); Qingyuan City, Lianzhou County, Xian Town; 18 Nov. 2019; bought by Hai-Ling Zhang on local market; ZMB.122693-1 • 3 specs (preserved in ethanol); Zhaoqing City, Bohai Park, Qixing Lake, 0.1–0.2 m deep under rocks; 19 Jan. 2020; Ji-Lin Jiang leg.; ZMB.122760. – **Guangxi** • 4 specs (preserved in ethanol); Guilin City, Yangshuo Town; 14 Mar. 2022; bought on local market by Le-Jia Zhang; ZMB.122727 • 2 specs (preserved in ethanol); Laibin City, Heshan County, Renyi Village, Huaiji Reservoir, 0.5 m deep mud substrate; 7 Jan. 2020; Ri-Bao Huang leg.; KIZ.240088.

SINGAPORE • 3 specs (preserved in ethanol); Canal at Springleaf Rd; ZMB.192077.

Description

Adult shell (Fig. 14A–H, K–R) relatively small for the genus (20.87 ± 0.93 mm), thin but sturdy, conical, olive to olive brown, with five to six whorls, apex acute; teleoconch whorls inflated, sometimes with shoulder, with three smooth primary keels, with one to two weaker smooth secondary keels located between suture and first keel, sometimes one additional weak keel located between first and second/second and third keels, base of shell with three to five weak keels, all keels usually darker than rest of shell surface; aperture ovate, less than half of shell in height, inner shell surface bluish white, outer lip thin, always with an obvious angular periphery, columellar lip covered with thick inner shell layers, white or orange, adult columellar lip recurved, sometimes forming a relatively narrow crescent-shaped callus, this structure or columellar lip completely covering umbilicus.

Operculum (Fig. 14I–J) corneous, ovate, relatively thin, yellow to orange; exterior surface smooth; interior surface with small nuclear region, around 1/5 of inner opercular region, with shiny grains or veins or smooth glossy surface.

Radular (Fig. 15) (n = 3) central tooth with one broad central denticle and four to five small sharp cusps on either side; lateral tooth with one broad central denticle and four small sharp cusps on either side; inner marginal tooth narrow, about half of lateral tooth in width, with one broad central denticle and three to four small sharp cusps on either side; outer marginal tooth wide, almost same width as lateral tooth, with 28 to 30 small sharp cusps.

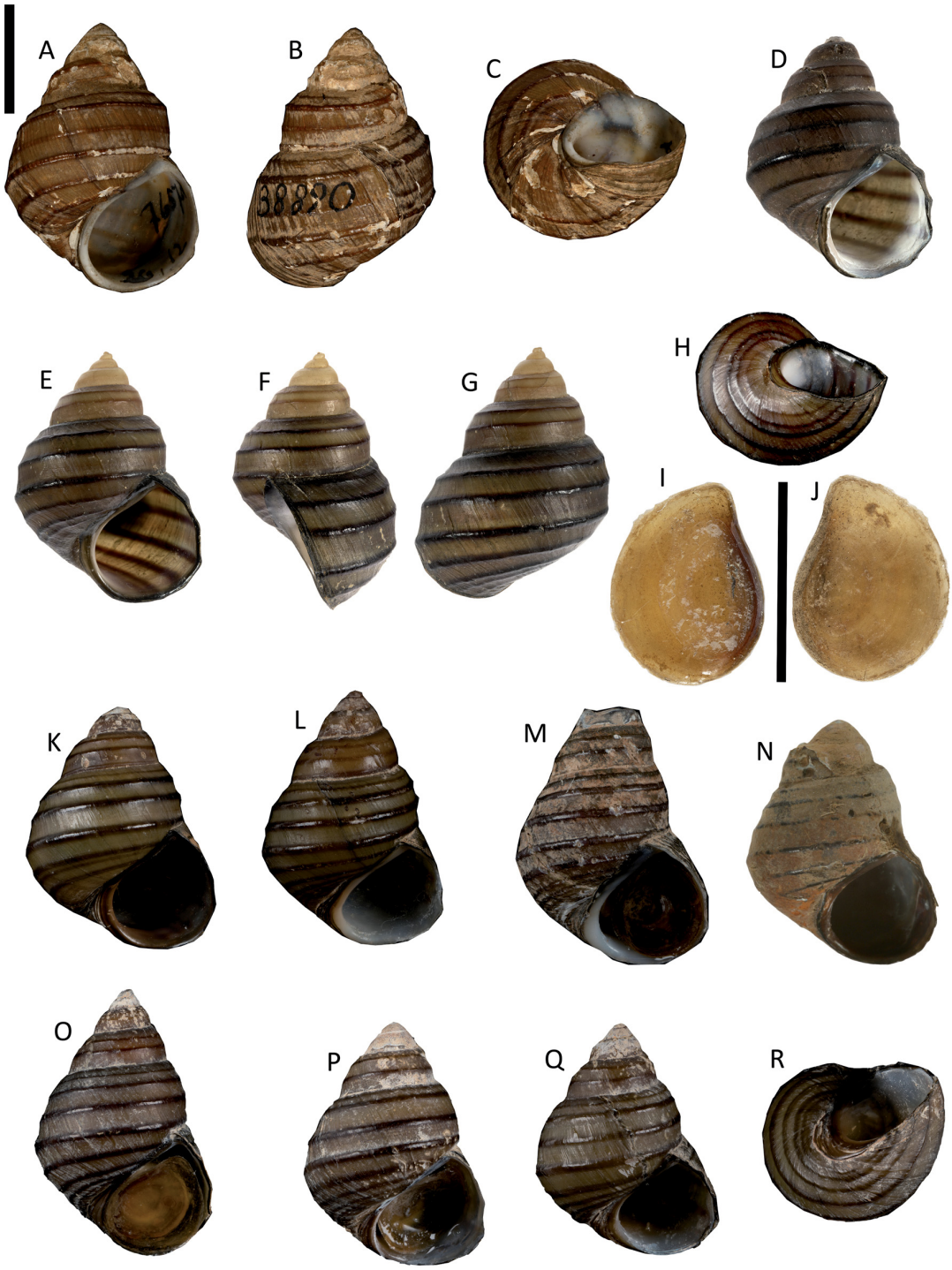


Fig. 14. Shells and operculum of *Bakyietaia guangdungensis* (Kobelt, 1906) gen. et comb. nov. **A–C**. Lectotype, SMF.38890, Guangdong, China. **D**. KIZ.240054, Guangzhou, Guangdong, China. **E–H**. ZMB.122727-1, Yangshuo, Guangxi, China. **I–J**. Operculum of ZMB.122727-1. **K**. ZMB.122727-2, Yangshuo, Guangxi, China. **L**. ZMB.122693-1, Lianzhou, Guangdong, China. **M**. ZMB.122768-2, Heshan, Guangxi, China. **N**. ZMB.192077, Singapore. **O–R**. ZMB.122760, Zhaoqing, Guangdong, China. Scale bars = 1 cm, top left bar applies to all shells, separate bar for operculum I–J.

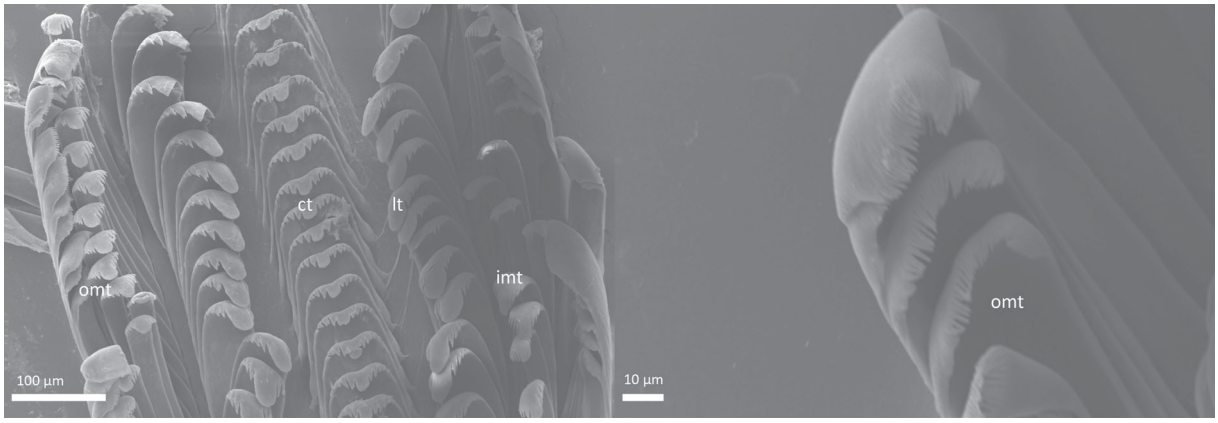


Fig. 15. SEM photo of the radula of *Bakyietaia guangdungensis* (Kobelt, 1906) gen. et comb. nov., ZMB.122693-1.

Remarks

The newly collected specimens from Guangzhou City of Guangdong have a shell that is very similar to that of the lectotype. *Bakyietaia guangdungensis* can be distinguished from most congeners based on its relatively small conical shell with inflated whorls, but largely falls within the range of variation of *Bakyietaia wilhelmi*. However, *B. guangdungensis* has a greater number of small cusps on the outer marginal teeth than *B. wilhelmi* (28–29 vs 18–25). Both of these species also overlap in geographic range, and, therefore, DNA barcoding is recommended for the unambiguous identification of these two species. The recommended Chinese name is 广东越田螺.

Habitat and distribution

Mud and rock substrate in the shallow water of rivers and lakes in Western Guangdong and Eastern Guangxi, China. Introduced into Singapore and Sydney, Australia, possibly also in Malaysia (pending confirmation using molecular evidence).

Bakyietaia mutica (Kobelt, 1909) gen. et comb. nov.
Figs 16–17

Vivipara boettgeri mutica Kobelt, 1909 in Kobelt 1906–1909: 194, pl. 39 figs 3–4 ("Hainan", Hainan Province, China).
Vivipara boettgeri Kobelt, 1909 in Kobelt 1906–1909: 137–138, pl. 26 figs 1–7. [non *Paludina boettgeri* Möllendorff, 1890, junior homonym].

Viviparus muticus – Yen 1939: 38, pl. 3 figs 18–19.
Sinotaia mutica – Zilch 1955: 77, figs 50–51.
Angulyagra mutica – Liu *et al.* 1995: 14.

Diagnosis

Shell medium in size (22.14 ± 1.74 mm), conical, whorls inflated, with weak primary keels, prominent keel above suture; columellar lip recurved, forming callus covering umbilicus completely; operculum with small nuclear region (around 1/4 of inner opercular region) with shiny grains or veins; outer marginal tooth of radula with 19 to 24 small sharp cusps.

Material examined

Holotype of *Vivipara boettgeri mutica*
CHINA • dry preserved spec.; Hainan Province, O.v. Möllendorff leg.; SMF.38817.

Holotype of *Vivipara boettgeri*
CHINA • dry preserved spec.; O.v. Möllendorff leg.; SMF.7652.

Paratypes of *Vivipara boettgeri mutica*
CHINA • 2 specs (preserved dry); Hainan Island; SMF.38815 • 3 specs (preserved dry); Hainan Island; SMF.38816.

Other material
CHINA – **Hainan Province** • 3 specs (preserved in ethanol); Haikou, wetlands near Yangshan Reservoir; 20 Oct. 2019; bought by Sheng-Zhuo Huang on local market; ZMB.122711 • 3 specs (preserved in ethanol); Dingan County, Shuikou Village, 0.5 m deep on wall of cement canal; 6 Mar. 2022; Le-Jia Zhang leg.; ZMB.122724 • 1 spec. (preserved dry); same data as for preceding; YHY-BAKMUT-XC-1 • 2 specs (preserved in ethanol); Haikou City, wetland in Xue Village, 0.1 m deep on rock substrate; 5 Mar. 2022; Le-Jia Zhang leg.; ZMB.122746 • 3 specs (preserved in ethanol); Haikou City, a canal in a farming field near Yangshan Reservoir, 0.1 m deep on rock; 5 Mar. 2022; Le-Jia Zhang leg.; ZMB.122752 • 2 specs (preserved in ethanol); Wenchang City, a pond in Jinjiahu Village, 0.5 m deep on rock; 9 Nov. 2020; Ji-Ze Ruan leg.; ZMB.122772 • 6 specs (preserved dry); same data as for preceding; YHY-BAKMUT-WC-19, YHY-BAKMUT-WC-36, YHY-BAKMUT-WC-1, YHY-BAKMUT-WC-22, YHY-BAKMUT-WC-37, YHY-BAKMUT-WC-39.

Description

Adult shell (Fig. 16A–K) medium in size (22.14 ± 1.74 mm), thin but sturdy, conical, olive to dark olive brown, with five to six whorls, apex acute; teleoconch whorls inflated, sometimes with shoulder, with three weak, smooth primary keels, with one to two even weaker smooth secondary keels located between suture and first keel, sometimes one additional weak keel located between first and second/second and third keels, base of shell with two to four weak keels, all keels usually darker than rest of shell surface; aperture ovate, less than half of shell height, inner shell surface bluish white, outer lip thin, always with an obvious angular periphery, columellar lip covered with thick inner shell layers, always white, adult columellar lip recurved, sometimes forming a relatively wide crescent-shaped callus, this structure or columellar lip completely covering umbilicus.

Operculum (Fig. 16L–M) corneous, ovate, relatively thin, dark orange to red; exterior surface smooth; interior surface with small nuclear region, around 1/4 of inner opercular region, with shiny grains or veins or smooth glossy surface.

Radular (Fig. 17) (n = 3) central tooth with one broad central denticle and four to five small sharp cusps on either side; lateral tooth with one broad central denticle and four to five small sharp cusps on either side; inner marginal tooth narrow, about half of lateral tooth in width, with one broad central denticle and five to six small sharp cusps on either side; outer marginal tooth wide, almost same width as lateral tooth, with 19 to 24 small sharp cusps.

Remarks

The newly collected specimens from Haikou City of Hainan have a shell that is very similar to that of the holotype. *Bakyietaia mutica* is one of the species of *Bakyietaia* gen. nov. with weak primary keels. It can be easily distinguished from most congeners based on its medium-sized thin conical shell with three very weak primary keels. It is morphologically similar to *Bakyietaia fontinalis* gen. et sp. nov. and *Bakyietaia*

naiadica gen. et sp. nov. However, it can be distinguished from *B. fontinalis* based on the inflated whorls (vs non-inflated whorls in *B. fontinalis*) and fewer cusps on the outer marginal teeth (19–24 vs 26–29); it can be distinguished from *B. naiadica* based on its more conical shell with prominent keel above suture. The distribution of *Bakyietaia mutica* does not overlap with those of *B. fontinalis* and *B. naiadica*. The recommended Chinese name is 钝形越田螺.

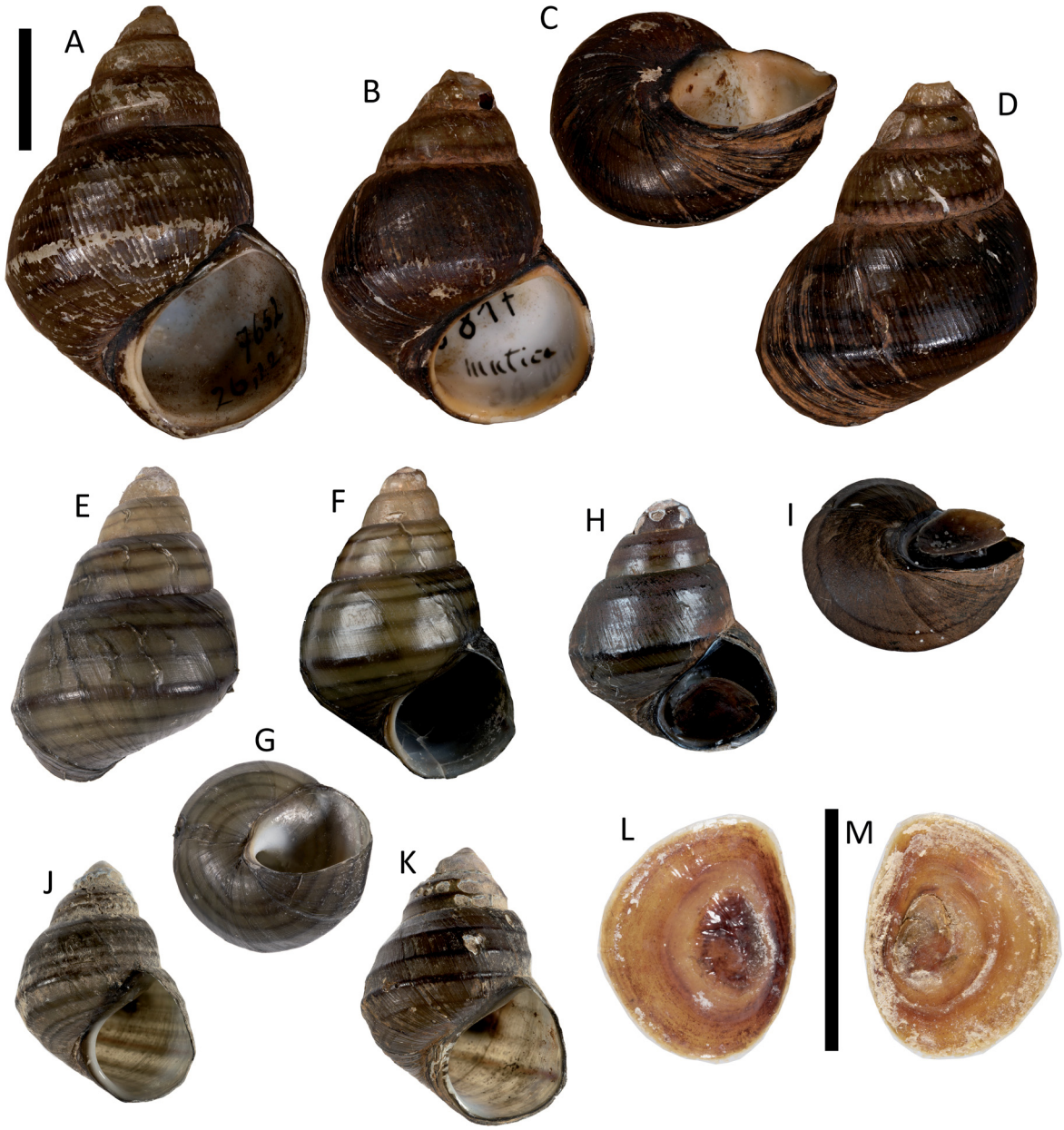


Fig. 16. Shells and operculum of *Bakyietaia mutica* (Kobelt, 1909) gen. et comb. nov. **A**. Paratype SMF.7652, Hainan, China. **B–D**. Holotype, SMF.38817, Hainan, China. **E–G**. ZMB.122711-1, Yangshan, Hainan, China. **H–I**. ZMB.122752, Yangshan, Hainan, China. **J**. ZMB.122724, Shuikou, Hainan, China. **K**. ZMB.122746 Xue Village, Hainan, China. **L–M**. Operculum of ZMB.122711-1. Scale bars = 1 cm, top left bar applies to all shells, separate bar for operculum L–M.

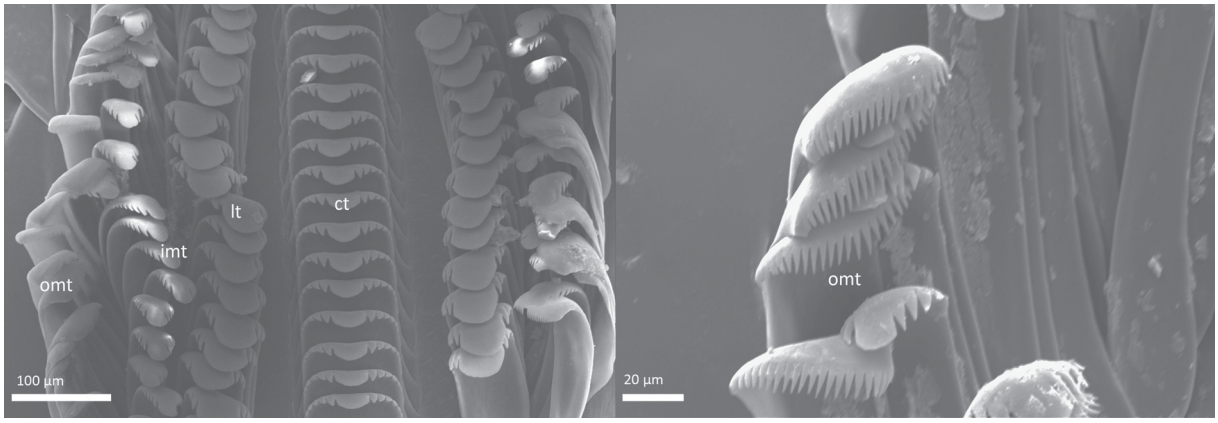


Fig. 17. SEM photo of the radula of *Bakyietaia mutica* (Kobelt, 1909) gen. et comb. nov., ZMB.122752 (left), ZMB.122711 (right).

Habitat and distribution

Rock substrate in the shallow water of rivers and lakes in northern Hainan Province, China.

Bakyietaia wilhelmi (Yen, 1939) gen. et comb. nov.
Figs 18–19

Viviparus wilhelmi Yen, 1939: 37, pl. 3 fig. 16 ("Kanton", Guangzhou City, Guangdong, China).

Viviparus polyzonatus – Yen 1938: 448, fig. 1 [non *Vivipara polyzonata* Frauenfeld, 1862].
Sinotaia wilhelmi – Zilch 1955: 77, fig. 56.
Angulyagra wilhelmi – Starobogatov 1970: 202. — Liu *et al.* 1995: 14.
Angulyagra boettgeri – Do *et al.* 2014: 3–4, fig. 5 [non *Paludina boettgeri* Möllendorff, 1890 in Heude 1882–1890].
Sinotaia guangdungensis – Ng *et al.* 2017 [non *Vivipara heudei* var. *guangdungensis* Kobelt, 1906 in Kobelt 1906–1909].

Diagnosis

Shell small to medium in size (25.53 ± 3.72 mm), whorls usually not inflated, moderate keel above suture; columellar lip recurved, forming callus covering umbilicus completely; operculum with small nuclear region (around 1/4 to 1/5 of inner opercular region) with shiny grains or veins; outer marginal tooth of radula with 18 to 25 small sharp cusps.

Material examined

Holotype

CHINA • dry preserved spec.; Guangdong Province, Guangzhou City; O.v. Möllendorff leg.; SMF.40812.

Paratypes

CHINA • 18 specs (preserved dry); Guangdong Province, Guangzhou City; O.v. Möllendorff leg.; SMF.40243.

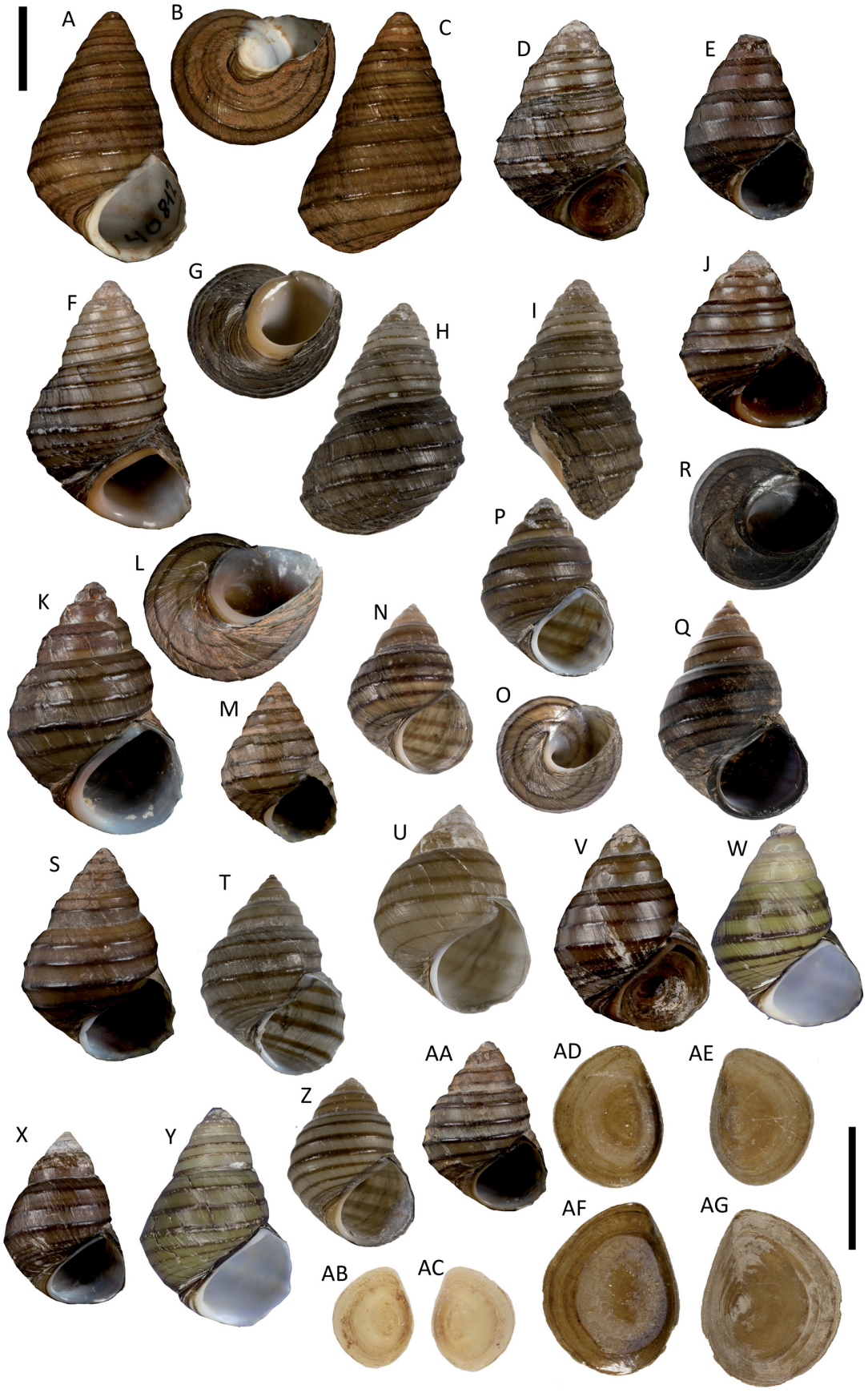
Other material

CHINA – **Guangdong Province** • 2 specs (preserved in ethanol); Yunfu City, Xinxing County, Liuzu Town, 0.14 m deep on mud or rock substrate in creeks; 4 Jan. 2020; Fu-Ying Liang leg.; ZMB.122771 • 4 specs (preserved dry); same data as for preceding; YHY-BAKWIL-YF-1, YHY-BAKWIL-YF-13

to YHY-BAKWIL-YF-15 • 1 spec. (preserved in ethanol); Zhaoqing City, Bohai Park, Qixing Lake, 0.1–0.2 m deep under rocks; 10 Jan. 2020; Ji-Lin Jiang leg.; ZMB.122760-1 • 4 specs (preserved in ethanol); Zhuhai City, Pingsha Town, a canal in Nanxin, 0.1–0.2 m deep on mud substrate; 12 Oct. 2022; ZMB.122688 • 1 spec. (preserved dry); same data as for preceding; YHY-BAKWIL-ZH-1 • 4 specs (preserved dry); Meizhou City, Dapu County, Sanhe Town, in a canal; 2 Apr. 2022; Le-Jia Zhang leg.; KIZ.240088 • 3 specs (preserved in ethanol); Zhanjiang City, a pond in Zhiliao Village, 2 m deep on mud substrate; 3 Mar. 2022; Le-Jia Zhang leg.; ZMB.122751 • 3 specs (preserved in ethanol); Qingyuan City, Fogang County, Shijiao Town, Lianxi Village, under Longxi Bridge, Longxi River, 0.5 m deep on mud or rock substrate; 6 Dec. 2019; Chang-Le Huang leg.; ZMB.122689 • 3 specs (preserved in ethanol); Meizhou City, Wuhua County, Changxing Village, Xiaodu River, 0.1–0.25 m deep on rock; 28 Nov. 2019; Yu-Hui Cai leg.; ZMB.122700 • 1 spec. (preserved in ethanol); Qingyuan City, Lianzhou County, Xian Town; 18 Nov. 2019; bought by Hai-Ling Zhang on local market; ZMB.122693B • 4 specs (preserved in ethanol); Heyuan City, Dongyuan County, Xinfengjiang Reservoir, 0.4 m deep in pond; 18 Nov. 2019; Chun-Di Chen leg.; ZMB.122696 • 4 specs (preserved in ethanol); Shanwei City, Luhe County, Xintian Town, Tianxin Village, Laozhutang, 1–2 m deep on mud substrate in fish pond; 15 Dec. 2019; Yuan-Shan Qiu leg.; ZMB.122702 • 4 specs (preserved in ethanol); Shaoguan City, Shixing County, Taiping Town, Diba, Mojiangping Lake, 0.2 m deep on mud or rock substrate; 5 Dec. 2019; Yong-Ming Nie leg.; ZMB.122699 • 4 specs (preserved in ethanol); Jieyang City, Puning County, Nanxi Town, Xiashanweijiao, 4–5 m deep in creek; 4 Dec. 2019; Mei Yang leg.; ZMB.122704 • 4 specs (preserved in ethanol); Qingyuan City, Yangshan County, Jiangxikong, 0.4 m deep on sand and rock substrate; 4 Dec. 2019; Jian-Guo Chen leg.; ZMB.122686 • 2 specs (preserved in ethanol); Guangzhou City, Zengcheng District, Lingshan, Yakoukan Village, 0.5 m deep on mud substrate in creek; 4 Dec. 2019; Da-Ming Shi leg.; ZMB.122695 • 2 specs (preserved in ethanol); Shenzhen City, Baoan District, outlet of a reservoir near Dawang Cemetery, 0.5 m deep on mud substrate; 18 Dec. 2019; Fan Qiu leg.; ZMB.122692. – **Guangxi** • 4 specs (preserved in ethanol); Laibin City, Heshan County, Renyi Village, Huaiji Reservoir, 0.5 m deep mud substrate; 7 Jan. 2020; Ri-Bao Huang leg.; ZMB.122768A • 3 specs (preserved dry); same data as for preceding; YHY-BAKWIL-HS-2, YHY-BAKWIL-HS-18, YHY-BAKWIL-HS-3 • 2 specs (preserved in ethanol); Guigang City, Gangbei District, Niuyun Reservoir, 0.5 m deep on mud substrate; 7 Jan. 2020; Ri-Bao Huang leg.; ZMB.122770 • 2 specs (preserved dry); same data as for preceding; YHY-BAKWIL-NY-1, YHY-BAKWIL-NY-4 • 2 specs (preserved in ethanol); Liuzhou City, Liujiang District, Baipeng Village, Hepingtun, canal near lotus fields, 0.5 m deep on mud substrate; 19 Oct. 2019; Ping Zeng leg.; ZMB.122685 • 1 spec. (preserved in ethanol); Guangxi, Baise City, creek near Nawang Village, 0.1 m deep on sand or rock substrate; 20 Mar. 2022; Le-Jia Zhang leg.; ZMB.122723-2. – **Hainan Province** • 2 specs (preserved in ethanol); Haikou, wetlands near Yangshan Reservoir; bought by Sheng-Zhuo Huang on local market; 20 Oct. 2019; ZMB.122709 • 1 spec. (preserved in ethanol); Ledong Li Autonomous County, Honghu Village, in Honghu Lake, 0.1 m deep on sand substrate; 9 Mar. 2022; Le-Jia Zhang leg.; ZMB.122737-3. – **Sichuan Province** – 2 specs (preserved in ethanol); Chengdu City, Donghu Park, East Lake; 12 Oct. 2022; ZMB.122769. – **Yunnan Province** • 4 specs (preserved in ethanol); Gejiu City, Zhadian Village, 0.1 m deep canal; 21 Mar. 2022; Le-Jia Zhang leg.; ZMB.122729 • 5 specs (preserved dry); Gejiu City, Zhadian Village, 0.3 m deep canal; 20 Apr. 2020; Yan Tan leg.; YHY-BAKWIL-ZD-1, YHY-BAKWIL-ZD-2, YHY-BAKWIL-NY-1, YHY-BAKWIL-NY-4, YHY-BAKWIL-ZD-18.

MALAYSIA • 1 spec. (preserved in ethanol); Sabah, Kota Marudu, stream in paddy field; 4 Apr. 2016; A. Zieritz leg.; BORMOL8674 (MZ596234.1).

VIETNAM • 4 specs (preserved in ethanol); Cao Bang, Pac Bo at Chinese border, Ha Quang River; 21 Mar. 2006; bought by Frank Köhler on local market; ZMB.114206 • 4 specs (preserved in ethanol); Cao Bang, Bang River; 21 Mar. 2006; Frank Köhler leg.; ZMB.114202.


A
B
C
D
E
F
G
H
I
J
K
L
M
N
O
P
Q
R
S
T
U
V
W
X
Y
Z
AA
AB
AC
AD
AE
AF
AG

Description

Adult shell (Fig. 18A–AA) small to medium (25.53 ± 3.72 mm), thin to thick, sturdy, conical, olive to dark olive brown, with five to six whorls, apex acute; teleoconch whorls sometimes without shoulder, sometimes inflated and with shoulder, with three smooth primary keels, with one to two weaker smooth secondary keels located between suture and first keel, sometimes one additional weak keel located between first and second/second and third keels, base of shell with two to five weak keels, all keels usually darker than rest of shell surface; aperture ovate, less than half of shell in height, inner shell surface bluish white, outer lip thin, always with an angular periphery, columellar lip covered with thick inner shell layers, white or orange, adult columellar lip recurved, sometimes forming a rather wide crescent-shaped callus, this structure or columellar lip completely covering umbilicus.

Operculum (Fig. 18AB–AG) corneous, ovate, relatively thin, yellow to orange; exterior surface smooth; interior surface with small nuclear region, around 1/4 to 1/5 of inner opercular region, with shiny grains or veins or smooth glossy surface.

Radular (Fig. 19) (n = 6) central tooth with one broad central denticle and four to five small sharp cusps on either side; lateral tooth with one broad central denticle and four small sharp cusps on either side; inner marginal tooth narrow, about half of lateral tooth in width, with one broad central denticle and three to five small sharp cusps on either side; outer marginal tooth wide, almost same width as lateral tooth, with 18 to 25 small sharp cusps.

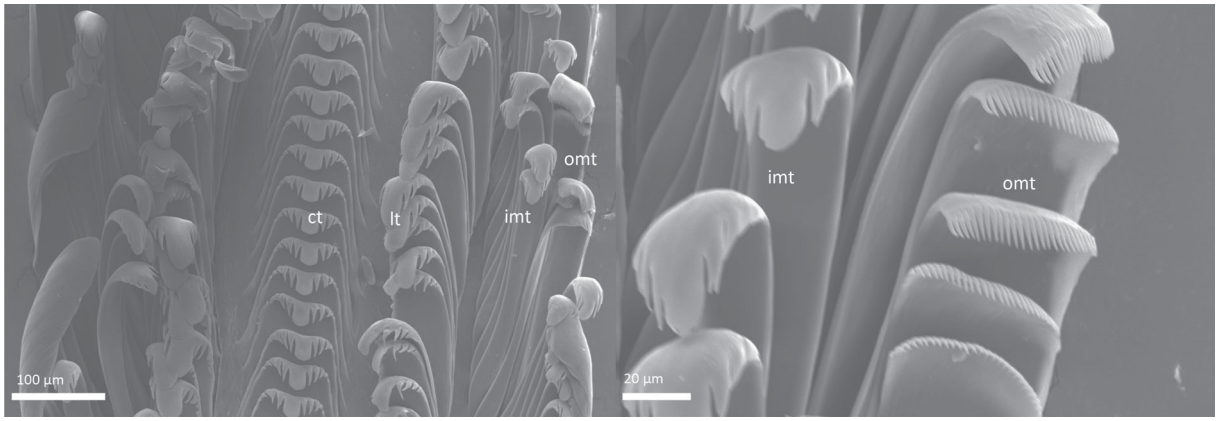


Fig. 19. SEM photo of the radula of *Bakyietaia wilhelmi* (Yen, 1939) gen. et comb. nov., ZMB.122686.

Fig. 18 (preceding page). Shells and opercula of *Bakyietaia wilhelmi* (Yen, 1939) gen. et comb. nov. **A–C**. Holotype, SMF.40812, Guangdong, China. **D**. ZMB.122686-2, Jiangxikong, Guangdong, China. **E**. ZMB.122696, Heyuan, Guangdong, China. **F–I**. ZMB.122686-1, Jiangxikong, Guangdong, China. **J**. ZMB.122689, Fogang, Guangdong, China. **K–L**. ZMB.122688, Zhuhai, Guangdong, China. **M**. ZMB.122692, Shenzhen, Guangdong, China. **N–O**. ZMB.122685, Liuzhou, Guangxi, China. **P**. ZMB.122751, Zhanjiang, Guangdong, China. **Q–R**. ZMB.122729, Gejiu, Yunnan, China. **S**. ZMB.122737-3, Ledong, Hainan, China. **T**. ZMB.122709, Yangshan, Hainan, China. **U**. ZMB.114206, Ha Quang, Vietnam. **V**. ZMB.122770, Niuyun, Guangxi, China. **W**. P1010042, Niuyun, Guangxi, China. **X**. ZMB.122760-1, Zhaoqing, Guangdong, China. **Y**. YHY-BAKWIL-HS-2, Heshan, Guangxi, China. **Z**. 122693-2, Lianzhou, Guangdong, China. **AA**. ZMB.122704, Jieyang, Guangdong, China. **AB–AC**. Operculum of ZMB.122685. **AD–AE**. Operculum of ZMB.122686-1. **AF–AG**. Operculum of ZMB.114206. Scale bars = 1 cm, top left bar applies to all shells, separate bar for opercula AB–AG.

Remarks

The newly collected specimens from Qingyuan City in Guangdong have a shell that is very similar to that of the holotype. *Bakyietaia wilhelmi* is the most common species of this genus. It has the widest distribution range, and displays extremely high polymorphism of shell characters. This species was also found sympatrically with other species of *Bakyietaia* gen. nov. (*B. boettgeri*, *B. duchieri* and *B. guangdungensis*) in some localities (such as Qixing Lake in Zhaoqing City in Guangdong and Honghu Lake in Ledong County of Hainan). The morphotype that is similar to the holotype can be distinguished from most congeners based on its comparatively small conical shell with non-inflated whorls and moderately keeled suture. However, some morphotypes cannot be distinguished from *Bakyietaia guangdungensis* based on their shell morphology. The COI tree supports the status of *B. wilhelmi* and *B. guangdungensis* as distinct species that are quite distantly related. In addition, *B. wilhelmi* always has fewer small cusps on the outer marginal teeth than *B. guangdungensis* (18–25 vs 28–30). DNA barcoding is considered necessary to unambiguously differentiate *B. wilhelmi* and *B. guangdungensis*. The recommended Chinese name is 威廉越田螺.

Habitat and distribution

Mud, sand and rock substrate in the shallow water of rivers, wetlands and lakes in Guangdong, Hainan, Guangxi and southern Yunnan Province, China and northern Vietnam. Introduced into Chengdu City, Sichuan Province, China and northern Borneo, Malaysia.

Bakyietaia chenghuang Zhang, Yen & von Rintelen gen. et sp. nov.
urn:lsid:zoobank.org:act:24C0929E-836B-4AC5-9829-294C4C6345B4
Figs 20–21

Diagnosis

Shell medium in size (23.70 ± 5.37 mm), rounded and thin, teleoconch with weak primary keels; columellar lip recurved, forming callus covering umbilicus completely; operculum with small nuclear region (around 1/5 of inner opercular region) with shiny grains or veins; outer marginal tooth of radula with 15 to 16 small sharp cusps.

Etymology

'Cheng Huang' means 'city god' in Chinese, referring to the type locality in Chenghuang Town. Formed as a noun in apposition. The recommended Chinese name is 城隍越田螺.

Material examined

Holotype

CHINA • spec. preserved in ethanol; Guangxi, Yulin City, Chenghuang Town, a river near Shirentou Mountain, 0.5 m deep on rock; 13 Mar. 2022; Le-Jia Zhang leg.; KIZ.240001.

Paratypes

CHINA • 4 specs (preserved in ethanol); same data as for holotype; KIZ.240002 to KIZ.240005 • 2 specs (preserved in ethanol); same data as for holotype; ZMB.122722-1 • 4 specs (preserved in ethanol); same data as for holotype; KIZ.240089.

Other material

1 spec. (preserved dry); same data as for holotype; YHY-BAKCHE-CH-1.

Description

Adult shell (Fig. 20A–E, H–J) medium in size (23.70 ± 5.37 mm), thin but sturdy, broadly conical or rounded, olive to olive brown, with five whorls, apex acute; teleoconch whorls inflated, with three weak,

smooth primary keels, with one to two weaker smooth secondary keel located between suture and first keel, sometimes one additional weak keel located between first and second/second and third keels, base of shell with three to five weak keels; aperture ovate, large, around half of shell in height, inner

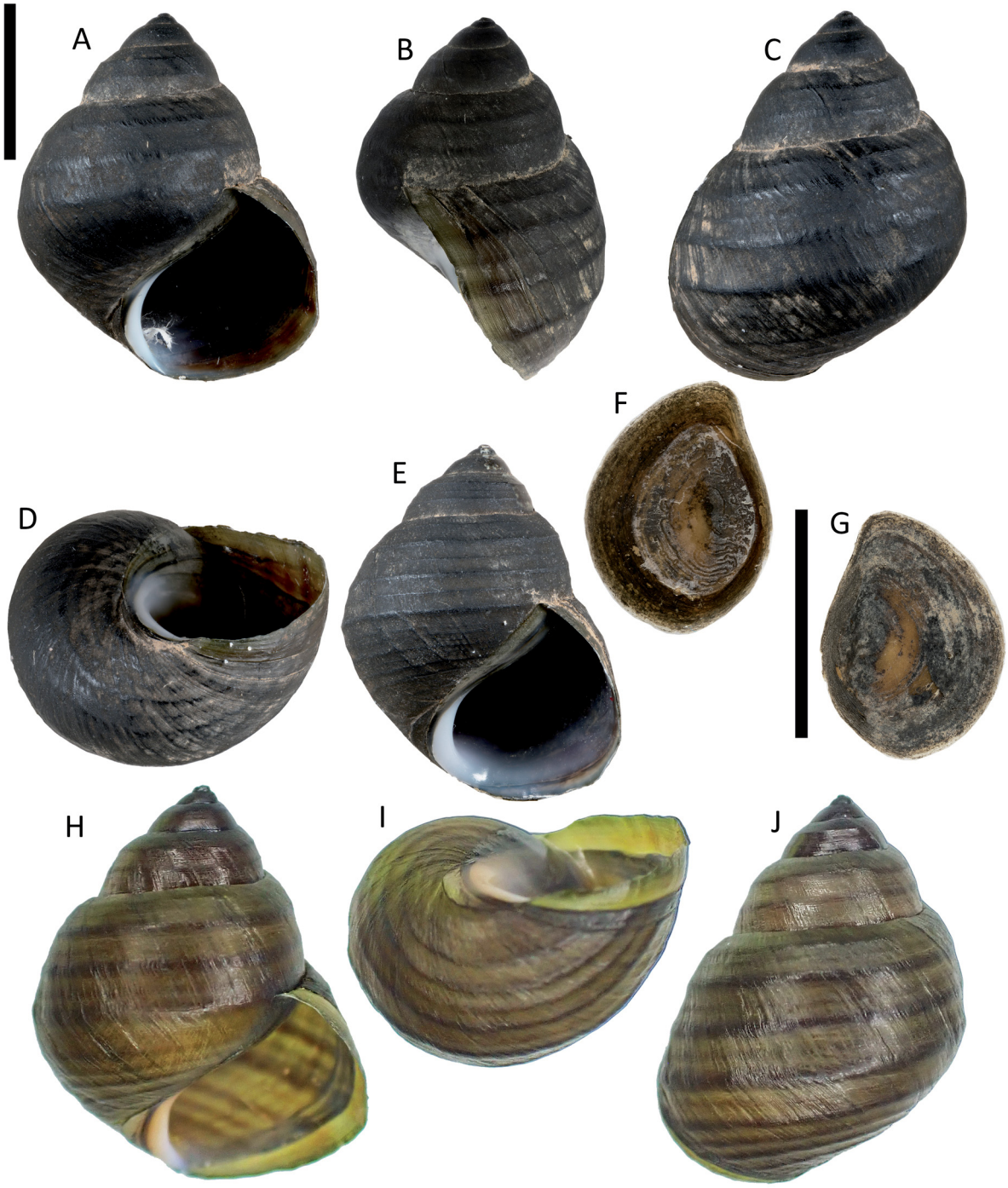


Fig. 20. Shells and operculum of *Bakyietaia chenghuang* Zhang, Yen & von Rintelen gen. et sp. nov. **A–D**. Holotype, KIZ.240001, Chenghuang Town, Guangxi, China. **E**. Paratype, ZMB.122722-1, Chenghuang Town, Guangxi, China. **F–G**. Operculum of KIZ.240002. **H–J**. YHY-BAKCHE-CH-1, Chenghuang Town, Guangxi, China. Scale bars = 1 cm, top left bar applies to all shells, separate bar for operculum F–G.

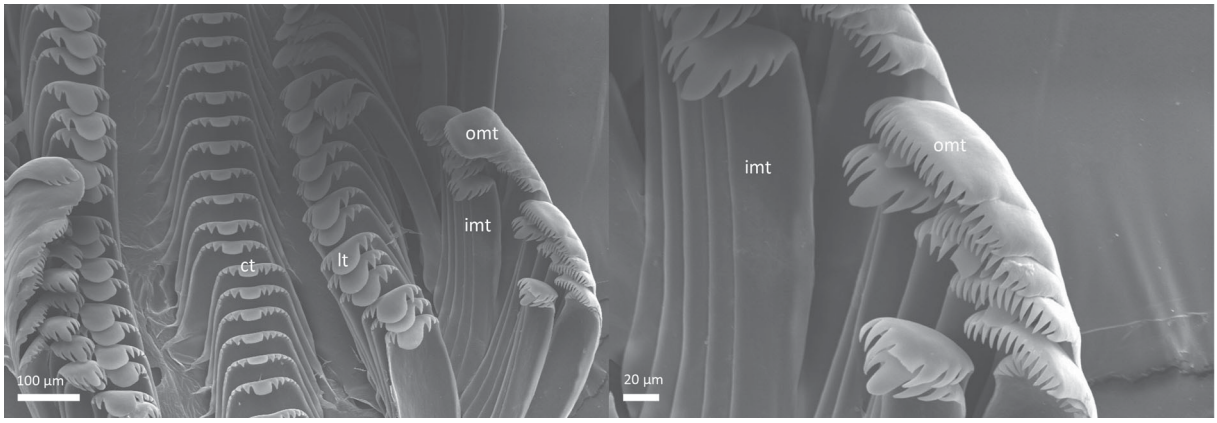


Fig. 21. SEM photo of the radula of *Bakyietaia chenghuang* Zhang, Yen & von Rintelen gen. et sp. nov., paratype, ZMB.122722-1.

shell surface bluish white to purple white, outer lip thin, always with a relatively rounded periphery, columellar lip covered with thick inner shell layers, always white, adult columellar lip recurved, forming a very narrow crescent-shaped callus or without this structure, columellar lip or this structure completely covering umbilicus.

Operculum (Fig. 20F–G) corneous, ovate, thin, yellow; exterior surface smooth; interior surface with small nuclear region, around 1/5 of inner opercular region, with shiny grains or veins.

Radular (Fig. 21) (n = 2) central tooth with one broad central denticle and four to five small sharp cusps on either side; lateral tooth with one broad central denticle and four small sharp cusps on either side; inner marginal tooth narrow, about half width of lateral tooth, with one broad central denticle and three small sharp cusps on either side; outer marginal tooth wide, almost same width as lateral tooth, with 15 to 16 small sharp cusps.

Remarks

Bakyietaia chenghuang gen. et sp. nov. can be easily distinguished from most congeners based on its thin, rounded shell with a wide aperture and a very small operculum. It can be differentiated from the morphologically similar species *Bakyietaia subcostata* based on the smaller number of small cusps on outer marginal teeth of the radula (15–16 vs 29–43).

Habitat and distribution

Only known from the type locality in Guangxi, China, where it occurs on rocky substrates in the shallow water.

Bakyietaia jingweiae Yen, Zhang & von Rintelen gen. et sp. nov.
urn:lsid:zoobank.org:act:7D19E72D-8C68-4AB8-A41B-70CA77A28C0C
Figs 22–23

Diagnosis

Shell small to medium in size (26.79 ± 5.37 mm), sturdy, conical, whorls not inflated, prominent keel above suture; columellar lip recurved, forming callus covering umbilicus completely; operculum with small nuclear region (around 1/4 of inner opercular region) with shiny grains or veins; outer marginal tooth of radula with 26–28 small sharp cusps; distributed in northernVietnam, across the border in western Guangxi and in western Hainan Island, China.

Etymology

Named after 'Jingwei', a Chinese mythical bird into which the Flame Emperor Yandi's daughter Nüwa, who drowned in the sea, was transformed, and which tried to fill up the sea. The recommended Chinese name is 精卫越田螺.

Material examined

Holotype

CHINA • spec. preserved in ethanol; Guangxi, Baise City, Jingxi County, Xinjing Town, Longtan Wetland, 0.1 m on rock; 30 Dec. 2019; Hua-Pu Huang leg.; KIZ.240006.

Paratypes

CHINA – **Guangxi** • 4 specs (preserved in ethanol); same data as for holotype; KIZ.240056 to KIZ.240059 • 5 specs.(preserved in ethanol); same data as for holotype; ZMB.122701 • 1 spec. (preserved in ethanol); Guangxi, Baise City, creek near Nawang Village, 0.1 m deep on sand or rock substrate; 20 Mar. 2022; Le-Jia Zhang leg.; KIZ.240007. – **Hainan Province** • 3 specs (preserved in ethanol); Ledong Li Autonomous County, Honghu Village, Honghu Lake, 0.1 m deep sand substrate; 9 Mar. 2022; Le-Jia Zhang leg.; ZMB.122737-1, ZMB.122737-2, ZMB.122737-4 • 1 spec. (preserved in ethanol); Changjiang Li Autonomous County, Changhua Town, Sanjia Village, Changhua River, 0.5 m deep on rock; 9 Mar. 2022; Le-Jia Zhang leg.; KIZ.240008.

VIETNAM • 4 specs (preserved in ethanol); Cao Bang, river Sông Bằng; 2000; IEBR leg.; MZMB.114431 • 3 specs (preserved in ethanol); Ca River drainage, Ho-Chi-Minh-Highway between Yen Cat and Thái Hòa, Nghê An; 21–31 Oct. 2006; Frank Köhler leg.; ZMB.114407 • 2 specs (preserved in ethanol); Ba Be Lakes, Bac Kan; 2001; IEBR leg.; ZMB.114430 • 10 specs (preserved in ethanol); Ba Be Lakes, Bac Kan, ferry port; 21 Mar. 2006; Frank Köhler leg.; ZMB.114189.

Other material

CHINA • 3 specs (preserved dry); same data as for holotype; YHY-BAKDUC-JX-1, YHY-BAKDUC-JX-10, YHY-BAKDUC-JX-15.

Description

Adult shell (Fig. 22A–N) small to medium (26.79 ± 5.37 mm), thin to thick, sturdy, conical, olive to olive brown, with five to six whorls, apex acute; teleoconch whorls slightly inflated, with three smooth primary keels, with one to two weaker smooth secondary keels located between suture and first keel, sometimes one additional weak keel located between first and second/second and third keels, base of shell with one to three weak keels, all keels usually darker than rest of shell surface; aperture ovate, less than half of shell in height, inner shell surface bluish white, outer lip thin, always with a strong angular periphery, columellar lip covered with thick inner shell layers, white or orange-red, adult columellar lip recurved, sometimes forming a narrow to wide crescent-shaped callus, this structure or columellar lip completely covering umbilicus.

Operculum (Fig. 22O–P) corneous, ovate, relatively thick, dark red; exterior surface smooth; interior surface with small nuclear region, around 1/4 of inner opercular region, with shiny grains or veins or smooth glossy surface.

Radular (Fig. 23) (n = 4) central tooth with one broad central denticle and four to six small sharp cusps on either side; lateral tooth with one broad central denticle and five to six small sharp cusps on either side; inner marginal tooth narrow, about half of lateral tooth in width, with one broad central denticle and four to five small sharp cusps on either side; outer marginal tooth wide, almost same width as lateral tooth, with 26 to 28 small sharp cusps.

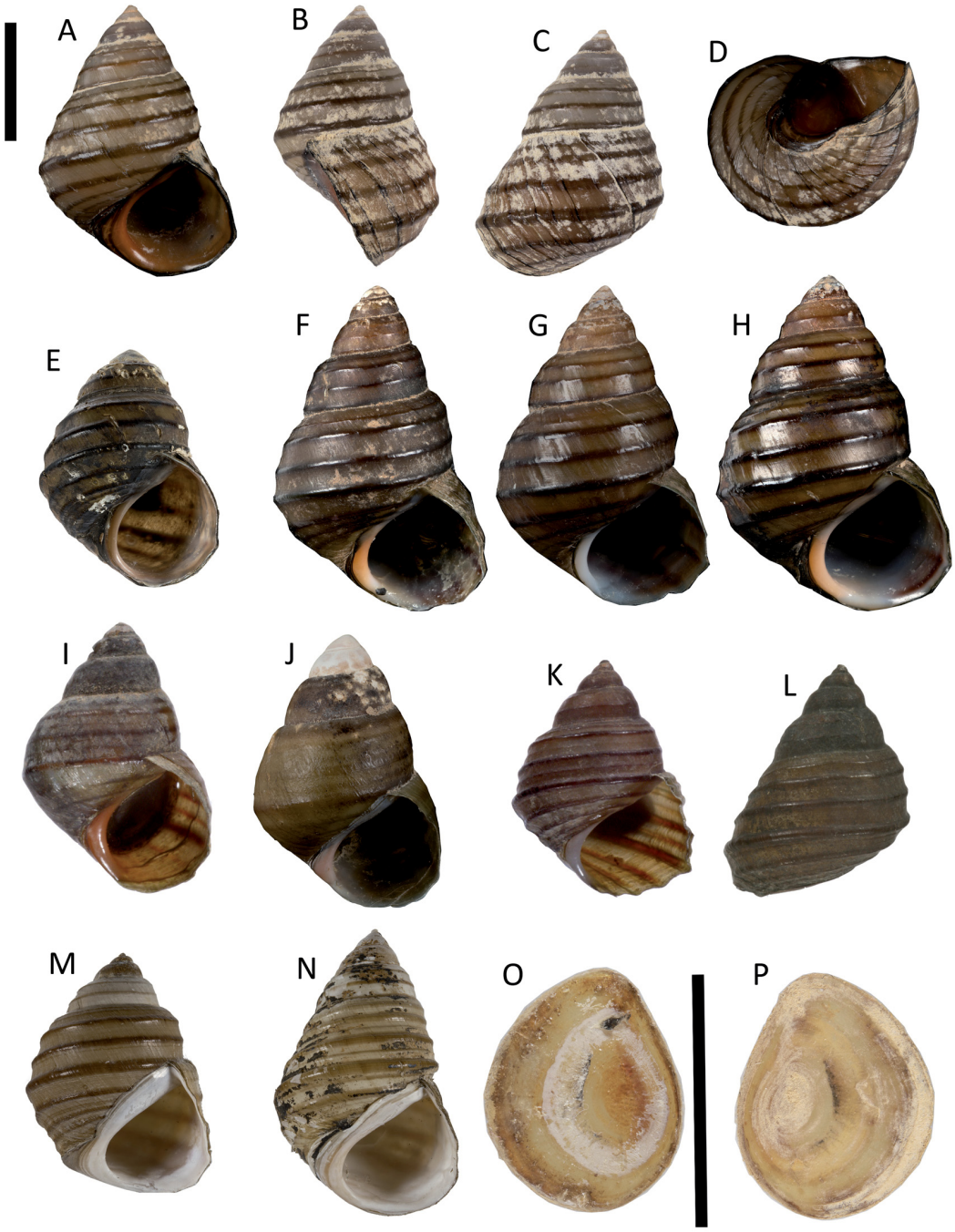


Fig. 22. Shells and operculum of *Bakyietaia jingweiae* Yen, Zhang & von Rintelen gen. et sp. nov. **A–D**. Holotype, KIZ.240006, Jingxi, Guangxi, China. **E**. Paratype, KIZ.240007, Nawang, Guangxi, China. **F–H**. Paratypes, ZMB.122737-1, ZMB.122737-2, ZMB.122737-4, Ledong, Hainan, China. **I**. Paratype, ZMB.114407, Nghê An, Vietnam. **J**. Paratype, KIZ.240008, Changhua, Hainan, China. **K–L**. Paratype, ZMB.114189, Ba Be Lakes, Bac Kan, Vietnam. **M–N**. Paratypes, ZMB.114430, Ba Be Lakes, Bac Kan, Vietnam. **O–P**. Operculum of ZMB.122701. Scale bars = 1 cm, top left bar applies to all shells, separate bar for operculum O–P.

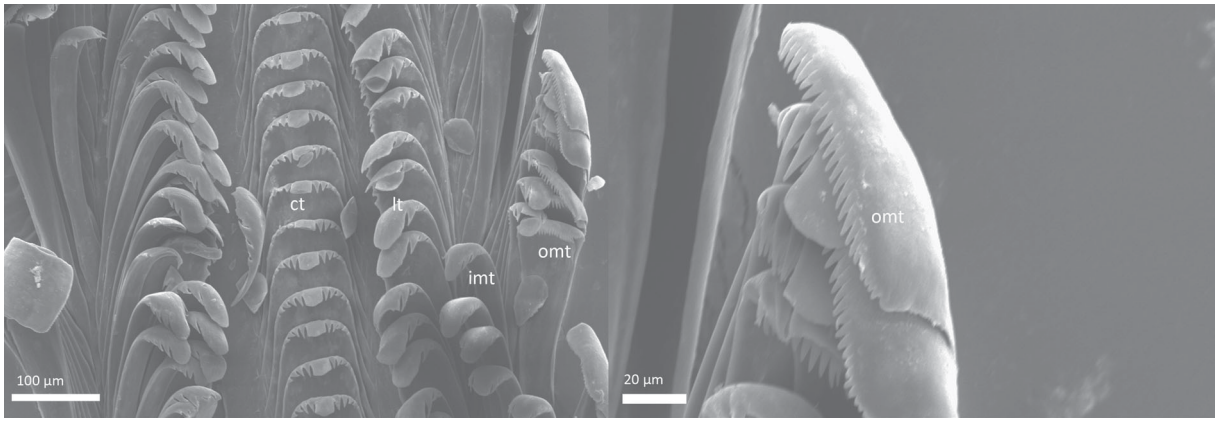


Fig. 23. SEM photo of the radula of *Bakyietaia jingweiae* Yen, Zhang & von Rintelen gen. et sp. nov., ZMB.122701.

Remarks

Bakyietaia jingweiae gen. et sp. nov. is most similar to *Bakyietaia boettgeri* based on shell morphology, but differs in possessing a smaller shell and greater number of small cusps on outer marginal teeth (26–28 vs 23–24). The distribution areas of these two species are close to each other but not overlapping near the border between Guangxi, China and Vietnam.

Habitat and distribution

Sand substrate and rocks in the shallow water of rivers and lakes of western Guangxi and western Hainan Province, China and northern Vietnam.

Bakyietaia liusanjieae Zhang, Yen & von Rintelen gen. et sp. nov.
urn:lsid:zoobank.org:act:16B296D0-9634-4460-B0EB-770DB94244DD
Figs 24–25

Diagnosis

Shell medium in size (25.69 ± 3.35 mm), sturdy, conical shell with lower spire, whorls not inflated; columellar lip recurved, forming callus covering umbilicus completely; operculum with small nuclear region (around 1/4 of inner opercular region) with shiny grains or veins; outer marginal tooth of radula with 26–27 small sharp cusps; distributed in northern Guangxi, China.

Etymology

Named after 'Liu Sanjie' (刘三姐, Liu family's third daughter), a legendary folk singer of the Zhuang people in Guangxi. The type locality of this species is close to her hometown. The recommended Chinese name is 歌仙越田螺.

Material examined

Holotype

CHINA • spec. preserved in ethanol; Guangxi, Hechi City, Luocheng Mulao Autonomous County, near Hemu Town, river in Xinhui Village, 0.5 m deep on dam; 16 Mar. 2022; Le-Jia Zhang leg.; KIZ.240009.

Paratypes

CHINA – **Guangxi** • 2 specs (preserved in ethanol); same data as for holotype; KIZ.240010, KIZ.240011 • 2 specs (preserved in ethanol); same data as for holotype; ZMB.122722-2 • 2 specs (preserved dry);

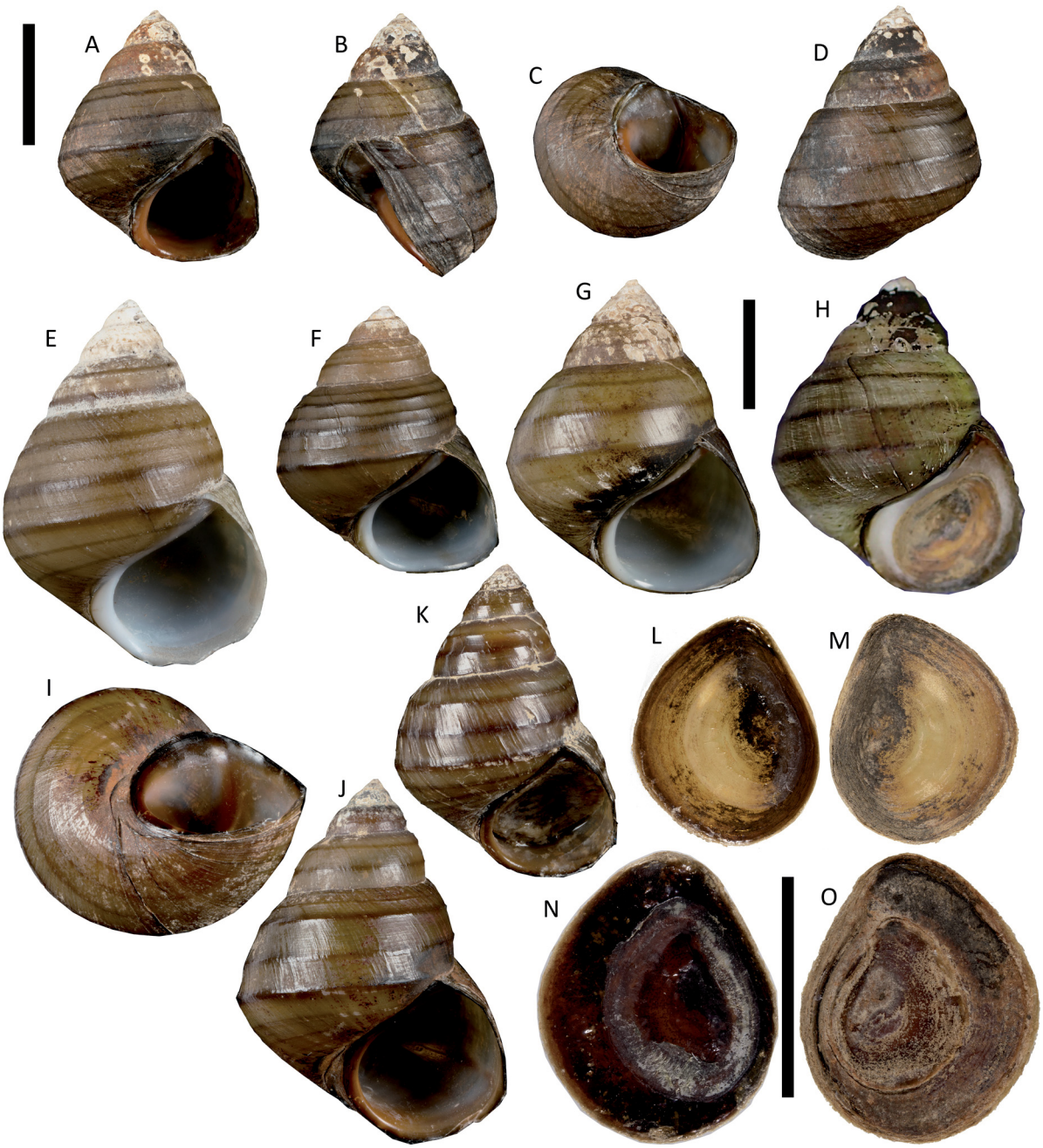


Fig. 24. Shells and operculum of *Bakyietaia liusanjieae* Zhang, Yen & von Rintelen gen. et sp. nov. **A–D**. Holotype, KIZ.240009, Xinhui, Guangxi, China. **E**. Paratype, KIZ.240092, Liusanjie Town, Guangxi, China. **F–G**. Paratypes, KIZ.240010, KIZ.240011, Xinhui, Guangxi, China. **H**. YHY-BAKLIU-XH-1 Xinhui, Guangxi, China. **I–J**. Paratype, ZMB.122722-2, Baishou, Guangxi, China. **K**. Paratype, ZMB.122763, Hezhou, Guangxi, China. **L–M**. Operculum of paratype KIZ.240010. **N–O**. Operculum of ZMB.122722-2. Scale bars = 1 cm, top left bar applies to all shells, separate bar for opercula L–O.

same data as for holotype; KIZ.240090 • 2 specs (preserved in ethanol); Guilin City, Baishou Town, Baishou River, 0.5 m deep on mud and sand substrate; 15 Mar. 2022; Le-Jia Zhang leg.; KIZ.240012, KIZ.240013 • 2 specs (preserved in ethanol); same data as for preceding; ZMB.122738 • 1 spec.; same data as for preceding; KIZ.240091 • 1 spec. (preserved dry); Hechi City, Yizhou District, Liusanjie Town, on bank of Xiajian River; 16 Mar. 2022; Le-Jia Zhang leg.; KIZ.240092 • 2 specs (preserved dry); same data as for preceding; 17 Mar. 2022; KIZ.240093 • 2 specs (preserved in ethanol); Hezhou City, Zhongshan County, Tonggu Town, Fengzhen Village, Shangpu, 0.5 m deep on mud substrate in a pond; 9 Mar. 2020; Shui-Yang Huang leg.; KIZ.240014, KIZ.240015 • 1 spec. (preserved in ethanol); same data as for preceding; ZMB.122763.

Other material

CHINA • 1 spec. (preserved dry); same data as for holotype; YHY-BAKLIU-XH-1.

Description

Adult shell (Fig. 24A–K) medium in size (25.69 ± 3.35 mm), thin but sturdy, conical shell with low spire, olive to olive brown, with five to six whorls, apex acute; teleoconch whorls not inflated, with three smooth relatively weak primary keels, with one to two even weaker smooth secondary keels located between suture and first keel, sometimes one additional weak keel located between first and second/second and third keels, base of shell with one to five weak keels, all keels usually darker than rest of shell surface; aperture ovate, less than half of shell in height, inner shell surface bluish white, orange-red or dark purple, outer lip thin, always with a strong basal angular periphery, columellar lip covered with thick inner shell layers, white or orange red, adult columellar lip recurved, sometimes forming a relatively wide crescent-shaped callus, this structure or columellar lip completely covering umbilicus.

Operculum (Fig. 24L–O) corneous, ovate, relatively thick, dark orange to dark red; exterior surface smooth; interior surface with small nuclear region, around 1/4 of inner opercular region, with shiny grains or veins or smooth glossy surface.

Radular (Fig. 25) (n = 3) central tooth with one broad central denticle and three to four small sharp cusps on either side; lateral tooth with one broad central denticle and two to three small sharp cusps on either side; inner marginal tooth narrow, about half of lateral tooth in width, with one broad central denticle and five small sharp cusps on either side; outer marginal tooth wide, almost same as lateral tooth in width, with 26 to 27 small sharp cusps.

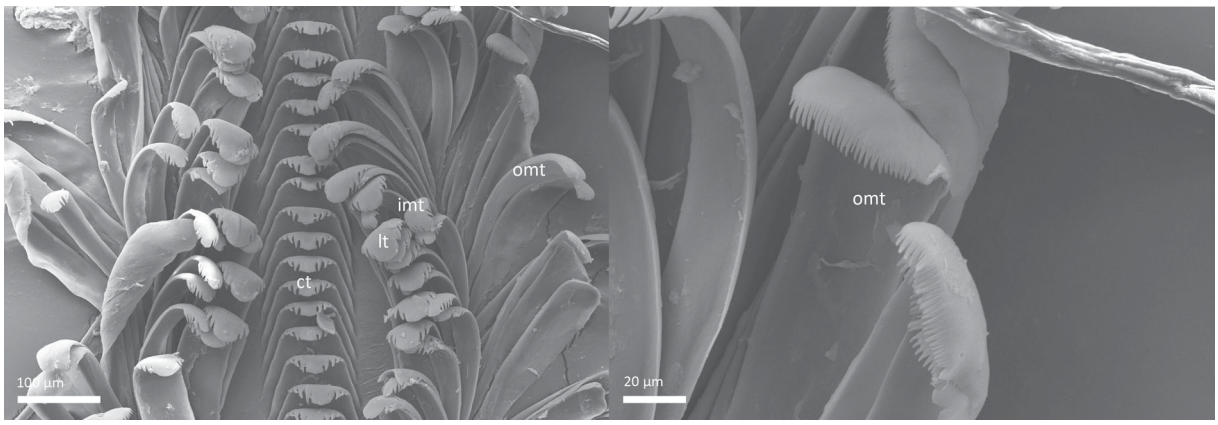


Fig. 25. SEM photo of the radula of *Bakyietaia liusanjieae* Zhang, Yen & von Rintelen gen. et sp. nov., ZMB.122722-2.

Remarks

Bakyietaia liusanjieae gen. et sp. nov. can be distinguished from its congeners based on its medium-sized conical shell with whorls not inflated and lower spire. It differs from *Bakyietaia liangzhuorum* gen. et sp. nov. by having less prominent primary keels, thin outer lip and greater number of small cusps on outer marginal teeth (26–27 vs 20–25). The distributions of *B. liusanjieae* and *B. liangzhuorum* are allopatric (Northern Guangxi vs Southern Guangxi & West Guangdong).

Habitat and distribution

Rock substrate in the shallow water of rivers of northern Guangxi, China.

Bakyietaia avisvenatoris Yen, Zhang & von Rintelen gen. et sp. nov.
urn:lsid:zoobank.org:act:DE6AD35F-6629-4C6B-A180-F4C1298C0DDB
Figs 26–27

Diagnosis

Shell small to large (19.78–27.84 mm) thin, sturdy, conical, shoulder angular, whorls inflated, prominent keel above suture, outer lip angular; columellar lip recurved, forming callus covering umbilicus completely; operculum with small nuclear region (around 1/4 of inner opercular region) with shiny grains or veins; outer marginal tooth of radula with 24–27 small sharp cusps.

Etymology

In memory of one of the ancestors of the collector of the type material, who was a bird hunter and moved to the type locality due to the abundance of birds there. The recommended Chinese name is 猎人越田螺.

Material examined

Holotype

CHINA • spec. preserved in ethanol; Guangdong Province, Guangzhou City, Zengcheng District, Paitan Town, a pond in Shi Village; 18 Jun. 2020; Da-Ming Shi leg.; KIZ.240020.

Paratypes

CHINA – **Guangdong Province** • 2 specs (preserved in ethanol); same data as for holotype; KIZ.240021, KIZ.240022 • 1 spec. (preserved in ethanol); same data as for holotype; ZMB.122757 • 1 spec. (preserved in ethanol); same data as for holotype; KIZ.240095. – **Guangxi** • 2 specs (preserved in ethanol); Yulin City, Luchuan County, Wangsha Village, Shuikou, 0.4 m deep on mud substrate or rock; 15 Nov. 2019; Bei-Hua Liang leg.; KIZ.240023, KIZ. 240055 • 1 spec. (preserved in ethanol); same data as for preceding; ZMB.122698 • 1 spec. (preserved in ethanol); same data as for preceding; KIZ.240096 • 2 specs (preserved in ethanol); Yulin City, Luchuan County, Wangsha Village, Baishiling, 0.4 m deep on mud substrate or rock; 15 Nov. 2019; Bei-Hua Liang leg.; KIZ.240052, KIZ.240053.

Other material

CHINA – **Guangxi** • 1 spec. (preserved dry); Yulin City, Luchuan County, Wangsha Village, Shuikou, 0.4 m deep on mud substrate or rock; 15 Nov. 2019; Bei-Hua Liang leg.; YHY-BAKAVI-SK-4 • 1 spec. (preserved dry); Yulin City, Luchuan County, Wangsha Village, Baishiling, 0.4 m deep on mud substrate or rock; 15 Nov. 2019; Bei-Hua Liang leg.; YHY-BAKAVI-BSL-15.

Description

Adult shell (Fig. 26A–E, J–Q) small to large (19.78–27.84 mm), thin but sturdy, conical, olive to olive brown, with five whorls, apex acute; teleoconch whorls sometimes with shoulder, with three relatively weak and smooth primary keels, with one to two weaker smooth secondary keels located between suture

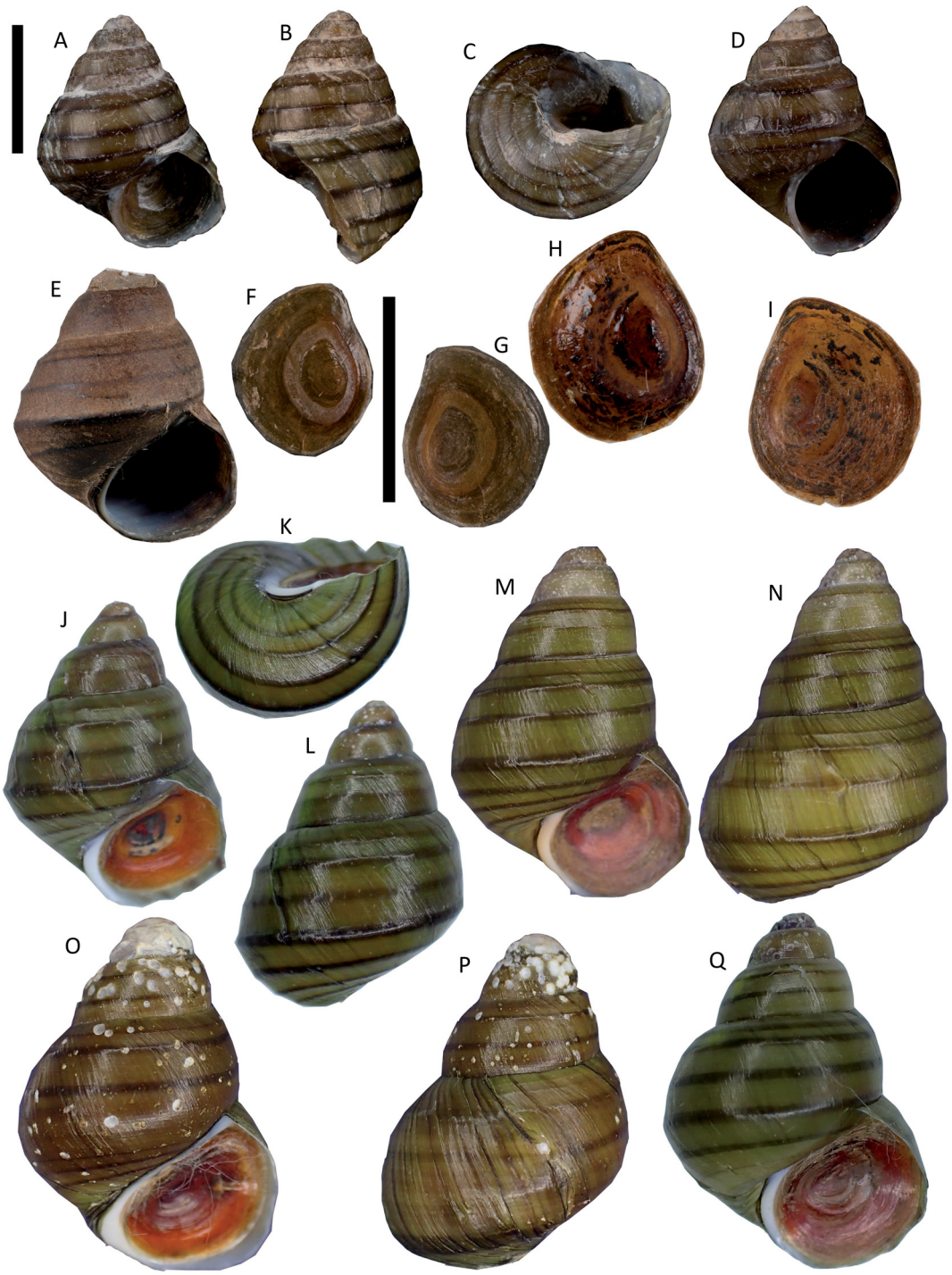


Fig. 26. Shells and operculum of *Bakyietaia avisvenatoris* Yen, Zhang & von Rintelen gen. et sp. nov. **A–C**. Holotype, KIZ.240020, Paitan Town, Guangdong, China. **D**. Paratype, ZMB.122757, Paitan Town, Guangdong, China. **E**. Paratype, ZMB.122698, Shuikou, Guangxi, China. **F–G**. Operculum of paratype, ZMB.122757. **H–I**. Operculum of paratype, ZMB.122698. **J–L**. Paratype, KIZ.240052, Baishiling, Guangxi, China. **M–N**. YHY-BAKAVI-SK-1, Shuikou, Guangxi, China. **O–P**. YHY-BAKAVI-BSL-4, Baishilin, Guangxi, China. **Q**. Paratype, KIZ.240055, Shuikou, Guangxi, China. Scale bars = 1 cm, top left bar applies to all shells, separate bar for opercula F–I.

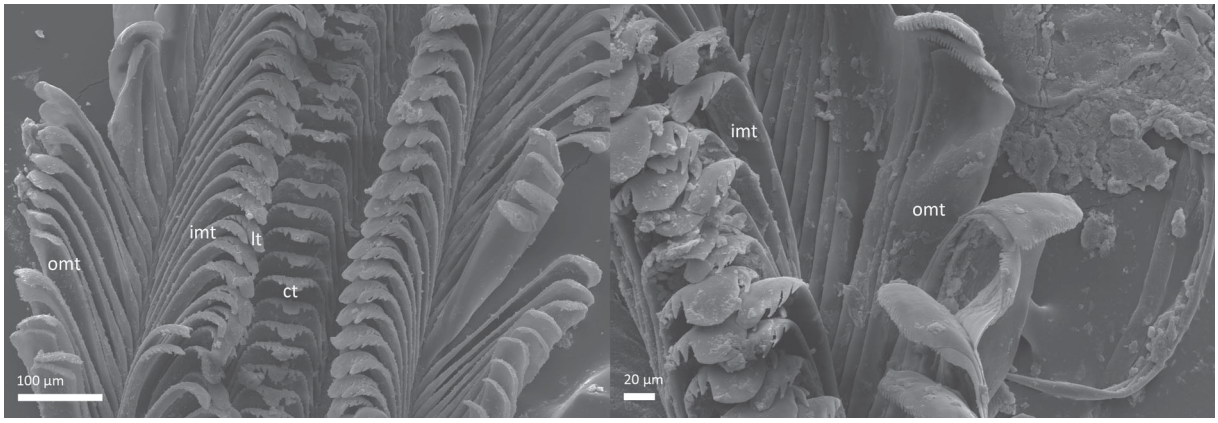


Fig. 27. SEM photo of the radula of *Bakyietaia avisvenatoris* Yen, Zhang & von Rintelen gen. et sp. nov., paratypes, MB.122757 (left), ZMB.122698 (right).

and first keel, sometimes one additional weak keel located between first and second/second and third keels, base of shell with one to three weak keels, all keels usually darker than rest of shell surface, prominent keel above suture; aperture ovate, less than half of shell in height, inner shell surface bluish white, outer lip thin, always with a strong angular periphery,, columellar lip covered with thin inner shell layers, white, columellar lip outward folding, completely or partly covering umbilicus.

Operculum (Fig. 26F–I) corneous, ovate, relatively thin, yellow to red; exterior surface smooth; interior surface with small nuclear region, around 1/4 of inner opercular region, with shiny grains or veins or smooth glossy surface.

Radular (Fig. 27) (n = 2) central tooth with one broad central denticle and four to five small sharp cusps on either side; lateral tooth with one broad central denticle and four to five small sharp cusps on either side; inner marginal tooth narrow, about half of lateral tooth in width, with one broad central denticle and three to four small sharp cusps on either side; outer marginal tooth wide, almost same width as lateral tooth, with 24 to 27 small sharp cusps.

Remarks

Bakyietaia avisvenatoris gen. et sp. nov. can be distinguished from most of its congeners based on its thin conical shell with inflated whorls, angular shoulder and strongly keeled suture. This species can be differentiated from *Bakyietaia indrapura* gen. et sp. nov. from Central Vietnam based on its less inflated whorls and less prominent keel at suture. The distributions of these two species are far apart.

Habitat and distribution

Mud substrate or rock in the shallow water of ponds and creeks in eastern Guangxi and central Guangdong Province, China.

Bakyietaia liangzhuorum Yen, Zhang & von Rintelen gen. et sp. nov.
urn:lsid:zoobank.org:act:AB0084ED-D1BE-4F3C-A448-B06D8386E028
Figs 28–29

Diagnosis

Shell medium in size (25.25 ± 3.07 mm), conical, spire low, teleoconch with prominent primary keels, columellar lip recurved, forming callus covering umbilicus completely, outer lip thick; operculum with small nuclear region (around 1/5 of inner opercular region) with shiny grains or veins; outer marginal tooth of radula with 20–25 small sharp cusps.

Etymology

'Liang Zhu' is the abbreviated title of one of China's four great folktales, 'Liang Shanbo and Zhu Yingtai'. They loved each other, but Zhu was forcibly betrothed to someone else. Liang, grief-stricken, became ill and died. When Zhu's wedding procession passed Liang's tomb, a strong wind suddenly blew up, forcing them to stop. In front of the tomb, Zhu told Liang how much she loved him. The tomb burst open and Zhu immediately jumped into it. Afterwards a pair of colourful butterflies appeared from the tomb: their spirits emerged in the form of butterflies and flew away together, never to be separated again.

Inspiration for the name *liangzhuorum* for this species is drawn from seven Han Dynasty (202 BC–220 AD) tombs in Basi, which are near the type locality. The recommended Chinese name is 彩蝶越田螺.

Material examined

Holotype

CHINA • spec. preserved in ethanol; Guangxi, Laibin City, Wuxian County, Tongwan Town, a river in Jin Village, 0.5 m deep in crack of rocks; 20 Dec. 2019; Han-Zhi Tan leg.; KIZ.240024.

Paratypes

CHINA – **Guangdong Province** • 2 specs (preserved in ethanol); Qingyuan City, Qingxin District, Bin River near Shitan Town, 0.6 m deep on rock with sand and mud substrate; 24 Sep. 2022; Mr Chen leg.; KIZ.240031, KIZ.240032 • 1 spec. (preserved in ethanol); Qingyuan City, Qingxin District, Bin River near Shitan Town, 0.6 m deep on rock with sand and mud substrate; 24 Sep. 2022; Mr Chen leg.; ZMB.122762 • 1 spec. (preserved in ethanol); same data as for preceding; KIZ.240099. – **Guangxi** • 4 specs (preserved in ethanol); same data as for holotype; KIZ.240025 to KIZ.240028 • 1 spec. (preserved in ethanol); same data as for holotype; ZMB.122691 • 4 specs (preserved in ethanol); same data as for holotype; KIZ.240097 • 2 specs (preserved in ethanol); Yulin City, Chenghuang Town, a river near Shirentou Mountain, 0.1 m deep on mud and sand substrate; 13 Mar. 2022; Le-Jia Zhang leg.; KIZ.240029, KIZ.240030 • 1 spec. (preserved in ethanol); Yulin City, Chenghuang Town, a river near Shirentou Mountain, 0.1 m deep on mud and sand substrate; 13 Mar. 2022; Le-Jia Zhang leg.; ZMB.122719 • 1 spec. (preserved in ethanol); Yulin City, Chenghuang Town, a river near Shirentou Mountain, 0.1 m deep on mud and sand substrate; 13 Mar. 2022; Le-Jia Zhang leg.; KIZ.240098 • 4 specs (preserved in ethanol); Qinzhou City, Pubei County, Liuken Town, Hengtong, 0.2 m deep on mud substrate; 25 Sep. 2020; Mr Huang leg.; KIZ.240033 to KIZ.240036 • 2 specs (preserved in ethanol); same data as for preceding; ZMB.122761 • 4 specs (preserved in ethanol); same data as for preceding; KIZ.240100.

Other material

CHINA – **Guangdong Province** • 3 specs (preserved dry); Qingyuan City, Qingxin District, Bin River near Shitan Town, 0.6 m deep on rock with sand and mud substrate; 24 Sep. 2022; Mr Chen leg.; YHY-BAKLIA-ST-18, YHY-BAKLIA-ST-17, YHY-BAKLIA-ST-2. – **Guangxi** • 1 spec. (preserved dry); Yulin City, Chenghuang Town, a river near Shirentou Mountain, 0.1 m deep on mud and sand substrate; 13 Mar. 2022; Le-Jia Zhang leg.; YHY-BAKLIA-CH-1 • 3 specs (preserved dry); Qinzhou City, Pubei County, Liuken Town, Hengtong, 0.2 m deep on mud substrate; 25 Sep. 2020; Mr Huang leg.; YHY-BAKLIA-QZ-1, YHY-BAKLIA-QZ-18, YHY-BAKLIA-QZ-2.

Description

Adult shell (Fig. 28A–I, H–L) medium in size (25.25 ± 3.07 mm), thin to thick, sturdy, conical, olive to greenish brown, with six whorls, teleoconch whorls not inflated, with three smooth strong primary keels, with one to two weak smooth keels located between suture and first keel, sometimes one additional weak keel located between first and second/second and third keels, base of shell with one to four weak keels, all keels usually darker than rest of shell surface; aperture ovate, less than half of the shell in height, inner

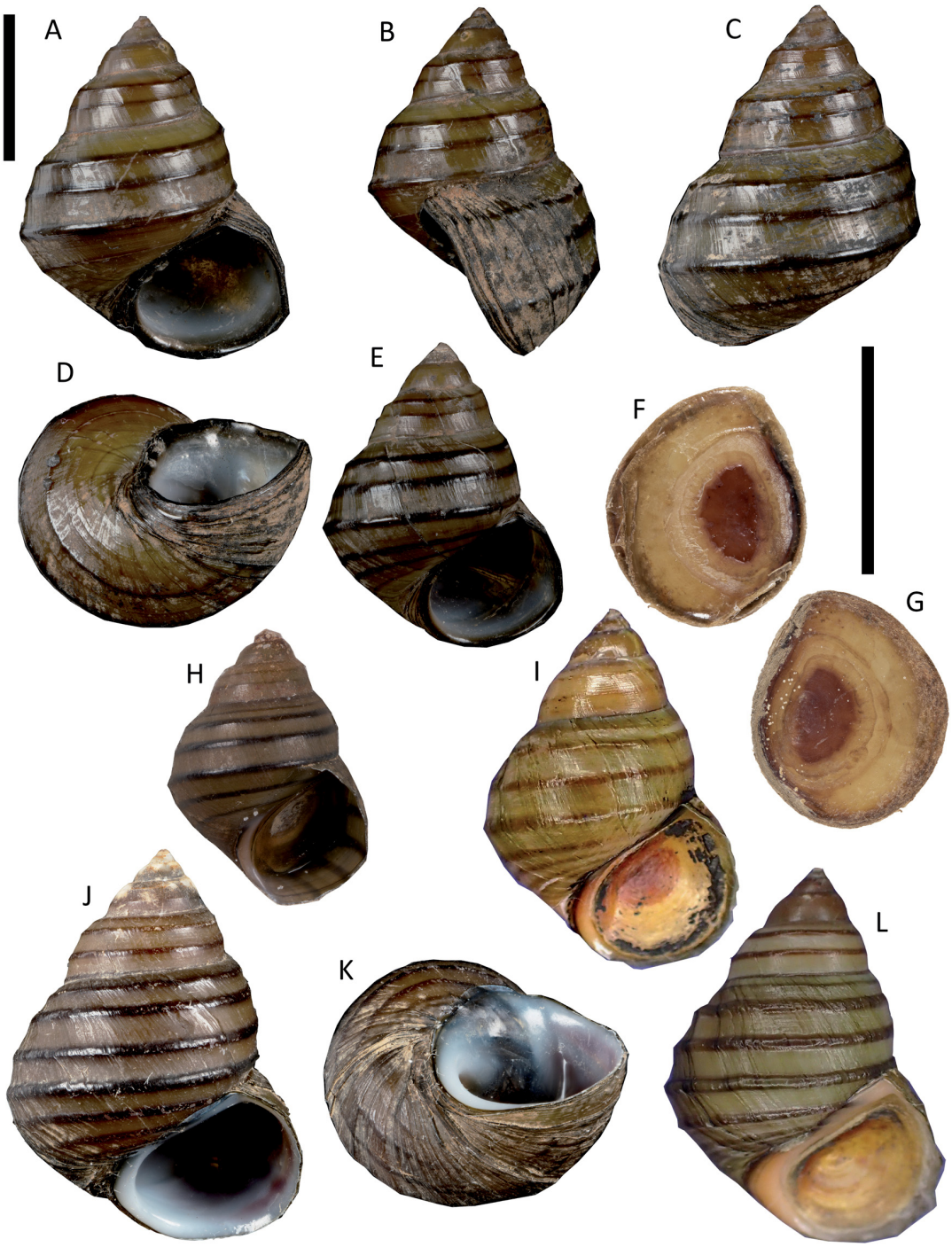


Fig. 28. Shells and operculum of *Bakyietaia liangzhuorum* Yen, Zhang & von Rintelen gen. et sp. nov. **A–D, F–G**. Holotype, KIZ.240024, Laibin, Guangxi, China. **E**. Paratype, ZMB.122691, Laibin, Guangxi, China. **F–G**. Operculum. **H**. Paratype, ZMB.122761, Qinzhou, Guangxi, China. **I**. YHY-BAKLIA-CH-1, Chenghuang Town, Guangxi, China. **J–K**. Paratype, KIZ.240031, Shitan Town, Guangdong, China. **L**. YHY-BAKLIA-ST-18, Shitan Town, Guangdong, China. Scale bars = 1 cm, top left bar applies to all shells, separate bar for operculum F–G.

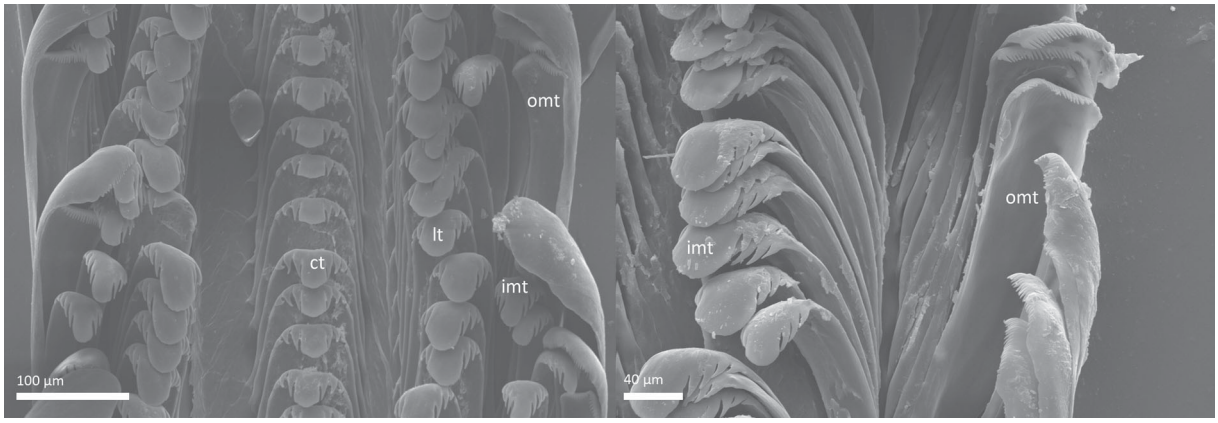


Fig. 29. SEM photo of the radula of *Bakyietaia liangzhuorum* Yen, Zhang & von Rintelen gen. et sp. nov. Paratypes, ZMB.122691 (left), ZMB.122719 (right).

shell surface bluish white to pale purple, margin of outer and columellar lip stained black or white, outer lip slightly thickened, always with a strong angular periphery, columellar lip covered with thick inner shell layers, white or pale orange, adult columellar lip recurved, forming a relatively narrow crescent-shaped callus, this structure completely covering umbilicus.

Operculum (Fig. 28F–G) corneous, ovate, relatively thick, yellow to orange, sometimes with red nuclear region; exterior surface smooth; interior surface with small nuclear region, around 1/5 of inner opercular region, with shiny grains or veins or smooth glossy surface.

Radular (Fig. 29) (n = 5) central tooth with one broad central denticle and three to four small sharp cusps on either side; lateral tooth with one broad central denticle and three to four small sharp cusps on either side; inner marginal tooth narrow, about half of lateral tooth in width, with one broad central denticle and three to four small sharp cusps on either side; outer marginal tooth wide, almost same as lateral tooth in width, with 20 to 25 small sharp cusps.

Remarks

Bakyietaia liangzhuorum gen. et sp. nov. can be distinguished from its congeners based on its medium-sized conical shell with low spire, prominent primary keels and thick outer lip. This species occurs sympatrically with *B. chenghuang* gen. et sp. nov. in Chenghuang Town. However, *B. liangzhuorum* prefers a sandy/muddy substrate, while *B. chenghuang* lives on large rocks.

Habitat and distribution

Mostly sand or mud substrate (occasionally on rocks) in the shallow water of rivers in eastern Guangxi and central Guangdong Province, China.

Bakyietaia luikongi Yen, Zhang & von Rintelen gen. et sp. nov.
urn:lsid:zoobank.org:act:4A1410D8-7530-4344-8041-08948593A02E
Figs 30–31

Diagnosis

Shell relatively small (20.66 ± 0.70), thin, spiral whorls low, shoulder angular, teleoconch with very weak primary keels. Outer marginal tooth of radula with 19–20 small sharp cusps; columellar lip recurved, forming callus covering umbilicus completely; operculum with small nuclear region (around 1/5 of inner opercular region) with shiny grains or veins.

Etymology

Named after 'Lui Kong', the god of thunder in the local Min Nan Chinese dialect, popular in the folklore of Leizhou County which includes the type locality of this species. The recommended Chinese name is 雷神越田螺.

Material examined

Holotype

CHINA • spec. preserved in ethanol; Guangdong Province, Zhanjiang City, Leizhou County, Liren Village, near Nanguang Farm Second Team, 0.1–0.5 m deep on mud and rock substrate in ponds; 6 Apr. 2020; Yu-Xuan Zhou leg.; KIZ.240037.

Paratypes

CHINA • 4 specs (preserved in ethanol); same data as for holotype; KIZ.240038 to KIZ.240041 • 2 specs (preserved in ethanol); same data as for holotype; ZMB.122764 • 3 specs (preserved in ethanol); same data as for holotype; KIZ.240101.

Other material

CHINA • 1 spec. (preserved dry); same data as for holotype; YHY-BAKLK-LR-1.

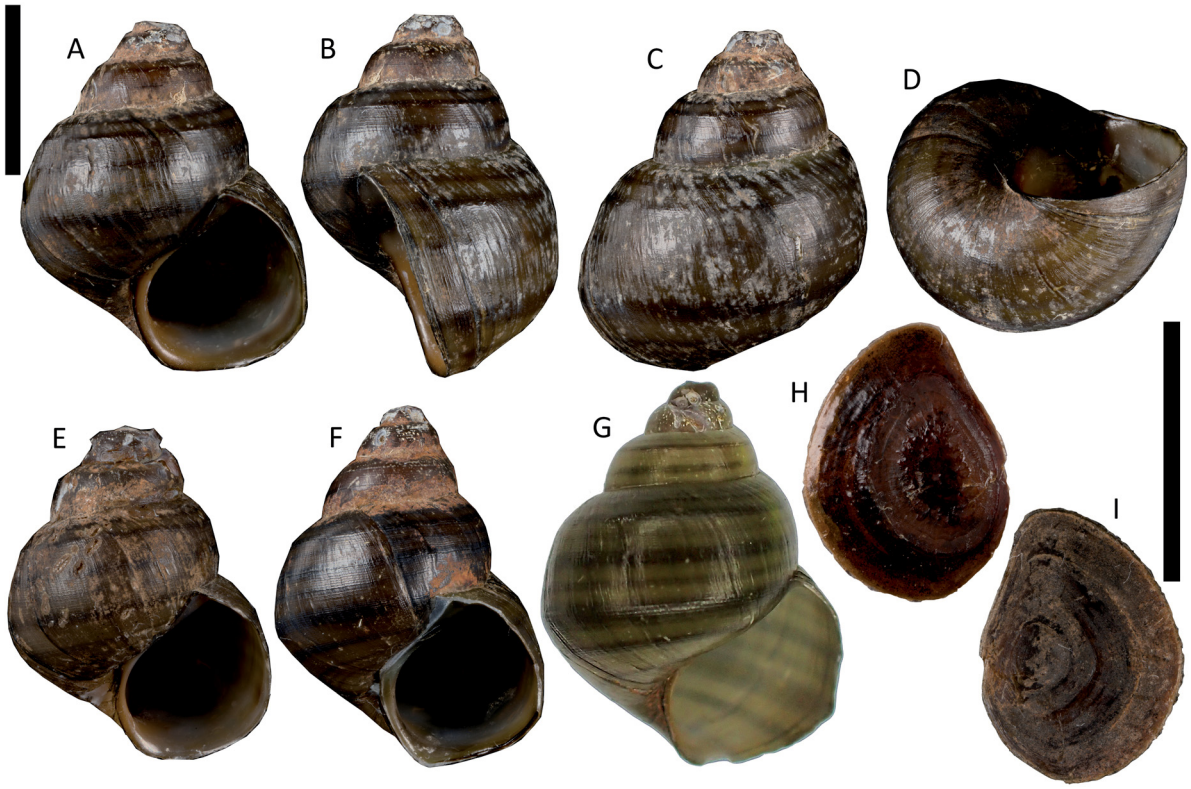


Fig. 30. Shells and operculum of *Bakyietaia luikongi* Yen, Zhang & von Rintelen gen. et sp. nov. **A–D**. Holotype, KIZ.240037, Leizhou, Guangdong, China. **E–F**. Paratype, ZMB.122764, Leizhou, Guangdong, China. **G**. YHY-BAKLK-LR-1, Leizhou, Guangdong, China. **H–I**. Operculum of holotype, KIZ.240037. Scale bars = 1 cm, top left bar applies to all shells, separate bar for operculum G–H.

Description

Adult shell (Fig. 30A–G) relatively small for the genus (20.66 ± 0.70 mm), thin but sturdy, broad conical to conical, dark olive brown, with five whorls, apex acute; teleoconch whorls sometimes with shoulder, with three weak but obvious smooth primary keels, with one to two weaker smooth secondary keels located between suture and first keel, always with one weak keel located between first and second/second and third keels, base of shell with three to four weak keels, all keels usually darker than rest of shell surface; aperture ovate, lnearly half of shell in height, inner shell surface bluish white, outer lip thin, always with an obvious angular periphery, columellar lip covered with thin inner shell layers, white to orange, columellar lip folded outwards, completely covering umbilicus.

Operculum (Fig. 30H–I) corneous, ovate, thin, dark orange to dark red; exterior surface smooth; interior surface with small nuclear region, around 1/5 of inner opercular region, with shiny grains or veins or smooth glossy surface.

Radular (Fig. 31) (n = 2) central tooth with one broad central denticle and four small sharp cusps on either side; lateral tooth with one broad central denticle and four small sharp cusps on either side; inner marginal tooth narrow, about half of lateral tooth in width, with one broad central denticle and three to four small sharp cusps on either side; outer marginal tooth wide, almost same width as lateral tooth, with 19 to 20 small sharp cusps.

Remarks

Bakyietaia luikongi gen. et sp. nov. is the only species of *Bakyietaia* gen. nov. with a conical shell and weak primary keels distributed outside Hainan Island and is the sister species of the clade including all species with weak primary keels from Hainan. It can be easily distinguished from all congeners based on the small thin conical shell with three very weak primary keels and lower spire. It is the smallest species among those with weak primary keels.

Habitat and distribution

Only known from mud and rock substrate in the shallow water of ponds in Leizhou Peninsula, Guangdong Province, China.

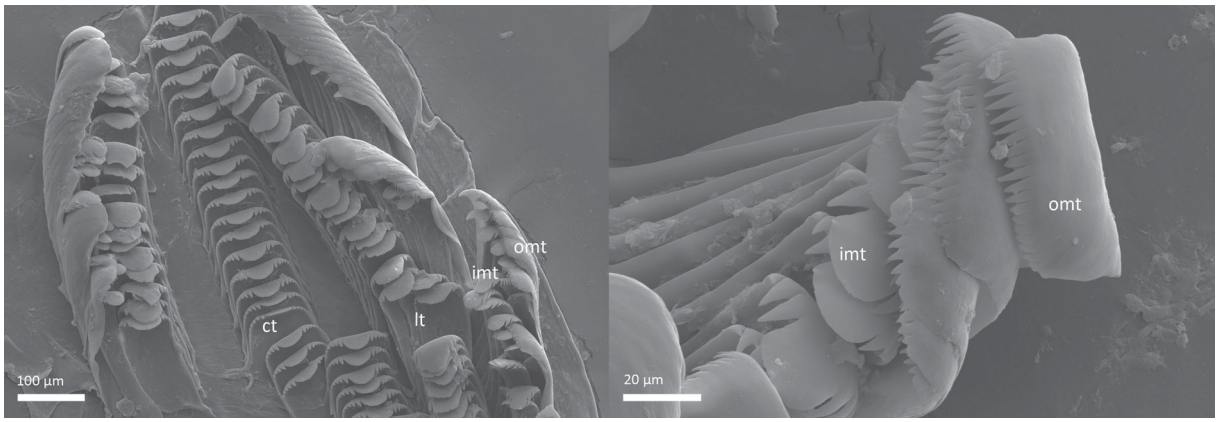


Fig. 31. SEM photo of the radula of *Bakyietaia luikongi* Yen, Zhang & von Rintelen gen. et sp. nov., paratype, ZMB.122764.

Bakyietaia fontinalis Zhang, Yen & von Rintelen gen. et sp. nov.
urn:lsid:zoobank.org:act:8DFECB0B-656C-42B6-B3FE-51C2BC907619
Figs 32–33

Diagnosis

Shell medium in size (24.25 ± 2.59 mm), sturdy, conical, whorls not inflated, with weak primary keels, shoulder rounded; columellar lip recurved, forming callus covering umbilicus completely; operculum with small nuclear region (around 1/5 of inner opercular region) with shiny grains or veins; outer marginal tooth of radula with 26–29 small sharp cusps.

Etymology

Refers to the cold spring habitat of the type locality. The recommended Chinese name is 冷泉越田螺.

Material examined

Holotype

CHINA • spec. preserved in ethanol; Hainan Province, Dingan County, Jiuwentang Town, Jiuwentang Cold Spring, 0.5 m deep on mud and sand substrate; 6 Mar. 2022; Le-Jia Zhang leg.; KIZ.240042.

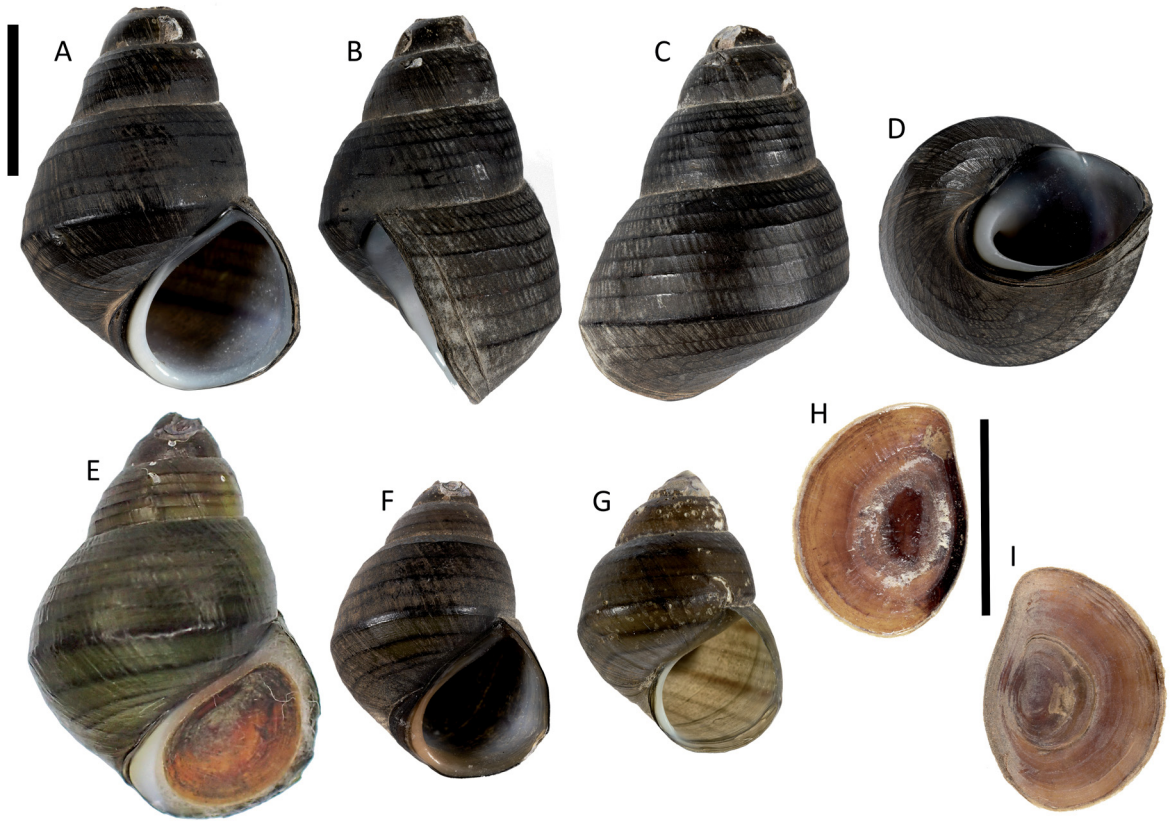


Fig. 32. Shells and operculum of *Bakyietaia fontinalis* Zhang, Yen & von Rintelen gen. et sp. nov. **A–D**. Holotype, KIZ.240042, Jiuwentang, Hainan, China. **E**. YHY-BAKFON-LQ-1, Jiuwentang, Hainan, China. **F**. Paratype, ZMB.122764, Jiuwentang, Hainan, China. **G**. Paratype, KIZ.240104, Wanquan River, Hainan, China. **H–I**. Operculum of holotype, KIZ.240042. Scale bars = 1 cm, top left bar applies to all shells, separate bar for operculum H–I.

Paratypes

CHINA • 1 spec. (preserved in ethanol); same data as for holotype; KIZ.240043 • 2 specs (preserved in ethanol); same data as for holotype; ZMB.122733 • 1 spec. (preserved in ethanol); same data as for holotype; KIZ.240102 • 2 specs (preserved in ethanol); Hainan Province, Dingan County, river near Leiming Town; 2018; KIZ.240103 • 1 spec. (preserved in ethanol); Hainan Province, Qionghai City, Shibi Town, Wanquan River, 0.1 m deep on rock; 7 Mar. 2022; Le-Jia Zhang leg., KIZ.240104.

Other material

CHINA • 1 spec. (preserved dry); same data as for holotype; YHY-BAKFON-LQ-1.

Description

Adult shell (Fig. 32A–G) medium in size (24.25 ± 2.59 mm), thin to thick, sturdy, conical, olive to dark olive brown, with five whorls, apex acute; teleoconch whorls not inflated, with three weak but obvious smooth primary keels, with one to two weaker smooth secondary keel located between suture and first keel, always with one additional weak keel located between first and second/second and third keels, base of shell with two to four weak keels, all keels usually darker than the other part of shell surface in colour; aperture ovate, less than half of shell in height, inner shell surface bluish white, outer lip thin, always with a strong angular periphery, columellar lip covered with thick inner shell layers, white or orange, adult columellar lip recurved, sometimes forming a crescent-shaped callus, this structure or columellar lip completely covering umbilicus.

Operculum (Fig. 32H–I) corneous, ovate, thin, orange to dark red; exterior surface smooth; interior surface with small nuclear region, around 1/5 of inner opercular region, with shiny grains or veins or smooth glossy surface.

Radular (Fig. 33) (n = 2) central tooth with one broad central denticle and four to five small sharp cusps on either side; lateral tooth with one broad central denticle and four small sharp cusps on either side; inner marginal tooth narrow, about half width of lateral tooth, with one broad central denticle and four to five small sharp cusps on either side; outer marginal tooth wide, almost same as lateral tooth in width, with 26 to 29 small sharp cusps.

Remarks

Bakyietaia fontinalis gen. et sp. nov. is one of the species of *Bakyietaia* gen. nov. with weak primary keels. This species can be easily distinguished from all congeners, especially the morphologically similar

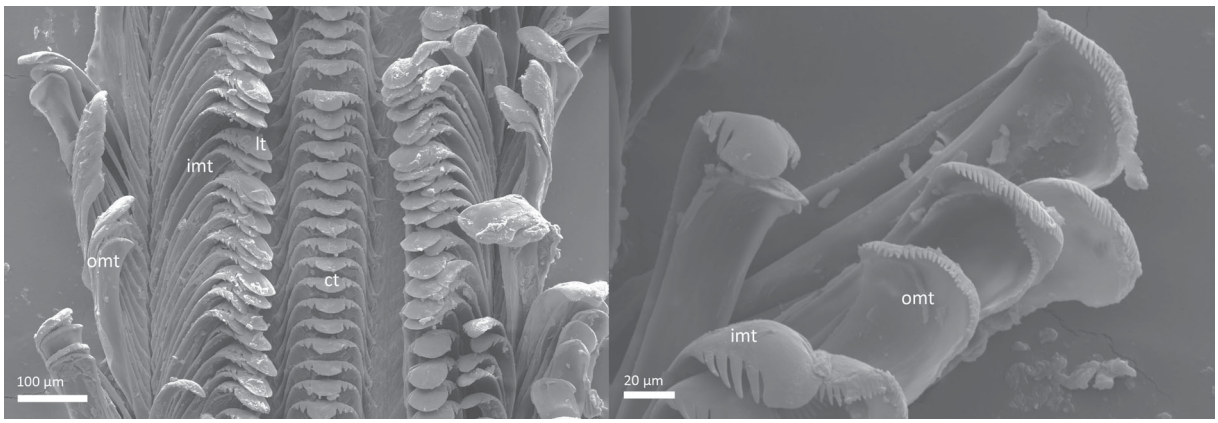


Fig. 33. SEM photo of the radula of *Bakyietaia fontinalis* Zhang, Yen & von Rintelen gen. et sp. nov., paratype, ZMB.122733.

species *B. mutica*, based on its medium-sized conical shell with whorls not inflated, rounded shoulder and more cusps on the outer marginal teeth (26–29 vs 19–24).

Habitat and distribution

Mud and rock substrate in the shallow water of springs and rivers of central-eastern Hainan Province, China.

Bakyietaia naiadica Zhang, Yen & von Rintelen gen. et sp. nov.
urn:lsid:zoobank.org:act:1E34D07F-05C1-4819-ADC6-D02399C18B8B
Figs 34–35

Diagnosis

Shell medium in size (25.73 ± 0.62 mm), sturdy, cylindrical outline, with very weak primary keels, weak keel above suture, outer lip angular; columellar lip recurved, forming callus covering umbilicus completely; operculum with small nuclear region (around 1/5 of inner opercular region) with shiny grains or veins; outer marginal tooth of radula with 19–22 small sharp cusps.

Etymology

Named after Naiads, the nymphs of freshwater bodies such as springs in Greek mythology. The recommended Chinese name is 龙婆越田螺.

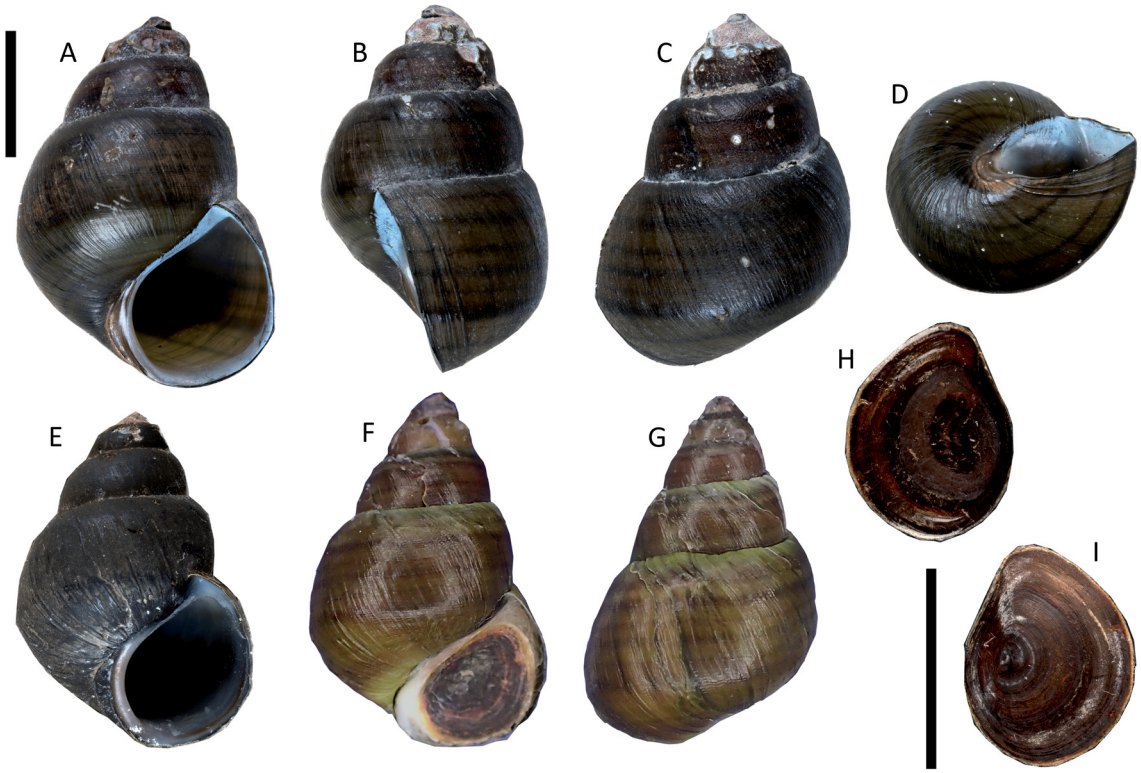


Fig. 34. Shells and operculum of *Bakyietaia naiadica* Zhang, Yen & von Rintelen gen. et sp. nov. **A–D**. Holotype, KIZ.240044, Longpo Temple, Hainan, China. **E**. Paratype, KIZ.240045, Xue Village, Hainan, China. **F–G**. YHY-BAKNAI-XC-1, Xue Village, Hainan, China. **H–I**. Operculum of holotype, KIZ.240044. Scale bars = 1 cm, top left bar applies to all shells, separate bar for operculum F–G.

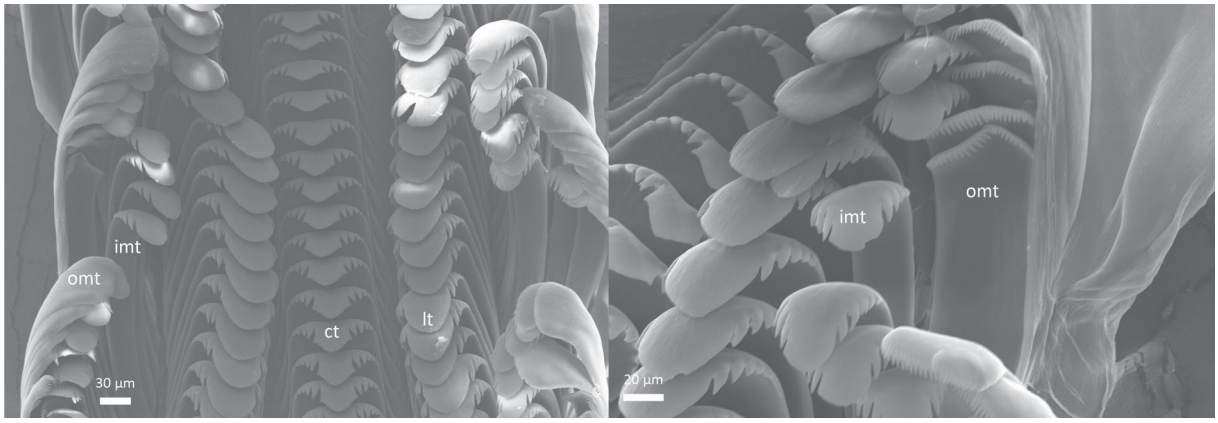


Fig. 35. SEM photo of the radula of *Bakyietaia naiadica* Zhang, Yen & von Rintelen gen. et sp. nov., paratype, ZMB.122743.

Material examined

Holotype

CHINA • spec. preserved in ethanol; Hainan Province, Haikou City, spring near Longpo Temple, 0.1 m deep on rock; 5 Mar. 2022; Le-Jia Zhang leg.; KIZ.240044.

Paratypes

CHINA • 1 spec. (preserved in ethanol); same data as for holotype; ZMB.122743 • 1 spec. (preserved in ethanol); Hainan Province, wetland in Xue Village, Haikou City, 0.1 m deep on rock substrate; 3 May 2022; Le-Jia Zhang leg.; KIZ.240045.

Other material

CHINA • 1 spec. (preserved dry); Hainan Province, wetland in Xue Village, Haikou City, 0.1 m deep on rock substrate; 3 May 2022; Le-Jia Zhang leg.; YHY-BAKNAI-XC-1.

Description

Adult shell (Fig. 34A–G) medium (25.73 ± 0.62 mm), thin but sturdy, conical, olive to dark olive brown, with five whorls; teleoconch whorls inflated, with shoulder, with three very weak smooth primary keels, with one to two even weaker smooth secondary keels located between suture and first keel, sometimes with one additional weak keel located between first and second/second and third keels, base of shell with two to four weak keels, all keels usually darker than rest of shell surface; aperture ovate, less than half of shell in height, inner shell surface bluish white, outer lip thin, always with an obvious angular periphery, columellar lip covered with thick inner shell layers, white or pale orange, adult columellar lip recurved, sometimes forming a crescent-shaped callus, this structure completely covering umbilicus.

Operculum (Fig. 34H–I) corneous, ovate, thin, dark red; exterior surface smooth; interior surface with small nuclear region, around 1/5 of inner opercular region, with shiny grains or veins or smooth glossy surface.

Radular (Fig. 35) (n = 1) central tooth with one broad central denticle and four to five small sharp cusps on either side; lateral tooth with one broad central denticle and four to five small sharp cusps on either side; inner marginal tooth narrow, about half width of lateral tooth, with one broad central denticle and five to six small sharp cusps on either side; outer marginal tooth wide, almost same as lateral tooth in width, with 19 to 22 small sharp cusps.

Remarks

Bakyietaia naiadica gen. et sp. nov. can be easily distinguished from all congeners, especially the morphologically similar *B. mutica*, based on its more cylindrical shell with weaker primary keels and less prominent keel at suture.

Habitat and distribution

Rock substrate in the shallow water of springs and wetlands of northern Hainan Province, China.

Bakyietaia luuemxlong Zhang, Yen & von Rintelen gen. et sp. nov.
urn:lsid:zoobank.org:act:3C33CDFF-1DD8-4AC2-A4D6-A28D0535B1A4
Figs 36–37

Diagnosis

Shell small to medium in size (23.56 ± 2.58 mm), sturdy, whorls inflated, with weak primary keels, moderate keel above suture; columellar lip recurved, forming callus covering umbilicus completely; operculum with small nuclear region (around 1/5 of inner opercular region) with shiny grains or veins; outer marginal tooth of radula with 20 small sharp cusps; distributed in southern Hainan Island.

Etymology

According to the mythology of the Hlai people of Hainan Island, 'luuemx long', which means 'forget to grow up' in the Hlai language, is a race of dwarves living in the forest. Formed as a noun in apposition. The recommended Chinese name is 阑咙越田螺.

Material examined

Holotype

CHINA • spec. preserved in ethanol; Hainan Province, Qionghai City, Huishan Town, creeks near farmland of Mutang Village, 0.1 m deep on mud substrate; 7 Mar. 2022; Le-Jia Zhang leg.; KIZ.240046.

Paratypes

CHINA • 2 specs (preserved in ethanol); same data as for holotype; KIZ.240047–240048 • 1 spec. (preserved in ethanol); same data as for holotype; ZMB.122739.

Other material

CHINA • 1 spec. (preserved dry); same data as for holotype; YHY-BAKLUU-MT-1.

Description

Adult shell (Fig. 36A–E, H–J) small to medium (23.56 ± 2.58 mm), thin but sturdy, conical, dark olive brown, with five whorls; teleoconch whorls inflated, with three weak but obvious primary keels, with one to two even weaker smooth secondary keels located between suture and first keel, always with one additional weak keel located between first and second/second and third keels, base of shell with two to four weak keels, all keels usually darker than rest of shell surface; aperture ovate, less than half of shell in height, inner shell surface bluish white, outer lip thin, always with an obvious angular periphery, columellar lip covered with thick inner shell layers, white, columellar lip folded outwards, covering umbilicus.

Operculum (Fig. 36F–G) corneous, ovate, thin, dark red; exterior surface smooth; interior surface with small nuclear region, around 1/5 of inner opercular region, with shiny grains or veins or smooth glossy surface.

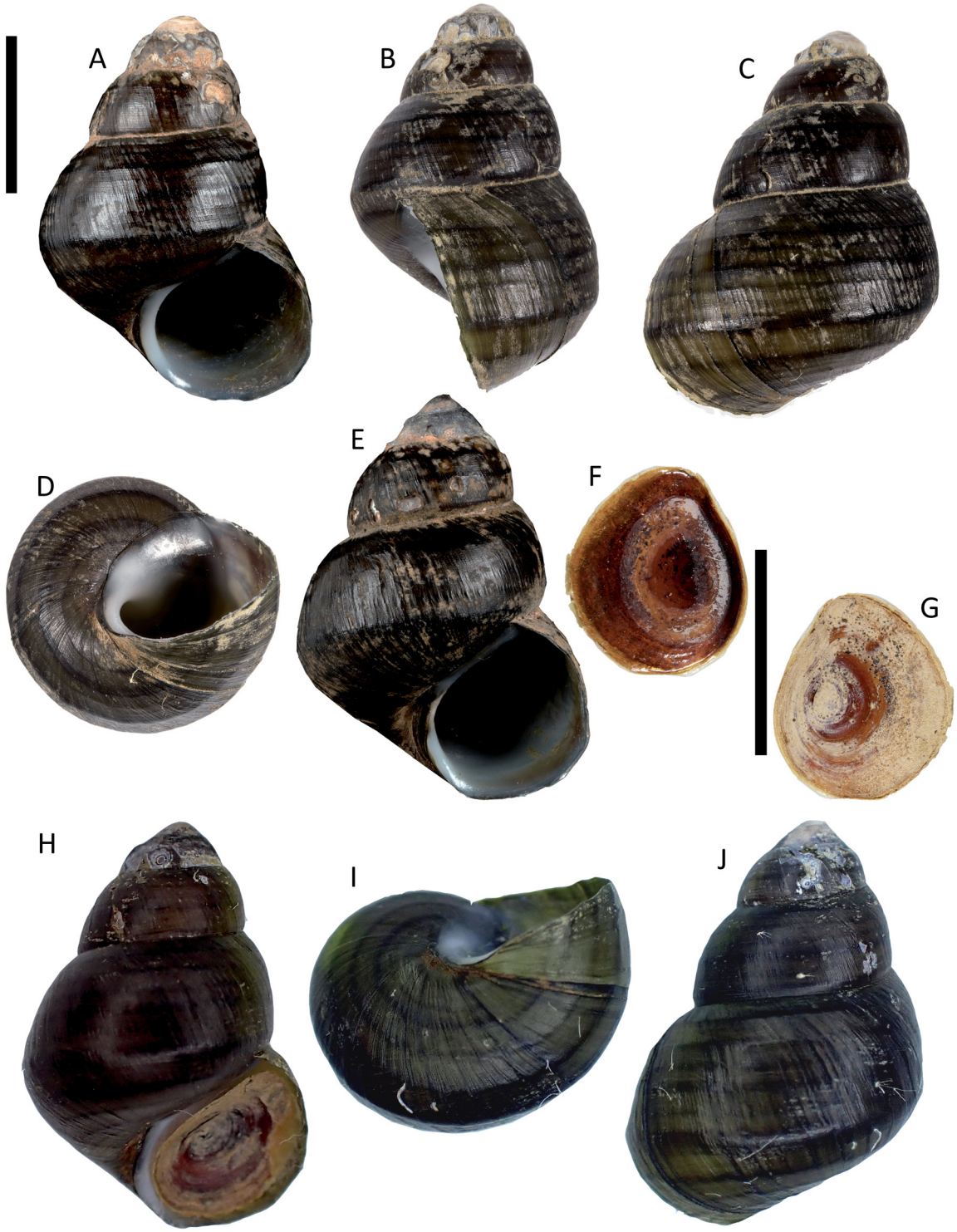


Fig. 36. Shells and operculum of *Bakyietaia luuemxlong* Zhang, Yen & von Rintelen gen. et sp. nov. **A–D**. Holotype, KIZ.240046, Mutang, Hainan, China. **E**. Paratype, ZMB.122739, Mutang, Hainan, China. **F–G**. Operculum of holotype, KIZ.240046. **H–J**. YHY-BAKLUU-MT-1, Mutang, Hainan, China. Scale bars = 1 cm, top left bar applies to all shells, separate bar for operculum F–G.

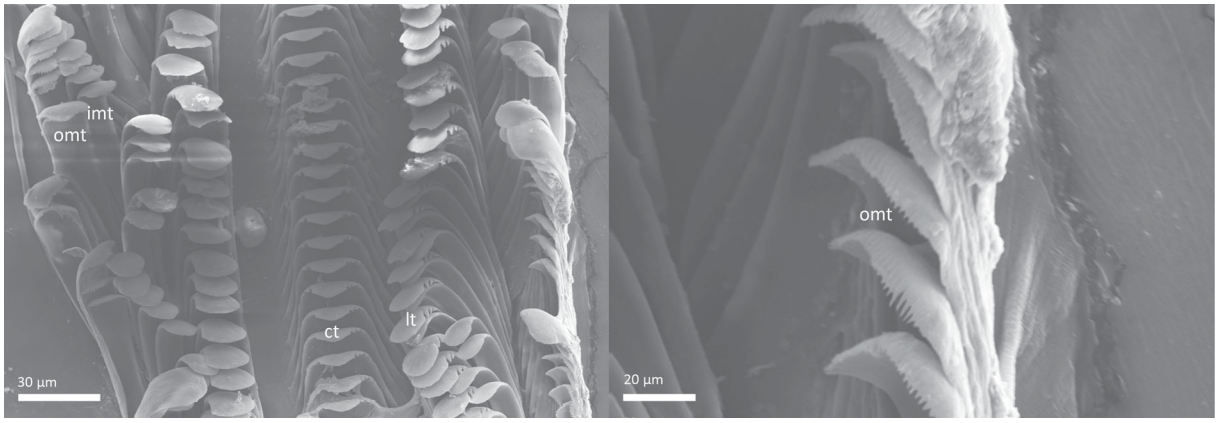


Fig. 37. SEM photo of the radula of *Bakyietaia luuemxlong* Zhang, Yen & von Rintelen gen. et sp. nov., paratype, ZMB.122739.

Radular (Fig. 37) (n = 1) central tooth with one broad central denticle and four small sharp cusps on either side; lateral tooth with one broad central denticle and three small sharp cusps on either side; inner marginal tooth narrow, about half of lateral tooth in width, with one broad central denticle and unknown number of small sharp cusps on either side (all heavily worn); outer marginal tooth wide, almost same as lateral tooth in width, with around 20 small sharp cusps.

Remarks

Bakyietaia luuemxlong gen. et sp. nov. is one of the species of *Bakyietaia* gen. nov. with weak primary keels. This species can be easily distinguished from all congeners based on the small- to medium-sized conical shell with inflated whorls and moderate keel above suture.

Habitat and distribution

Only known from the type locality on mud substrate in the shallow water of creeks in southern Hainan Province, China.

Bakyietaia indrapura Zhang, Yen & von Rintelen gen. et sp. nov.
urn:lsid:zoobank.org:act:D7B758FD-46BD-4DED-8C15-AD9BED3528AA
Figs 38–39

Diagnosis

Shell medium in size (26.92 ± 2.45 mm), thin, sturdy, whorls inflated, with prominent primary keels at suture; columellar lip recurved, forming callus covering umbilicus completely; operculum with small nuclear region (around 1/5 of inner opercular region) with shiny grains or veins; outer marginal tooth of radula with 21–26 small sharp cusps; distributed in central Vietnam.

Etymology

Named after Indrapura, capital of the ancient kingdom of Champa, which is close to the type locality. Formed as a noun in apposition. The recommended Chinese name is 占婆越田螺.

Material examined

Holotype

VIETNAM • 1 spec. (preserved in ethanol); Phuoc Son, Kham Duc, Cai River drainage; 21–31 Oct. 2006; Frank Köhler leg.; ZMB.114403.1.

Paratypes

VIETNAM • 2 specs (preserved in ethanol); same data as for holotype; ZMB.114403 • 5 specs (preserved in ethanol); Nghê An, Tân Duong District, Tam Quang, Truong Son Mts, mountain creek; 21–31 Oct. 2006; Frank Köhler leg.; ZMB.114402.1, ZMB.114402 • 3 specs (preserved in ethanol); same data as for preceding; ZMB.114406.

Description

Adult shell (Fig. 38A–F) medium in size (26.92 ± 2.45 mm), thin but sturdy, conical, olive to greenish brown, with five to six whorls, apex acute; teleoconch whorls, especially body whorl, slightly inflated, sometimes forming shoulder, with three smooth primary keels, with one to two weaker smooth secondary keels located between suture and first keel, sometimes one additional weak keel located between first and second/second and third keels, base of shell with three to five weak keels, keels usually darker than rest of shell surface; aperture ovate, less than half of shell in height, inner shell surface bluish white, outer lip thin, always with a strong angular periphery, columellar lip covered with thick inner shell layers, white or orange, adult columellar lip recurved, forming a very narrow crescent-shaped callus or without this structure, columellar lip or this structure usually covering umbilicus, umbilicus sometimes narrowly open, bordered by a keel.

Operculum (Fig. 38G–H) corneous, ovate, thin, yellow to orange; exterior surface smooth; interior surface with small nuclear region, around 1/5 of inner opercular region, with shiny grains or veins.

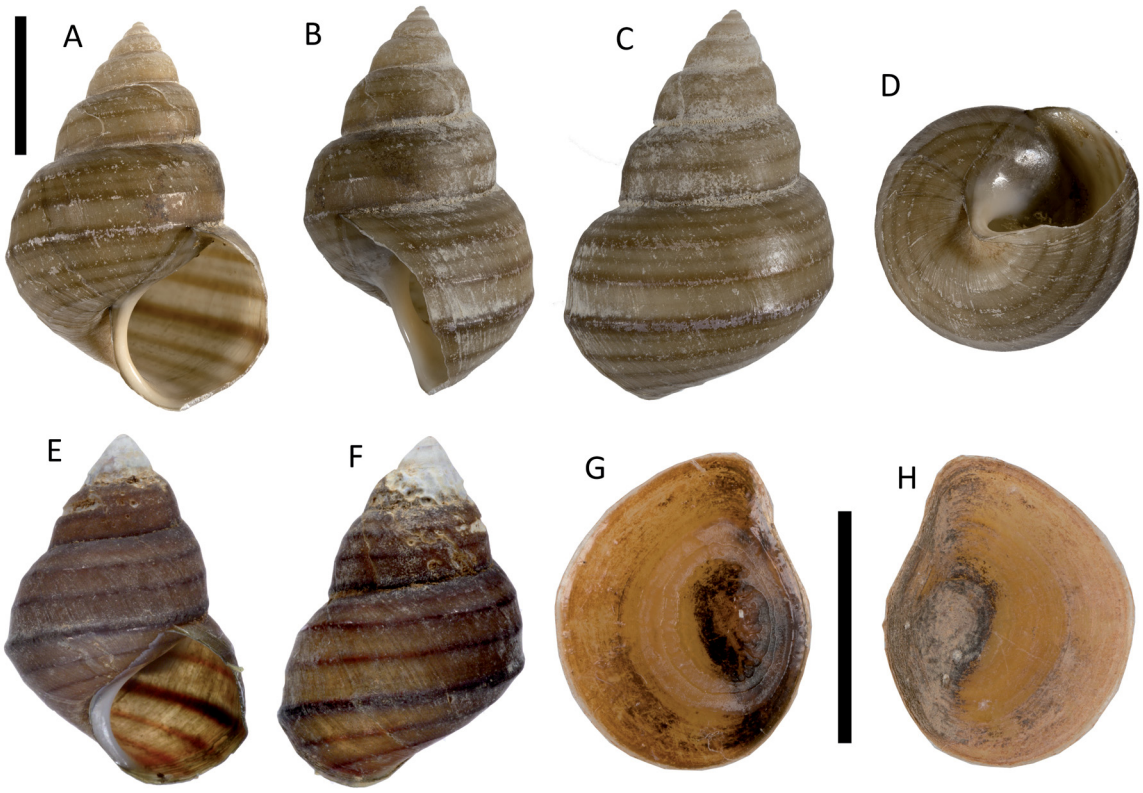


Fig. 38. Shells and operculum of *Bakyietaia indrapura* Zhang, Yen & von Rintelen gen. et sp. nov. **A–D**. Paratype, ZMB.114402.1, Nghe An, Vietnam. **E–F**. Holotype, ZMB.114403, Phuoc Son, Vietnam. **K–L**. Operculum of paratype ZMB.114402. Scale bars = 1 cm, top left bar applies to all shells, separate bar for operculum G–H.

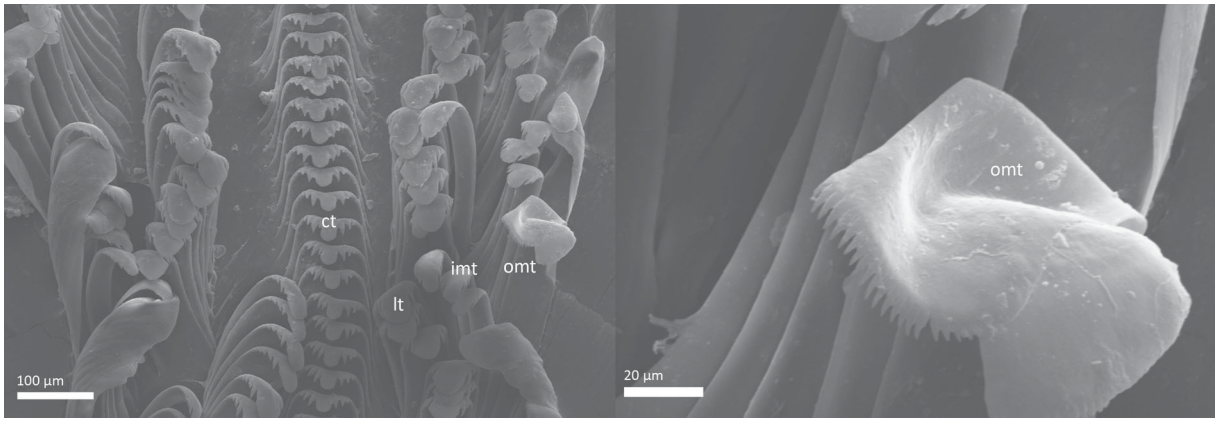


Fig. 39. SEM photo of the radula of *Bakyietaia indrapura* Zhang, Yen & von Rintelen gen. et sp. nov., paratype, ZMB.114402.1.

Radular (Fig. 39) (n = 4) central tooth with one broad central denticle and five small sharp cusps on either side; lateral tooth with one broad central denticle and five small sharp cusps on either side; inner marginal tooth narrow, about half width of lateral tooth, with one broad central denticle and five to six small sharp cusps on either side; outer marginal tooth wide, almost same width as lateral tooth, with 21 to 26 small sharp cusps.

Remarks

Bakyietaia indrapura gen. et sp. nov. can be distinguished from most congeners, especially *Bakyietaia polyzonata*, based on the medium-sized thin conical shell, more inflated whorls and stronger keel at suture. The distribution of *Bakyietaia indrapura* in central Vietnam is far from the distributions of other congeners. It is probably the southernmost non-introduced species of this genus.

Habitat and distribution

Rivers and mountain creeks of Central Vietnam.

Discussion

The present study is the first part of the revision of the 'wastebasket taxon' *Angulyagra*, focusing on the species of *Angulyagra* from South China and the Indochinese Peninsula, which are here assigned to the new genus *Bakyietaia*. We also included one species of *Angulyagra* from insular Southeast Asia. Our phylogeny, as well as that of Stelbrink *et al*. (2020), suggests that *Angulyagra costata* from Northern Sulawesi, Indonesia clusters with *Torotaia* cf. *mainitensis* from Lake Lanao, Mindanao Island, Philippines, and is not closely related to *Bakyietaia* (Fig. 2). *Torotaia* is mainly distributed in Mindanao, Philippines (Haas 1939), whereas Sulawesi is located to the south of Mindanao, separated by the Celebes Sea. Based on the phylogeny, shell morphology and distributions, we suspect that *Angulyagra costata* should be assigned to *Torotaia.* However, a systematic study of *Torotaia* is needed.

Although no material of the type species *Angulyagra oxytropis* has been available for the molecular phylogenetic part of this study, our investigation of the shell, operculum, radula and anatomy supports the assignment of the so-called "*Angulyagra*" species from South China and the Indochinese Peninsula to a new genus, *Bakyietaia*. In addition, the distribution of *Angulyagra oxytropis* in Manipur, India is located a long distance away from the known distribution of the new genus. A future molecular study including fresh material of *Angulyagra oxytropis* from Manipur will help to further understand the relationship between *Angulyagra* and *Bakyietaia*.

The integrative approach combining morphology, anatomy and COI sequence data supports the validity of the new genus *Bakyietaia*. All morphologically similar genera from China and Southeast Asia, such as *Sinotaia*, *Filopaludina*, *Anulotaia* and *Taia*, are shown to be distinct genera based on the COI phylogeny (Fig. 2), not least by the large p-distances between *Bakyietaia* and other genera (8.45%–15.65%). Althought the support values are quite low due to only using one marker, our COI tree is broadly consistent with the genus-level topology of the subfamily Bellamyinae based on multiple genes in Stelbrink *et al*. (2020). *Bakyietaia* falls within clade B of the Bellamyinae proposed by Stelbrink *et al*. (2020), which is widespread in Africa, Southeast Asia and Australia.

Several studies have shown that a species-level phylogeny based solely on single or several mitochondrial markers should not be used uncritically for the delimitation of closely related species in the Viviparidae (Zhang *et al.* 2015; Hirano *et al.* 2019b; Ye *et al.* 2021). However, in the present study, the monophyly of most species of *Bakyietaia* gen. nov. is modest to highly supported in the COI tree. In addition, although some species with high morphological intraspecific variation and wide distribution have not any OR no population structure in the COI tree, such as *B. wilhelmi*, some other species displayed a clear geographical population structure in the COI tree, such as *B. jingweiae* gen. et sp. nov. ("Ledong, Hainan" population, pp = 0.99) and *B. avisvenatoris* gen. et sp. nov. ("Paitan, Guangdong" population, pp = 0.99). Therefore, it is worthwhile to sample in more localities in the future to study the intraspecific diversity, especially for the species sampled at one site in the present study (such as *B. luikongi* gen. et sp. nov.). We found a high degree of congruence between morphology-based species delimitations and species level units inferred from the COI phylogeny. The numbers from both ASAP analyses show a total of 17 groups/OTUs, which is concordant with the result of 17 clades from the COI tree and the morphological study. Therefore, we consider that the 17 species recognised here are valid.

The radula is considered valuable in the classification of viviparid species (Zhang *et al.* 2015, 2023). In other freshwater snails, differences in radula morphology have been considered to be driven by trophic specialization, which may promote adaptive radiation of different species (von Rintelen *et al*. 2004; Hilgers *et al.* 2022). *Bakyietaia* gen. nov. displays a high interspecific diversity in some characteristics of the radula, especially regarding the number of cusps on the outer marginal teeth. Several species with similar shells can be differentiated based on radula characters, such as *Bakyietaia subcostata* and *B. chenghuang* gen. et sp. nov., *B. guangdungensis* and *B. wilhelmi*, *B. mutica* and *B. fontinalis* gen. et sp. nov. In one instance, two species occur sympatrically at the same site in a creek near Chenghuang Town, *B. chenghuang* and *B. liangzhuorum* gen. et sp. nov. *Bakyietaia chenghuang* with very few cusps on the outer marginal teeth is almost exclusively found on large rocks, while *B. liangzhuorum* with more cusps on the outer marginal teeth is almost exclusively restricted to soft sandy/muddy substrates. We consider that more ecological studies should be conducted to get a better understanding of radula differences and potential adaption in the group.

In conclusion, the new freshwater genus *Bakyietaia* is a highly diverse group of Viviparidae confined to South China and the Indochinese Peninsula. The distribution pattern of species of *Bakyietaia* and their differences in morphology and ecology also make it a good model to study speciation, adaption and biogeography in freshwater in this region. Further studies combining systematics, ecology and genomics and more intensive sampling in Laos, Vietnam and Guangxi, China, are needed to uncover the evolutionary history of this highly diverse group.

Acknowledgements

We thank Zheng-Yuan Zhang and Da-Ming Shi for the help in collecting specimens, Thor-Seng Liew for assistance in molecular work on material from Malaysia, Hwa Ja Götz and Michael Neumann (Museum für Naturkunde, Berlin), A. Schumacher and I. Gallmetzer (Naturhistorisches Museum, Vienna) and Romy Richter for providing some of the photos, Daniel Lorenz (Gymnasium der Franziskaner, Bozen),

Jonathan Ablett (Natural History Museum, London), Sigrid Hof (Naturmuseum Senckenberg, Frankfurt) for help in checking their collections , and Julian Joseph for English proofreading (Wiltshire, England). This work was funded by the CIBD at MfN, German Research Council (DFG) grant RI 1738-26/1, and Southeast Asia Biodiversity Research Institute, Chinese Academy of Sciences (Y4ZK111B01).

References

Annandale N. 1921. The aquatic and amphibious Mollusca of Manipur. The Prosobranchia. *Records of the Indian Museum* 22: 538–564. https://doi.org/10.5962/bhl.part.1480

Annandale T.N. & Seymour Sewell R.B. 1920. Progress report on a Survey of the freshwater gastropod molluscs of the Indian Empire and of their trematode parasites. *Indian Journal of Medical Research* 8: 93–124.

Benson W.H. 1836. Descriptive catalogue of a collection of land and fresh-water shells, chiefly contained in the Museum of the Asiatic Society. *Journal of the Asiatic Society of Bengal* 5: 741–750. Available from https://www.biodiversitylibrary.org/page/37188918 [accessed 9 Jun. 2023].

Chan S.Y. 1996. Some freshwater gastropods of Singapore. *Of Sea and Shore* 18: 184–187.

Clements R., Koh L.P., Lee T.M., Meier R. & Li D. 2006. Importance of reservoirs for the conservation of freshwater molluscs in a tropical urban landscape. *Biological Conservation* 128: 136–146. https://doi.org/10.1016/j.biocon.2005.09.023

Dautzenberg P. & Fischer H. 1908. Contribution à la faune malacologique de l'Indo-Chine. *Journal de Conchyliologie* 54: 145–226. Available from https://www.biodiversitylibrary.org/page/16298507 [accessed 9 Jun. 2023].

Do T.A., Do V.K., Do A D. 2014. The species composition, distribution, biomass of mollusk (Class: Gastropoda, Bivalvia, Cephalopoda) in coral reef in 19 surveyed islands in Vietnam. *Vietnam Journal of Marine Science and Technology* 14 (4): 358–367. https://doi.org/10.15625/1859-3097/14/4/5822

Fischer H. 1898. Notes sur la faune du Haut Tonkin. III. Liste des mollusques recueillis par le Dr. A. Billet. *Bulletin scientifique de la France et de Belgique* 28: 310–338.
Available from https://www.biodiversitylibrary.org/page/10724680 [accessed 9 Jun. 2023].

Fischer H. & Dautzenberg P. 1904. Catalogue des mollusques terrestres et fluviatiles de l'Indo-Chine orientale cités jusqu'à ce jour. *Mission Pavie, Études diverses* 3: 390–450.

Frauenfeld G. 1862. Versuch einer Aufzählung der Arten der Gattung *Bithynia* Lch. und *Nematura* Bns. nach der kaiserlichen und Cuming's Sammlung. *Verhandlungen der Kaiserlich-Königlichen Zoologisch-Botanischen Gesellschaft in Wien* 12: 1145–1170.
Available from https://www.biodiversitylibrary.org/page/30333254 [accessed 9 Jun. 2023].

Ghilardi R.P., Rodrigues S.C., Simone L.R.L., Carbonaro F.A. & Nava W.R. 2011. Moluscos fósseis do Grupo Bauru. *In*: Souza Carvalho I.D., Kumar Srivastava N., Strohschoen Jr. O., Cunha Lana C. (eds) *Paleontologia: Cenários de Vida* Vol. 4: 239–250. Interciência, Rio de Janeiro.

Gredler V.M. 1889. Zur Conchylien-Fauna von China. XIV. Stück. *Nachrichtsblatt der Deutschen malakozoologischen Gesellschaft* 21: 155–163.
Available from https://www.biodiversitylibrary.org/page/15599998 [accessed 9 Jun. 2023].

Griffith E. & Pidgeon E. 1833–1834. The Mollusca and Radiata, Vol. 12. *In*: Griffith E. 1824−1835. *The Animal Kingdom Arranged in Conformity with its Organization, by the Baron Cuvier*. Whittaker and Co., London. https://doi.org/10.5962/bhl.title.45021

Haas F. 1939. Malacological notes. *Zoological Series of Field Museum of Natural History* 24: 93–103. Available from https://www.biodiversitylibrary.org/page/2772848 [accessed 9 Jun. 2023].

Heude P.M. 1882–1890. Notes sur les mollusques terrestres de la Vallée du Fleuve Bleu. *Mémoires concernant l'histoire naturelle de l'Empire chinois* 1: 1–177. https://doi.org/10.5962/bhl.title.50365

Hilgers L., Hartmann S., Pfaender J., Lentge-Maaß N., Marwoto R.M., von Rintelen T. & Hofreiter M. 2022. Evolutionary divergence and radula diversification in two ecomorphs from an adaptive radiation of freshwater snails. *Genes* 13: 1029. https://doi.org/10.3390/genes13061029

Hirano T., Saito T., Tsunamoto Y., Koseki J., Prozorova L., Do V.T., Matsuoka K., Nakai K., Suyama Y. & Chiba S. 2019a. Role of ancient lakes in genetic and phenotypic diversification of freshwater snails. *Molecular Ecology* 28: 5032–5051. https://doi.org/10.1111/mec.15272

Hirano T., Saito T., Tsunamoto Y., Koseki J., Ye B., Do V.T., Miura O., Suyama Y. & Chiba S. 2019b. Enigmatic incongruence between mtDNA and nDNA revealed by multi-locus phylogenomic analyses in freshwater snails. *Scientific Reports* 9: e6223. https://doi.org/10.1038/s41598-019-42682-0

Hirano T., Saito T., Ito S., Ye B., Linscott T.M., Do V.T., Dong Z. & Chiba S. 2023. Phylogenomic analyses reveal incongruences between divergence times and fossil records of freshwater snails in East Asia. *Molecular Phylogenetics and Evolution* 182: 107728. https://doi.org/10.1016/j.ympev.2023.107728

Johnson D.S. 1973. Freshwater life. *In*: Chuang S.H. (ed.) *Animal Life and Nature in Singapore*. Singapore University Press, Singapore.

Kobelt W. 1906–1909. Die Gattung *Paludina* Lam. (*Vivipara* Montfort) in Abbildungen nach der Natur mit Beschreibungen. *Sytematisches Conchylien-Cabinet von Martini und Chemnitz,* Neue Folge Band 1, Abt. 21a. Bauer & Raspe, Nürnberg. https://doi.org/10.5962/bhl.title.119758

Kozlov A.M., Darriba D., Flouri T., Morel B. & Stamatakis A. 2019. RAxML-NG: A fast, scalable and user-friendly tool for maximum likelihood phylogenetic inference. *Bioinformatics* 35: 4453–4455. https://doi.org/10.1093/bioinformatics/btz305

Kumar S., Stecher G., Li M., Knyaz C. & Tamura K. 2018. MEGA X: Molecular Evolutionary Genetics Analysis across computing platforms. *Molecular Biology and Evolution* 35: 1547–1549. https://doi.org/10.1093/molbev/msy096

Liu Y.Y., Zhang W.Z. & Wang Y.X. 1995. Distribution of the Viviparidae from China (Mollusk: Gastropoda). *Transactions of the Chinese Society of Malacology* 5–6: 8–16. [In Chinese.]

Maassen W.J.M. 2001. *A Preliminary Checklist of the Non-marine Mollusks of Malaysia: "A hand list"*. De Kreukel Extra Editie.

Madsen H. & Hung N.M. 2014. An overview of freshwater snails in Asia with main focus on Vietnam. *Acta Tropica* 140: 105–17. https://doi.org/10.1016/j.actatropica.2014.08.005

MolluscaBase eds. 2023. MolluscaBase. Viviparidae J.E. Gray, 1847.
Available from https://www.molluscabase.org/aphia.php?p=taxdetails&id=154000 [accessed 9 Jun. 2023].

Ng P.K.L. 1992. *A Guide to Freshwater Life in Singapore*. Science Centre Singapore, Singapore.

Ng P.K.L., Chou L.M. & Lam T.J. 1993. The status and impact of introduced freshwater animals in Singapore. *Biological Conservation* 64: 19–24. https://doi.org/10.1016/0006-3207(93)90379-F

Ng T.H., Tan S.K. & Yeo D.C. 2014. The taxonomy, distribution and introduction history of the earliest reported alien freshwater mollusc in Singapore — *Sinotaia guangdungensis* (Gastropoda: Viviparidae). *Malacologia* 57: 401–408. https://doi.org/10.4002/040.057.0211

Ng T.H., Dulipat J., Foon J.K., Lopes-Lima M., Zieritz A. & Liew T.S. 2017. A preliminary checklist of the freshwater snails of Sabah (Malaysian Borneo) deposited in the BORNEENSIS collection, Universiti Malaysia Sabah. *ZooKeys* 673: 105–123. https://doi.org/10.3897/zookeys.673.12544

Palmieri M., Palmeiri J. & Sullivan J. 1980. A chemical analysis of the habitat of nine commonly occurring Malaysia freshwater snails. *The Malayan Nature Journal* 34: 1–7.

Philippi R.A. 1842–1850. *Abbildungen und Beschreibungen neuer oder wenig gekannter Conchylien unter Mithülfe mehrerer deutscher Conchyliologen*. T. Fischer, Cassel. https://doi.org/10.5962/bhl.title.10589

Prashad B. 1928. Recent and fossil Viviparidae. A study in distribution, evolution and palaeogeography. *Memoirs of the Indian Museum* 8: 153–253.

Preece R.C., White T.S., Raheem D.C., Ketchum H., Ablett J., Taylor H., Webb K. & Naggs F. 2022. William Benson and the golden age of malacology in British India. Biography, illustrated catalogue and evaluation of his molluscan types. *Tropical Natural History* Supplement 6: 1–434. https://doi.org/10.58837/tnh.22.6.257073

Preston H.B. 1915. Freshwater Gastropoda & Pelecypoda. *In*: Blanford W.T. (ed.) *The Fauna of British India, Including Ceylon and Burma. Mollusca Vol. 4*. Taylor & Francis, London. https://doi.org/10.5962/bhl.title.13091

Puillandre N., Brouillet S. & Achaz G. 2020. ASAP: Assemble Species by Automatic Partitioning. *Molecular Ecology Resources* 21: 609–620. https://doi.org/10.1111/1755-0998.13281

Qian Z.X., Fang Y.F. & He J. 2014. A conchological review of Bellamyinae (Gastropoda: Viviparidae) of China. *Shell Discoveries* 1: 3–12.

Rao H.S. 1925. On the comparative anatomy of Oriental Viviparidae. *Records of the Zoological Survey of India* 27: 129–135. https://doi.org/10.26515/rzsi/v27/i2/1925/163463

Rao H.S. 1931. *Angulyagra oxytropis* (Benson) nom. nov. – A correction. *Records of the Zoological Survey of India* 33: 301. https://doi.org/10.26515/rzsi/v33/i3/1931/162505

Richter R. 2015. *Die Evolution und Biogeographie der südostasiatischen Sumpfdeckelschnecken (Viviparidae): ein molekularer und morphologischer Ansatz*. PhD thesis, Humboldt Universität, Berlin.

Ronquist F., Teslenko M., Van Der Mark P., Ayres D.L., Darling A., Höhna S., Larget B., Liu L., Suchard M.A. & Huelsenbeck J.P. 2012. MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* 61: 539–542. https://doi.org/10.1093/sysbio/sys029

Schultheiß R., Wilke T., Jørgensen A. & Albrecht C. 2011. The birth of an endemic species flock: Demographic history of the *Bellamya* group (Gastropoda, Viviparidae) in Lake Malawi. *Biological Journal of the Linnean Society* 102: 130–143. https://doi.org/10.1111/j.1095-8312.2010.01574.x

Schultheiß R., Van Bocxlaer B., Riedel F., von Rintelen T. & Albrecht C. 2014. Disjunct distributions of freshwater snails testify to a central role of the Congo system in shaping biogeographical patterns in Africa. *BMC Evolutionary Biology* 14: 1–2. https://doi.org/10.1186/1471-2148-14-42

Sengupta M.E., Kristensen T.K., Madsen H. & Jørgensen A. 2009. Molecular phylogenetic investigations of the Viviparidae (Gastropoda: Caenogastropoda) in the lakes of the Rift Valley area of Africa. *Molecular Phylogenetics and Evolution* 52: 797–805. https://doi.org/10.1016/j.ympev.2009.05.007

Shea M. 1994. The Chinese viviparid snail *Bellamya heudei guangdungensis* (Kobelt, 1906) in Australia (Prosobranchia: Viviparidae). *Molluscan Research* 15: 3–11. https://doi.org/10.1080/13235818.1994.10673652

Sivan N., Heller J. & Van Damme D. 2006. Fossil Viviparidae (Mollusca: Gastropoda) of the Levant. *Journal of Conchology* 39: 207–219.

Starobogatov Y.I. 1970. *Fauna mollyuskov i zoogeograficheskoe raionirovanie kontinental'nykh vodoemov zemnogo shara*. Nauka, Leningrad.

Stelbrink B., von Rintelen T., Albrecht C., Clewing C. & Naga P.O. 2019. Forgotten for decades: Lake Lanao and the genetic assessment of its mollusc diversity. *Hydrobiologia* 843: 31–49. https://doi.org/10.1007/s10750-018-3666-0

Stelbrink B., Richter R., Köhler F., Riedel F., Strong E.E., van Bocxlaer B., Albrecht C., Hauffe T., Page T.J., Aldridge D.C., Bogan A.E., Du L.N., Manuel-Santos M.R., Marwoto R.M., Shirokaya A.A. & von Rintelen T. 2020. Global diversification dynamics since the Jurassic: Low dispersal and habitat-dependent evolution explain hotspots of diversity and shell disparity in river snails (Viviparidae). *Systematic Biology* 69: 944–961. https://doi.org/10.1093/sysbio/syaa011

Strong E.E., Gargominy O., Ponder W.F. & Bouchet P. 2008. Global diversity of gastropods (Gastropoda; Mollusca) in freshwater. *Hydrobiologia* 595: 149–166. https://doi.org/10.1007/s10750-007-9012-6

Subba Rao N.V. 1989. Handbook: freshwater molluscs of India. Zoological Survey of India, Calcutta.

Tan S.K. & Woo H.P.M. 2010. *A Preliminary Checklist of the Molluscs of Singapore*. Raffles Museum of Biodiversity Research, Singapore.

Tan S.K., Chan S.Y. & Clements G.R. 2012. *A Guide to Snails and other Non-marine Mollucs of Singapore*. Science Centre Singapore, Singapore.

Thanh D.N., Hai H.T. & Cuong D. 2004. Snail species of Viviparidae in Vietnam. *Academia Journal of Biology* 26: 1–5.

Tracey S., Todd J.A. & Erwin D.H. 1993. Mollusca: Gastropoda. *In*: Benton M.J. (ed.) *The Fossil Record* 2: 131–167. Chapman and Hall, London.

von Rintelen T., Wilson A.B., Meyer A. & Glaubrecht M. 2004. Escalation and trophic specialization drive adaptive radiation of freshwater gastropods in ancient lakes on Sulawesi, Indonesia. *Proceedings of the Royal Society of London. Series B: Biological Sciences* 271: 2541–2549. https://doi.org/10.1098/rspb.2004.2842

Winnepenninckx B., Backeljau T. & De Wachter R. 1993. Extraction of high molecular weight DNA from molluscs. *Trends in Genetics* 9: e407. https://doi.org/10.1016/0168-9525(93)90102-N

Ye B., Saito T., Hirano T., Dong Z., Do V.T. & Chiba S. 2020. Human-geographic effects on variations in the population genetics of *Sinotaia quadrata* (Gastropoda: Viviparidae) that historically migrated from continental East Asia to Japan. *Ecology and Evolution* 10: 8055–8072. https://doi.org/10.1002/ece3.6456

Ye B., Hirano T., Saito T., Dong Z., Do V.T. & Chiba S. 2021. Molecular and morphological evidence for a unified, inclusive *Sinotaia quadrata* (Caenogastropoda: Viviparidae: Bellamyinae). *Journal of Molluscan Studies* 87: eyab013. https://doi.org/10.1093/mollus/eyab013

Yen T.C. 1938 Notes on the gastropod fauna of Szechwan Province. *Mitteilungen aus dem Zoologischen Museum in Berlin* 23: 438–457.

Yen T.C. 1939. Die chinesischen Land- und Süsswasser-Gastropoden des Natur-Museums Senckenberg. *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft* 444: 1–233.

Yen T.C. 1943. A preliminary revision of the recent species of Chinese Viviparidae. *The Nautilus* 56: 124–130. Available from https://www.biodiversitylibrary.org/page/8520239 [accessed 9 Jun. 2023].

Yeo D.C.J. & Chia C.S.W. 2010. Introduced species in Singapore: An overview. *COSMOS* 6: 23–37. https://doi.org/10.1142/S0219607710000486

Zhang L.J. & von Rintelen T. 2021. The neglected operculum: A revision of the opercular characters in river snails (Caenogastropoda: Viviparidae). *Journal of Molluscan Studies* 87: eyab008. https://doi.org/10.1093/mollus/eyab008

Zhang L.J., Chen S.C., Yang L.T., Jin L. & Köhler F. 2015. Systematic revision of the freshwater snail *Margarya* Nevill, 1877 (Mollusca: Viviparidae) endemic to the ancient lakes of Yunnan, China, with description of new taxa. *Zoological Journal of the Linnean Society* 174: 760–800. https://doi.org/10.1111/zoj.12260

Zhang L.J., Du L.N. & von Rintelen T. 2023. A new genus of river snails, *Dalipaludina* (Gastropoda, Viviparidae), endemic to the Yunnan Plateau of SW China. *Zoosystematics and Evolution* 99: 285–297. https://doi.org/10.3897/zse.99.102586

Zhu X.G. 1994. Jurassic-Cretaceous nonmarine gastropods from northern Xinjiang. *Acta Palaeontologica Sinica* 33: 85–105.

Zilch A. 1938. Das Vorkommen von *Buliminopsis incerta* (Pfr.) auf Formosa und in China. *Archiv für Molluskenkunde* 7: 3.

Zilch A. 1955. Die Typen und Typoide des Natur-Museums Senckenberg, 14: Mollusca, Viviparidae. *Archiv für Molluskenkunde* 84: 45–87.

Zilch A. 1974. Zur Geschichte der deutschen Malakozoologie, XIV. Vinzenz Gredler und die Erforschung der Weichtiere Chinas durch Franziskaner aus Tirol. *Archiv für Molluskenkunde* 104: 171–228.

Printed versions of all papers are deposited in the libraries of four of the institutes that are members of the *EJT* consortium: Muséum national d'Histoire naturelle, Paris, France; Meise Botanic Garden, Belgium; Royal Museum for Central Africa, Tervuren, Belgium; Royal Belgian Institute of Natural Sciences, Brussels, Belgium. The other members of the consortium are: Natural History Museum of Denmark, Copenhagen, Denmark; Naturalis Biodiversity Center, Leiden, the Netherlands; Museo Nacional de Ciencias Naturales-CSIC, Madrid, Spain; Leibniz Institute for the Analysis of Biodiversity Change, Bonn – Hamburg, Germany; National Museum of the Czech Republic, Prague, Czech Republic; The Steinhardt Museum of Natural History, Tel Aviv, Israël.

Supplementary files

Supp. file 1. The alignment of the COI sequences in the present study.
https://doi.org/10.5852/ejt.2025.1005.2985.13431

Supp. file 2. ML tree based on the COI sequences in the present study
https://doi.org/10.5852/ejt.2025.1005.2985.13433