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Revision of the genus *Metalycaeus* Pilsbry, 1900 in the Himalayan region with description of five new species (Gastropoda, Cyclophoridae, Alycaeinae)

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Abstract. The *Metalycaeus* species of the Himalaya and Myanmar are revised. Five new species are described: *Dicharax zayai* Páll-Gergely & Meng sp. nov., *Metalycaeus gittenbergeri* Páll-Gergely & Aravind sp. nov., *M. tuyae* Páll-Gergely & Meng sp. nov., *M. kempi* Páll-Gergely & Aravind sp. nov. and *Metalycaeus adiorum* Páll-Gergely & Aravind sp. nov. Ten taxa are moved to synonymy: *Alycaeus macgregori* Godwin-Austen, 1914 and *A. burtii* var. *yetayensis* Godwin-Austen, 1914 are synonyms of *M. bhutanensis* (Godwin-Austen, 1914); *A. luyorensis* Godwin-Austen, 1914 is a synonym of *M. dikrangensis* (Godwin-Austen, 1914); *A. lohitensis* Godwin-Austen, 1914 is a synonym of *Metalycaeus brahma* (Godwin-Austen, 1886); *M. karmademaae* Gittenberger, Choki Gyeltshen & Kezang Tobgay, 2024 is a synonym of *M. crenulatus* (Benson, 1859); *A. subinflatus* Godwin-Austen, 1914 and *A. varius* Godwin-Austen, 1914 (replacement name: *M. suhajdai* Páll-Gergely, 2020) are synonyms of *M. beddomei* (Godwin-Austen, 1914); *A. toruputuensis* Godwin-Austen, 1914 is a

synonym of *M. mundulus* (Godwin-Austen, 1914); and *A. polygonoma* Blanford, 1862 and *A. neglectus* Godwin-Austen, 1914 are synonyms of *M. stylifer* (Benson, 1857). A neotype is designated for *Dicharax zayuensis* (Zhang, Chen & Zhou, 2008).

Keywords. India, Myanmar, China, taxonomy.

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Introduction

Alycaeinae Blanford, 1864, a subfamily within the terrestrial caenogastropod family Cyclophoridae Gray, 1847, is widely distributed across South, Southeast, and East Asia, spanning the Western Ghats in the west to Japan in the east (Páll-Gergely *et al.* 2020, 2025). The group is remarkably diverse, currently comprising 352 accepted species (MolluscaBase 2026). Three major centres of species richness have been recognised within its range: (1) the southeastern Himalaya, (2) northern Vietnam and southern China, and (3) peninsular Malaysia and Sumatra, each harbouring five genera of Alycaeinae (Páll-Gergely *et al.* 2020). A recent taxonomic revision has clarified the diversity and systematic placement of several Himalayan genera, including *Chamalycaeus* Möllendorff, 1897, *Cycloryx* Godwin-Austen, 1914, and *Dicharax* Kobelt & Möllendorff, 1900 (Páll-Gergely *et al.* 2025). Despite this progress, the species-rich genus *Metalycaeus* Pilsbry, 1900, a key component of the Himalayan Alycaeinae group, has not yet been comprehensively revised, leaving substantial ambiguity in its taxonomy and species boundaries.

The present study provides the first detailed revision of the Himalayan members of *Metalycaeus*. We organise the species into coherent species groups based on comparative shell morphology and other diagnostic characters, and we present high-quality photographs of all known type specimens from the region. In addition to re-examining historical type material, including species described prior to the end of the 19th century, we also incorporate newly collected specimens from the Himalaya. Based on this material, we describe four species of *Metalycaeus* and one of *Dicharax* new to science, thereby contributing to a clearer understanding of the diversity, taxonomy, and biogeographical significance of Alycaeinae in the Himalaya.

Material and methods

The new material of *Metalycaeus* was collected from the Siang Valley in Arunachal Pradesh, India, in April–May 2022 as part of a broader study on regional molluscan diversity. The Siang Valley spans the districts of Upper Siang, Siang, and East Siang, which together form the principal catchment of the Siang River, a major tributary of the Brahmaputra. Sampling was conducted on both the eastern and western banks of the river, in areas that were historically explored during the "Abor Expedition" of 1911–1912. The region is characterized by tropical evergreen and semi-deciduous forests, with sampling sites ranging from 160 m to 1200 m above mean sea level. Rainfall occurs during both the Southwest and Northeast Monsoons, although the majority is received during the former. Specimens were collected across a variety of habitats by systematically searching suitable microhabitats such as the bases of large trees, buttress roots, litter-filled ground depressions, and beneath sizeable rocks. Live-collected specimens were preserved in absolute ethanol for subsequent examination.

Shells of Alycaeinae were photographed using a Nikon SMZ25 digital microscope with Nikon Nis-Elements software (Institute for Soil Sciences, HUN-REN Centre for Agricultural Research, Budapest). Following photography, all shells were measured using a Keyence VHX-5000 digital microscope or a Vernier calliper. The counting of the shell whorls (to the closest 0.25 whorl) follows Kerney & Cameron

(1979: 13). The sculpture of the body whorl along the sutural tube is always different from that of the other regions of the shell (Godwin-Austen 1882–1920), because of the presence of microtunnels running to the sutural tube (Páll-Gergely *et al.* 2016). Therefore, three regions of the teleoconch are distinguished following Páll-Gergely *et al.* (2017: fig. 1a–b, see also Páll-Gergely *et al.* 2025: fig. 2): Region 1 (R1) extends from the beginning of the teleoconch to the beginning of the differently ribbed region where the sutural tube lies; Region 2 (R2) extends from the differently ribbed area to the constriction; and Region 3 (R3) extends from the constriction to the peristome. The latter region usually bears 1–3 swellings of various morphology (Páll-Gergely *et al.* 2025: fig. 2).

Historical localities mentioned in the text are compiled in Supp. file 1.

Abbreviations

D = shell diameter
H = shell height
R1 = Region 1 (see above)
R2 = Region 2 (see above)
R3 = Region 3 (see above)

Repositories

ATREE = collection of the Ashoka Trust for Research in Ecology and the Environment, Bangalore, India
IZCAS = National Zoological Museum of China, Institute of Zoology, Chinese Academy of Sciences, Beijing, China
NBCB = National Biodiversity Centre, Serbithang, Thimphu, Bhutan
NHM = The Natural History Museum, London, UK
NHMUK = when citing lots deposited in the NHM
NZSI = National Zoological Collection of the Zoological Survey of India, Kolkata, India
ZSI/SRC = Zoological Survey of India, Southern Regional Centre, Chennai, India

Results

Class Gastropoda Cuvier, 1795
Subclass Caenogastropoda Cox, 1960
Order Architaenioglossa Haller, 1890
Superfamily Cyclophoroidea Gray, 1847
Family Cyclophoridae Gray, 1847
Subfamily Alycaeinae Blanford, 1864

Genus ***Dicharax*** Kobelt & Möllendorff, 1900

Remarks

The Himalayan members or the genus *Dicharax* were revised in an earlier paper (Páll-Gergely *et al.* 2025). Here, we treat two species of *Dicharax* (one of them is a new species), which were revealed during the revision of the genus *Metalycaeus*.

Dicharax zayai Páll-Gergely & Meng sp. nov.
urn:lsid:zoobank.org:act:6B295457-2373-496C-A05E-22E720BCA85E
Fig. 1

Diagnosis

A species of *Dicharax* with rounded outline, finely ribbed R1, a long R2 and a slightly shorter R3 (together nearly reaching half whorl), R2 with widely-spaced, curved ribs, R3 with a sharp, central swelling, aperture finely undulating.

Etymology

This new species is named after the son of the species' second author, Menghe Zaya.

Proposed Chinese name

扎雅垒螺

Type material

Holotype

CHINA • shell (originally labelled as paratype of *Chamalycaeus zayuensis*) (D: 4.29 mm, H: 3.2 mm); Tibet Autonomous Region, Tashan Town, Zayu County; 28°04′ N, 97° E; 3 Jul. 1980; Chen Deniu leg.; IZCAS TM_094545.

Paratypes

CHINA • 1 shell (originally labelled as paratype of *Chamalycaeus zayuensis*); same data as for holotype; IZCAS TM_094546 • 1 shell (originally labelled as paratype of *Chamalycaeus zayuensis*); same data as for holotype; 7 Jun. 1980; IZCAS TM_094552.

Description

Shell medium-sized, light grey to off-white, body colour dark. Shell depressed, apical whorls conical, dorsal outline rounded. Protoconch consists of ca 1.5 whorls, smooth. R1 with ca 2–2.25 whorls, rather regularly, finely ribbed/wrinkled (ca 50 ribs on last half whorl). R1–R2 boundary clearly visible because of the more widely-spaced and elevated ribs of R2, and that R2 is swollen. R2+R3 nearly reaching half a whorl, R2 is longer than R3. R2 with ca 30–35 widely-spaced, curved ribs. Constriction deep, followed by a centrally located, elevated, rather sharp swelling. Swelling parallel with peristome. R3 more densely and finely ribbed than R2. Inner peristome only slightly protruding, outer peristome expanded, the boundary between the two peristomes visible but not conspicuous. Aperture relatively large, strongly oblique to shell axis in lateral view, the upper part of peristome strongly protruding. Peristome slightly fringed. Umbilicus narrower than one third of shell width, rather asymmetrical (oval due to nearly straight R2 side).

Measurements

D = 3.8–4.3 mm, H = 2.8–3.2 mm (n = 3).

Differential diagnosis

Other species of the *Dicharax* species group 2 have a less expanded, more fringed peristome. This new species was found in the same series of paratypes as the neotype of *D. zayuensis*, which has a blunter and longer R3 swelling and lower R2 ribs.

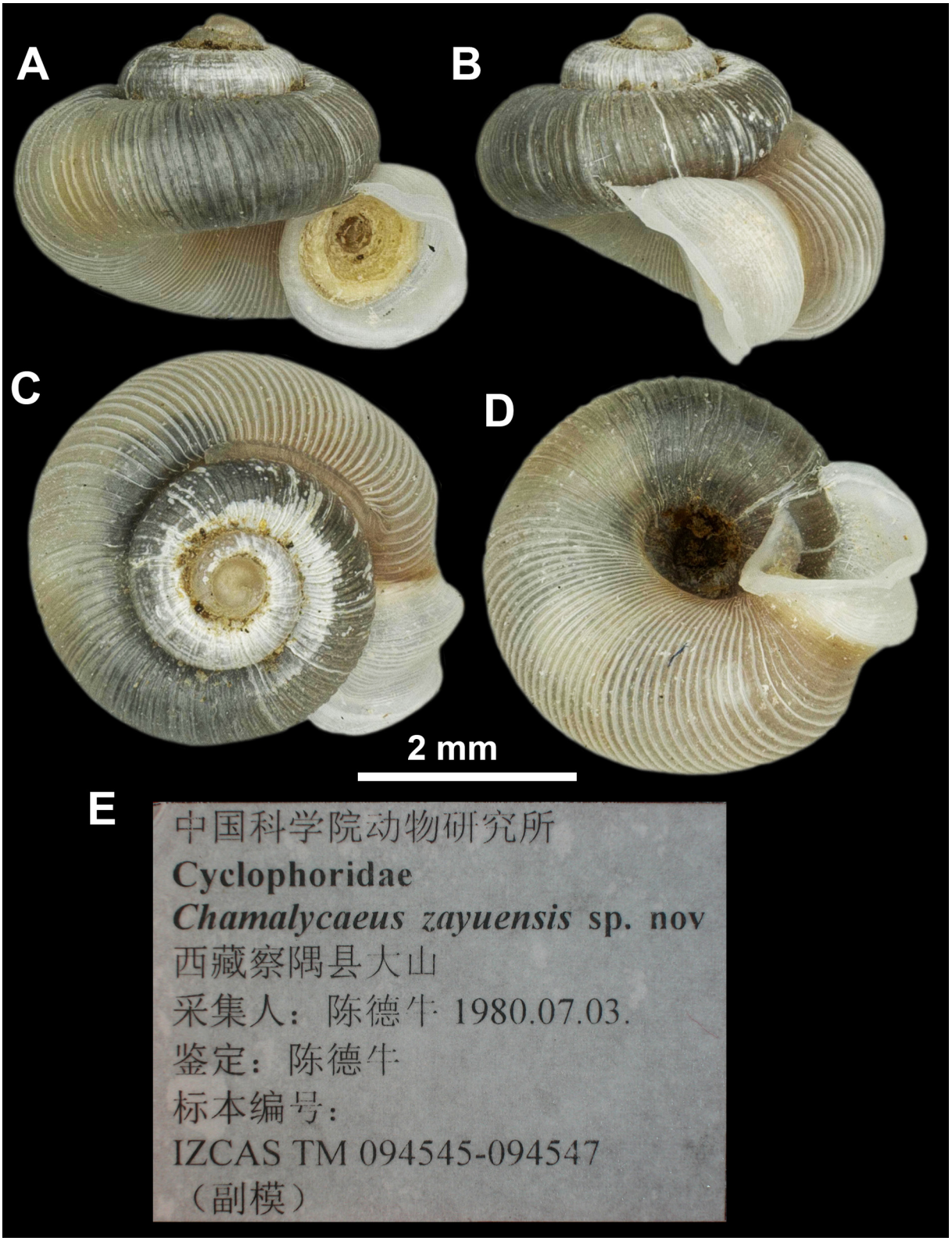


Fig. 1. *Dicharax zayai* Páll-Gergely & Meng sp. nov. **A–D**. Holotype (IZCAS TM_094545). **E**. Original label. All photos: K. Meng.

Remarks

Due to the sharp R3 swelling, this species is a member of the *Dicharax* species group 2 defined by Páll-Gergely *et al.* (2025).

Dicharax zayuensis (Zhang, Chen & Zhou, 2008)
Fig. 2

Chamalycaeus zayuensis Zhang, Chen & Zhou, 2008: 745, figs 1–4.

Chamalycaeus zayuensis – Qian & Zhou 2013: 26, species 27, unnumbered figures.
Metalycaeus (?) *zayuensis* – Páll-Gergely *et al.* 2017: 108; 2020: 160 (partim).

Diagnosis

This species of *Dicharax* is characterized by a conical dorsal side, a finely ribbed shell (all shell regions), a combined length of R2+R3 of ca quarter whorl, a low, central R3 swelling, and a rounded, slightly undulating peristome.

Type material examined

Neotype (hereby designated)
CHINA • shell (originally labelled as paratype of *Chamalycaeus zayuensis*); Tibet Autonomous Region, Tashan Town, Zayu County; 28°04′ N, 97° E; 7 Jun. 1980; Chen Deniu leg.; IZCAS TM_094553. See also Remarks.

Type locality

"Tashan Town, Zayu County (28°04'N, 97°E), Tibet Autonomous Region, China".

Measurements

D = 5 mm, H = 3. 9 mm.

Differential diagnosis

Among the species known from the Himalaya, the most similar is *D. strangulatus* (Pfeiffer, 1846), but *D. zayuensis* has a higher, more conical spire, a slightly undulating (not perfectly rounded) peristome (rounded in *D. strangulatus*). The Bhutanese *D. bhudepressus* Gittenberger, Choki Gyeltshen & Kezang Tobgay, 2024 is also similar in shell sculpture and the ratios of shell region, but it is more depressed, and has a much more oblique aperture compared to the shell axis. Interestingly, several Japanese species, such as *Dicharax oshimanus* (Pilsbry & Y. Hirase, 1904), are very similar to *D. zayuensis* in shell and aperture shape, relative lengths of shell regions, and sculpture, but have more depressed shells. See also *D. zayai* sp. nov.

Remarks

The photos in the original description (Zhang *et al.* 2008) show a shell (not specified as the holotype in the figure captions) in three views, and an SEM micrograph of its radula. Páll-Gergely *et al.* (2017) tentatively classified this species in the genus *Metalycaeus*, based on the spiral lines visible on the photos published by Qian & Zhou (2013). In a later paper, Páll-Gergely *et al.* (2020) published photos of the specimen labelled as the holotype (IZCAS TM_094538), and noted that it represents a species different from the one figured in the original description. Therefore, the holotype was considered lost (Páll-Gergely *et al.* 2020). For this revision, we examined and photographed all specimens housed in the IZCAS. The original description mentions the holotype and 19 paratypes. In the IZCAS, 17 specimens were catalogued. Among them, TM_094538 was labelled as the holotype, while TM_094539 to TM_094554

were labelled as paratypes. Among the paratypes, TM_094551 is a plant seed, and TM_094539 is a juvenile Cyclophoroidea Gray, 1847, while the remaining ones belong to three species of Alycaeinae (see Table 1). Specimens TM_094538, TM_094540, TM_094541, TM_094542, TM_094543, TM_094544, TM_094547, TM_094548, TM_094549, TM_094550, and TM_094554 belong to an undescribed species of *Metalycaeus* (described here as *M. tuyae* sp. nov.), TM_094545, TM_094546, and TM_094552 belong to an undescribed species of *Dicharax* (described here as *D. zayai* sp. nov.). Lastly, specimen TM_094553 is conspecific with the specimen figured in the original description, although it is not the same shell (corrosion marks are different). Nevertheless, we consider the shell figured in the original description (Zhang *et al.* 2008) to be conspecific with shell TM_094553 due to the similar shell shape



Fig. 2. Photos of *Dicharax zayuensis* (Zhang, Chen & Zhou, 2008). **A–C**. Photos from the original description. **D–F**. Photos from Qian & Zhou (2013). **G–J**. Neotype (same specimen as 2D–F, IZCAS TM_094553). **K**. Original label of the neotype. Photos: K. Meng (G–K).

Table 1. Identifications of type specimens of *Chamalycaeus zayuensis* Zhang, Chen & Zhou, 2008.

inventory number	originally labelled as	current status
TM_094538	holotype of *Chamalycaeus zayuensis*	paratype of *Metalycaeus tuyae* sp. nov.
TM_094539	paratype of *Chamalycaeus zayuensis*	Cyclophoroidea sp.
TM_094540	paratype of *Chamalycaeus zayuensis*	paratype of *Metalycaeus tuyae* sp. nov.
TM_094541	paratype of *Chamalycaeus zayuensis*	paratype of *Metalycaeus tuyae* sp. nov.
TM_094542	paratype of *Chamalycaeus zayuensis*	paratype of *Metalycaeus tuyae* sp. nov.
TM_094543	paratype of *Chamalycaeus zayuensis*	paratype of *Metalycaeus tuyae* sp. nov.
TM_094544	paratype of *Chamalycaeus zayuensis*	paratype of *Metalycaeus tuyae* sp. nov.
TM_094545	paratype of *Chamalycaeus zayuensis*	holotype of *Dicharax zayai* sp. nov.
TM_094546	paratype of *Chamalycaeus zayuensis*	paratype of *Dicharax zayai* sp. nov.
TM_094547	paratype of *Chamalycaeus zayuensis*	paratype of *Metalycaeus tuyae* sp. nov.
TM_094548	paratype of *Chamalycaeus zayuensis*	paratype of *Metalycaeus tuyae* sp. nov.
TM_094549	paratype of *Chamalycaeus zayuensis*	holotype of *Metalycaeus tuyae* sp. nov.
TM_094550	paratype of *Chamalycaeus zayuensis*	paratype of *Metalycaeus tuyae* sp. nov.
TM_094551	paratype of *Chamalycaeus zayuensis*	plant seed
TM_094552	paratype of *Chamalycaeus zayuensis*	paratype of *Dicharax zayai* sp. nov.
TM_094553	paratype of *Chamalycaeus zayuensis*	neotype of *Dicharax zayuensis*

(especially in dorsal and ventral views), and the similar relative lengths of the shell regions (R2 is shorter than in *D. zayai* and *M. tuyae*). The latter shell (TM_094553) can be clearly identified as the shell in the book of Qian & Zhou (2013) based on corrosion marks (both authors of that book are also authors of the species). As the holotype (i.e., originally figured shell) is considered lost, and the specimens labelled as holotype and paratypes belong to four different snail species, the best solution seems to be to designate shell TM_094553 as the neotype of *D. zayuensis*. It is designated with the express purpose of clarifying the taxonomic status of *D. zayuensis*. The original description mostly lacks information that would be sufficient to distinguish between the three species (i.e., understand to which species of the three it belongs). However, the length of the sutural tube is described to be less than 1 mm long, which is much larger in the other two species.

The 78 Himalayan (including Myanmar) species of the genus *Dicharax* were grouped into species groups based on a combination of shell characters (Páll-Gergely *et al.* 2025). *Dicharax zayuensis* mostly fits in the *Dicharax* species group 9, which includes *D. montanus* (G. Nevill, 1881), *D. rechilaensis* (Godwin-Austen, 1914), *D. strangulatus* (Pfeiffer, 1846) and *D. strigatus* (Godwin-Austen, 1874), based on the finely ribbed R1, a relatively short R2 and R3. Nevertheless, most species of that species group (with the exception of *D. strangulatus*) have an R3 swelling situated close to the peristome, and the peristome of *D. zayuensis* is slightly undulating (rounded in the other species of the *Dicharax* species group 9). In shell shape and the formation of shell regions, *D. zayuensis* could also be classified in *Dicharax* species group 10 (with 3 species, all known from Bhutan).

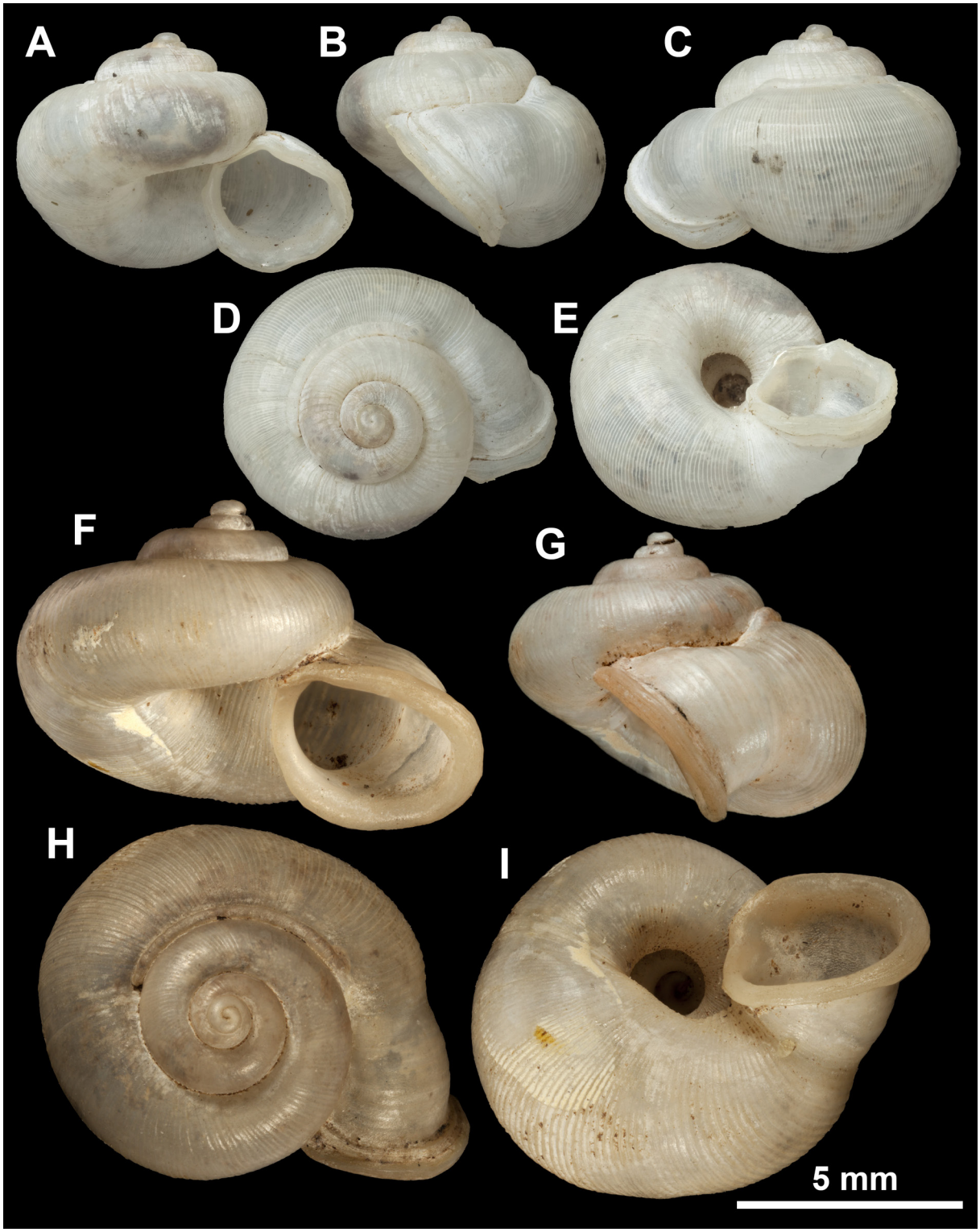


Fig. 3. Species of the *Metalycaeus aborensis* species group. **A–E**. *M. aborensis* (Godwin-Austen, 1914), syntype (NHMUK 1903.7.1.3102). **F–I**. *M. physis* (Benson, 1859), syntype (UMZC I.102735). All photos: Kevin Webb.

Genus ***Metalycaeus*** Pilsbry, 1900

Alycaeus (*Metalycaeus*) Pilsbry, 1900: 382 (section of *Alycaeus*).

Chamalycaeus (*Metalycaeus*) – Thiele 1929: 108. — Wenz 1938: 478. — Egorov 2013: 37.
Metalycaeus – Páll-Gergely & Asami 2017: 4. — Páll-Gergely *et al.* 2017: 73; 2020: 137.

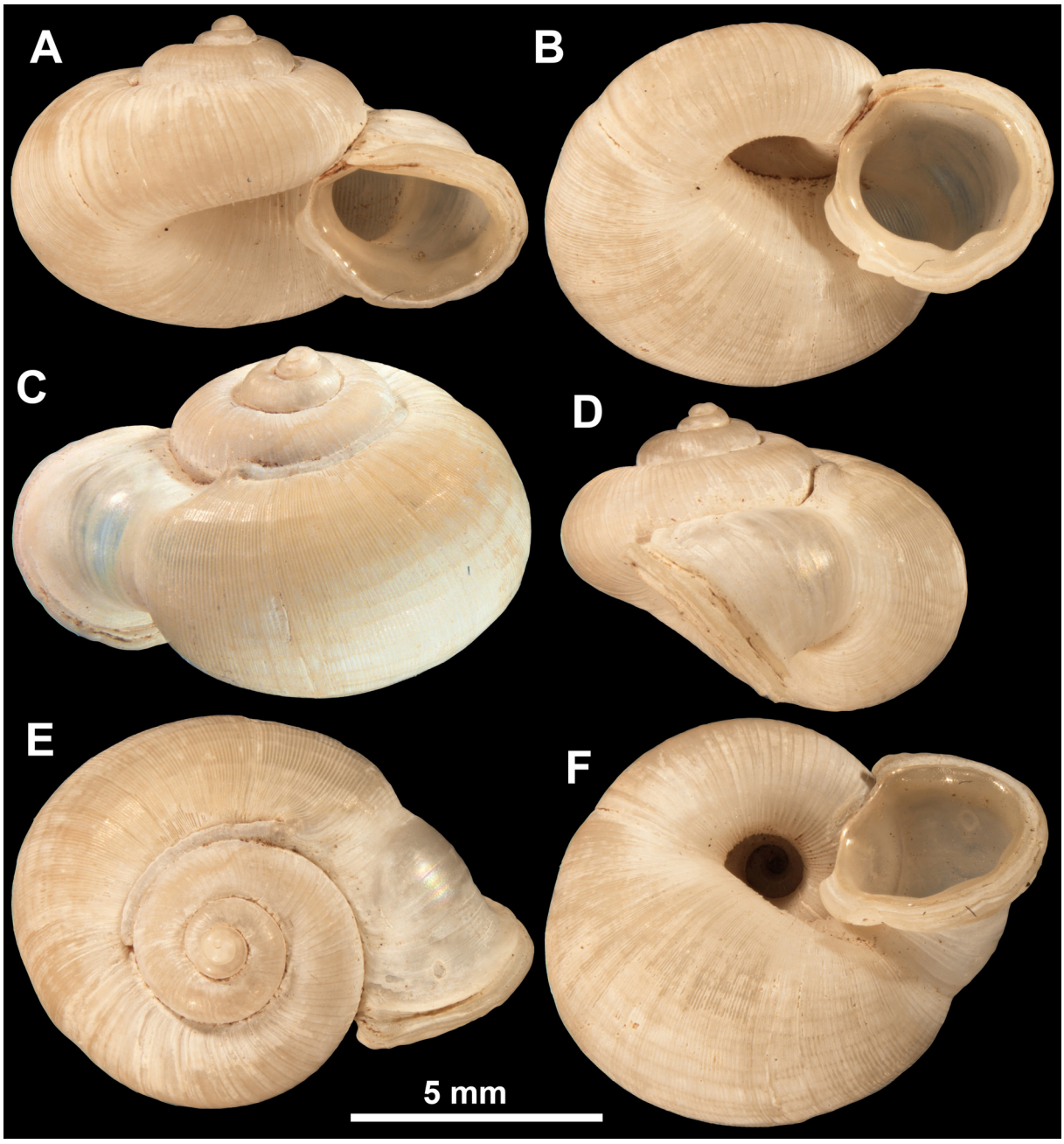


Fig. 4. Shell of *Metalycaeus aborensis* (Godwin-Austen, 1914) from the Kaleg-Rotung Road (ZSI/SRC/LM2232). All photos: B. Páll-Gergely.

Metalycaeus aborensis species group

Remarks

This species group is characterized by a long and smooth R2, and a long, only slightly inflated R3 swelling. Operculum calcareous.

Metalycaeus aborensis (Godwin-Austen, 1914)
Figs 3A–E, 4–5

Alycaeus aborensis Godwin-Austen, 1914: 364, pl. 149 fig. 9.

Alycaeus (*Chamalycaeus*) *aborensis* – Gude 1921: 223.
Chamalycaeus (*Chamalycaeus*) *aborensis* – Ramakrishna *et al.* 2010: 52.
Metalycaeus (?) *aborensis* – Páll-Gergely *et al.* 2020: 161.

Diagnosis

A large, depressed conical species of *Metalycaeus* with strongly swollen, long, R2 with smooth surface (R2+R3 exceeds half a whorl), an R3 with a central, low swelling, a short distance between inner and outer peristomes and an internally slightly fringed inner peristome.

Type material examined

Syntypes
INDIA • 5 shells (one of them separated with pink wool); Abor Hills; Oakes leg.; NHMUK 1903.7.1.3.102.

Additional material examined

INDIA – **Arunachal Pradesh** • 1 shell; Penin, Upper Siang; 28°46.881′ N, 94°45.529′ E; 1040 m a.s.l.; 11 May 2022; Aravind N.A. and Surya Narayanan leg.; ZSI/SRC/LM2229 • 1 shell; Kumsing, Siang; 28°14.141′ N, 94°59.654′ E, 2 May 2022; Aravind N.A. and Surya Narayanan leg.; ZSI/SRC/LM2230 • 2 shells; Sissen, East Siang; 28°7.917′ N, 95°7.372′ E; 235 m a.s.l.; 26 Apr. 2022; Aravind N.A. and Surya Narayanan leg.; ZSI/SRC/LM2231 • 1 shell; Kaleg-Rotung Road, East Siang; 28°6.507′ N, 95°10.159′ E; 936 m a.s.l.; 24 Apr. 2022; Aravind N.A. and Surya Narayanan leg.; ZSI/SRC/LM2232.

Type locality

"Bapu Peak, Abor Hills".

Differential diagnosis

The most similar species is *M. physis* (Benson, 1859) in terms of general shell and aperture shape. Typical *M. physis* shells are larger than typical *M. aborensis* shells, but one of the *M. aborensis* shells we collected (Kaleg-Rotung Road) is as large as typical *M. physis* shells. *Metalycaeus physis* has a smooth lip of the inner peristome, but *M. aborensis* shells can be slightly fringed. The R1 of *M. aborensis* shells tend to be more densely ribbed than those of *M. physis*, but this character shows variability between shells of both species. The only consistent difference we could find between the two species is the denser R2 striping in *M. aborensis*.

Remarks

Our specimens from Sissen, Kumsing and Penin agree with typical specimens of *M. aborensis* in terms of shell size and shape, but there are differences regarding the formation of the inner peristome, and the R2 ribs inside the umbilicus. Typical *M. aborensis* shells have a slightly fringed aperture (4 low denticles

separated by incisions). Among our newly collected material, only a shallow basal incision is discernible in specimens from Sissen and Penin.

Inside the umbilicus, ca every 4th rib is more elevated than the others, which is visible in all examined samples, including the types. However, the density of those elevated ribs is variable. Namely, the rib density of the specimen from Kumsing agrees with that of the types of *M. aborensis*, while the shells from Sissen and Penin have more widely-spaced ribs inside the umbilicus. The single specimen we collected on Kaleg-Rotung Road is larger than all other specimens (D: 10.2 mm, H: 6.6 mm vs D: 7.5–8.10 mm, H: 5.4–5.7 mm), but we could not detect any other differences.

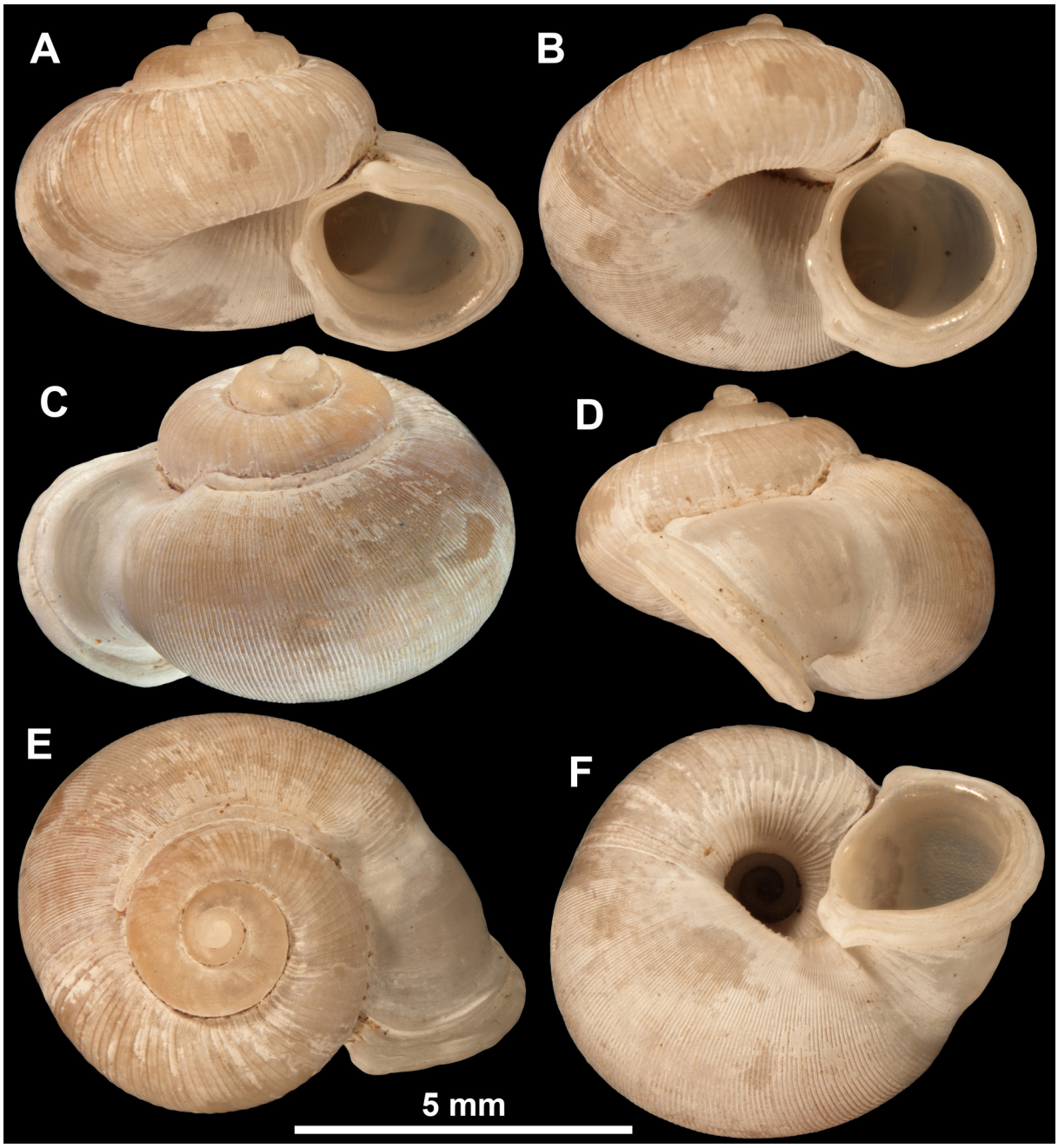


Fig. 5. Shell of *Metalycaeus aborensis* (Godwin-Austen, 1914) from Kumsing (ZSI/SRC/LM2230). All photos: B. Páll-Gergely.

Metalycaeus physis (Benson, 1859)
Fig. 3F–I

Alycaeus physis Benson, 1859: 179.

Alycaeus physis – Sowerby 1877: pl. 6, species 51. — Godwin-Austen 1914: 342, pl. 134 fig. 1, 1a.
Alycaeus (*Chamalycaeus*) *physis* – Kobelt 1902: 361. — Gude 1921: 231–232, fig. 34.
Alycaeus (*Orthalycaeus*) *physis* – Rees 1964: 64, pl. 5 fig. 27.
Chamalycaeus (*Chamalycaeus*) *physis* – Ramakrishna *et al.* 2010: 55.
Metalycaeus physis – Páll-Gergely *et al.* 2020: 151. — Preece *et al.* 2022: 81, fig. 30b–c. — Gittenberger *et al.* 2024: 194, figs 12–16, 44, 47.

Diagnosis

A very large, depressed conical species of *Metalycaeus* with fine ribs on R1 and R3, a strongly swollen, long R2 (R2+R3 exceeds half a whorl) with low, rather widely-spaced ribs, an R3 with a central, low swelling, a short distance between inner and outer peristomes and a circular peristome (unfringed).

Type material examined

Syntype
INDIA • Sikkim; UMZC I.102735;

Additional material examined

INDIA • 2 shells; Darjeeling; "Sow M/R 7/3/91, 626"; V.W. MacAndrew Collection, Acc. no. 1563; NHMUK 20150124 • 3 shells; Darjiling; NHMUK 1888.12.4.895-871.

Type locality

"in valle Rungit (alt. 2000 ped.), prope Darjiling".

Metalycaeus sibbumensis (Godwin-Austen, 1914)
Fig. 6A–E

Alycaeus sibbumensis Godwin-Austen, 1914: 367, pl. 156 fig. 4, 4a.

Alycaeus sibbumensis – Gude 1921: 219.
Alycaeus (*Alycaeus*) *sibbumensis* – Ramakrishna *et al.* 2010: 51.
Metalycaeus (?) *sibbumensis* – Páll-Gergely *et al.* 2020: 166.

Diagnosis

A large, depressed conical species of *Metalycaeus* with fine ribs on R1, widely-spaced ribs on R3, a swollen, long, smooth R2 (R2+R3 reaches half a whorl), an R3 with a central, low swelling, a short distance between inner and outer peristomes and a circular peristome (unfringed).

Type material examined

Syntypes
INDIA • 2 shells; Sibbum, Abor Hills; Oakes leg.; NHMUK 1903.7.1.3142.

Type locality

"Sibbum, Abor Hills".

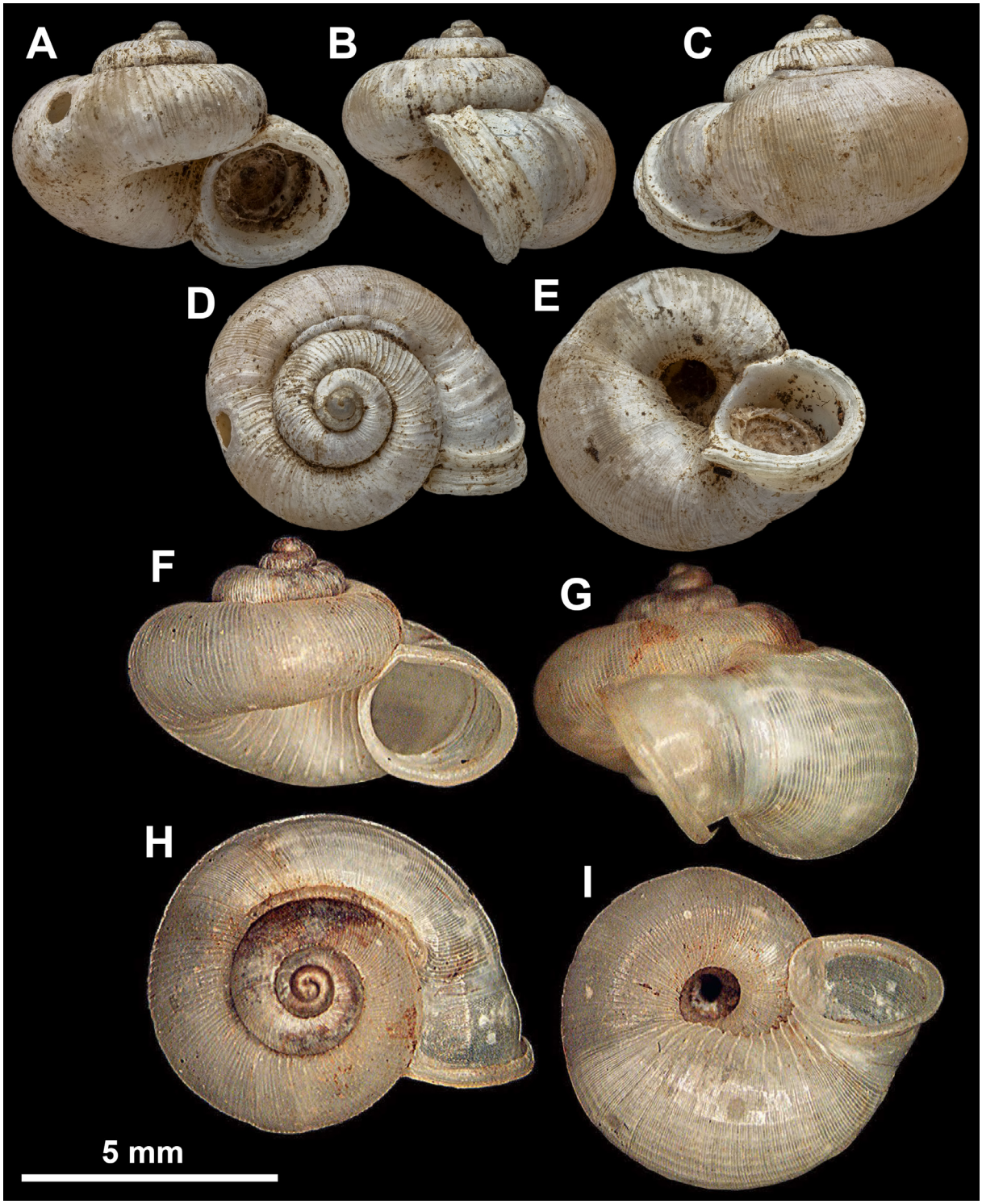


Fig. 6. Species of the *Metalycaeus aborensis* species group. **A–E**. *M. sibbumensis* (Godwin-Austen, 1914), syntype (NHMUK 1903.7.1.3142). **F–I**. *M. umbidistinctus* Gittenberger & Choki Gyeltshen, 2024, holotype (NBCB 1501). Photos: K. Webb (A–E), Figs F–I are from Gittenberger *et al.* (2024).

Differential diagnosis

Smaller than typical *M. aborensis*, its shape is identical, but it has a rounded aperture (in *M. aborensis* it is slightly fringed) and a greater distance between inner and outer peristomes.

Metalycaeus umbidistinctus Gittenberger & Choki Gyeltshen, 2024
Fig. 6F–I

Metalycaeus umbidistinctus Gittenberger & Choki Gyeltshen in Gittenberger *et al.*, 2024: 197, figs 11, 16–17.

Diagnosis

This species is characterized by a long, smooth R2 and a conspicuously short R3.

The species of the *M. bhutanensis* species group also possess a short R3, but they differ from *M. umbidistinctus* by the deeper constriction and the ribbed (not smooth) R2.

Type material examined

Holotype

BHUTAN • shell; Mongar Dzongkhag, 4 km SW of Mongar; 27°14′ N, 91°11′ E; 725 m a.s.l.; 12 Apr. 2015; E. Gittenberger and Pema Leda leg.; NBCB 1501 (photos examined).

Type locality

"Mongar Dzongkhag: 4 km SW of Mongar, 725 m a.s.l., 27°14′ N 91°11′ E" (Bhutan).

Metalycaeus bhutanensis species group

Remarks

Long, smooth R2, short R3, strongly reflected outer peristome. Operculum calcareous.

Metalycaeus bhutanensis (Godwin-Austen, 1914)
Figs 7–8

Alycaeus bhutanensis Godwin-Austen, 1914: 350, pl. 148 fig. 8.
Alycaeus macgregori Godwin-Austen, 1914: 356–357, pl. 141 fig. 2, 2a–b. **Syn. nov.**
Alycaeus burtii var. *yetayensis* Godwin-Austen, 1914: 353–354, pl. 149 fig. 7. **Syn. nov.**

Alycæus ingrami var. *nagaensis* – Nevill 1878: 292 (see remarks under *M. macgregori*).
Alycaeus burtii var. *yetaiensis* [sic] – Gude 1921: 207.
Alycaeus (*Chamalycaeus*) *bhutanensis* – Gude 1921: 224.
Alycaeus (*Chamalycaeus*) *macgregori* – Gude 1921: 229.
Chamalycaeus (*Chamalycaeus*) *macgregori* – Ramakrishna *et al.* 2010: 54.
Metalycaeus bhutanensis – Páll-Gergely *et al.* 2020: 139.
Metalycaeus burtii yetayensis – Páll-Gergely *et al.* 2020: 141.
Metalycaeus macgregori – Páll-Gergely *et al.* 2020: 147.

Diagnosis

This species is characterized by fine, rather widely-spaced ribs and slightly lower spiral striation on R1, a long, swollen R2, a short R3 with a low central swelling, and an internally fringed aperture.

Type material examined

Syntypes of *Alycaeus bhutanensis* Godwin-Austen, 1914
INDIA/BHUTAN • 2 shells; Bhutan; "Beddome coll."; NHMUK 1912.4.16.290.

Syntypes of *Alycaeus burtii* var. *yetayensis* Godwin-Austen, 1914
INDIA • 6 shells; Yetay ravine, No. 24 Pk, Dafla No. 7 camp; NHMUK 1903.7.1.2535.

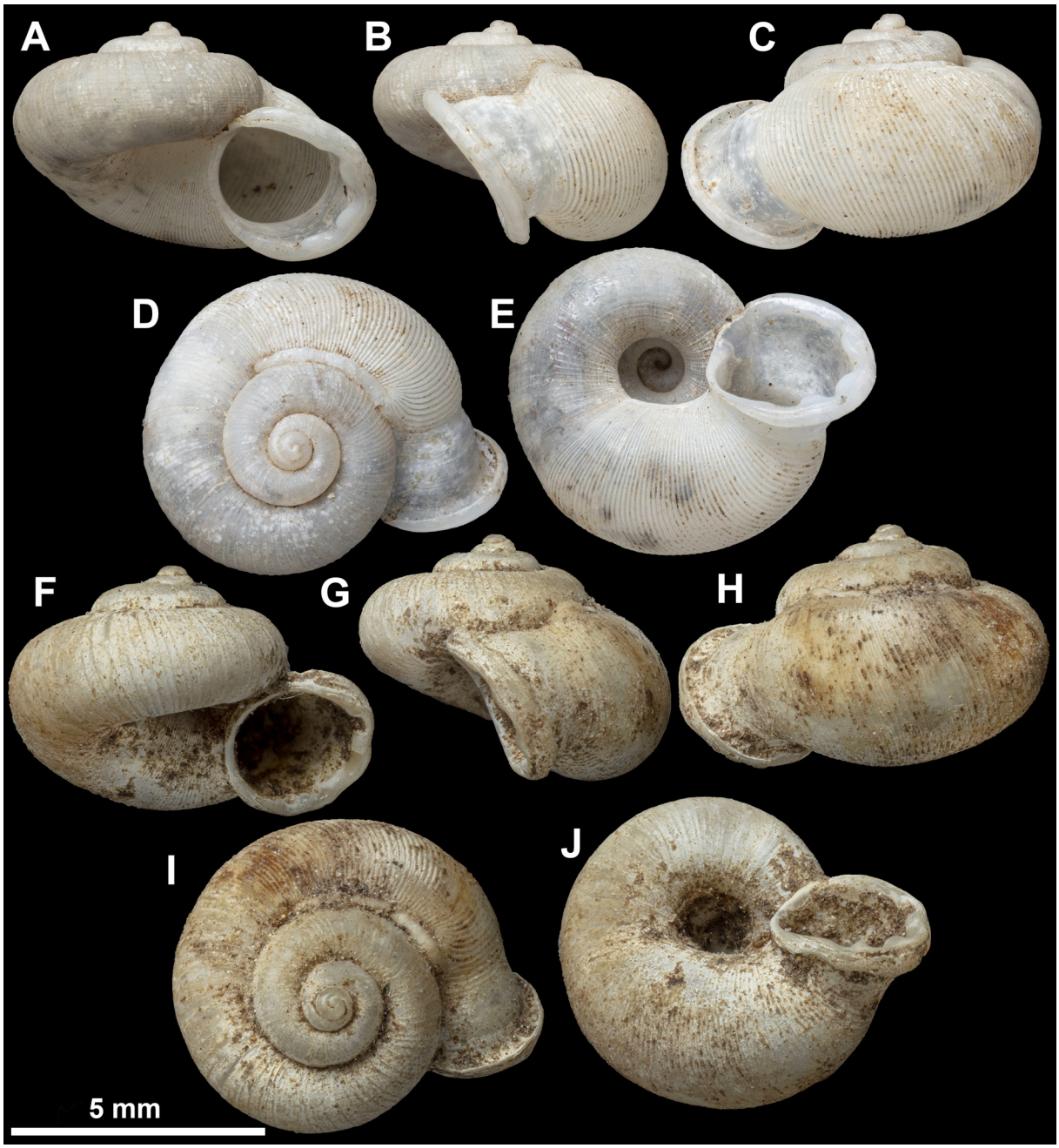


Fig. 7. Shells of *Metalycaeus bhutanensis* (Godwin-Austen, 1914). **A–E**. Syntype of *Alycaeus bhutanensis* (NHMUK 1912.4.16.290). **F–J**. Syntype of *A. burtii* var. *yetayensis* Godwin-Austen, 1914 (NHMUK 1903.7.1.2535). All photos: K. Webb.

Holotype of *Alycaeus macgregori* Godwin-Austen, 1914
INDIA • (fixed by original description); Dafla Hills; NHMUK 1903.7.1.2621.

Paratypes of *Alycaeus macgregori* Godwin-Austen, 1914
INDIA • 2 shells; Shengorh (at 27°18′41″ N, 93°44′43″ E according to Szekeres *et al.* 2021), Dafla Hills; "Godwin-Austen coll."; NZSI M.8058.

Type localities

"Bhutan Frontier, probably on Eastern, or Aka Hills, side" (*A. bhutanensis*); "Yetay Ravine, No. 24 Peak, Dafla Hills" (*A. burtii* var. *yetayensis*); "Dafla Hills" (*A. macgregori*).



Fig. 8. Shells of *Metalycaeus bhutanensis* (Godwin-Austen, 1914). **A–B**. Holotype of *Alycaeus macgregori* Godwin-Austen, 1914 (NHMUK 1903.7.1.2621). **C–H**. Paratype and labels of *A. macgregori* (ZSI/SRC/M.8058). Photos: K. Webb (A–B) and S. Sajan (C–H).

Remarks

We found no difference between *M. bhutanensis* and *M. burtii yetayensis*, therefore the latter is a synonym of the former.

In the original description of *A. macgregori*, Godwin-Austen (1914) stated that the holotype was in his collection ("single type-specimen in my collection"). Unfortunately, that shell is damaged on its R2. Godwin-Austen (1914) also states that he received two shells from the Indian Museum collected at the Shengorh Peak (Dafla Hills), and "at a hasty glance", identified them as *Alycaeus nagaensis* Godwin-Austen, 1871 (currently *Dicharax ingrami* (Blanford, 1862), see Páll-Gergely *et al.* 2025). Thus, those two shells were listed as *Alycaeus ingrami* var. *nagaensis* by Nevill (1878), and, fortunately, they were found in the ZSI. Godwin-Austen (1914) stated that the two shells from the Shengorh Peak were "finer, better grown specimens, with crenulated outer lower margin, showing well, with three well-marked folds", while those are "only just indicated in my drawing" (referring to the holotype of *A. macgregori*). The holotype of *A. macgregori* is nearly identical to the syntypes of *A. bhutanensis* with the exception of the rounded aperture, which is probably due to the immature developmental stage of the *A. macgregori* shell. Therefore, we treat *A. macgregori* as a junior synonym of *A. bhutanensis*. The two shells from the Shengorh peak are also very similar to the syntypes of *M. bhutanensis*, but they have a less conspicuous constriction.

Metalycaeus dikrangensis (Godwin-Austen, 1914)
Fig. 9

Alycaeus dikrangensis Godwin-Austen, 1914: 355, pl. 148 fig. 6, 6a.
Alycaeus luyorensis Godwin-Austen, 1914: 365–366, pl. 157 fig. 6, 6a. **Syn. nov.**

Alycaeus (*Raptomphalus*) *luyorensis* – Gude 1921: 288.
Alycaeus dikrangensis – Gude 1921: 209.
Alycaeus (*Alycaeus*) *dikrangensis* – Ramakrishna *et al.* 2010: 48.
Chamalycaeus (*Raptomphalus*) *luyorensis* – Ramakrishna *et al.* 2010: 69.
Metalycaeus luyorensis – Páll-Gergely *et al.* 2020: 147.
Metalycaeus (?) *dikrangensis* – Páll-Gergely *et al.* 2020: 163.

Diagnosis

R1 finely ribbed, R2+R3 reaches nearly half a whorl, R2 smooth, twice as long as R3, R3 almost smooth, with a slight indication of a central swelling, outer peristome reflected, inner peristome strongly fringed (including its outer rim).

Type material examined

Syntypes of *Alycaeus dikrangensis* Godwin-Austen, 1914
INDIA • 13 shells in 3 different vials; Toruputu Peak, Dafla Hills; Godwin-Austen leg.; NHMUK 1903.7.1.2533.

Syntypes of *Alycaeus luyorensis* Godwin-Austen, 1914
INDIA • 2 shells; Luyor, Abor Hills; 7200 ft; Oakes leg.; NHMUK 1903.7.1.3527.

Type localities

"Toruputu Peak, Dafla Hills" (*A dikrangensis*); "Luyor, Abor Hills, 7200 ft" (*A. luyorensis*).

Remarks

The only difference between the type specimens of *M. dikrangensis* and *M. luyorensis* is the strongly reflected outer peristome in the former. This character is not regarded as sufficient for species-level

distinction in other cases (see *Dicharax notus* (Godwin-Austen, 1914) in Páll-Gergely *et al.* 2021: fig. 26), therefore we treat *M. luyorensis* as a junior synonym of *M. dikrangensis*. The strongly protruding, fringed inner peristome on the photographed syntype of *M. luyorensis* protrudes considerably less in the other syntype, so this is not a consistent difference between the two 'species'.

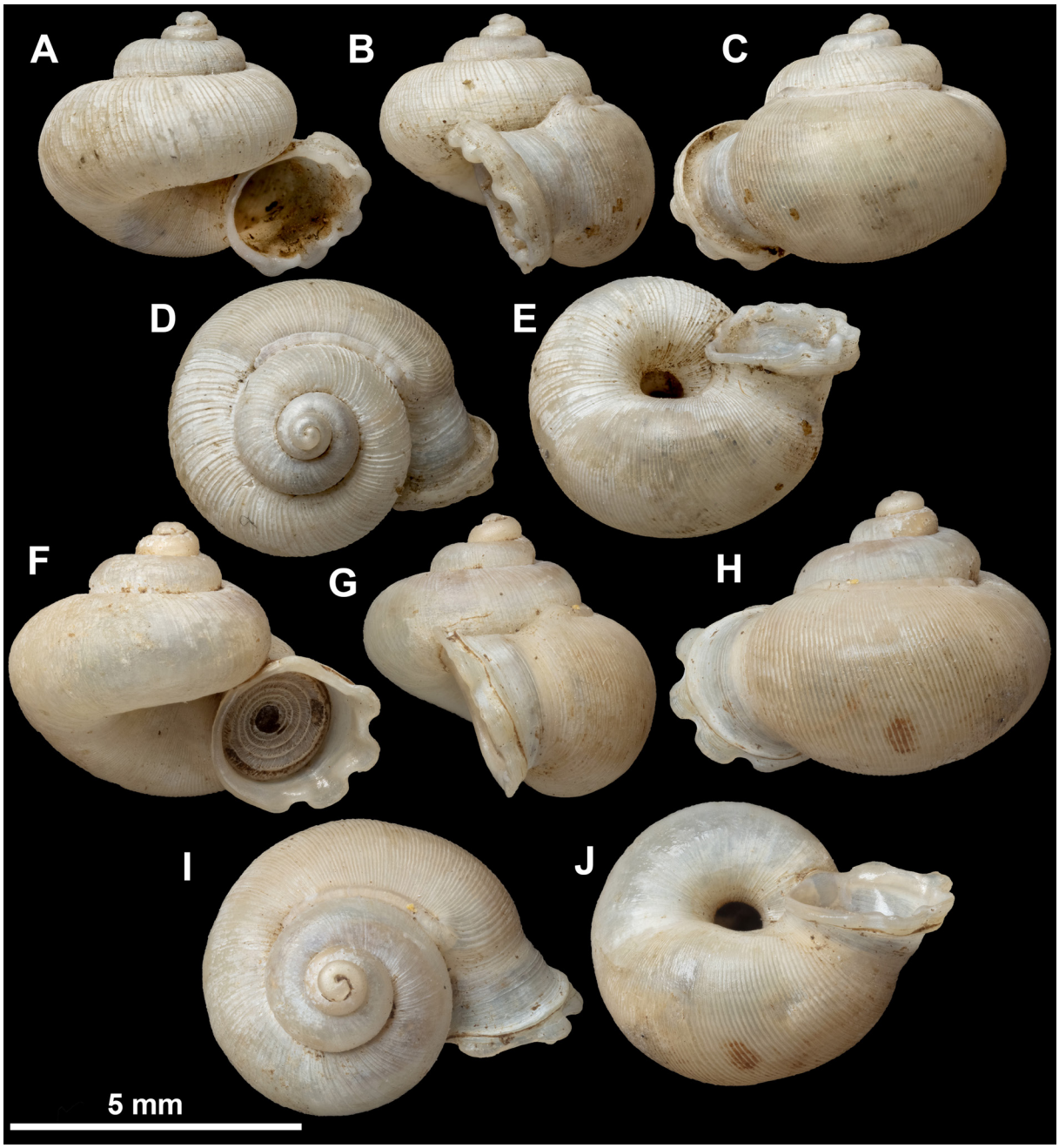


Fig. 9. Species of *Metalycaeus dikrangensis* (Godwin-Austen, 1914). **A–E**. Syntype of *M. dikrangensis* (Godwin-Austen, 1914) (NHMUK 1903.7.1.2533). **F–J**. Syntype of *Alycaeus luyorensis* Godwin-Austen, 1914 (NHMUK 1903.7.1.3527). All photos: K. Webb.

Metalycaeus gittenbergeri Páll-Gergely & Aravind sp. nov.
urn:lsid:zoobank.org:act:4A16143C-8C7A-48CF-97DA-CA59F30D2B7C
Figs 10–12

Diagnosis

This species is characterized by a strongly depressed shell, fine, dense ribs on R1, a long, strongly swollen R2, a short R3 with a low central swelling, and an internally fringed aperture.

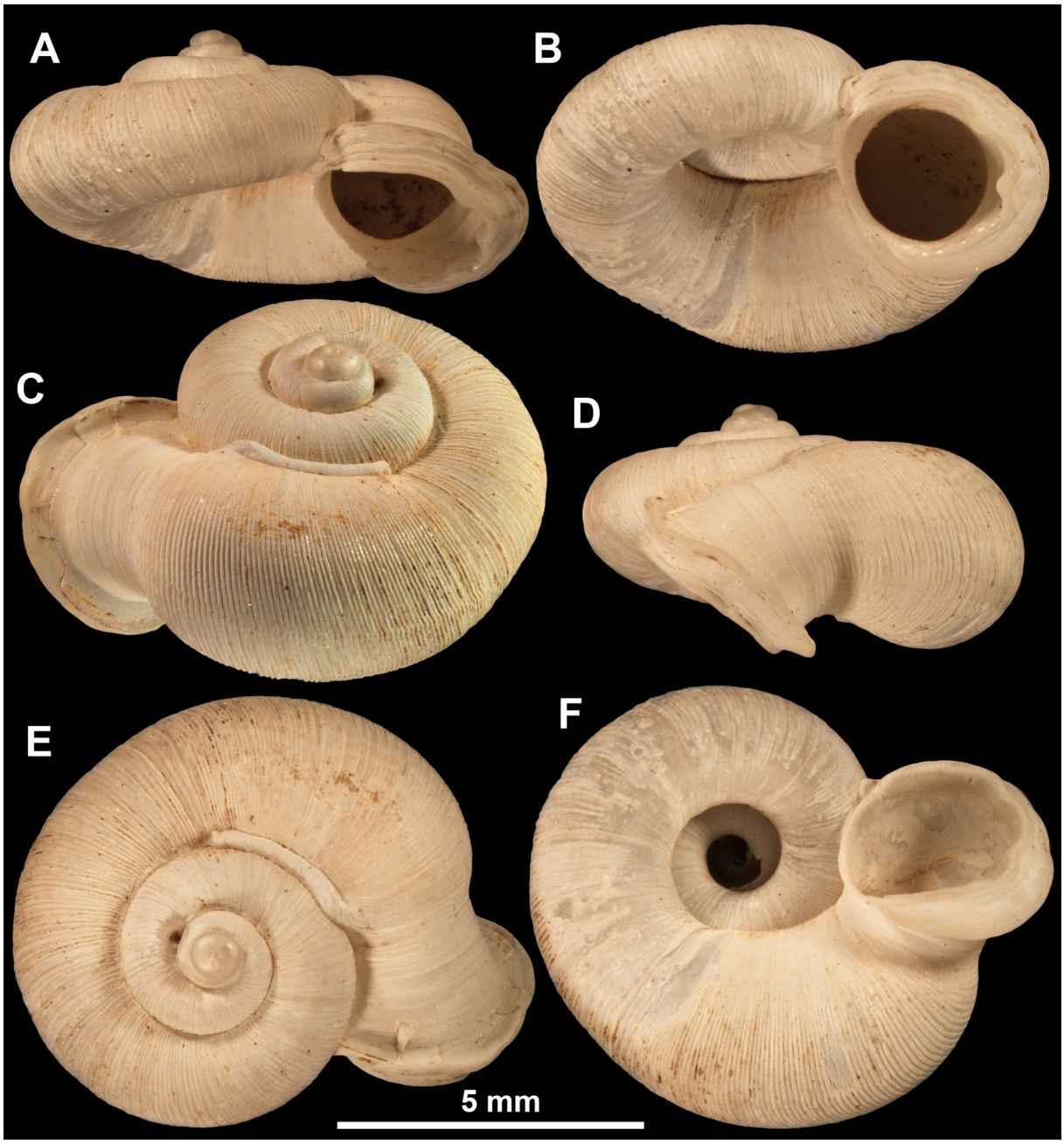


Fig. 10. Holotype of *Metalycaeus gittenbergeri* Páll-Gergely & Aravind sp. nov. (ZSI/SRC/LM2233). All photos: B. Páll-Gergely.

Etymology

This new species is dedicated to and named after Prof. Edmund Gittenberger, who is one of the leading experts on terrestrial snails, and he is especially acknowledged for his contribution to the knowledge of Himalayan molluscs.

Type material

Holotype

INDIA – **Arunachal Pradesh** • shell (D: 8.3 mm, H: 4.3 mm); Yemsing Cave, East Siang; 28°8.198′ N, 95°0.773′ E; 514 m a.s.l.; 26 Apr. 2022; Aravind N.A. and Surya Narayanan leg.; ZSI/SRC/LM2233.

Paratypes

INDIA – **Arunachal Pradesh** • 2 shells; Yemsing, East Siang; 28°6.387′ N, 95°0.427′ E; 590 m a.s.l.; 27 Apr. 2022; Aravind N.A. and Surya Narayanan leg.; ZSI/SRC/LM2234 • 5 specs in ethanol; same data as for preceding; ZSI/SRC/LM2235.

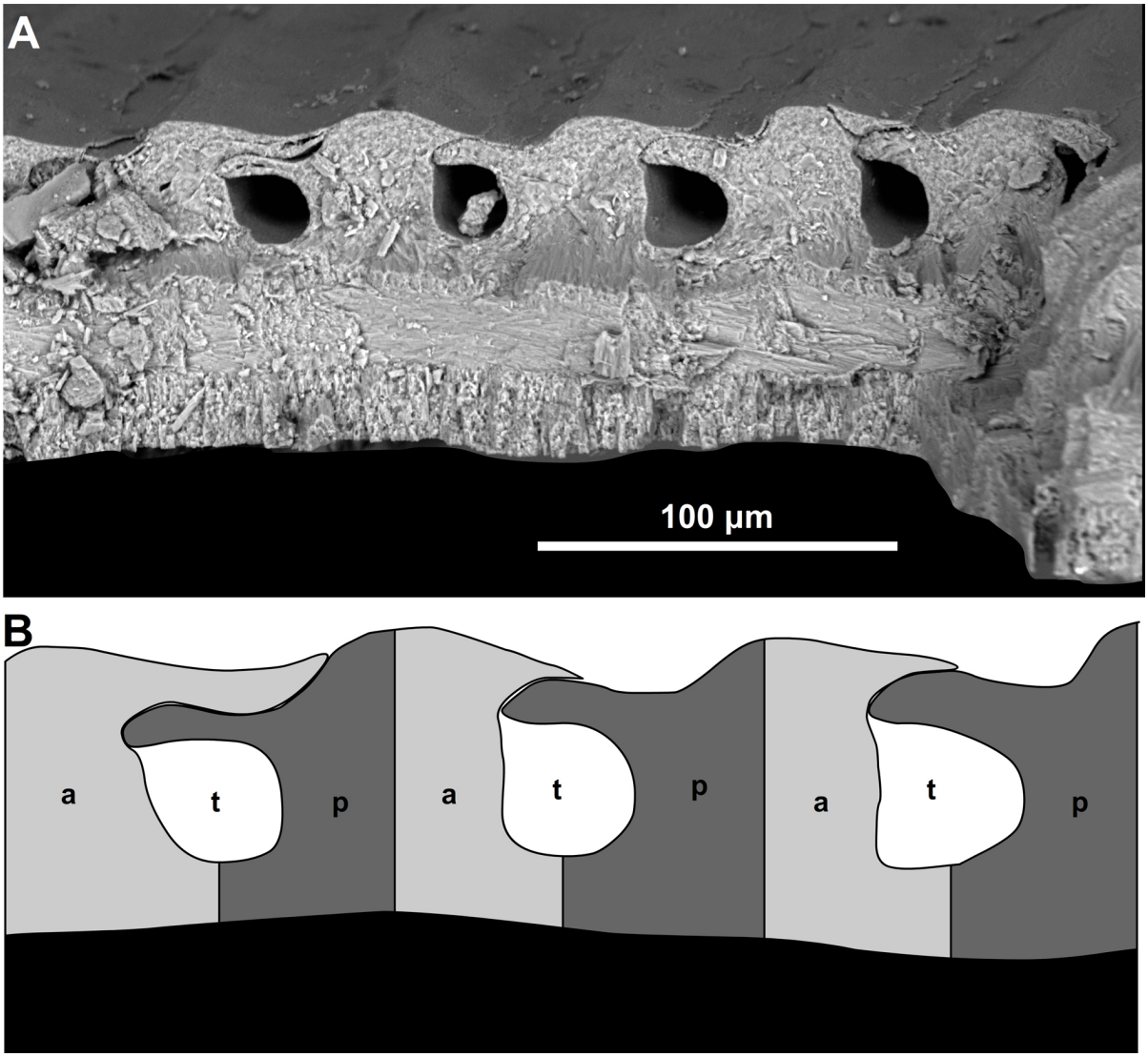


Fig. 11. Cross sectional view of R2 of *Metalycaeus gittenbergeri* Páll-Gergely & Aravind sp. nov., paratype (ZSI/SRC/LM2235). All images: B. Páll-Gergely. Abbreviations: a = anterior crust; p = posterior crust; t = microtunnel.

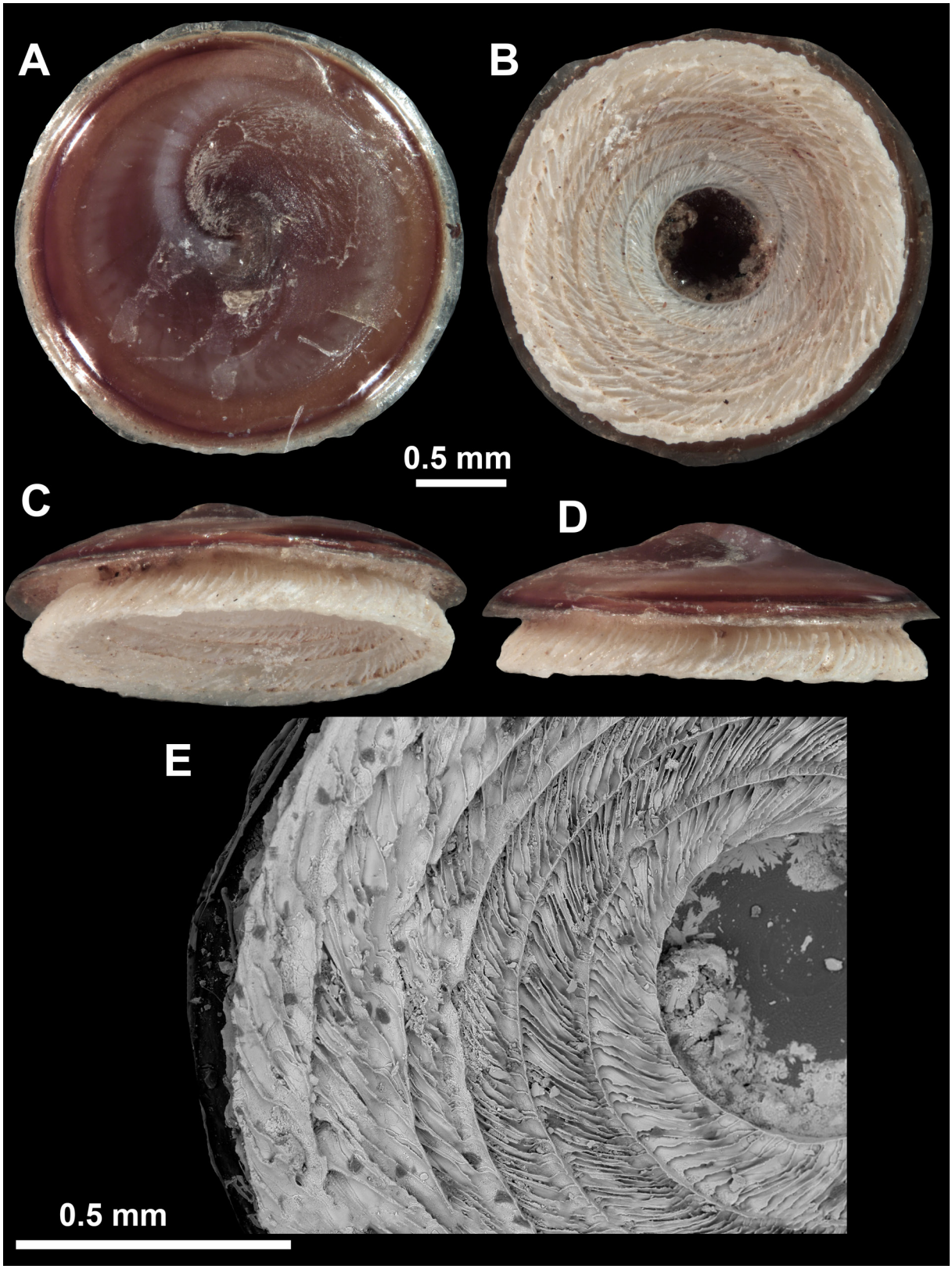


Fig. 12. Operculum of *Metalycaeus gittenbergeri* Páll-Gergely & Aravind sp. nov., paratype (ZSI/SRC/LM2235). All images: B. Páll-Gergely.

Description

Shell large, off-white, strongly depressed, with only the apex protruding above the dorsal surface. Protoconch consists of ca 1.5–1.75 whorls, practically smooth, with fine spirally striation. R1 with ca 2–2.25 whorls, with very dense, irregular ribs (ca 20 ribs on last half whorl) and denser, finer spiral striation. Shell surface relatively worn even in living specimens, therefore the spiral striation not clearly visible on last R1 whorl. R1–R2 boundary clearly visible due to strongly swollen R2, although no conspicuous change in rib density. R2 ca as long as R3, together they reach ca a quarter whorl. R2 with dense, blunt ribs. Number of R2 ribs ca 80. Constriction rather deep, long. R3 irregularly wrinkled, with a blunt, low, central swelling. Aperture strongly oblique to shell axis (strongly declines). Inner peristome slightly protruding, blunt, inner surface of the palatal part slightly fringed (3 slight chevrons demarcate 2 bays), and there is an additional, very slight incision at the meeting point of the columellar and parietal regions. Outer surface of inner peristome almost circular, with some signs of undulation on the parietal side. Outer peristome strongly expanded and reflected, with the exception of the parietal-umbilical area. Umbilicus relatively wide, oval, its outline straighter on the R2 side than elsewhere.

Operculum

Inner wall with a central, blunt, slightly elevated nipple, which gradually increases in height from the edge to the centre. Outer side with a multispiral, white, calcareous, wrinkled lamina, starting from the edge of the nucleus, and forming a funnel-shape structure parallel to the operculum surface.

Measurements

D = 8.1–8.4 mm, H = 4.2–4.9 mm (n = 3).

Differential diagnosis

The most similar species is *M. bhutanensis*, but the new species is more depressed, has a wider umbilicus, a denser radial sculpture (on both R1 and R2), a more inflated R2, a more oblique aperture, stronger distinction between inner and outer peristomes, a more expanded outer peristome and a more protruding inner peristome.

Metalycaeus brahma species group

Remarks

This species group is characterized by a long R2 with widely-spaced ribs, a relatively short R3 without a prominent swelling, and a fringed peristome. Operculum calcareous.

Metalycaeus brahma (Godwin-Austen, 1886)
Fig. 13

Alycaeus brahma Godwin-Austen, 1886: 195–196, pl. 48 fig. 3.
Alycaeus commutatus Godwin-Austen, 1914: 351, pl. 148 fig. 7.
Alycaeus lohitensis Godwin-Austen, 1914: 362–363, pl. 137 fig. 1, 1a. **Syn. nov.**
Alycaeus chanjukensis Godwin-Austen, 1914: 364–365, pl. 157 fig. 5, 5a

Alycaeus (*Chamalycaeus*) *brahma* – Kobelt 1902: 353.
Alycaeus brahma – Godwin-Austen 1914, Vol. II: 363.
Alycaeus brahma var. – Godwin-Austen 1914, Vol. II: 363.
Alycaeus lohitensis – Gude 1921: 210.
Alycaeus chanjukensis – Gude 1921: 207.
Alycaeus (*Chamalycaeus*) *brahma* – Gude 1921: 224–225.
Alycaeus (*Raptomphalus*) *commutatus* – Gude 1921: 286.

Alycaeus (*Alycaeus*) *chanjukensis* – Ramakrishna *et al.* 2010: 47.
Alycaeus (*Alycaeus*) *lohitensis* – Ramakrishna *et al.* 2010: 48.
Chamalycaeus (*Chamalycaeus*) *brahma* – Ramakrishna *et al.* 2010: 52.
Metalycaeus brahma – Páll-Gergely *et al.* 2020: 139, fig. 32 (treated *A. commutatus* and *A. chanjukensis* as junior synonyms). — Gittenberger *et al.* 2024: 190, figs 4, 7.
Metalycaeus lohitensis – Páll-Gergely *et al.* 2020: 146.

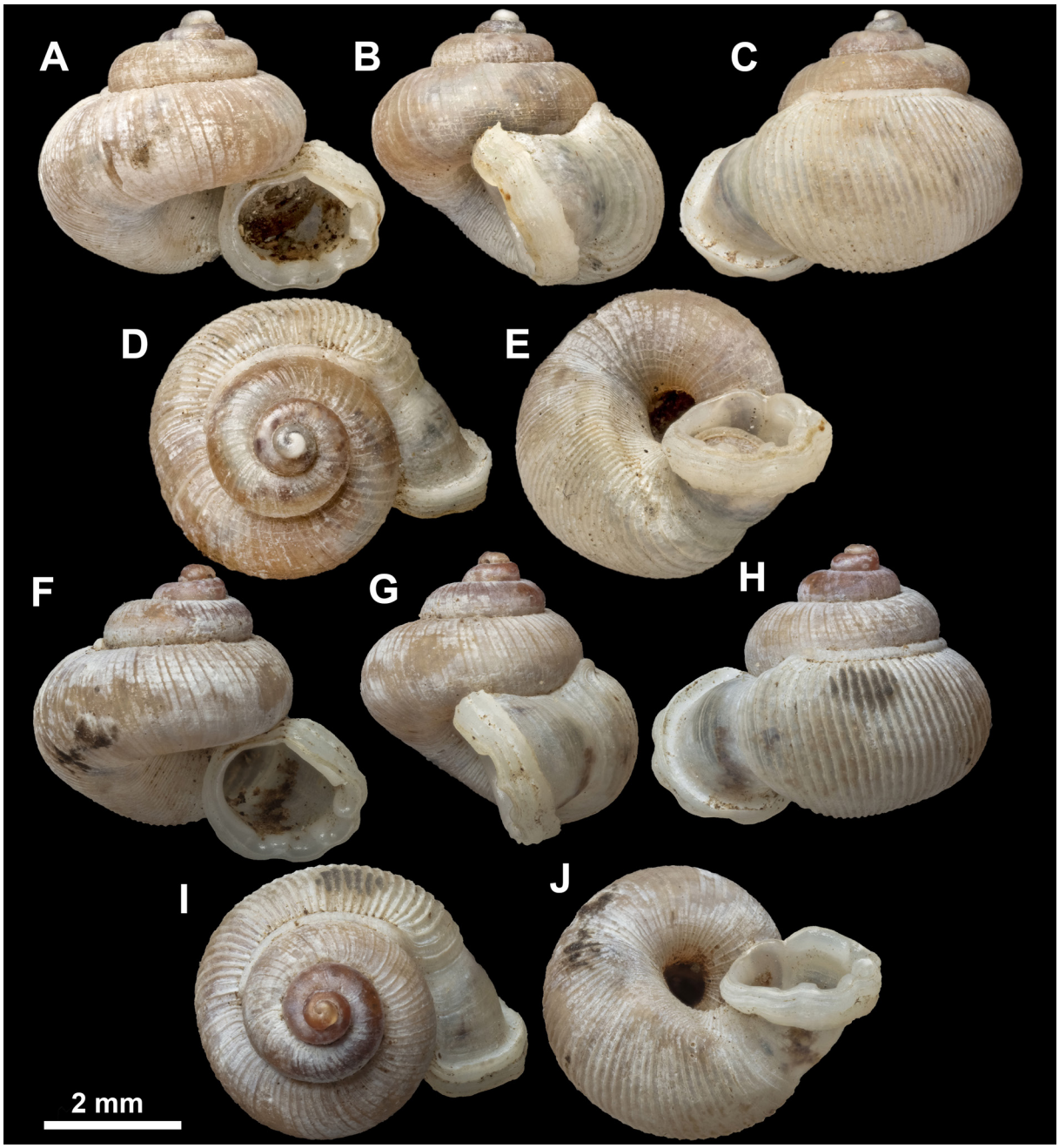


Fig. 13. Shells of *Metalycaeus brahma* (Godwin-Austen, 1886). **A–E**. Syntype of *M. brahma* (NHMUK 1903.7.1.2610). **F–J**. Syntype of *Alycaeus lohitensis* Godwin-Austen, 1914 (NHMUK 1903.7.1.2493). All photos: K. Webb.

Diagnosis

This species is characterized by a globular shell, a very long R2 with widely-spaced ribs, the very slightly indicated R3 swelling, and the fringed peristome.

Type material examined

Syntypes of *Alycaeus brahma* Godwin-Austen, 1886
INDIA • 16 shells (Fig. 82A–E); Brahmakund, E Assam; M. Ogle leg.; NHMUK 1903.7.1.2610.

Syntypes of *Alycaeus chanjukensis* Godwin-Austen, 1914
INDIA • 3 shells; Chanjuk La, Tsanspu Valley; 29°25′ N, 95°20′ W; "Oakes coll."; NHMUK 1903.7.1.3583.

Syntypes of *Alycaeus commutatus* Godwin-Austen, 1914
INDIA • 2 shells; Bhutan; "ex Beddome coll."; NHMUK 1912.4.16.293.

Syntypes of *Alycaeus lohitensis* Godwin-Austen, 1914
INDIA • 19 shells (Fig. 82F–J); Brahmakund, Eastern Assam; Ogle leg.; NHMUK 1903.7.1.2493.

Additional material examined

INDIA • 1 spec. of "*Metalycaeus brahma* (Godwin-Austen, 1886) var."; Dihung Valley, Singpho Hills; M. Ogle leg.; NHMUK 1903.7.1.2611.

Type localities

"Brahmakund" (*A. brahma*); "Chanjuk La, Tsanspu Valley, 4300 ft., Lat. 29° 25', Long. 95° 20'" (*A. chanjukensis*); "Bhutan" (*A. commutatus*); "Brahmakund, Eastern Assam" (*A. lohitensis*).

Remarks

Alycaeus commutatus and *A. chanjukensis* were synonymized with *M. brahma* by Páll-Gergely *et al.* (2020). Since *A. lohitensis* is not distinguishable from the other three species, we treat it as a junior synonym of *M. brahma*.

Metalycaeus burtii (Godwin-Austen, 1874)
Fig. 14A–E

Alycaeus Burtii Godwin-Austen, 1874: 149–150, pl. 3 fig. 9.

Alycaeus burtii – Sowerby 1877: pl. 3, species 27. — Godwin-Austen 1914: 352–353, pl. 144 fig. 8, 8a.
Alycaeus (*Alycaeus*) *burti* [sic] – Kobelt 1902: 342. — Ramakrishna *et al.* 2010: 47.
Alycaeus burti [sic] – Gude 1921: 206–207.
Metalycaeus burtii – Páll-Gergely *et al*. 2020: 141.

Diagnosis

This species has a slightly more depressed shell with wider umbilicus than *M. brahma*. Until more material becomes available, we treat it as a valid species.

Type material examined

Holotype
INDIA • single specimen mentioned in the original description; Barowli Gorge, Tezpur Dist., Assam; NHMUK 1903.7.1.2492.

Type locality

"Foot of the Bhutan Himalaya at the debouchement of the Barowli River, Assam".

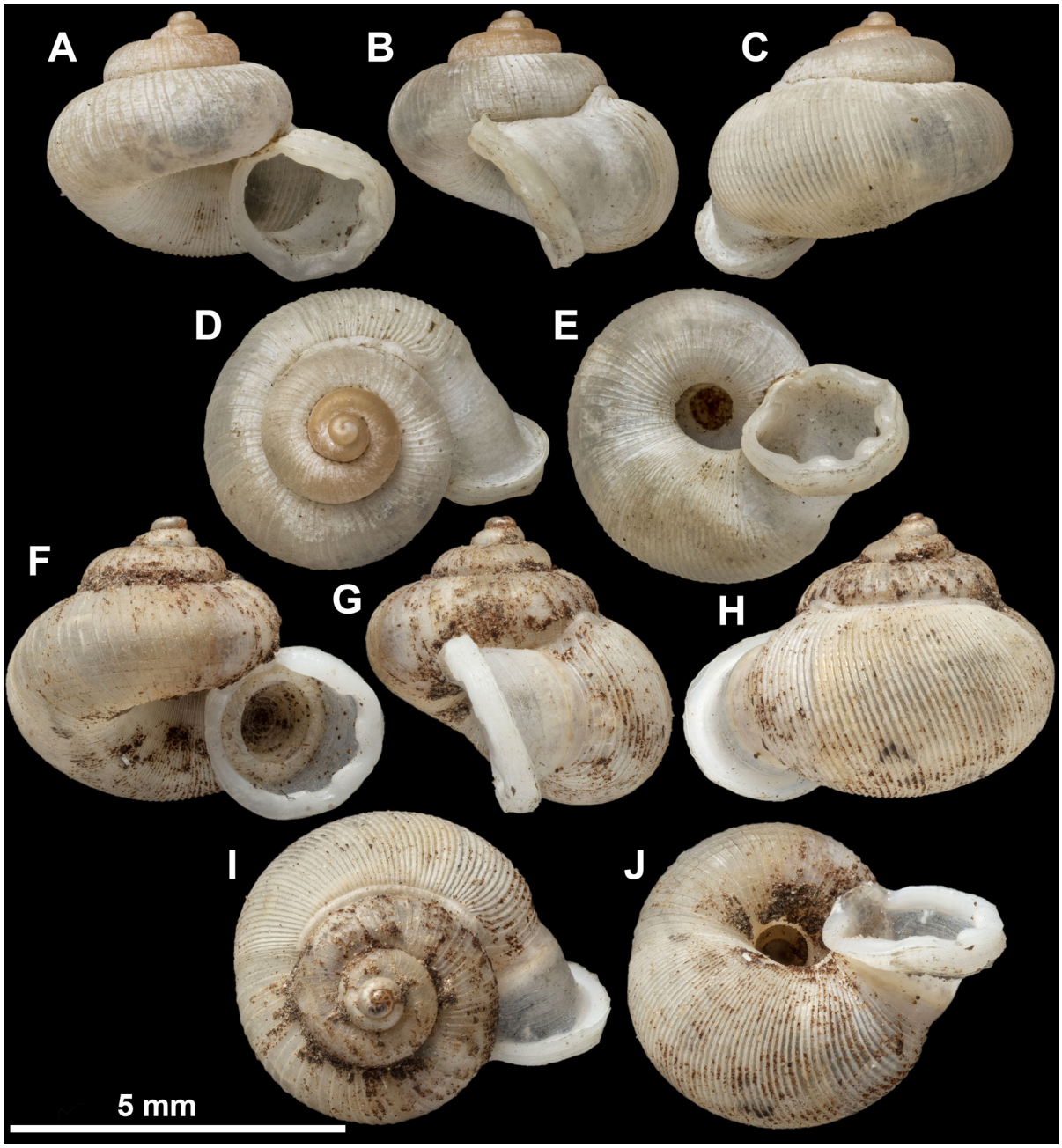


Fig. 14. Species of the *Metalycaeus brahma* species group. **A–E**. *M. burtii* (Godwin-Austen, 1874), holotype (NHMUK 1903.7.1.2492). **F–J**. *M. oglei* (Godwin-Austen, 1914), syntype (NHMUK 1903.7.1.2491). All photos: K. Webb.

Metalycaeus crenulatus (Benson, 1859)
Figs 15, 16A–E

Alycaeus crenulatus Benson, 1859: 180–181.
Metalycaeus karmademaae Gittenberger, Choki Gyeltshen & Kezang Tobgay in Gittenberger *et al.*, 2024: 194, figs 7–10. **Syn. nov.**

Alycaeus crenulatus – Godwin-Austen 1871: 90, pl. 3 fig. 4; 1914: 337–338, pl. 133 fig. 1, 1a–c. — Sowerby 1877: pl. 5, species 43.
Alycaeus (*Dicharax*) *crenulatus* – Kobelt 1902: 367. — Gude 1921: 242.
Chamalycaeus (*Dicharax*) *crenulatus* – Ramakrishna *et al.* 2010: 57.
Metalycaeus crenulatus – Páll-Gergely *et al.* 2020: 142. — Preece *et al.* 2022: 81, fig. 30b.

Diagnosis

R1 and R2 strongly ribbed, R2+R3 reaches nearly half a whorl, R3 short, without swelling, outer peristome reflected, inner peristome strongly fringed (including its outer rim).

Type material examined

Syntype of *Alycaeus crenulatus* Benson, 1859
INDIA • 1 shell; Darjiling; "R. McAndrew collection, Bens. coll."; UMZC I.102690.

Holotype of *Metalycaeus karmademaae* Gittenberger *et al.*, 2024
BHUTAN • shell; Lhuentse Dzongkhag: Garbrag (Phag Sang), 11 km W of Gorgon; 27°30′ N, 91°04′ E; 1800 m a.s.l.; 22 Feb. 2017; Ugyen Tenzin, Dawa Yoezer and Sherub Sherub leg.; NBCB 1314 (photographs examined).

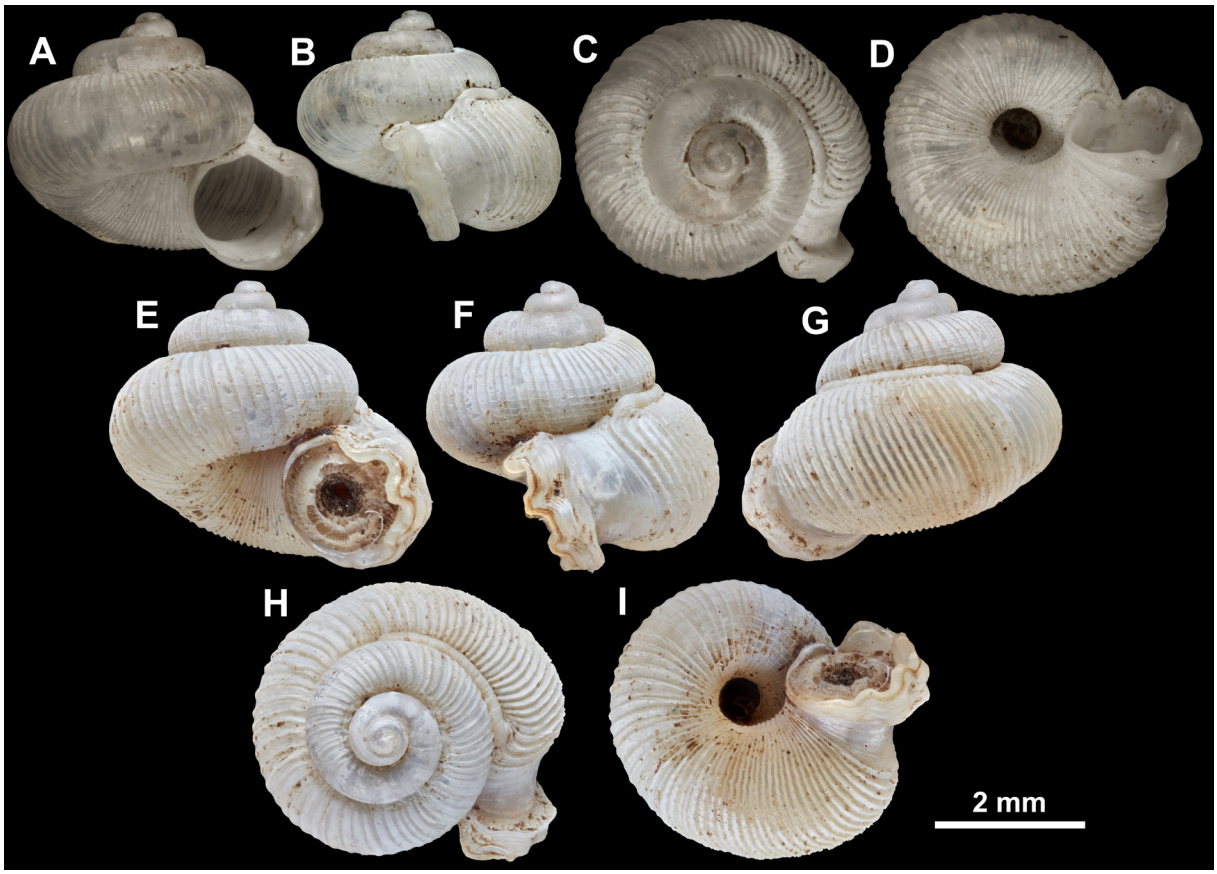


Fig. 15. Shells of *Metalycaeus crenulatus* (Benson, 1859). **A–D**. Syntype of *Alycaeus crenulatus* (UMZC I.102690). **E–I**. NHMUK 1903.7.1.2507. All photos: K. Webb.

Additional material examined

INDIA • 7 shells; Damsang, W Bhutan; Robert leg.; NHMUK 1903.7.1.1254 • ca 20 shells; Damsang, W. Bhutan; "Godwin-Austen coll."; NHMUK 1903.7.1.2507.

Type localities

"in valle Rungun" (*A. crenulatus*); "Lhuentse Dzongkhag: Garbrag (Phag Sang), 11 km W of Gorgon, 1800 m a.s.l., 27°30′ N 91°04′ E" (Bhutan) (*M. karmademaae*).

Remarks

Metalycaeus karmademaae agrees in all important traits with the examined shells of *M. crenulatus*. The only difference we could find is the thinner peristome in *M. karmademaae*, which seems insufficient for species-level distinction. Therefore, we treat *M. karmademaae* as a junior synonym of *M. crenulatus*.

Metalycaeus geduensis Gittenberger & Sherub Sherub, 2024
Fig. 16G–J

Metalycaeus geduensis Gittenberger & Sherub Sherub in Gittenberger *et al.*, 2024: 192, figs 5, 7.

Diagnosis

See under Remarks.

Type material examined

Holotype

BHUTAN • Chhukha Dzongkhag, NW of Gedu; 26°57′ N, 89°30′ E; 2447 m a.s.l.; 24 Mar. 2021; Choki Gyeltshen, Kezang Tobgay and Nima Gyeltshen leg.; NBCB 1326.

Type locality

"Chhukha Dzongkhag: NW of Gedu, 26°57′ N 89°30′ E, 2447 m a.s.l." (Bhutan).

Remarks

The R1 ribs of *Metalycaeus geduensis* are seemingly weaker than those of the specimens of *M. crenulatus* we examined. Nevertheless, this is a quantitative character that may not justify the distinction of *M. geduensis* as a separate species. Until more material becomes available, we treat this species differently from *M. crenulatus*. Furthermore, the holotype of *M. geduensis* has a slightly longer R3 than that of *M. crenulatus* we examined. The importance of this character should also be tested by a more extensive material. The type locality of *M. geduensis* is situated between those of *M. crenulatus* and *M. karmademaae* (treated here as a synonym of *M. crenulatus*).

Metalycaeus oglei (Godwin-Austen, 1914)
Fig. 14F–J

Alycaeus oglei Godwin-Austen, 1914: 362, pl. 148 fig. 2.

Alycaeus oglei – Gude 1921: 213.
Alycaeus (*Alycaeus*) *oglei* – Ramakrishna *et al.* 2010: 49.
Chamalycaeus oglei – Páll-Gergely *et al.* 2020: 42.
Metalycaeus oglei – Páll-Gergely *et al.* 2025: 7.

Diagnosis

R1 finely ribbed and spirally striated, R2 with relatively low ribs, R2+R3 reach half a whorl combined, R2 more than twice as long as R3, R3 with a very low, blunt swelling situated closer to R2 than to the peristome, outer peristome expanded, inner surface of inner peristome fringed.

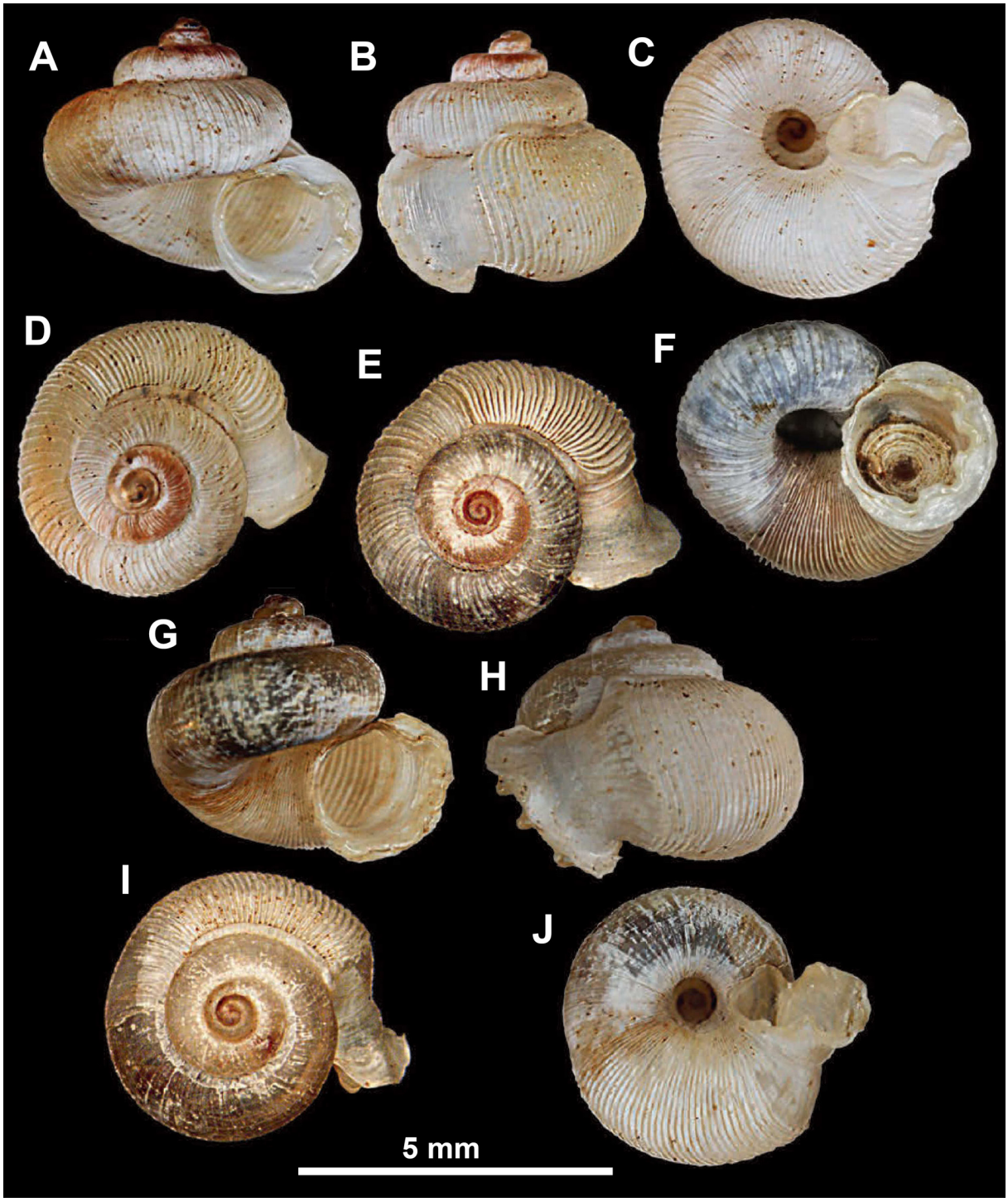


Fig. 16. Species of the *Metalycaeus brahma* species group. **A–F**. *Metalycaeus crenulatus* (Benson, 1859). **A–D**. *M. karmademaae* Gittenberger, Choki Gyeltshen & Kezang Tobgay, 2024, holotype (NBCB 1314). **E–F**. *M. karmademaae*, paratype (NBCB 1320). **G–J**. *M. geduensis* Gittenberger & Sherub Sherub, 2024, holotype (NBCB 1326). All photos from Gittenberger *et al.* (2024).

Material examined

Syntypes

INDIA • 2 shells in the vial; Noa Dihing; 500 ft; M. Ogle leg.; NHMUK 1903.07.01.2491 • 1 shell in the vial; Sadia; 350 ft; M. Ogle leg.; NHMUK 1903.07.01.2491. The box labelled *A. oglei* contained two glass vials.

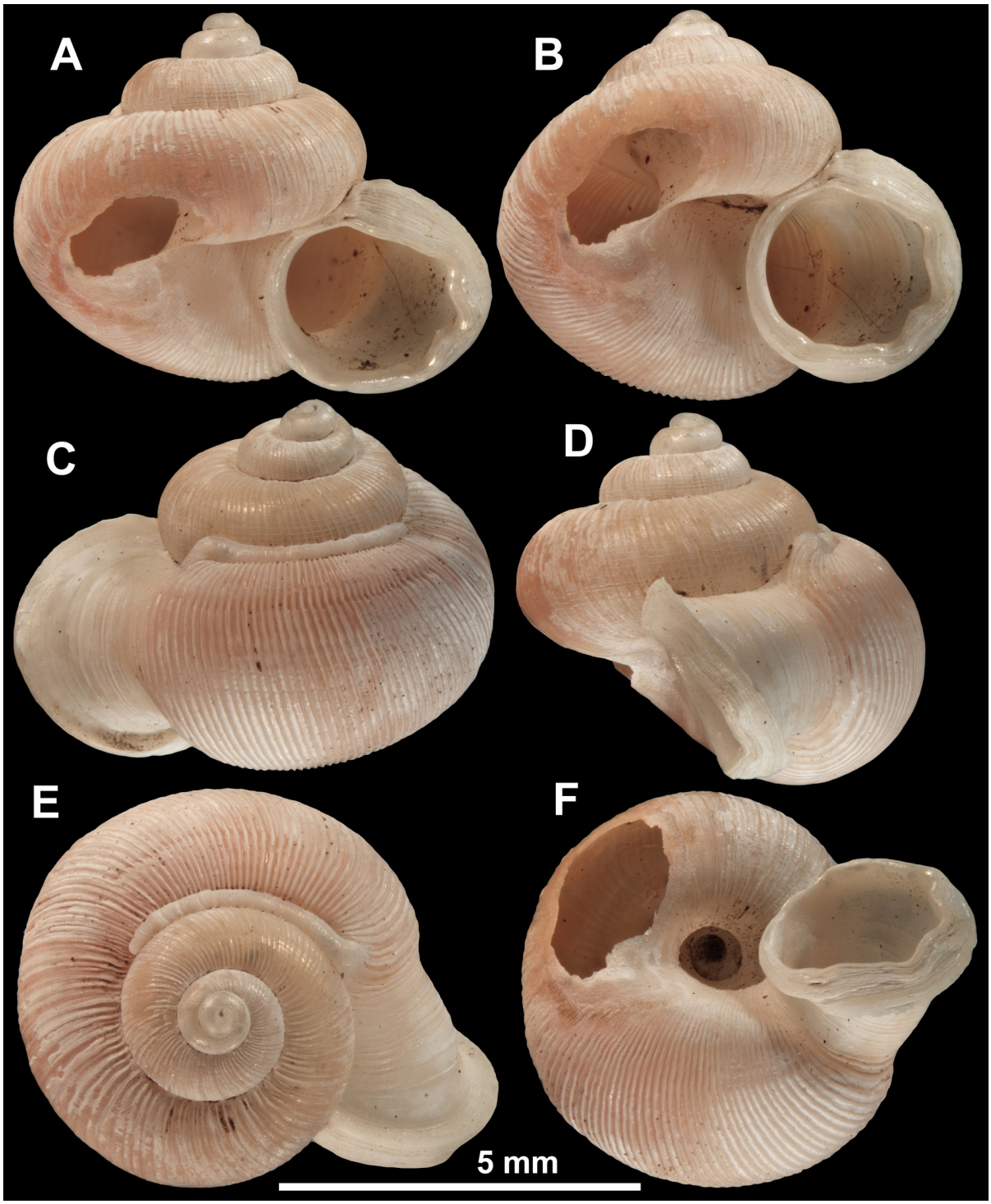


Fig. 17. *Metalycaeus* sp., Ramsing (ZSI/SRC/LM2236). All photos: B. Páll-Gergely.

Type locality

"Sadia"; "Dihing, 500 ft".

Remarks

Although no spiral striation was observed on the protoconch of *M. oglei*, it was moved to the genus *Metalycaeus* due to its close similarity with *M. brahma* (see Páll-Gergely *et al.* 2025).

Metalycaeus sp.
Fig. 17

Material examined

INDIA – **Arunachal Pradesh** • 1 shell; Upper Siang, from the back side of Ramsing forest guest house; 28°39.333′ N, 94°58.557′ E; 664 m a.s.l.; 10 May 2022; Aravind N.A. and Surya Narayanan leg.; ZSI/SRC/LM2236.

Measurements

D = 5.7 mm, H = 4.6 mm (n = 1).

Remarks

The most similar species is *Metalycaeus brahma*. However, that species has less dense R2 ribbing, a comparatively larger aperture with a more expanded, less reflected outer peristome, a more fringed inner peristome, and a sharper keel at the base of R2.

Metalycaeus oglei has less dense R1 ribs, stronger spiral striation in the same region, and a less oblique aperture to the shell axis.

This is probably a new species, but since it would be based on a single, damaged shell, we refrain from formally describing it.

Metalycaeus inflatus species group

Remarks

Shell rather small, R3 with no or low swelling, peristome expanded, practically absent towards the umbilicus. Besides the species listed here, *M. laosensis* Páll-Gergely, 2017 also belongs here. Operculum proteinaceous.

Metalycaeus beddomei (Godwin-Austen, 1914)
Fig. 18

Alycaeus beddomei Godwin-Austen, 1914: 386, pl. 149 fig. 5, 5a.
Alycaeus subinflatus Godwin-Austen, 1914: 400–401, pl. 154 fig. 8, 8a. **Syn. nov.**
Alycaeus (*Dioryx*) *varius* Godwin-Austen, 1914: 402, pl. 157 fig. 7, 7a (non *Alycaeus varius* Pilsbry & Y. Hirase, 1905). **Syn. nov.**
Metalycaeus suhajdai Páll-Gergely in Páll-Gergely *et al.*, 2020: 158 (replacement name for *Alycaeus varius* Godwin-Austen, 1914, non *Alycaeus varius* Pilsbry & Hirase, 1906).

Dioryx varius – Gude 1921: 204. — Ramakrishna *et al.* 2010: 75.
Alycaeus (*Chamalycaeus*) *subinflatus* – Gude 1921: 235.
Alycaeus (*Alycaeus*) *beddomei* – Ramakrishna *et al.* 2010: 46.
Chamalycaeus (*Chamalycaeus*) *subinflatus* – Ramakrishna *et al.* 2010: 56.

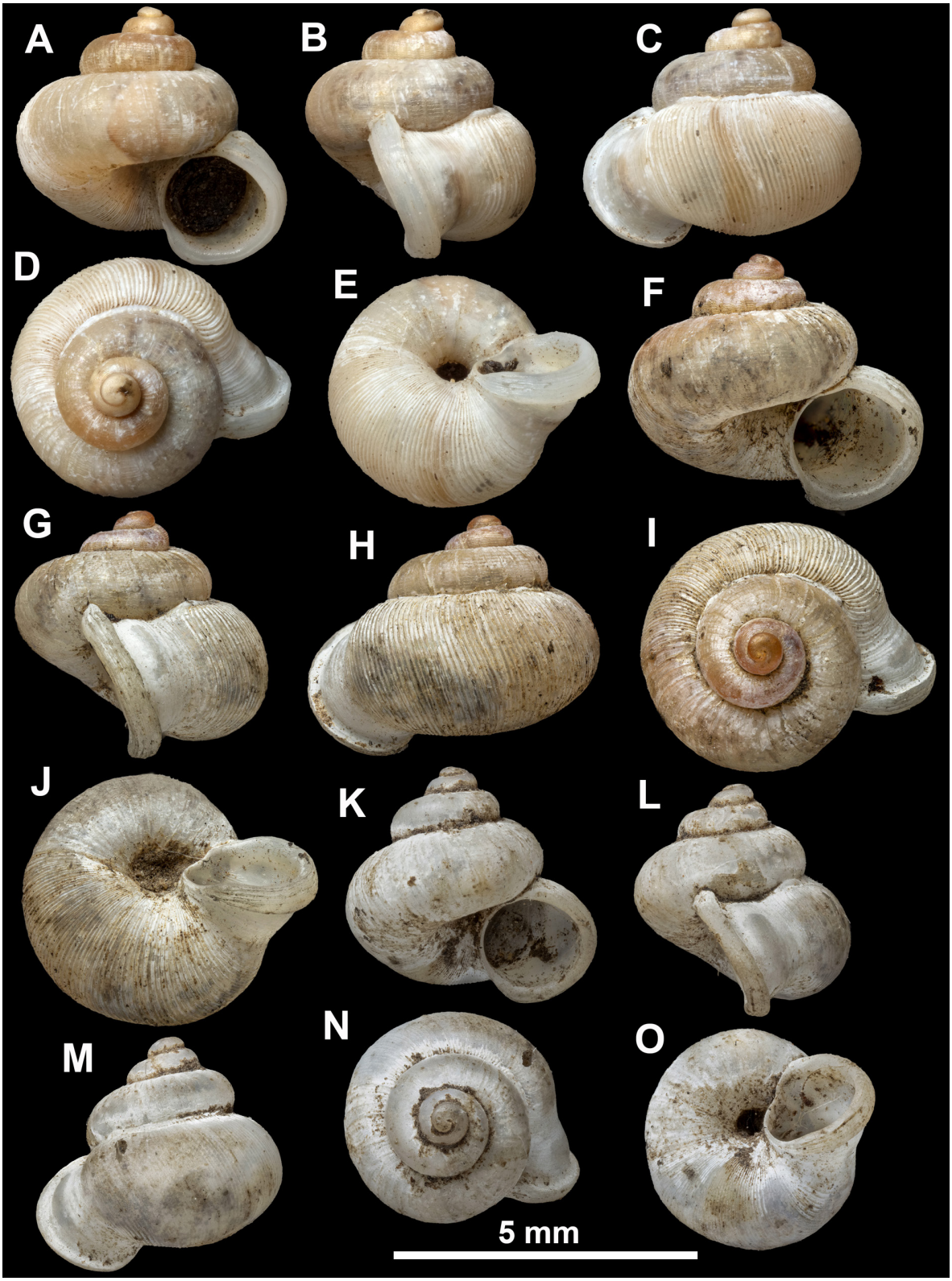


Fig. 18. Shells of *Metalycaeus beddomei* (Godwin-Austen, 1914). **A–E**. Syntype of *Alycaeus beddomei* (NHMUK 1912.4.16.294). **F–J**. Syntype of *A. subinflatus* Godwin-Austen, 1914 (NHMUK 1903.7.1.2489). **K–O**. Syntype of *A. varius* Godwin-Austen, 1914 (NHMUK 1903.7.1.2574) (= *Metalycaeus suhajdai* Páll-Gergely, 2020 is a replacement name). All photos: K. Webb.

Metalycaeus beddomei – Páll-Gergely *et al.* 2020: 138.
Metalycaeus subinflatus – Páll-Gergely *et al.* 2020: 158.

Diagnosis

Shell approximately as high as wide, R2+R3 combined are ca half a whorl long, R2 twice as long as R3, R3 with low, blunt swelling, outer peristome slightly expanded.

Type material examined

Syntypes of *Alycaeus beddomei* Godwin-Austen, 1914
INDIA • 5 shells; Naga Hills; "Beddome coll."; NHMUK 1912.4.16.294

Syntypes of *Alycaeus subinflatus* Godwin-Austen, 1914
INDIA • 7 shells (one spec. indicated with pink wool, other shells in another glass vial); Gaziphimi, NE Manipur; Godwin-Austen leg.; NHMUK 1903.7.1.2489.

Syntypes of *Alycaeus varius* Godwin-Austen, 1914
INDIA • 1 shell; Lhota Naga; Godwin-Austen leg.; NHMUK 1903.7.1.2574.

Type localities

"Naga Hills" (*A. beddomei*); "Gaziphimi, Lahupa Naga Hills, N.E. Munipur" (*A. subinflatus*); "Lhota Naga Hills" (*A. varius*).

Differential diagnosis

Metalycaeus beddomei differs from *M. inflatus* in the slight R3 swelling.

Remarks

The type specimens of *M. beddomei*, *M. subinflatus*, and *M. suhajdai* share traits such as the general shell and aperture shapes, the lengths of the regions, and the expanded outer peristome. The holotype of *Metalycaeus suhajdai* is slightly smaller than the photographed syntype of *M. beddomei*, but one syntype of the latter species agrees with *M. suhajdai* in size. The photographed syntype of *M. subinflatus* has a slightly more depressed shell than the imaged shell of *M. beddomei*, but this character is also not consistent between the two samples. Consequently, *M. subinflatus* and *M. suhajdai* are synonyms of *M. beddomei*.

Metalycaeus inflatus (Godwin-Austen, 1874)
Fig. 19A–E

Alycaeus inflatus Godwin-Austen, 1874: 146, pl. 3 fig. 1.

Alycaeus (*Chamalycaeus*) *inflatus* – Kobelt 1902: 356–357. — Gude 1921: 227–228.
Alycaeus inflatus – Godwin-Austen 1914: 392–393, pl. 144 fig. 1b–d.
Alycaeus inflatus var. – Godwin-Austen 1914: 394, pl. 144 fig. 1, 1a.
Chamalycaeus (*Chamalycaeus*) *inflatus* – Ramakrishna *et al.* 2010: 53.
Metalycaeus inflatus – Páll-Gergely *et al.* 2020: 145.

Diagnosis

Shell approximately as high as wide, R2+R3 are ca half a whorl long combined, R2 twice as long as R3, R3 with low, blunt swelling, outer peristome slightly expanded.

Type material examined

Syntypes

INDIA • 3 shells in 2 vials; Japvo Peak, Naga Hills; 10 000 ft; NHMUK 1903.7.1.2536.

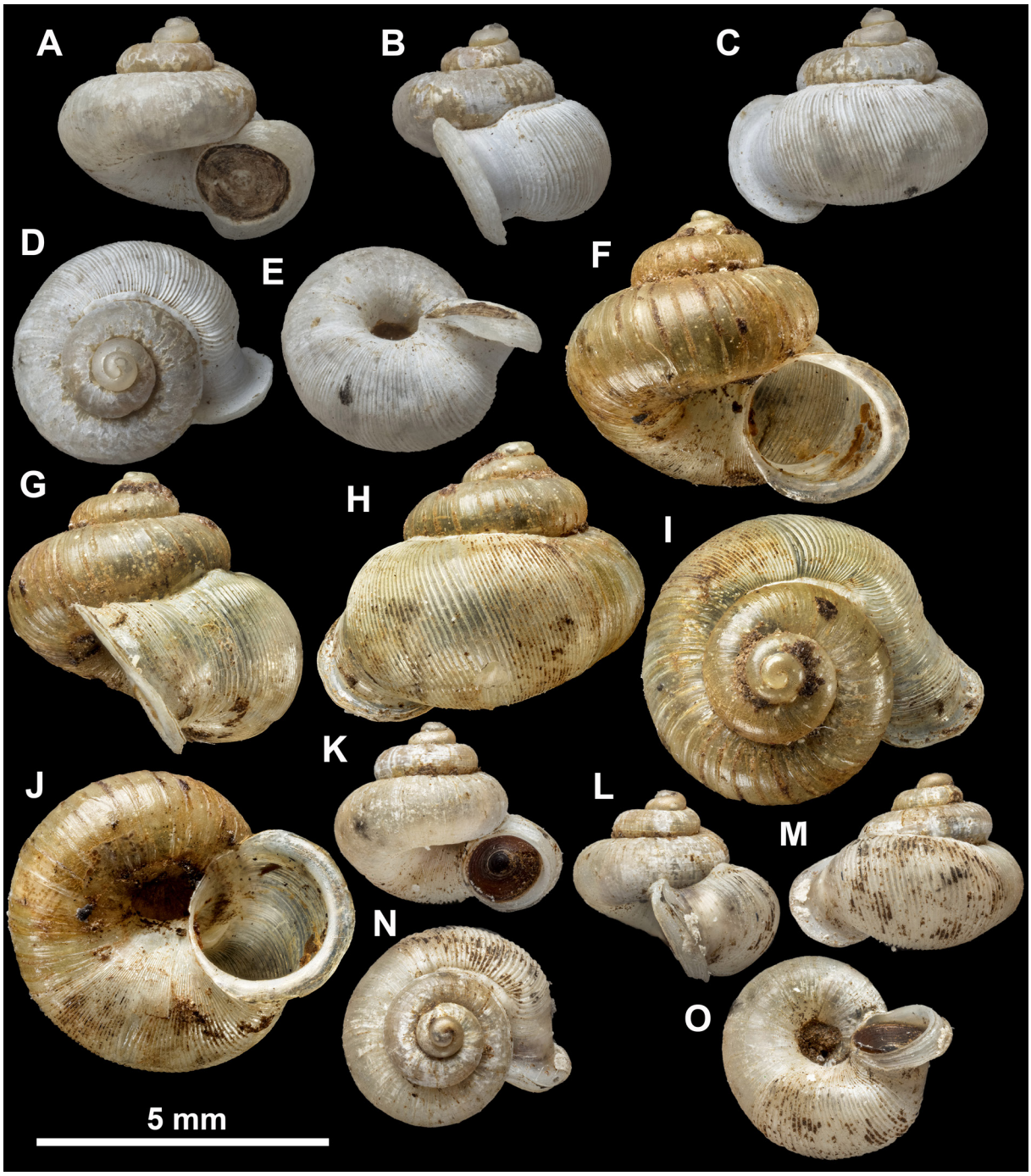


Fig. 19. Species of the *Metalycaeus inflatus* species group. **A–E**. *M. inflatus* (Godwin-Austen, 1874), syntype (NHMUK 1903.7.1.2536). **F–J**. *M. rubinus* (Godwin-Austen, 1893), syntype (NHMUK 1903.7.1.2685). **K–O**. *M. teriaensis* (Godwin-Austen, 1914), syntype (NHMUK 1903.7.1.2750). All photos: K. Webb.

Type locality

"Naga Hills under Japvo Peak"; "Yémi, Phúnngum, and Gaziphimi at the head of the Lanier River".

Remarks

See under *M. beddomei*.

Metalycaeus rubinus (Godwin-Austen, 1893)
Fig. 19F–J

Alycaeus rubinus Godwin-Austen, 1893: 594.

Alycaeus rubinus – Godwin-Austen 1897: 3–4, pl. 63 fig. 2, 2a; 1914: 412. — Gude 1921: 217–218.
Alycaeus (*Alycaeus*) *rubinus* – Kobelt 1902: 350.
Metalycaeus rubinus – Páll-Gergely *et al.* 2020: 166; 2021: 48, fig. 37.

Diagnosis

A species of *Metalycaeus* with a widely-spaced, glossy R1, a smooth R2, R2 and R3 are of the same size, together less than half a whorl long, aperture rounded.

Type material examined

Syntypes
MYANMAR • 2 shells; Ruby Mines District, Up. Burma; Doherty leg.; NHMUK 1903.7.1.2685.

Type locality

"Ruby Mines District, Upper Burmah".

Metalycaeus teriaensis (Godwin-Austen, 1914)
Fig. 19K–O

Alycaeus teriaensis Godwin-Austen, 1914: 382, pl. 154 fig. 10, 10a.

Alycaeus (*Dicharax*) *teriaensis* – Gude 1921: 272.
Chamalycaeus (*Dicharax*) *teriaensis* – Ramakrishna *et al.* 2010: 67.
Metalycaeus teriaensis – Páll-Gergely *et al.* 2020: 159.

Diagnosis

This species is characterized by the inflated R2, an R3 without swelling, and a slight keel on the basal part of R2.

Type material examined

Syntypes
INDIA • 7 shells (one shell indicated with pink wool, other shells in another glass vial); Teria Ghat, Khasi; NHMUK 1903.7.1.2750.

Type locality

"Teria Ghat, foot of the Khasi Hills".

Differential diagnosis

Metalycaeus teriaensis is very similar to *M. inflatus*, but is slightly smaller, its outer peristome is not reflected, and it has a slightly keeled basal part of its R2.

Metalycaeus mundulus species group

Remarks

Small, slightly keeled R2 on the umbilical side, no swelling of R3, outer peristome strongly expanding anteriorly. Note that *M. panggianus* (Godwin-Austen, 1914) could belong to the *M. magnificus* (Godwin-Austen, 1914) species group as well. Operculum calcareous.

Metalycaeus lectus (Godwin-Austen, 1914)
Fig. 20

Alycaeus lectus Godwin-Austen, 1914: 340, pl. 136 fig. 5, 5a–b.

Alycaeus (*Dicharax*) *lectus* – Gude 1921: 259.
Chamalycaeus (*Dicharax*) *lectus* – Ramakrishna *et al.* 2010: 62.
Dicharax (?) *lectus* – Páll-Gergely *et al.* 2020: 92, fig. 21.

Diagnosis

The shell shape and the short R2 of this species differ from all other species of this species group.

Material examined

Holotype

INDIA • shell (single specimen mentioned in the original description); near Chaukkalan, Darjeeling; "Dr. F. Stoliczka, coll."; NZSI M.8074.

Type locality

"in valle Rungun".

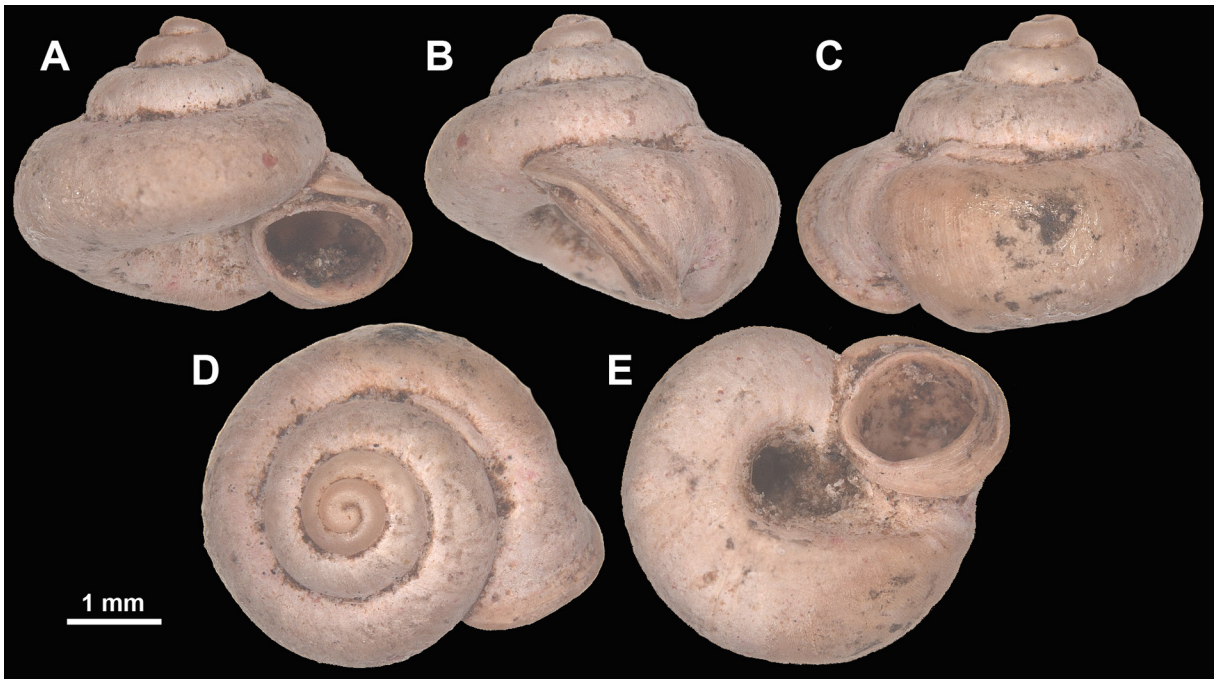


Fig. 20. *Metalycaeus lectus* (Godwin-Austen, 1914), holotype (ZSI/SRC/M.8074). All photos: S. Sajan.

Remarks

This species (known only from the holotype) was tentatively assigned to the genus *Dicharax* due to the absence of spiral striation; however, the shell is strongly corroded, making it difficult to discern the spiral lines.

The outer peristome, which extends beyond the inner peristome, and the R2, which is keeled on its umbilical side, suggest that this species belongs to the *Metalycaeus mundulus* species group instead. Therefore, *Alycaeus lectus* is moved to *Metalycaeus*.

Metalycaeus mundulus (Godwin-Austen, 1914)
Fig. 21

Alycaeus mundulus Godwin-Austen, 1914: 357–358, pl. 149 fig. 8.
Alycaeus toruputuensis Godwin-Austen, 1914: 359–360, pl. 149 fig. 3, 3a–b, pl. 145 fig. 10 (operculum).
Syn. nov.

Alycaeus Theobaldi – Godwin-Austen 1876: 175–176, pl. 7 fig. 10 (operculum).
Alycaeus theobaldi – Nevill 1878: 290.
Alycaeus mundulus – Gude 1921: 212.
Alycaeus (*Dicharax*) *toruputuensis* – Gude 1921: 274.
Alycaeus (*Alycaeus*) *mundulus* – Ramakrishna *et al.* 2010: 49.
Chamalycaeus (*Dicharax*) *toruputuensis* – Ramakrishna *et al.* 2010: 68.
Metalycaeus mundulus – Páll-Gergely *et al.* 2020: 148.
Metalycaeus (?) *toruputuensis* – Páll-Gergely *et al.* 2020: 167, fig. 38.

Diagnosis

Shell low conical, R1 strongly ribbed (mostly on the dorsal side), R2 smooth, R2+R3 slightly shorter than half a whorl, R2 slightly longer than R3, R3 with a low, blunt central swelling, end of R3 keeled on the ventral side, aperture with a conspicuous upper incision, outer peristome expanded, inner peristome slightly protruding, not fringed.

Type material examined

Holotype of *Alycaeus mundulus* Godwin-Austen, 1914
INDIA • single specimen mentioned in the original description; Toruputu, Dafla Hills; Godwin-Austen leg.; NHMUK 1906.1.1.955.

Holotype of *Alycaeus toruputuensis* Godwin-Austen, 1914
INDIA • shell; slope of Toruputu Peak, Dafla Hills, Assam; "Godwin-Austen coll."; NZSI M.8037. "the specimen figured is the type shell", "type in Indian Museum, Calcutta": Godwin-Austen 1914: 360).

Paratypes of *Alycaeus toruputuensis* Godwin-Austen, 1914
INDIA • 6 shells (in two different vials, one shell is indicated with pink wool); Toruputu Peak, Dafla Hills; Godwin-Austen leg.; NHMUK 1903.7.1.2496.

Type localities

"Torúpútú, Dafla Hills" (*A. mundulus*); "on the slopes of Torúpútú peak in the Dafla Hills" (in Godwin-Austen 1914; *A. toruputuensis*).

Remarks

There are no differences between the type specimens of *M. mundulus* and *M. toruputuensis*; therefore, they are synonyms. The former appeared earlier in the same publication. Therefore, it is selected to be the senior synonym. Moreover, they are from the same locality.

Metalycaeus panggianus (Godwin-Austen, 1914)
Figs 22–23

Alycaeus panggiana Godwin-Austen, 1914: 367, pl. 156 fig. 3, 3a.

Alycaeus panggianus – Gude 1921: 213–214.
Alycaeus (*Alycaeus*) *panggianus* – Ramakrishna *et al.* 2010: 50.
Metalycaeus (?) *panggianus* – Páll-Gergely *et al.* 2020: 166.

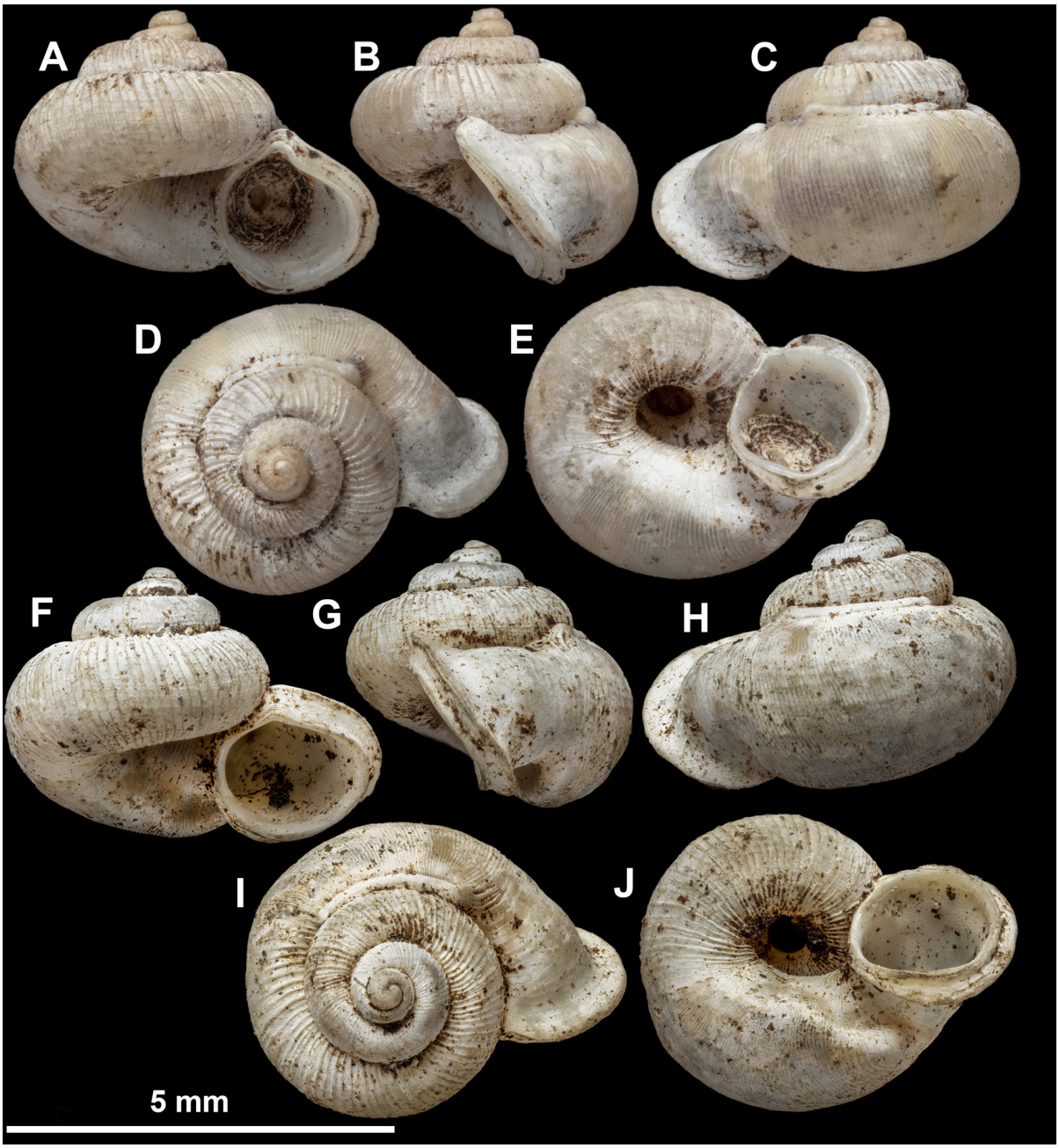


Fig. 21. Shells of *Metalycaeus mundulus* (Godwin-Austen, 1914). **A–E**. Holotype of *Alycaeus mundulus* (NHMUK 1906.1.1.955). **F–J**. Paratype of *A. toruputuensis* Godwin-Austen, 1914 (NHMUK 1903.7.1.2496). All photos: K. Webb.

Diagnosis

Shell low conical, R1 strongly ribbed (mostly on the dorsal side), R2 smooth, R2+R3 of ca half whorl combined, R2 slightly longer than R3, R3 practically without swelling, or it is very slightly indicated, end of R3 keeled on ventral side, aperture with conspicuous upper incision, outer peristome expanded, inner peristome slightly protruding, inner side fringed.

Type material examined

Holotype

INDIA • single specimen mentioned in the original description; Sibbum, Abor Hills; "Oakes coll."; NHMUK 1903.7.1.3143.

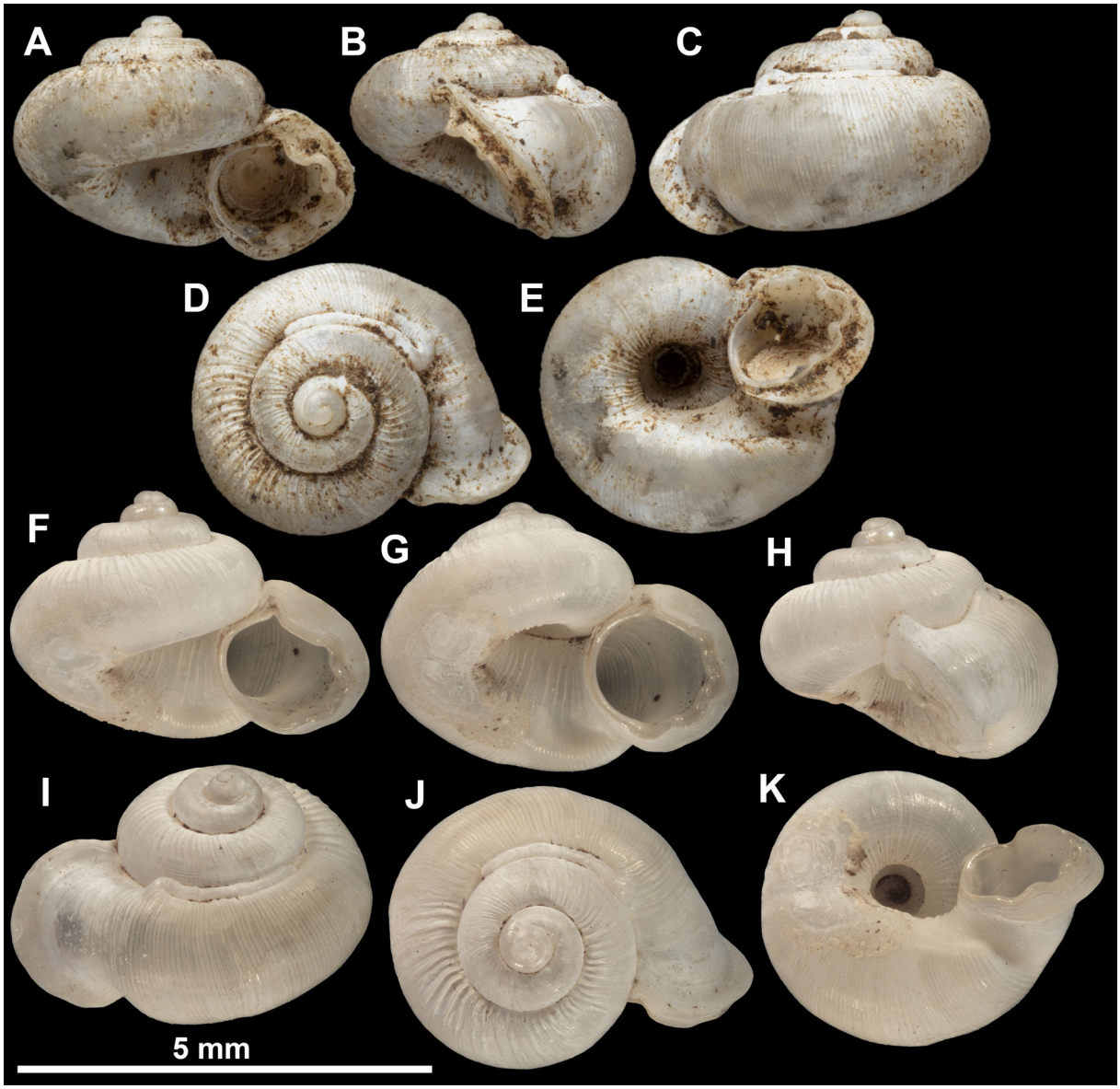


Fig. 22. Shells of *Metalycaeus panggianus* (Godwin-Austen, 1914). **A–E**. Holotype (NHMUK 1903.7.1.3143). **F–K**. Specimen from the Kaleg-Rotung Road (ZSI/SRC/LM2241). Photos: B. Páll-Gergely (F–K) and K. Webb (A–E).

Additional material examined

INDIA – **Arunachal Pradesh** • 1 shell; Yemsing Cave, East Siang; 28°8.198′ N, 95°0.773′ E; 514 m a.s.l.; 27 Apr. 2022; Aravind N.A. and Surya Narayanan leg.; ZSI/SRC/LM2237 • 1 shell; Yemsing, 1.3 km from Yem-Siang, East Siang; 28°6.649′ N, 95°0.744′ E; 545 m a.s.l.; 27 Apr. 2022; Aravind N.A. and Surya Narayanan leg.; ZSI/SRC/LM2238 • 1 shell; Penin, Upper Siang; 28°46.881′ N, 94°45.529′ E; 400 m a.s.l.; 11 May 2022; Aravind N.A. and Surya Narayanan leg.; ZSI/SRC/LM2239 • 1 shell; 3 km Yemsing-Along road, East Siang; 28°5.980′ N, 94°59.878′ E; 535 m a.s.l.; 29 Apr. 2022; Aravind N.A. and Surya Narayanan leg.; ZSI/SRC/LM2240 • 3 shells; Kaleg-Rotung Road, East Siang; 28°6.507′ N, 95°10.159′ E; 936 m a.s.l.; 24 Apr. 2022; Aravind N.A. and Surya Narayanan leg.; ZSI/SRC/LM2241.

Type locality

"Sibbum, Abor Hills".

Remarks

The newly collected shells match the types of *M. panggianus*.

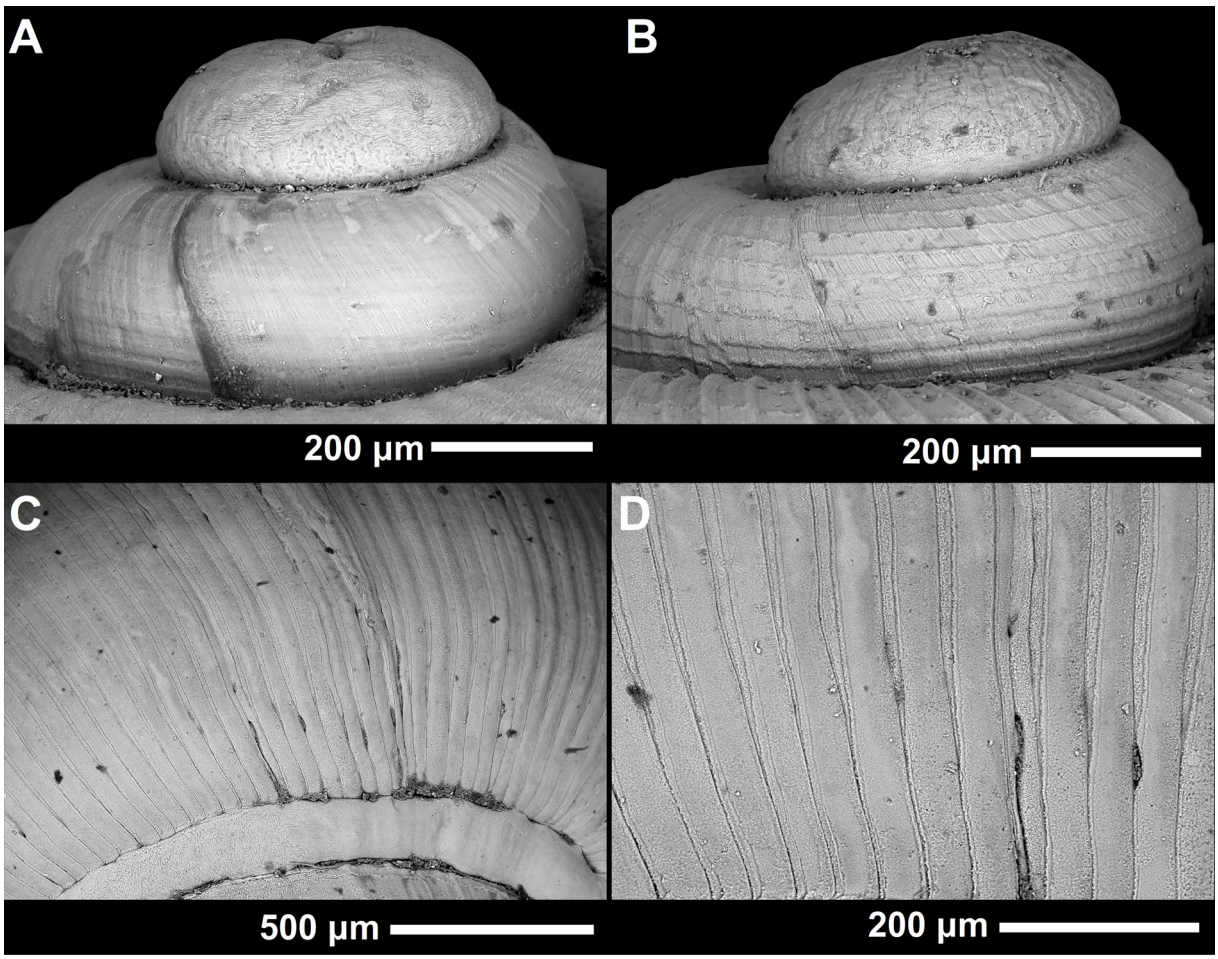


Fig. 23. Shell sculpture of *Metalycaeus panggianus* (Godwin-Austen, 1914). **A**. Protoconch of a specimen from the Kaleg-Rotung Road (same shell as Fig. 22F–K , ZSI/SRC/LM2241). **B**. Protoconch of a shell collected 3 km from Yemsing, along road. **C–D**. R2 surface of a specimen from the Kaleg-Rotung Road (same shell as Fig. 22F–K). All images: B. Páll-Gergely.

Metalycaeus oakesi species group

Remarks

This species group is characterized by a prominent R3 swelling and widely spaced ribs on R2. Operculum proteinaceous.

Metalycaeus heudei (Bavay & Dautzenberg, 1900)
Fig. 24A–E

Alycaeus (*Charax*) *heudei* Bavay & Dautzenberg, 1900a: 121–122.
Alycaeus paviei Bavay & Dautzenberg, 1912: 50–51, pl. 4 figs 5–8.
Alycaeus paviei var. *minor* Bavay & Dautzenberg, 1912: 51, pl. 4 fig. 9.
Alycæus kengtungensis Godwin-Austen, 1914: 409, pl. 139 fig. 6, 6a.
Chamalycaeus (*Dicharax*) *compressicosta* Zilch, 1957: 145–146, fig. 33.
Chamalycaeus (*Dicharax*) *fractus* Varga, 1974: 165–167, figs 1–5.
Alycaeus zhuangiyucuii Yang, Fan, Qiao & He, 2012: 32, fig. 2.

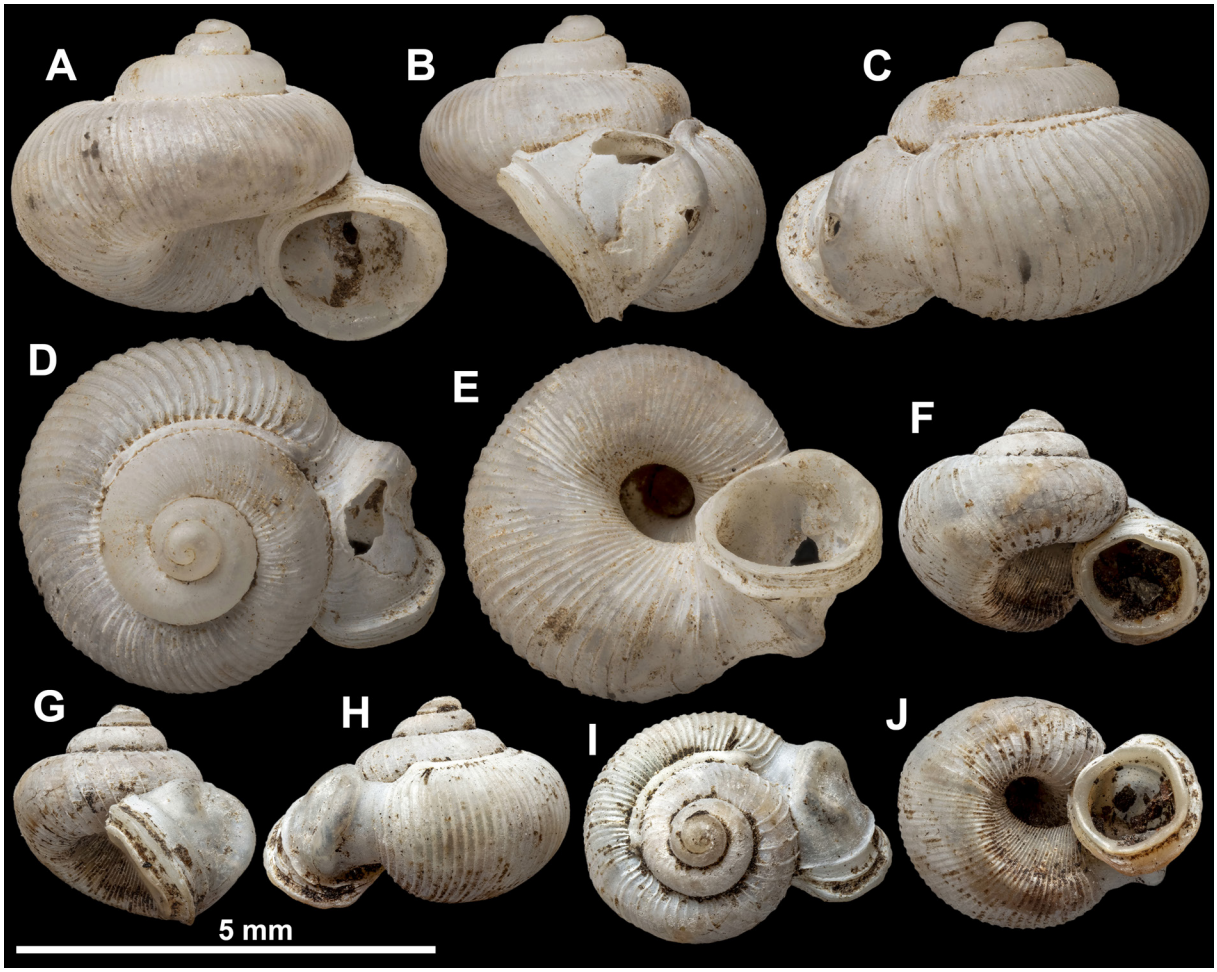


Fig. 24. Species of the *Metalycaeus oakesi* species group. **A–E**. *M. heudei* (Bavay & Dautzenberg, 1900), holotype of *Alycaeus kengtungensis* Godwin-Austen, 1914 (NHMUK 1903.7.1.3037). **F–J**. *M. oakesi* (Godwin-Austen, 1914), syntype (NHMUK 1903.7.1.3578). All photos: K. Webb.

Alycaeus (*Charax*) *heudei* – Bavay & Dautzenberg 1900b: 458–459, pl. 11 figs 15–18.
Metalycaeus heudei – Páll-Gergely *et al.* 2017: 74–84, figs 49c–d, 50–52, 53c–d (*paviei* Bavay & Dautzenberg, 1912, *paviei* var. *minor* Bavay & Dautzenberg, 1912, *compressicosta* Zilch, 1957, *fractus* Varga, 1974 and *zhuangiyucuii* Yang, Fan, Qiao & He, 2012 are considered synonyms); 2020: 143; 2021: 53, fig. 41 (*A. kengtungensis* considered as synonym). — Inkhavilay *et al.* 2019: 16, fig. 6c.
Metalycaeus kengtungensis – Páll-Gergely *et al.* 2020: 145.

Diagnosis (of "*A. kengtungensis*")

Shell low conical, R1 finely, strongly ribbed, R2 with widely-spaced, strong ribs; R2+R3 ca half a whorl combined, R2 ca 1.5 times as long as R3, R3 with a strongly elevated swelling that is situated closer to its posterior end, and flattened from the anterior side, aperture not fringed.

Type material examined

Holotype of *Alycaeus kengtungensis* Godwin-Austen, 1914
MYANMAR • shell; Shan State, "Kengtung, Siam Frontier"; Woodthorpe leg.; NHMUK 1903.7.1.3037.

For other types and non-type material, see Páll-Gergely *et al.* (2017, 2020, 2021).

Type localities

"Haut-Tonkin" (*A. heudei*); "Kengtung, Shan Frontier" (*A. kengtungensis*). For the other synonyms, see Páll-Gergely *et al.* (2017).

Remarks

This species probably has the widest distributional range in the subfamily Alycaeinae. It is distributed from Myanmar (Kayah and Shan states) through northern Vietnam and northern Laos to the Chinese provinces of Yunnan, Guangxi, Hunan, and Hubei (Páll-Gergely *et al.* 2017, 2021). Given the considerable variability in some shell characters and size (see Páll-Gergely *et al.* 2017), it is possible that it is rather a species complex. The population in the Shan States, Myanmar, was originally described as *A. kengtungensis*.

Metalycaeus oakesi (Godwin-Austen, 1914)
Fig. 24F–J

Alycaeus oakesi Godwin-Austen, 1914: 366–367, pl. 157 fig. 4, 4a.

Alycaeus (*Raptomphalus*) *oakesi* – Gude 1921: 289.
Chamalycaeus (*Raptomphalus*) *oakesi* – Ramakrishna *et al.* 2010: 69.
Metalycaeus oakesi – Páll-Gergely *et al.* 2020: 150.

Diagnosis

Characterized by a strong R3 swelling, a keeled R2 base, and a circular (not fringed) aperture.

Type material examined

Syntypes
INDIA • 5 shells; Abor Hills; 29°25′ N, 95°20′ E; NHMUK 1903.7.1.3578.

Type locality

"Chanjuk La, in Tsanspu Valley 4300 ft., Lat. 29°25′, Long. 95°20′".

Metalycaeus tuyae Páll-Gergely & Meng sp. nov.
urn:lsid:zoobank.org:act:EFC74C87-C3A0-4951-A905-496D5A73EEDD
Figs 25–26

Metalycaeus zayuensis – Páll-Gergely *et al.* 2020: 160, fig. 36 (partim.)

Diagnosis

A species of *Metalycaeus* with strong, lamella-like R1 ribs and strong spiral striation, a combined length of R2 and R3 almost reaching half a whorl, a prominent R3 swelling with a depression on the anterior side, and a large distance between inner and outer peristomes.

Etymology

This species is named after the wife of the species' second author, Aodeng Tuya.

Proposed Chinese name

图雅后阿氏螺

Type material

Holotype

CHINA • shell (originally labelled as paratype of *Chamalycaeus zayuensis*) (D: 4.2 mm, H: 3.5 mm); Tibet Autonomous Region, Tashan Town, Zayu County; 28°04′ N, 97° E; 10 Jun. 1980; Chen Deniu leg.; IZCAS TM_094549.

Paratypes

CHINA • 1 shell (originally labelled as holotype of *Chamalycaeus zayuensis*, see Páll-Gergely *et al.* 2020: fig. 36); same data as for holotype; 13 Jul. 1980; Chen Deniu leg.; IZCAS TM_094538 • 1 shell (originally labelled as paratype of *Chamalycaeus zayuensis*); same data as for preceding; IZCAS TM_094540 • 2 shells (originally labelled as paratype of *Chamalycaeus zayuensis*); same data as for preceding; IZCAS TM_094541, TM_094542 • 2 shells (originally labelled as paratype of *Chamalycaeus zayuensis*); same locality as for preceding; 26 May 1980; Chen Deniu leg.; IZCAS TM_094543, TM_094544 • 1 shell (originally labelled as paratype of *Chamalycaeus zayuensis*); same locality as for preceding; 3 Jul. 1980; Chen Deniu leg.; IZCAS TM_094547 • 1 shell (originally labelled as paratype of *Chamalycaeus zayuensis*); same locality as for preceding; 10 Jun. 1980; Chen Deniu leg.; IZCAS TM_094548 • 1 shell (originally labelled as paratype of *Chamalycaeus zayuensis*); same data as for preceding; IZCAS TM_094550 • 1 shell (originally labelled as paratype of *Chamalycaeus zayuensis*); same locality as for preceding; 7 Jun. 1980; Chen Deniu leg.; IZCAS TM_094554.

Description

Shell large, off-white, depressed, apical whorls conical, entire shell dominated by last whorl. Shell outline slightly oval in dorsal view. Protoconch consists of ca 1.5–1.75 whorls, finely spirally striated. R1 with ca 1.75–2 whorls, regularly, finely ribbed. Ribs elevated, mostly straight (or sometimes bent, mostly close to the suture), lamella-like, widely-spaced (ca 25 ribs on last half whorl). Spiral striation slightly denser than radial ribs, much weaker than the lamella-like ribs, although stronger than that of the congeners. R1–R2 boundary obscure due to the similar rib morphology and density on the two regions, although the swollen R2 makes the boundary obvious. Combined length of R2 and R3 reaches half a whorl, R2 being slightly longer than R3. R2 with ca 20–25 ribs. Constriction after R2 deep, long. R3 rather regularly ribbed, rib density increases towards the aperture, generally it is ca twice as dense as that of R1 and R2, and the ribs are lower than on R1 and R2. Spiral striation prominent between the ribs on R3 as well. R3 swelling prominent, situated closer to the posterior end of R3, its anterior part with a central, trapezoid

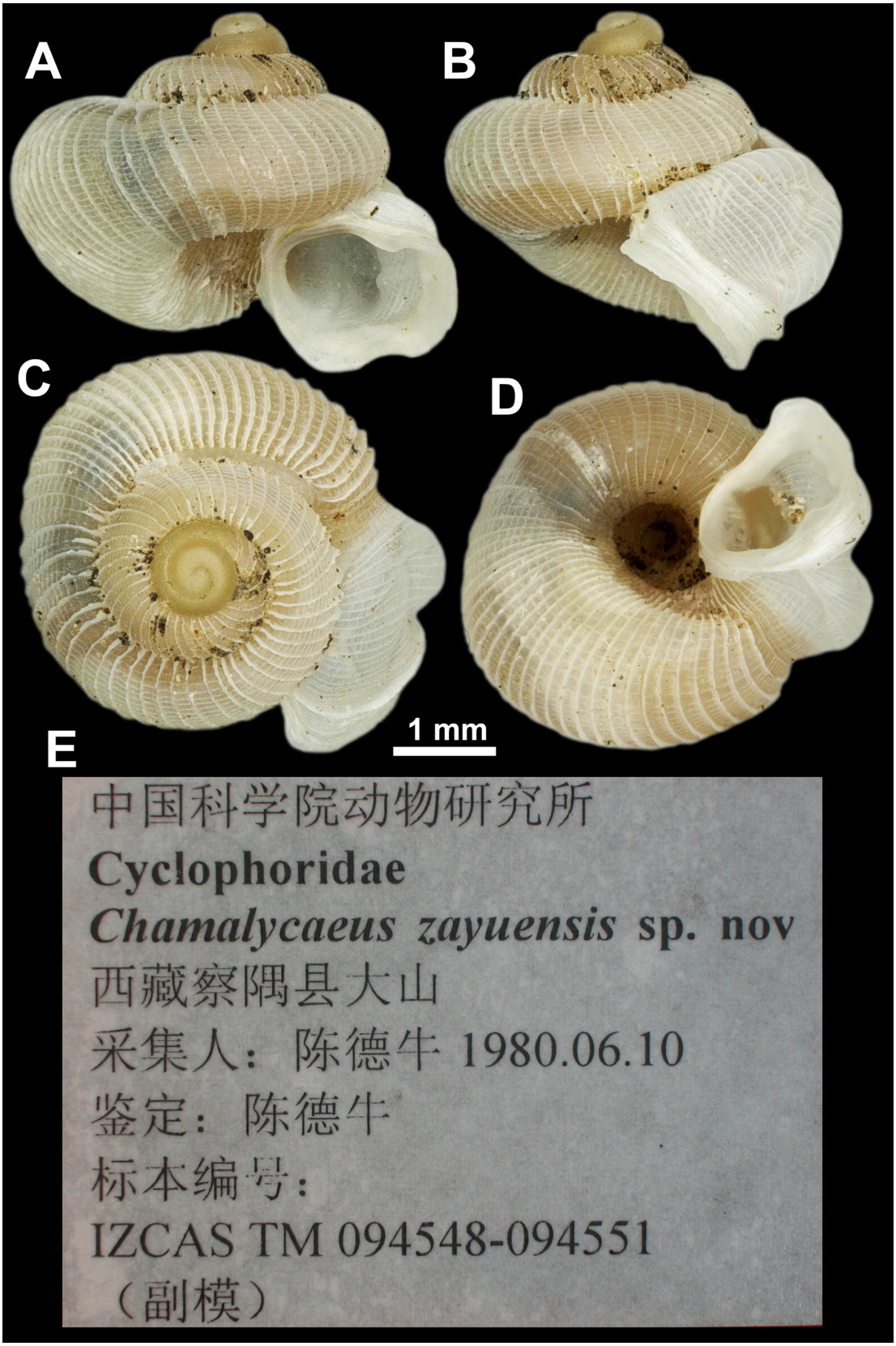


Fig. 25. A–D. *Metalycaeus tuyae* Páll-Gergely & Meng sp. nov., holotype (IZCAS TM_094549). **E**. Original label. All photos: K. Meng.

depression. Aperture strongly oblique to shell axis. Distance between inner and outer peristomes large. Surface between the inner and outer peristomes irregularly, densely wrinkled, due to multiple calcareous layers. Outer peristome expanded, slightly elongated basally and at the parietal-palatal meeting point, reduced towards umbilicus. Inner peristome protruding, sharp. Aperture mostly rounded, inside aperture there is a small and a large tooth-like projection, corresponding with the depression of the R3 swelling. Umbilicus very narrow, open, shows all the whorls, elliptical. Umbilical side of R3 with a slight groove.

Measurements

D = 3.9–5.2 mm, H = 3.2–4.4 mm (n = 11).

Differential diagnosis

The most similar species to *M. tuyae* sp. nov. is *M. oakesi* due to the long R2 with widely-spaced ribs, the prominent R3 swelling having a central depression and the great distance between the inner and outer peristomes. Nevertheless, the new species has a more rounded outline in dorsal view, has a shorter

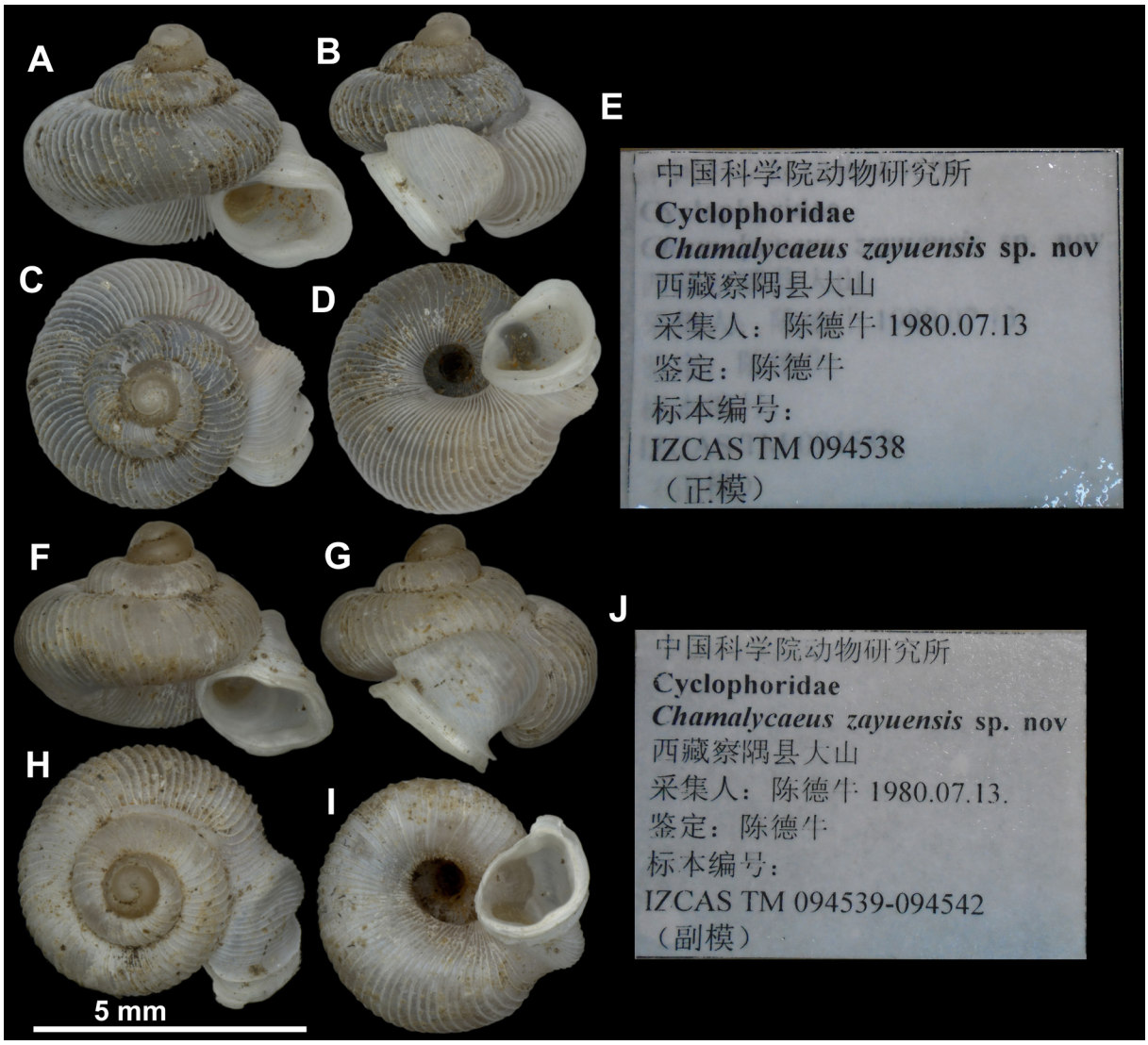


Fig. 26. *Metalycaeus tuyae* Páll-Gergely & Meng sp. nov., paratypes. **A–D**. IZCAS TM_094538. **F–I**. IZCAS TM_094540. All photos: K. Meng.

combined R2+R3 length, denser R1 ribs, a ribbed R3 (smooth in *M. oakesi*), and a less prominent keel on the base of R3.

Remarks

The specimen in the Beijing Museum labelled as the holotype of *Chamalycaeus zayuensis* (IZCAS TM 094538) belongs to a different species than that figured in the original description of *C. zayuensis* in Qian & Zhou (2013), and they are therefore described here as a new species.

Metalycaeus stylifer species group

Remarks

R1 with fine ribs, R2 with lamella-like ribs, R3 with a blunt, central swelling, aperture comparatively large, rounded or slightly fringed. Operculum proteinaceous.

Metalycaeus perplexus (Godwin-Austen, 1914)
Fig. 27A–E

Alycaeus perplexus Godwin-Austen, 1914: 380, pl. 155 fig. 11.

Alycaeus perplexus – Gude 1921: 214.
Alycaeus (*Alycaeus*) *perplexus* – Ramakrishna *et al.* 2010: 50.
Chamalycaeus perplexus – Páll-Gergely *et al.* 2020: 42.
Metalycaeus perplexus – Páll-Gergely *et al.* 2025: 7.

Differential diagnosis

This species is smaller than *M. polygonoma*, has finer R2 ribs, and a more rounded aperture (without crenulation on the peristome and basal incision).

Material examined

Syntypes
INDIA • 3 shells; Khasi Hills; "Godwin-Austen coll."; NHMUK 1903.7.1.2756.

Type locality

"Khasi Hills".

Remarks

Although no spiral striation was observed on the protoconch, this species is re-classified in the genus *Metalycaeus* due to its similarity with *M. polygonoma* (see Páll-Gergely *et al.* 2025).

Metalycaeus prosectus (Benson, 1857)
Fig. 27F–I

Alycaeus prosectus Benson, 1857: 203–204.

Alycaeus prosectus – Sowerby 1877: pl. 6, species 49. — Godwin-Austen 1914: 380–381, pl. 143 fig. 1, 1a, 1b.
Alycaeus (*Dicharax*) *prosectus* – Kobelt 1902: 375–376. — Gude 1921: 266–267.
Chamalycaeus (*Dicharax*) *prosectus* – Ramakrishna *et al.* 2010: 65.
Metalycaeus prosectus – Páll-Gergely *et al.* 2020: 151. — Preece *et al.* 2022: 82, fig. 30e.

Diagnosis

A large species of *Metalycaeus* with lamella-like ribs on R2, R2 and R3 of the same length, a very strongly oblique aperture (to the shell axis), and a strongly expanded outer peristome with an elongated basal projection.

Type material examined

Syntypes

INDIA • 4 shells; UMZC I.102775.

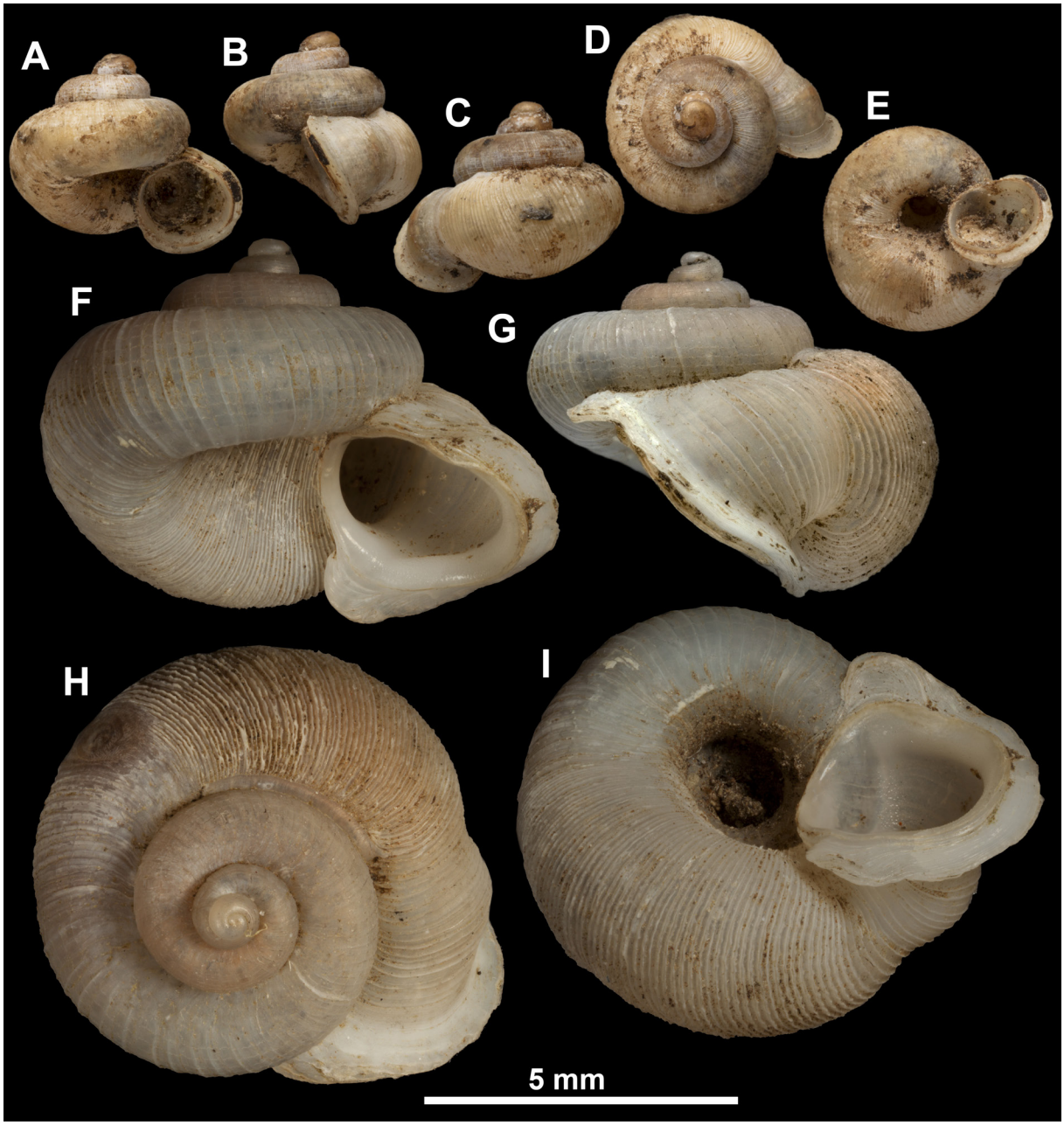


Fig. 27. Species of the *Metalycaeus stylifer* species group. **A–E**. *M. perplexus* (Godwin-Austen, 1914), syntype (NHMUK 1903.7.1.2756). **F–I**. *M. prosectus* (Benson, 1857), syntype (UMZC I.102775.A). All photos: K. Webb.

Additional material examined

INDIA • 5 shells; Khasi Hills; NHMUK 1906.4.4.63 • 3 shells; NHMUK 1888.12.4.873 to 1888.12.4.875.

Type locality

"ad Teria Ghát".

Metalycaeus stylifer (Benson, 1857)
Fig. 28

Alycaeus stylifer Benson, 1857: 204.
Alycaeus polygonoma Blanford, 1862: 140–141. **Syn. nov.**
Alycaeus distinctus Godwin-Austen, 1893: 592.
Alycaeus kamakiaensis Godwin-Austen, 1914: 375–376, pl. 141 fig. 8.
Alycaeus neglectus Godwin-Austen, 1914: 358, pl. 154 fig. 5 (non *Alycaeus neglectus* Heude, 1885). **Syn. nov.**
Alycaeus rotundatus Godwin-Austen, 1914: 359, pl. 154 fig. 6.
Metalycaeus godwinausteni Páll-Gergely, 2020 (replacement name for *A. neglectus* Godwin-Austen, 1914, non *Alycaeus neglectus* Heude, 1885)
Metalycaeus posteriobulbus Gittenberger & Sherub Sherub in Gittenberger *et al.*, 2024: 193, figs 1, 6–7.

Alycaeus ingrami var. – Godwin-Austen 1871: 91–92, pl. 4 fig. 3.
Alycaeus polygonus [sic] – Sowerby 1877: pl. 2, species 11.
Alycaeus stylifer – Benson 1859: 181. — Sowerby 1877: pl. 6, species 46. — Godwin-Austen 1914: 344, pl. 133 fig. 2, 2a–c.
Alycaeus (*Dicharax*) *polygonoma* – Kobelt 1902: 375. — Gude 1921: 265–266.
Alycaeus (*Dicharax*) *stylifer* – Kobelt 1902: 376–377. — Gude 1921: 269–270, fig. 35.
Alycaeus polygonoma – Godwin-Austen 1914: 423, pl. 141 fig. 5.
Alycaeus distinctus – Godwin-Austen 1914: 363, 390, pl. 145 fig. 3, 3a–b.
Alycaeus distinctus var. – Godwin-Austen 1914: 363, pl. 137, fig. 2, 2a–b; 1914: 391, pl. 149, fig. 4 (2 varieties).
Alycaeus kamakiaensis – Gude 1921: 209.
Alycaeus rotundatus – Gude 1921: 217.
Alycaeus (*Dicharax*) *neglectus* – Gude 1921: 261.
Alycaeus (*Chamalycaeus*) *distinctus* – Gude 1921: 226–227.
Alycaeus (*Alycaeus*) *kamakiaensis* – Ramakrishna *et al.* 2010: 48.
Alycaeus (*Alycaeus*) *rotundatus* – Ramakrishna *et al.* 2010: 51.
Chamalycaeus (*Chamalycaeus*) *distinctus* – Ramakrishna *et al.* 2010: 53.
Chamalycaeus (*Dicharax*) *neglectus* – Ramakrishna *et al.* 2010: 64.
Chamalycaeus (*Dicharax*) *stylifer* – Ramakrishna *et al.* 2010: 66.
Metalycaeus distinctus – Páll-Gergely *et al.* 2020: 142.
Metalycaeus kamakiaensis – Páll-Gergely *et al.* 2020: 145.
Metalycaeus polygonoma – Páll-Gergely *et al.* 2020: 151; 2025: 142, figs 83–88.
Metalycaeus rotundatus – Páll-Gergely *et al.* 2020: 153.
Metalycaeus stylifer – Páll-Gergely *et al.* 2020: 157. — Preece *et al.* 2022: 82, fig. 30f.

Diagnosis

This is a widespread, variable species, which is characterized by a conical shape (shell usually wider than high), R2+R3 ca 150 degrees, and of the same length, R2 with elevated, bent ribs, R3 with a conical central swelling, aperture comparatively large, peristome undulating, basal incision present.

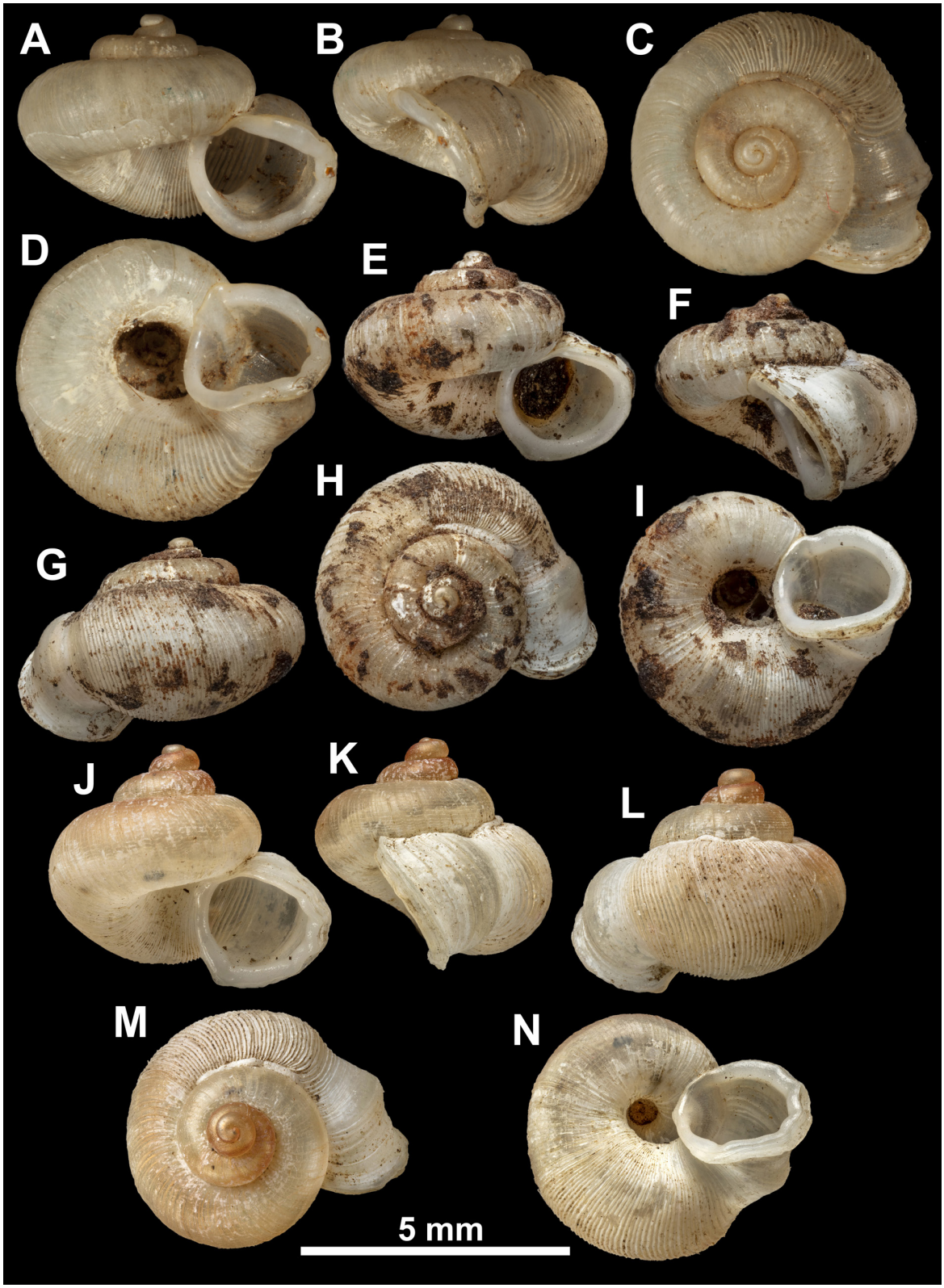


Fig. 28. Shells of *Metalycaeus stylifer* (Benson, 1857). **A–D**. Shell found in the same lot with the holotype (UMZC I.102630.B). **E–I**. *Alycaeus neglectus* Godwin-Austen, 1914, syntype (NHMUK 1903.7.1.2494). **J–N**. *A. polygonoma* W.T. Blanford, 1862, syntype (NHMUK 1906.4.4.51). All photos: K. Webb.

Type material examined

Holotype of *Alycaeus stylifer* Benson, 1857
INDIA • shell; Darjeeling; "R. McAndrew collection, Bens. col."; UMZC I.102630.A.

Syntypes of *Alycaeus neglectus* Godwin-Austen, 1914
INDIA • 2 shells; Toruputu Peak, Dafla Hills; Godwin-Austen leg.; NHMUK 1903.7.1.2494.

Syntypes of *Alycaeus distinctus* Godwin-Austen, 1893
INDIA • 10 shells; Naga Hills; NHMUK 1903.7.1.2619.

Syntype of *Alycaeus kamakiaensis* Godwin-Austen, 1914
INDIA • 1 shell; Kamakia Hill, Gowhatty, Assam; NHMUK 1903.7.1.2705.

Holotype of *Alycaeus rotundatus* Godwin-Austen, 1914
INDIA • single shell mentioned in the original description; Dafla Hills (?); NHMUK 1903.7.1.2543.

Syntypes of *Alycaeus polygonoma* Blanford, 1862
MYANMAR • 2 shells, in different vials; Tongoop Pass, Arakan Hills; NHMUK 1906.4.4.51.

Additional material examined

BHUTAN • 1 shell (labelled as *A. stylifer*); Damsang, W Bhutan; NHMUK 1903.7.1.1255.

INDIA • 1 shell from the same lot with the holotype of *A. stylifer*; Darjeeling; "R. McAndrew collection, Bens. col."; UMZC I.102630.B.

Type localities

"ad Darjiling" (*A. stylifer*); "in montibus Arakanensibus" (*A. polygonoma*); "Neighbourhood of Asálú, N. Cachar Hills" (*A. distinctus*); "Kamakia Temple Hill near Gowhatty, Assam" (*A. kamakiaensis*); "Dafla hills" (*A. rotundatus*); "Zhemgang Dzongkhag: between Duenmang Tsachu and Gongphu Zero Point, 24 km SE of Zhemgang, 335 m a.s.l., 27°02′ N 90°48′ E, scree in warm broadleaf forest" (*M. posteriobulbus*); "Torúpútú Peak, Dafla Hills" (*A. neglectus*).

Remarks

Páll-Gergely *et al.* (2025) showed that *Alycaeus distinctus*, *A. rotundatus*, *A. kamakiaensis*, *A. polygonoma* and *Metalycaeus posteriobulbus* represent the same species. *Metalycaeus godwinausteni* and *A. stylifer* also fall within the morphological variability of that species. Since *A. stylifer* is the oldest name, the accepted name must be *Metalycaeus stylifer*.

The holotype of *A. stylifer* was figured by Preece *et al.* (2022). Here, we show the shell that was found in the same lot in the UMZC (see Preece *et al.* 2022). The two shells are slightly different: the holotype looks teratological, it has a more inflated R2, and a shorter distance between the R2 swelling and the peristome than the other shell. Nevertheless, they are treated as conspecific.

Metalycaeus yamneyensis species group

Remarks

Large shell, inner and outer peristomes in large distance from each other, strongly fringed aperture. Operculum calcareous.

Metalycaeus adiorum Páll-Gergely & Aravind sp. nov.
urn:lsid:zoobank.org:act:0013C234-22B7-4C20-B3A3-4AE71152B0CB
Figs 29–30

Diagnosis

A medium-sized, conical species of *Metalycaeus* with a strongly swollen, long, finely ribbed R2 (R2+R3 exceeds half a whorl), an R3 with a central, low swelling, a short distance between inner and outer peristomes and an internally fringed inner peristome.

Etymology

This species is named after the *Adi* tribal communities. The *Adi* are one of the major indigenous tribal groups of Arunachal Pradesh and form a culturally, linguistically, and historically significant community in the Siang region. The *Adi* tribes vehemently fought against the British military during the "Abor Expedition". This species honours them for protecting forests and their culture.

Type material

Holotype

INDIA – **Arunachal Pradesh** • shell (D: 8.2 mm, H: 6.5 mm); Sissen, East Siang; 28°7.917′ N, 95°7.372′ E; 235 m a.s.l.; 26 Apr. 2022; Aravind N.A. and Surya Narayanan leg.; ZSI/SRC/LM2242.

Paratypes

INDIA – **Arunachal Pradesh** • 2 shells; same data as for the holotype; ZSI/SRC/LM2243 • 1 spec. in ethanol; Kaleg, 2 km from village to falls road, East Siang; 28°6.124′ N, 95°10.038′ E; 755 m a.s.l.; 24 Apr. 2022; Aravind N.A. and Surya Narayanan leg.; ZSI/SRC/LM2244 • 1 spec. in ethanol; Kaleg-Rotung road, East Siang; 28°6.507′ N, 95°10.159′ E; 936 m a.s.l.; 24 Apr. 2022; Aravind N.A. and Surya Narayanan leg.; ZSI/SRC/LM2245.

Description

Shell medium-sized, white, conical, entire shell dominated by last whorl. Protoconch consists of ca 1.5–1.75 whorls, finely, densely spirally striated. R1 with ca 2.25 whorls, with rather irregular, widely-spaced ribs and denser, finer spiral striation (ca 20 ribs on last half whorl). R1–R2 boundary clearly visible due to the abrupt change of rib density, and swollen R2. Length of R2 almost half a whorl. R2 with dense ribs of triangular cross section. Number of ribs is ca 80, including the ones situated posterior to the deepest point of the constriction. Constriction rather shallow, long. R3 irregularly wrinkled, of ca 30–45 degrees long, with a blunt, low, central swelling. Distance between inner and outer peristomes small (ca 1 mm). Surface between the inner and outer peristomes is irregularly, densely wrinkled, due to multiple calcareous layers. Outer peristome strongly expanded, sharp, disappears at the basal/columellar region (not reaching the umbilicus). Inner peristome strongly expanded (with the exception of the parietal-umbilical area), forms an almost flat surface. Outer perimeter mostly rounded, with the exception of a slight projection above the parieto-palatal transition and one on the basal-columellar transition due to the abrupt reduction in peristome height at the umbilical region. Inner side of the outer peristome fringed, with 4 main knobs (termed chevrons by Gittenberger *et al.* 2024) on the palatal side, separating 3 U-shaped bays. There is an additional, small upper incision immediately below the projection above the parieto-palatal transition. Umbilicus very narrow, open, shows all whorls, its shape is determined by the nearly straight line of R2.

Operculum

Inner wall with a central, blunt, slightly elevated nipple. Outer side with a multispiral, white, calcareous, wrinkled lamina, starting from the edge of the nucleus, and forming a funnel-shaped structure parallel to the operculum surface.

Measurements

D = 7.9–8.5 mm, H = 6.3–6.5 mm (n = 3).

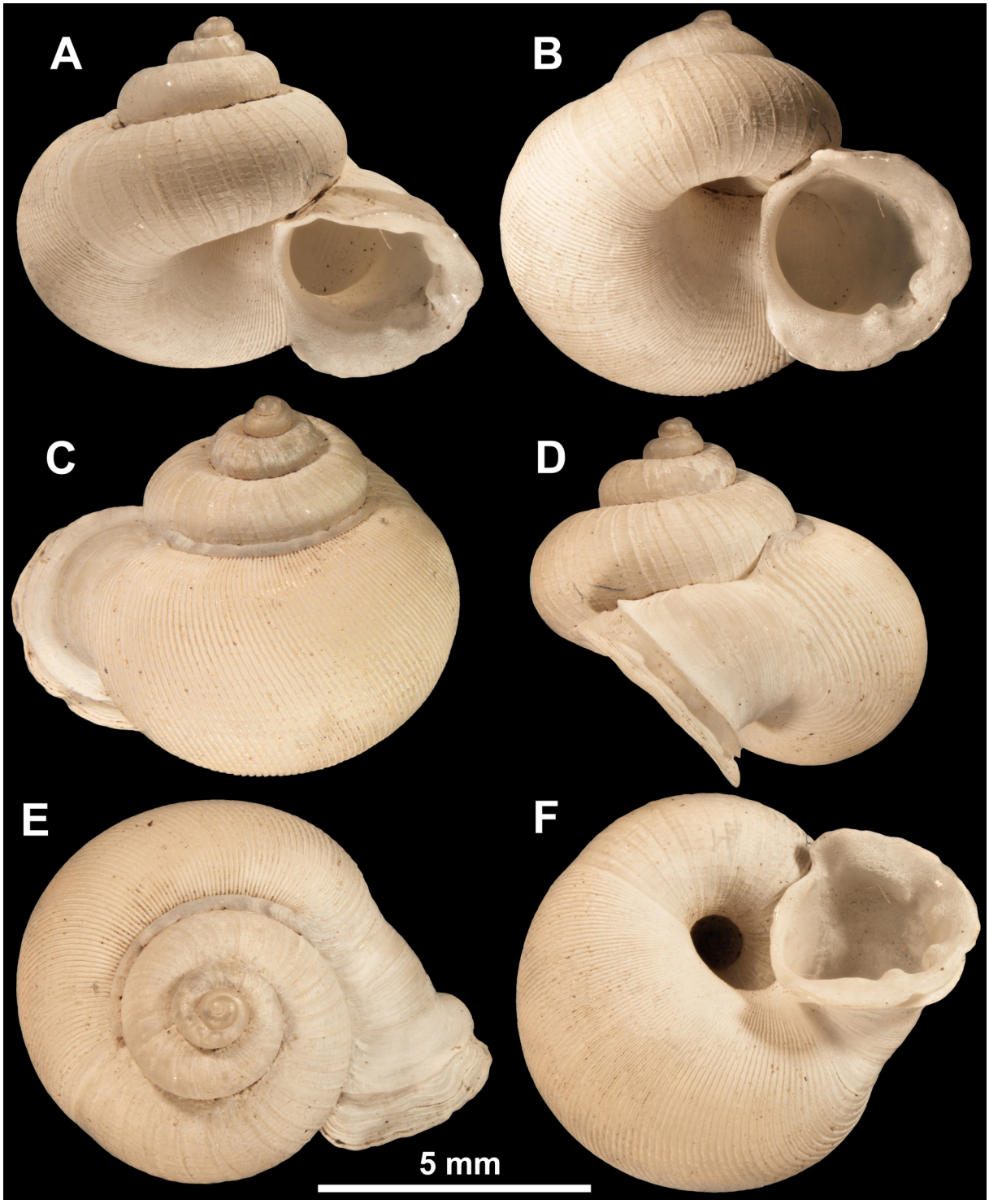


Fig. 29. *Metalycaeus adiorum* Páll-Gergely & Aravind sp. nov., holotype (ZSI/SRC/LM2242). All photos: B. Páll-Gergely.

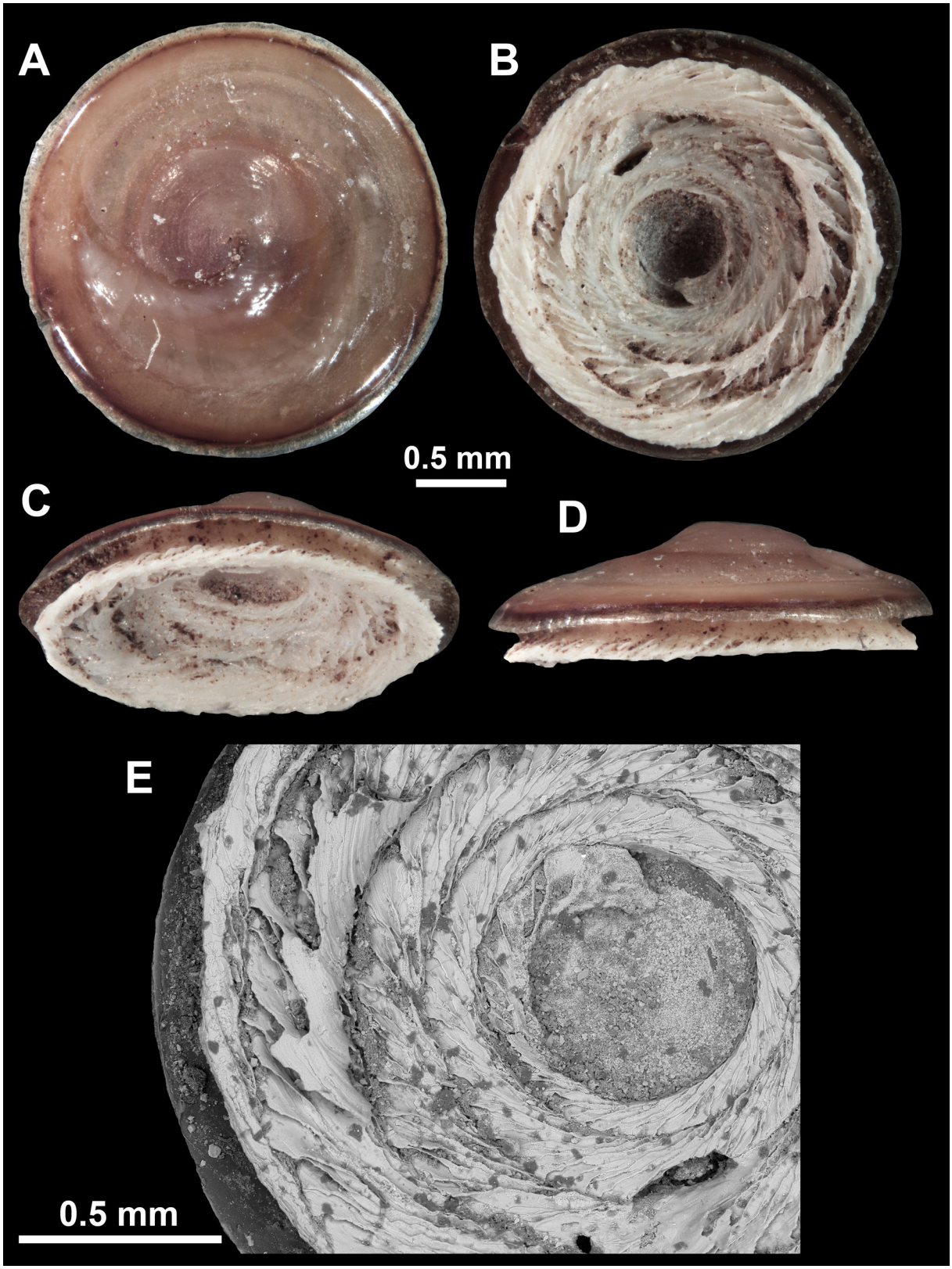


Fig. 30. Operculum of *Metalycaeus adiorum* Páll-Gergely & Aravind sp. nov., paratype (ZSI/SRC/LM2245) All images: B. Páll-Gergely.

Differential diagnosis

Metalycaeus vesica (Godwin-Austen, 1914) is smaller; its outer peristome is approximately as wide as the inner one, and the inner peristome is strongly fringed (its edge is undulating, while in this new species, only the inner part has apertural barriers).

Metalycaeus kempi sp. nov. is larger, its outline more oval, there is a larger space between the two peristomes, and the inner side of the inner peristome is less strongly fringed.

Metalycaeus aborensis has a more depressed and glossy shell, and weaker and less fringed inner peristome.

Metalycaeus kempi Páll-Gergely & Aravind sp. nov.
urn:lsid:zoobank.org:act:E4BE872F-FB07-45B8-BBC1-A3794248077E
Fig. 31

Diagnosis

A large, depressed species of *Metalycaeus* with strongly swollen, long, nearly smooth R2 (R2+R3 exceeds half a whorl), an R3 with a central, low swelling, a very large distance between inner and outer peristomes and an internally fringed inner peristome.

Etymology

This species is named after Stanley Wells Kemp, former Superintendent of the Indian Museum, Kolkata, who undertook an extensive collection of molluscs during the "Abor Expedition" in 1911–1912 (see, e.g., Kemp 1913). He also made extensive contributions to our understanding of the crustaceans of India.

Type material

Holotype

INDIA – **Arunachal Pradesh** • shell; Waterfall, Ramsing, Upper Siang; 28°40.275′ N, 94°57.587′ E; 1040 m a.s.l.; 12 May 2022; Aravind N.A. and Surya Narayanan leg.; ZSI/SRC/LM2246.

Paratype

INDIA – **Arunachal Pradesh** • 1 shell (D: 10.3 mm, H: 7.2 mm); same data as for the holotype; ZSI/SRC/LM2247.

Description

Shell large, off-white (although both shells are corroded), depressed, apical whorls conical, entire shell dominated by last whorl. Protoconch consists of ca 1.5 whorls, its sculpture is not discernible as both available shells are corroded. R1 with ca 2.25 whorls, rather regularly, finely ribbed (ca 50 ribs on last half whorl). Due to the corroded state of both shells, fine sculpture of R1 is not clearly visible. However, fine spiral striation is visible inside the umbilicus, where the sculpture is most intact. R1–R2 boundary clearly visible because of the denser ribs of R2, and R2 is conspicuously swollen. Length of R2 nearly reaches a half whorl. R2 sculpture also not visible clearly, although almost smooth with blunt ribs. Number of ribs is ca 90–96, including the ones situated posterior to the deepest point of the constriction. Constriction rather shallow, long. R3 irregularly wrinkled, of ca 60 degrees long, with a blunt, low swelling situated close to the constriction. Distance between inner and outer peristomes conspicuously large, outer peristome situated close to the centre of R3. Surface between the inner and outer peristomes irregularly, densely wrinkled, due to multiple calcareous layers. Outer peristome slightly expanded, sharp, only reflected towards the umbilicus at the meeting point of the last and penultimate whorl. Inner peristome strongly expanded (with the exception of the parietal-umbilical area), tuba-like. Outer perimeter mostly rounded, with the exception of a slight projection above the parieto-palatal transition

and a slight undulation at the lower palatal region (where there are the two strongest denticles inside the peristome). Inner side of the outer peristome slightly fringed, with 6 blunt, longitudinal ridges on the inner edge of the peristome, separating 5 shallow bays, which are elongated between the position of the inner peristome (visible from inside the peristome) and the edge of the outer peristome. There is an additional upper incision just below the projection above the parieto-palatal transition. Umbilicus very narrow, open, shows all whorls, its shape is determined by the nearly straight line of R2.

Measurements

D = 10.3–10.6 mm, H = 6.9–7.2 mm (n = 2).

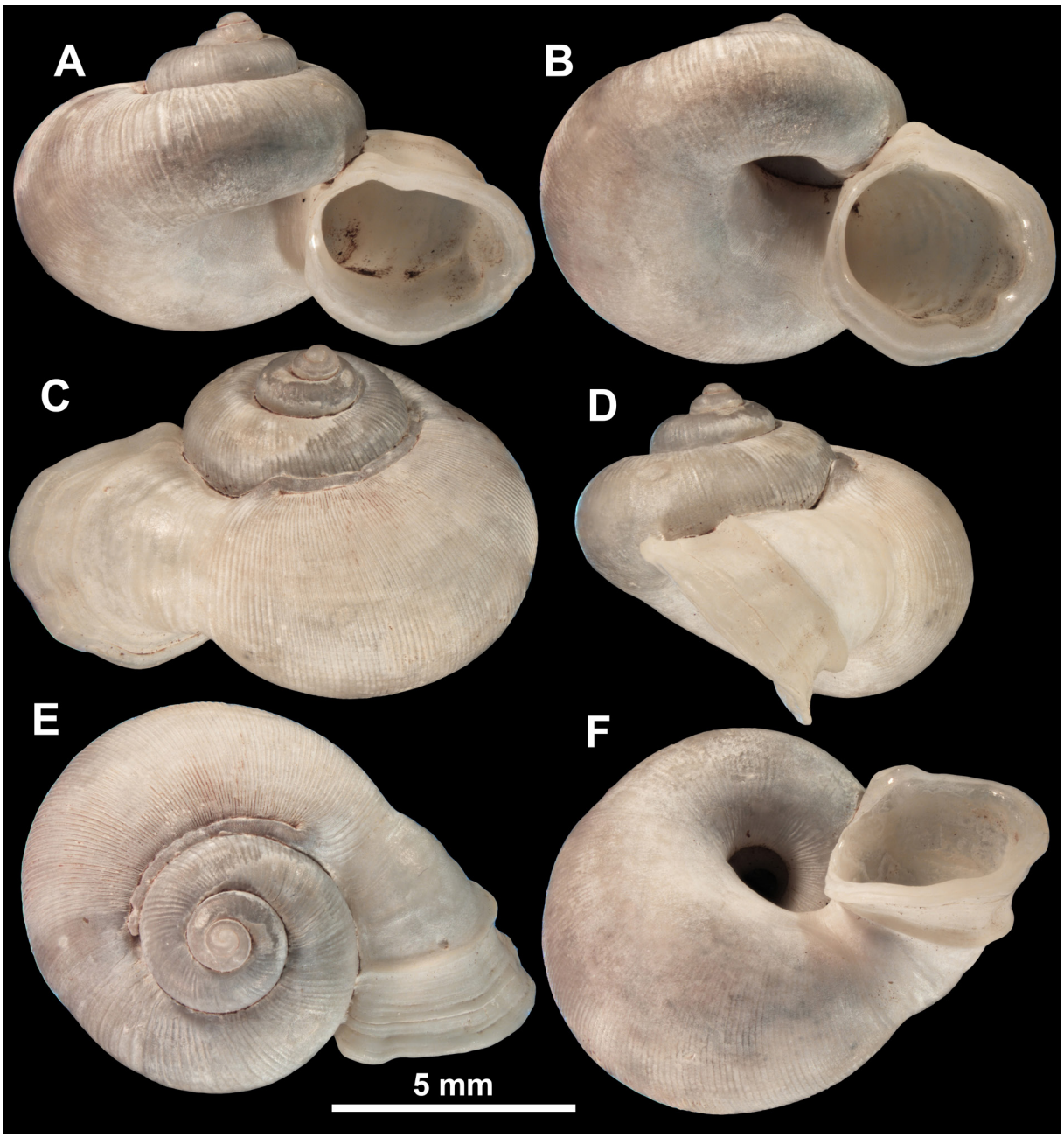


Fig. 31. *Metalycaeus kempi* Páll-Gergely & Aravind sp. nov., holotype (ZSI/SRC/LM2246). All photos: B. Páll-Gergely.

Differential diagnosis

Metalycaeus physis has no longitudinal ridges on the inner part of the aperture, it has a much smaller distance between the inner and outer peristomes, and its shell is less dominated by the last whorl.

Metalycaeus aborensis is usually smaller, has a more rounded outline, and the distance between the two peristomes is smaller.

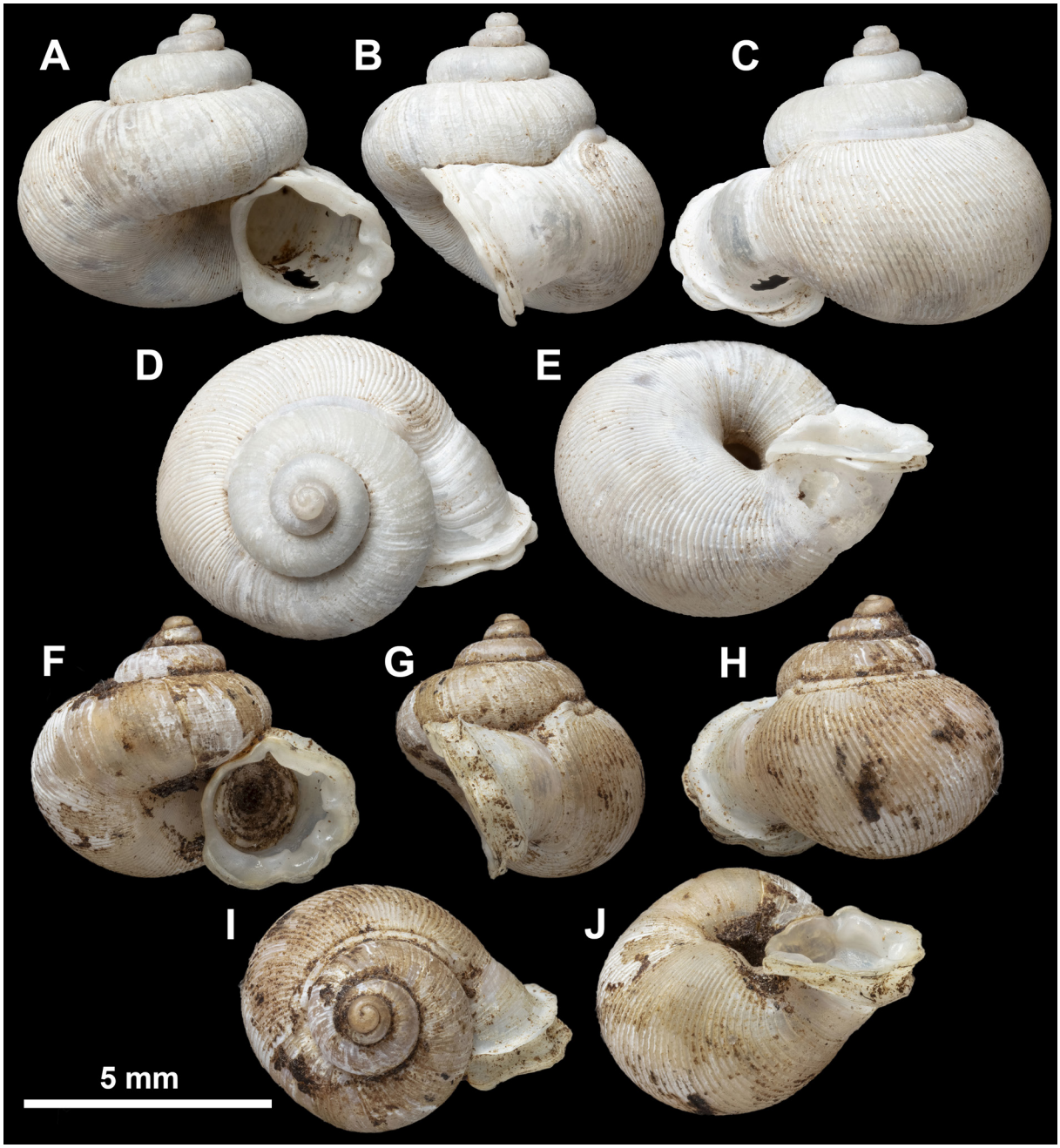


Fig. 32. Species of the *Metalycaeus yamneyensis* species group. **A–E**. *M. yamneyensis* (Godwin-Austen, 1914), syntype (NHMUK 1903.7.1.3114). **F–J**. *M. vesica* (Godwin-Austen, 1914), syntype (NHMUK 1903.7.1.3101). All photos: K. Webb.

Metalycaeus yamneyensis (Godwin-Austen, 1914)
Fig. 32A–E

Alycaeus yamnayensis (in the headings) and *A. yamneyensis* (in the text) Godwin-Austen, 1914: 368, pl. 156 fig. 2.

Alycaeus yamneyensis – Gude 1921: 222–223.
Alycaeus (*Alycaeus*) *yamneyensis* – Ramakrishna *et al.* 2010: 51.
Metalycaeus yamneyensis – Páll-Gergely *et al.* 2020: 159.

Diagnosis

This species of *Metalycaeus* is characterized by a strongly swollen, long R2 (R2+R3 more than half a whorl), short distance between the inner and outer peristomes, and a slightly fringed inner peristome (both inner and outer surfaces).

Type material examined

Syntypes
INDIA • 3 shells (one of them separated with pink wool); Yamney Valley, Abor Hills; NHMUK 1903.7.1.3114.

Type locality

"Yamne Valley, Abor Hills".

Differential diagnosis

See under *Metalycaeus vesica*.

Metalycaeus vesica (Godwin-Austen, 1914)
Figs 32F–J, 33–36

Alycaeus vesica Godwin-Austen, 1914: 368, pl. 149 fig. 10.

Alycaeus vesica – Gude 1921: 220.
Metalycaeus (?) *vesica* – Páll-Gergely *et al.* 2020: 167.

Diagnosis

This species of *Metalycaeus* is characterized by a strongly swollen, long R2 (R2+R3 more than half a whorl), relatively large distance between the inner and outer peristomes, and a fringed inner peristome.

Type material examined

Syntypes
INDIA • 2 shells in different vials; Abor Hills, Nr. Shimang; Oakes leg.; NHMUK 1903.7.1.3101.

Additional material examined

INDIA – **Arunachal Pradesh** • 20 shells; Penin, Upper Siang; 28°46.884′ N, 94°45.528′ E; 1040 m a.s.l.; 11 May 2022; Aravind N.A. and Surya Narayanan leg.; ZSI/SRC/LM2248 • 8 specs in ethanol (4 of them are empty shells); same data as for preceding; ZSI/SRC/LM2249 • 2 shells; Yemsing, East Siang; 28°6.387′ N, 95°0.427′ E; 590 m a.s.l.; 30 Apr. 2022; Aravind N.A. and Surya Narayanan leg.; ZSI/SRC/LM2250 • 2 specs in ethanol; same data as for preceding; ZSI/SRC/LM2251 • 2 shells; Yemsing stream, East Siang; 28°5.303′ N, 94°59.388′ E; 587 m a.s.l.; 27 Apr. 2022; Aravind N.A. and Surya Narayanan leg.; ZSI/SRC/LM2252 • 2 shells; Waterfall, Ramsing, Upper Siang; 28°40.275′ N, 94°57.587′ E; 1040 m a.s.l.; 12 May 2022; Aravind N.A. and Surya Narayanan leg.; ZSI/SRC/LM2253

• 2 specs in ethanol; same data as for preceding; ZSI/SRC/LM2254 • 12 specs in ethanol; Kumsing, Siang; 28°14.141′ N, 94°59.654′ E; 300 m a.s.l.; 2 May 2022; Aravind N.A. and Surya Narayanan leg.; ZSI/SRC/LM2255 • 3 shells; next to Gandhi Bridge, Mariyang-Ramsing Road, Upper Siang; 28°39.766′ N, 95°0.612′ E; 375 m a.s.l.; 10 May 2022; Aravind N.A. and Surya Narayanan leg.; ZSI/

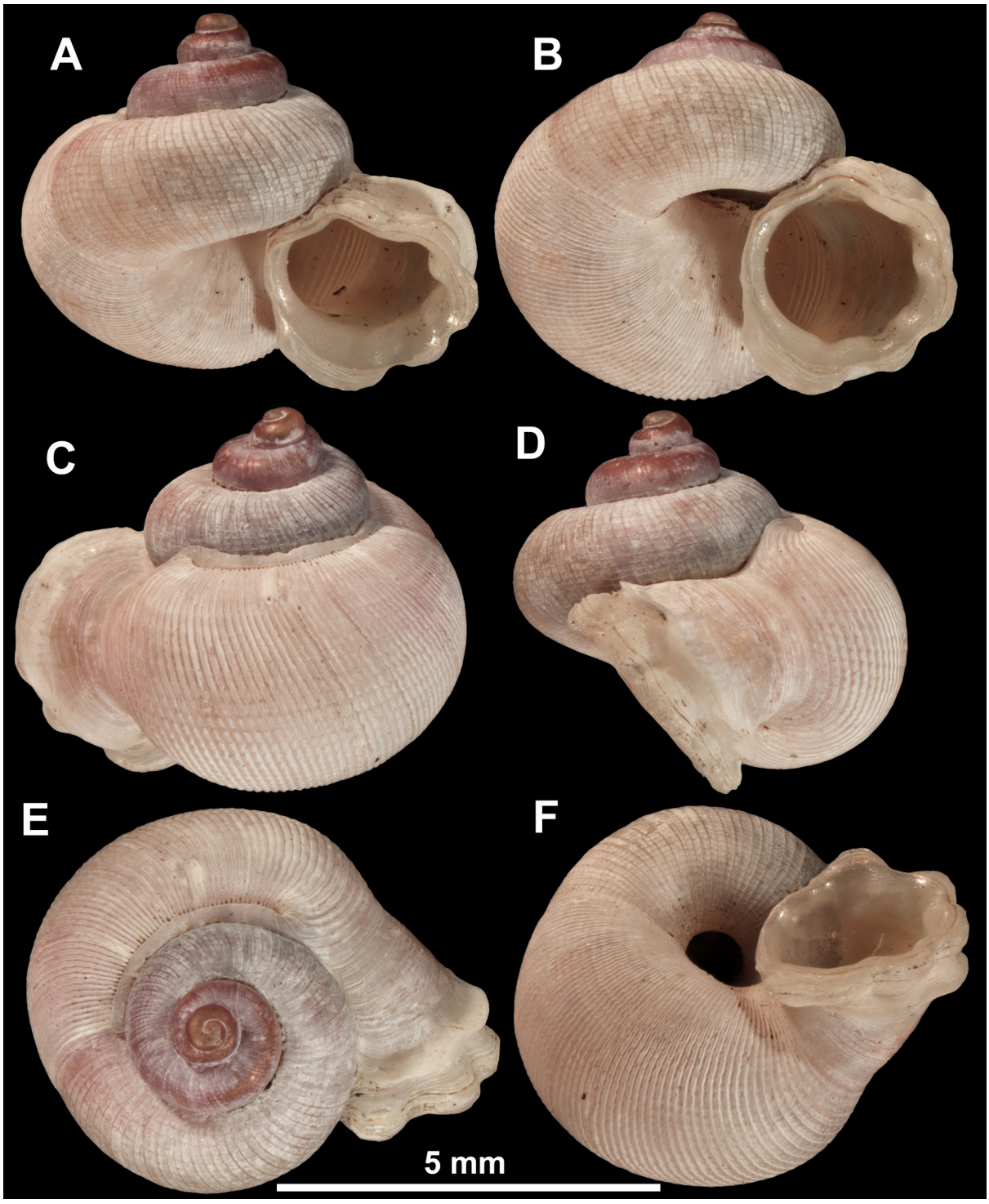


Fig. 33. Shell of *Metalycaeus vesica* (Godwin-Austen, 1914) from Ramsing waterfall (ZSI/SRC/LM2256). All photos: B. Páll-Gergely.

SRC/LM2256 • 3 specs in ethanol; same data as for preceding; ZSI/SRC/LM2257 • 1 shell; Sissen, East Siang; 28°7.917′ N, 95°7.372′ E; 235 m a.s.l.; 26 Apr. 2022; Aravind N.A. and Surya Narayanan leg.; ZSI/SRC/LM2258.

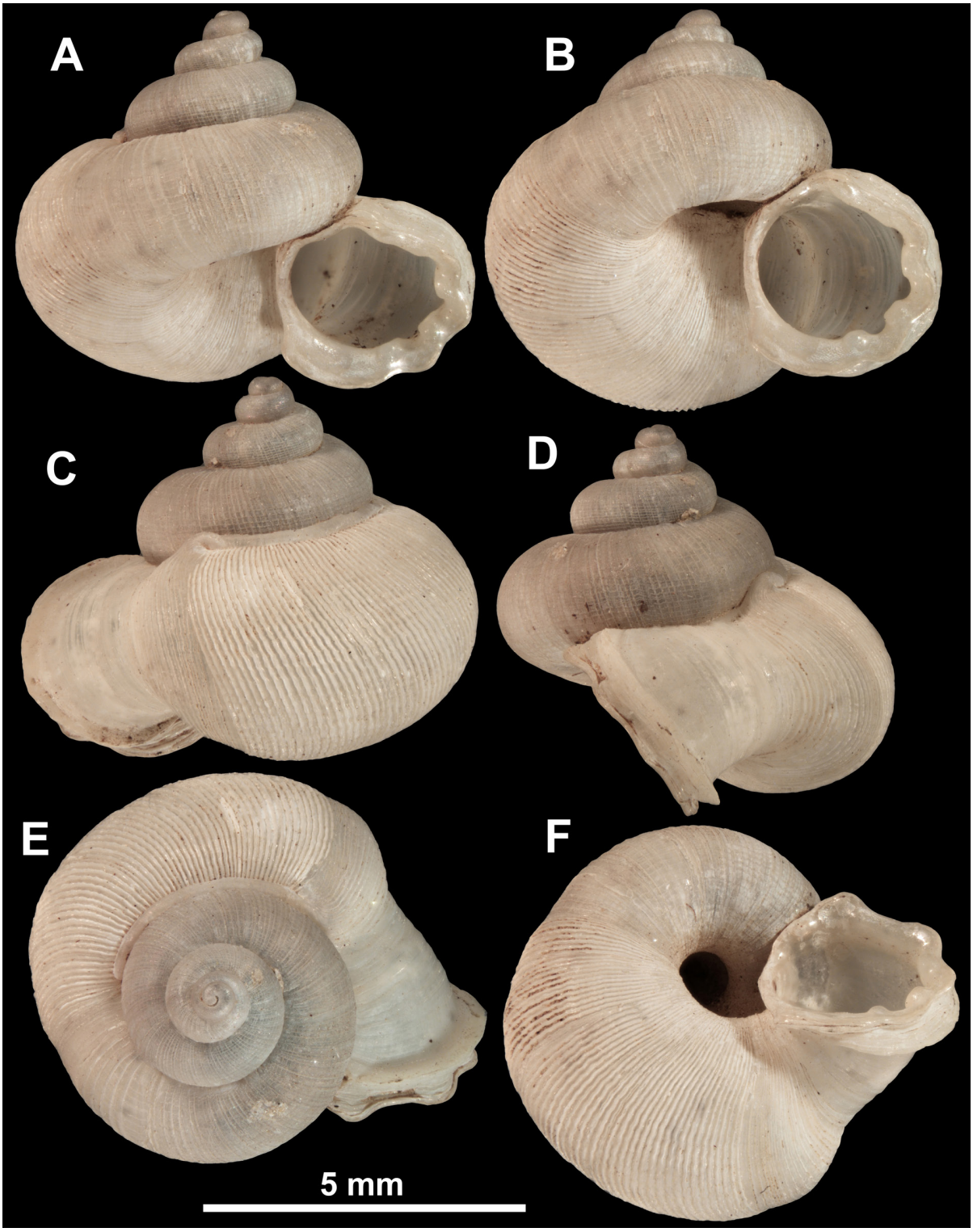


Fig. 34. Shell of *Metalycaeus vesica* (Godwin-Austen, 1914) from Penin (ZSI/SRC/LM2248). All photos: B. Páll-Gergely.

Type locality

"Bapu Peak, Abor Hills".

Differential diagnosis

Metalycaeus yamneyensis is larger, the distance between their two peristomes is smaller, and the inner peristome is less fringed (mostly on the palatal region).

Metalycaeus brahma (compared with the types of *M. brahma*, *M. chanjukensis* and *M. commutatus*) is slightly smaller, its inner and outer peristomes are not separated, the outer outline of the outer peristome is not undulating, it has a wider umbilicus, and a stronger keel on the base of R2. *Metalycaeus burtii* is also slightly smaller; its inner and outer peristomes are not separated, the outer outline of the outer peristome is not undulating, and it has a wider umbilicus.

Remarks

Our newly collected specimens match the typical *M. vesica* shells.

Discussion

This paper presents a comprehensive taxonomic revision of the genus *Metalycaeus* from the Himalayan region and Myanmar. With the addition of four new species described herein, the total number of

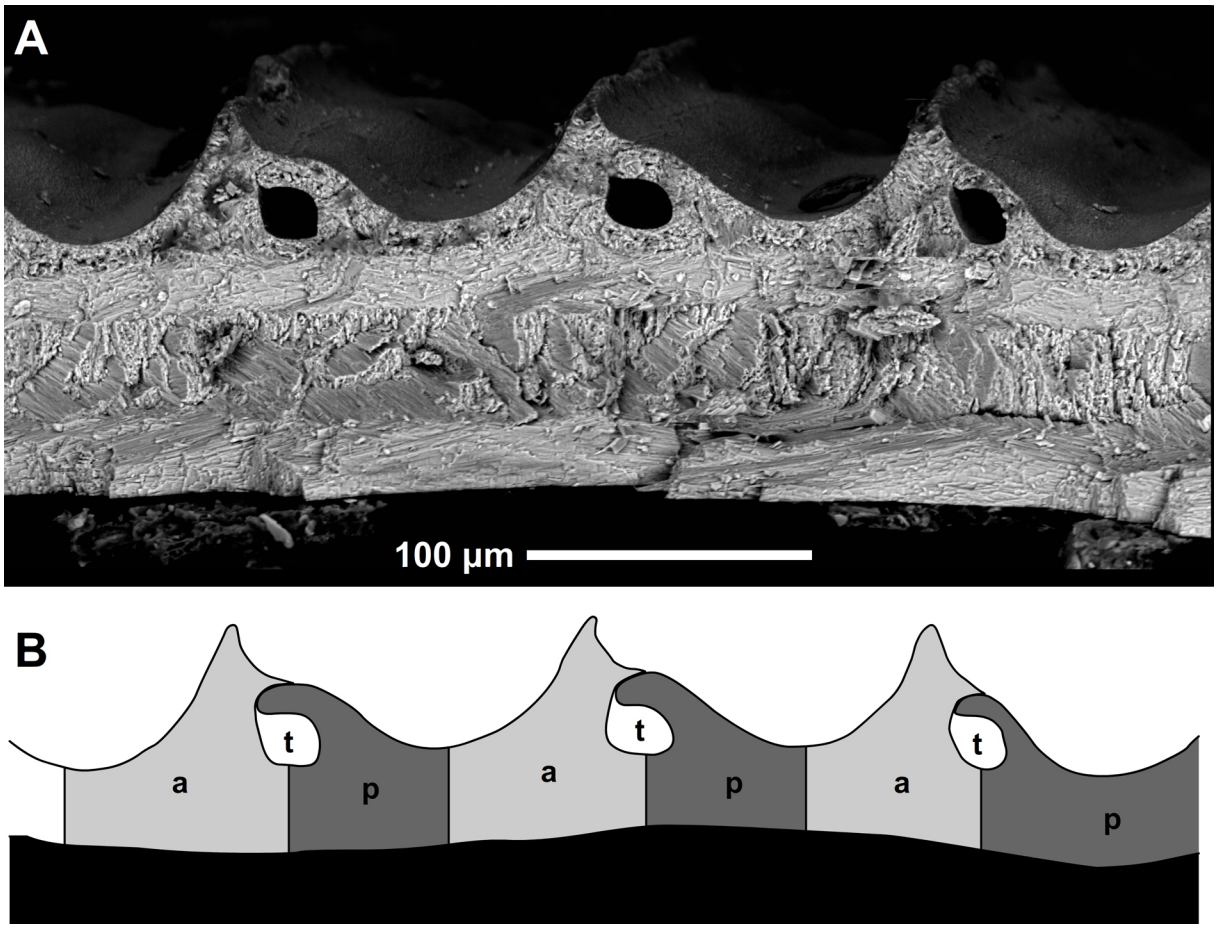


Fig. 35. Cross sectional view of R2 of *Metalycaeus vesica* (Godwin-Austen, 1914) (ZSI/SRC/LM2250). All images: B. Páll-Gergely. Abbreviations: a = anterior crust; p = posterior crust; t = microtunnel.

Metalycaeus species recognised from the Himalaya now stands at 29 (MolluscaBase 2026). In addition to documenting new species, this study reassesses all previously known species of the genus from this region. Based on revised diagnostic criteria and a contemporary understanding of species boundaries, several nominal species, primarily those described by Godwin-Austen in the early 20th century, are synonymised here (10 species and "forms") to reflect more accurate taxonomic placements.

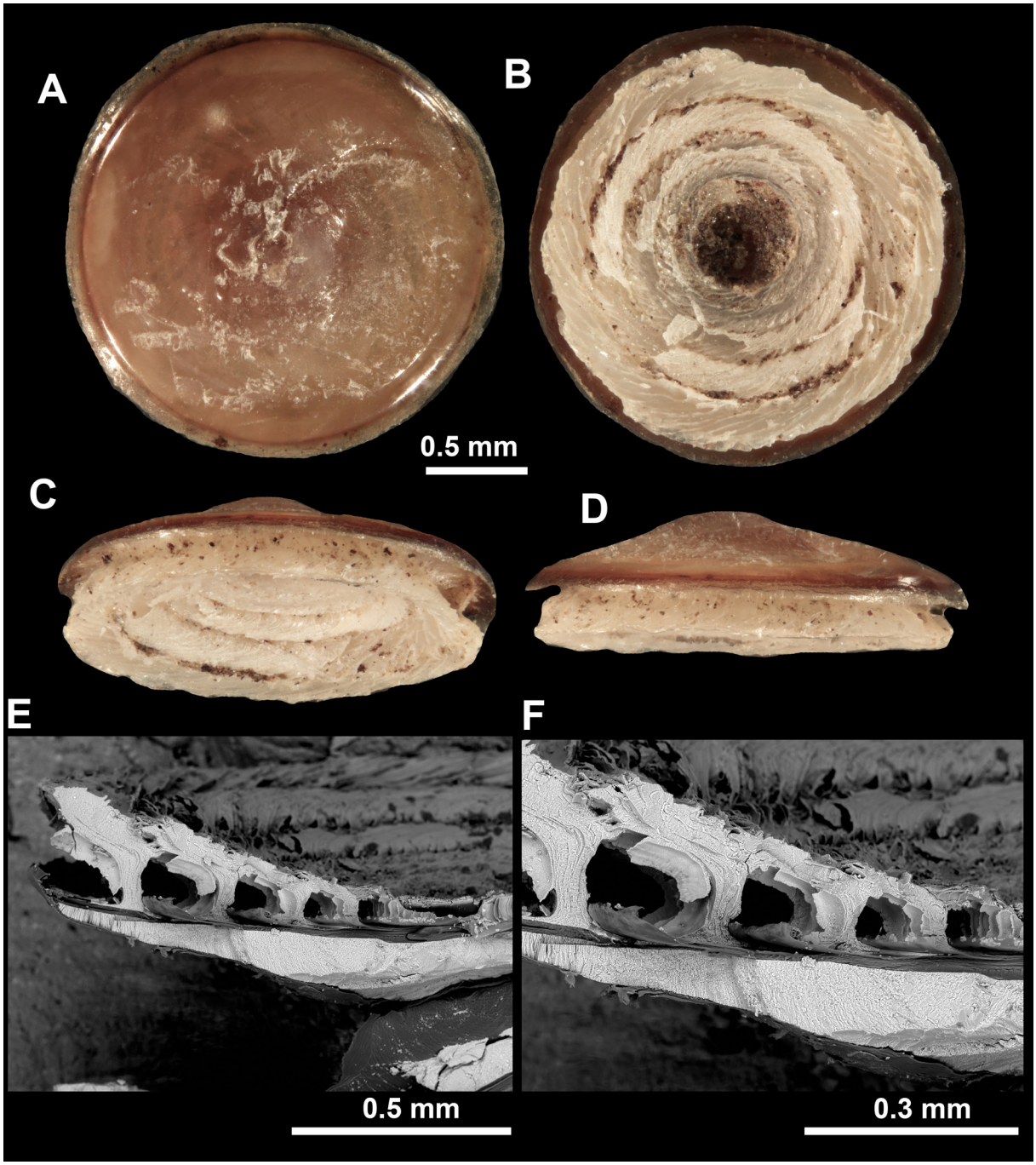


Fig. 36. Operculum of *Metalycaeus vesica* (Godwin-Austen, 1914) (ZSI/SRC/LM2250). All photos: B. Páll-Gergely.

Despite these advances, it is important to acknowledge that the present study relies primarily on shell morphology, which, although informative, may not fully capture the underlying evolutionary distinctiveness among populations. Land snails are well known for cryptic diversity, and the complex Himalayan landscape, with its deep river valleys, steep elevational gradients, and long-term barriers to dispersal, provides suitable conditions for allopatric speciation while retaining strong morphological similarities. Under such conditions, morphological characters alone may underestimate true species richness or underestimate evolutionary lineages that are distinct yet not readily diagnosable by shell features.

Future work incorporating molecular datasets will therefore be critical in testing the hypotheses proposed in this revision. DNA-based phylogenetic approaches can help clarify whether morphologically similar populations represent single widespread species or multiple independently evolving lineages shaped by geographic isolation. Integrative taxonomy, combining morphology, molecular phylogenetics, ecological data, and geographic information, will offer a more robust framework for resolving species limits within the genus *Metalycaeus*. Such an approach may ultimately reveal additional cryptic diversity or refine the systematic arrangement proposed here, thereby contributing to a deeper understanding of diversification processes in Himalayan land snails.

The Eastern Himalayas represents the centre for *Metalycaeus* diversity. Out of the eight species group defined here, five possess calcareous operculae, while that of three groups are proteinaceous ("horny"). The calcareous operculum (described here for *Metalycaeus gittenbergeri* sp. nov. and *M. adiorum* sp. nov., and for *M. physis* by Gittenberger *et al*. 2024) does not occur in species of *Metalycaeus* outside of the Himalayas, and seemingly represents a plesiomorphic character state known in other Cyclophoroidean groups (Gittenberger *et al*. 2024; Tran *et al*. 2026).

The new species of *Metalycaeus* described here were collected from the same region in Arunachal Pradesh, which was extensively sampled during the "Abor Expedition" in 1911 and 1912 by Stanley Kemp of the erstwhile Indian Museum (see, e.g., Kemp 1913). In addition to the already known species, the senior author collected four new species (three named here and one unnamed), indicating that the region harbours extraordinary levels of diversity. The other region in Arunachal Pradesh remains unexplored; further exploration of these regions might yield biogeographically interesting as well as new species for science.

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References

Bavay A. & Dautzenberg P. 1900a. Diagnoses de coquilles nouvelles de l'Indo-Chine. *Journal de Conchyliologie* 48: 108–122. Available from https://www.biodiversitylibrary.org/page/25146858 [accessed 12 Feb. 2026].

Bavay A. & Dautzenberg P. 1900b. Description de coquilles nouvelles de l'Indo-Chine. *Journal de Conchyliologie* 48: 435–460. Available from https://www.biodiversitylibrary.org/page/25147193 [accessed 12 Feb. 2026].

Bavay A. & Dautzenberg P. 1912. Description de coquilles nouvelles de l'Indo-Chine. *Journal de Conchyliologie* 60: 1–54. Available from https://www.biodiversitylibrary.org/page/16358455 [accessed 12 Feb. 2026].

Benson W.H. 1857. Characters of *Streptaulus*, a new genus, and several species of the *Cyclostomacea* from Sikkim, the Khasi Hills, Ava, and Pegu. *The Annals and Magazine of Natural History, Series 2* 19: 201–211. https://doi.org/10.1080/00222935708681840

Benson W.H. 1859. A sectional distribution of the genus *Alycæus*, Gray, with characters of six new species and of other Cyclostomidæ collected at Darjiling by W.T. Blanford, Esq., Geol. Survey. *The Annals and Magazine of Natural History*, *Series 3* 3: 176–184.
Available from https://www.biodiversitylibrary.org/page/2317897 [accessed 12 Feb. 2026].

Blanford W.T. 1862. Contributions to Indian Malacology, No. III. Descriptions of new operculated land-shells from Pegu, Arakan and the Khasi Hills. *Journal of the Asiatic Society of Bengal* 31: 135–144.
Available from https://www.biodiversitylibrary.org/page/56711841 [accessed 12 Feb. 2026].

Egorov R.V. 2013. *Treasure of Russian Shells. Supplement 3. A Review of the Genera of the Terrestrial Pectinibranch Molluscs (Synopsis Mainly Based on Published Data). Part III. Littoriniformes: Liareidae, Pupinidae, Diplommatinidae, Alycaeidae, Cochlostomidae.* R. Egorov, Moscow.

Gittenberger E., Choki Gyeltshen, Kezang Tobgay & Sherub Sherub 2024. The genera *Metalycaeus* and *Dicharax* (Caenogastropoda, Cyclophoroidea, Alycaeidae) in Bhutan, with the description of 16 new species. *Basteria* 88 (2): 187–219.

Godwin-Austen H.H. 1871. Descriptions of the species of Alycæinæ known to inhabit the Khasi Hill ranges. *Journal of the Asiatic Society of Bengal* 40: 87–93.
Available from https://www.biodiversitylibrary.org/page/35630903 [accessed 12 Feb. 2026].

Godwin-Austen H.H. 1874. Descriptions of nine species of Alycæinæ from Assam and the Naga Hills. *Journal of the Asiatic Society of Bengal* 43 (2): 145–150.
Available from https://www.biodiversitylibrary.org/page/35549500 [accessed 12 Feb. 2026].

Godwin-Austen H.H. 1876. On the Cyclostomacea of the Dafla Hills, Assam. *The Journal of the Asiatic Society of Bengal* 45 (Part 2, 3): 171–184.
Available from https://www.biodiversitylibrary.org/page/37118189 [accessed 12 Feb. 2026].

Godwin-Austen H.H. 1882–1920. *Land and Freshwater Mollusca of India, including South Arabia, Baluchistan, Afghanistan, Kashmir, Nepal, Burmah, Pegu, Tenasserim, Malay Peninsula, Ceylon and other islands of the Indian Ocean; Supplementary to Messrs. Theobald and Hanley's Conchologica Indica* Taylor and Francis, London, Vol. 1 (1): [i–iv] 1–18, pls 1–4 [Feb. 1882]; 1 (2): 19–66, pls 5–12 [Jul. 1882]; 1 (3): 67–94, pls 13–21 [Jan. 1883]; 1 (4): pls 22–42 [Sep. 1883], 95–164 [Oct. 1883]; 1 (5): pls 43–51 [Jun. 1884], 165–206 [May 1886]; 1 (6): pls 52–62 [Sep. 1887], 207–257 [Apr. 1888]. 2 (7): 1–46, pls 63–69 [Oct. 1897]; 2 (8): 47–86, pls 70–82 [Jan. 1898]; 2 (9): 87–146, pls 83–100 [Nov. 1899]; 2 (10): 147–238, pls 101–117 [Apr. 1907]; 2 (11): 239–310, pls 118–132 [Mar. 1910]; 2 (12): 311–442, pls 133–158 [Dec. 1914]. Vol. 3: 1–65, pls 159–165. https://doi.org/10.5962/bhl.title.12719

Godwin-Austen H.H. 1893. On some new species of the land-molluscan genus *Alycaeus* from the Khasi and Naga Hill Country, Assam, Munipur, and the Ruby Mine District, Upper Burma; and on one species from the Nicobars. *Proceedings of the Zoological Society of London* 61 (3): 592–595. Available from https://www.biodiversitylibrary.org/page/30981683 [accessed 12 Feb. 2026].

Gude G.K. 1921. *The Fauna of British India Including Ceylon and Burma. Mollusca III. Land Operculates (Cyclophoridae, Truncatellidae, Assimineidae, Helicinidae)*. Taylor and Francis, London. https://doi.org/10.5962/bhl.title.12890

Inkhavilay K., Sutcharit C., Bantaowong U., Chanabun R., Siriwut W., Srisonchai R., Pholyotha A., Jirapatrasilp P. & Panha S. 2019. Annotated checklist of the terrestrial molluscs from Laos (Mollusca, Gastropoda). *ZooKeys* 834: 1–166. https://doi.org/10.3897/zookeys.834.28800

Kemp S. 1913. Zoological results of the Abor Expedition 1911–12. Crustacea Decapoda. *Records of the Indian Museum* 8: 289–310. https://doi.org/10.5962/bhl.part.1191

Kerney M.P. & Cameron R.A.D. 1979. *A Field Guide to the Land Snails of Britain and North-west Europe*. Collins, London.

Kobelt W. 1902. *Das Tierreich. Eine Zusammenstellung und Kennzeichnung der rezenten Tierformen. In Verbindung mit der Deutschen Zoologischen Gesellschaft herausgegeben von der Königlich Preussischen Akademie der Wissenschaften zu Berlin. Mollusca: Cyclophoridae*. R. Friedländer und Sohn, Berlin. Available from https://www.biodiversitylibrary.org/page/1000211 [accessed 12 Feb. 2026].

Möllendorff O.F. von. 1897. Neue Landschnecken von Java. *Nachrichtsblatt der deutschen Malakozoologischen Gesellschaft* 29 (5–6, 7–8): 57–72, 89–97.
Available from https://www.biodiversitylibrary.org/page/28228249 [accessed 12 Feb. 2026].

MolluscaBase 2026. MolluscaBase. Available from https://www.molluscabase.org [accessed 12 Feb. 2026]. https://doi.org/10.14284/448

Nevill G. 1878. *Hand List of Mollusca in the Indian Museum, Calcutta. Part I. Gastropoda. Pulmonata and Prosobranchia–Neurobranchia*. Order of the Trustees, Calcutta. https://doi.org/10.5962/bhl.title.11957

Páll-Gergely B. & Asami T. 2017. A new species of *Metalycaeus* hitherto undistinguished from *M. vinctus* (Pilsbry, 1902). *Venus* 75 (1–4): 1–16. https://doi.org/10.18941/venus.75.1-4_1

Páll-Gergely B., Naggs F. & Asami T. 2016. Novel shell device for gas exchange in an operculated land snail. *Biology Letters* 12: 20160151. https://doi.org/10.1098/rsbl.2016.0151

Páll-Gergely B., Hunyadi A., Đỗ Đ.S., Naggs F. & Asami T. 2017. Revision of the Alycaeidae of China, Laos and Vietnam (Gastropoda: Cyclophoroidea) I: The genera *Dicharax* and *Metalycaeus*. *Zootaxa* 4331 (1): 1–124. https://doi.org/10.11646/zootaxa.4331.1.1

Páll-Gergely B., Sajan S., Tripathy B., Meng K., Asami T. & Ablett J.D. 2020. Genus-level revision of the Alycaeidae (Gastropoda, Cyclophoroidea), with an annotated species catalogue. *ZooKeys* 981: 1–220. https://doi.org/10.3897/zookeys.981.53583

Páll-Gergely B., Hunyadi A., Grego J., Reischütz A. & Auffenberg K. 2021. Nineteen new species of Alycaeidae from Myanmar and Thailand (Gastropoda: Caenogastropoda: Cyclophoroidea). *Zootaxa* 4973 (1): 1–61. https://doi.org/10.11646/zootaxa.4973.1.1

Páll-Gergely B., Gojšina V. & Aravind N.A. 2025. A review of *Chamalycaeus*, *Cycloryx* and *Dicharax* species of the Himalaya and Myanmar and seven new species of Alycaeinae from the Blue Mountain, Mizoram, India (Gastropoda, Caenogastropoda, Cyclophoridae. *European Journal of Taxonomy* 1029 (1): 1–158. https://doi.org/10.5852/ejt.2025.1029.3131

Pilsbry H.A. 1900. Notices of new Japanese land shells. *Proceedings of the Academy of Natural Sciences of Philadelphia* 52: 381–384. Available from https://www.biodiversitylibrary.org/page/24694261 [accessed 1 May 2025].

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* 22 (Supp. 6): 1–434. https://doi.org/10.58837/tnh.22.6.257073

Qian Z.-X. & Zhou W.-C. (eds) 2013. *Illustrated Handbook of Terrestrial Mollusks in China*. Research Monographs of Zhejiang Natural History Museum. Zhejiang People's Fine Arts Publishing House, Hangzhou. [In Chinese.]

Ramakrishna Mitra S.C. & Dey A. 2010. *Annotated Checklist of Indian Land Molluscs*. Zoological Survey of India, Kolkata. Available from http://faunaofindia.nic.in/PDFVolumes/occpapers/306/index.pdf [accessed 1 May 2025].

Rees W.J. 1964. A review of breathing devices in land operculate snails. *Proceedings of the Malacological Society of London* 36: 55–67.

Sowerby G.B. II. 1877. Monograph of the genus *Alycaeus*. *In*: *Conchologia Iconica, or Illustrations of the Shells of Molluscous Animals Vol. 20*: pls 1–6 and unpaginated text. L.A. Reeve, London. https://doi.org/10.5962/bhl.title.8129

Szekeres M., Grego J., Páll-Gergely B. & Ablett J.D. 2021. Clausiliidae (Gastropoda: Pulmonata) from India, Myanmar, Pakistan and Sri Lanka in the collection of the Natural History Museum, London. *Journal of Conchology* 44 (2): 155–187.

Thiele J. 1929. *Handbuch der systematischen Weichtierkunde, Teil 1*. Verlag von Gustav Fischer, Jena.

Tran T.G., Bui C.T., Vu L., Le D.K.T., Ho H.N.V. & Páll-Gergely B. 2026. Rediscovery and redescription of an endemic land snail from Vietnam: *Cyclotus simonianus* (Heude, 1886) with its phylogenetic position. *Zootaxa* 5785 (1): 134–151. https://doi.org/10.11646/zootaxa.5785.1.5

Varga A. 1974. Eine neue *Chamalycaeus*-Art aus Vietnam (Gastropoda: Cyclophoridae, Alycaeninae). *Folia Historico Naturalia Musei Matraensis* 2: 165–167.

Wenz W. 1938–1944. Gastropoda I. Allgemeiner Teil und Prosobranchia. *In*: Schindewolf O.H. (ed.) *Handbuch der Paläozoologie. Bd. 6 (1). Gastropoda*. Borntraeger, Berlin.

Yang H., Fan Z., Qiao D. & He J. 2012. Description of four landsnails from China. *Shell Discoveries* 1 (1): 32–33.

Zhang W.-H., Chen D.-N. & Zhou W.-C. 2008. A new species of the genus *Chamalycaeus* from China (Gastropoda, Prosobranchia, Mesogastropoda, Cyclophoridae). *Acta Zootaxonomica Sinica* 33 (4): 745–747.

Zilch A. 1957. Die Typen und Typoide des Natur-Museums Senckenberg, 20: Mollusca, Cyclophoridae, Alycaeinae. *Archiv für Molluskenkunde* 86 (4/6): 141–150.

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Supplementary file

Supp. file 1. Historical localities mentioned in the text.
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