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A new species of cyclophorid land snail (Caenogastropoda: Cyclophoridae) from the coastal regions of Maharashtra, India

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ABSTRACT

We describe a new species of cyclophorid land snail, *Theobaldius*? *konkanensis* n. sp., from the coastal and lower elevational region of the northern Western Ghats in Maharashtra, India. *Theobaldius*? *konkanensis* n. sp. can be differentiated from other species of *Theobaldius* Nevill, 1878 by the combination of a conoidally depressed shell with a more elevated spire, a deep notch on the apertural margin overhung by a prominent raised fold, and an operculum with the edges of the whorls conspicuously raised and bearing short spines. We provide a detailed description of the new species, focusing on the shell, operculum, jaw and radula, and the external morphology of the living animal; we map its distribution using recently collected data, and compare it with other species of *Theobalidus* and other cyclophoroidean genera.

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Konkan; northern Western Ghats; operculum; taxonomy; *Theobaldius*?

Introduction

The terrestrial caenogastropod superfamily Cyclophoroidea Gray, 1847 is widespread across the forested tropics (Kobelt 1902; Wenz 1938–1939; Stanisic 1998; Raheem et al. 2018) and comprises eight extant families (Bouchet et al. 2017), of which Cyclophoridae Gray, 1847 is one. This taxonomically diverse group is distributed across Asia, Africa, southern Europe, Australia and various Pacific islands (Kobelt 1902; Solem 1959; Stanisic 1998; Raheem et al. 2018) and consists of three recognised subfamilies and five tribes (Bouchet and Rocroi 2005; Bouchet et al. 2017; MolluscaBase 2024). The Cyclophoridae is represented by a number of genera in South Asia, where it constitutes a substantial proportion of the endemic and near-endemic land snail fauna (Gude 1921; Raheem et al. 2014).

Theobaldius Nevill, 1878 is one such cyclophorid genus (Gude 1921; Raheem et al. 2014; Figure 1A). Nevill (1878, pp. 275–277) first described *Theobaldius* as a subgenus of *Cyclophorus* Montfort, 1810, including 14 named species and six varieties. *Cyclophorus annulatus*' Pfeiffer, 1852 from Sri Lanka was designated as the type species. *Theobaldius* was subsequently elevated by Kobelt and Möllendorff (1897, p. 88) to full generic rank, with 19 species included. *Theobaldius* is characterised by a shell that is depressed or discoidal, dull brownish-yellow or yellowish-white in colour, usually with dark, brownish/blackish markings; a wide umbilicus; a rounded aperture; and a corneous, flat disc-shaped and multiwhorled operculum (Gude 1921). While 22 species are currently recognised in the genus (Kobelt 1902; Gude 1921; Raheem et al. 2014; MolluscaBase 2024), we would argue that two of the species are probably better placed in other genera. On the basis of shell morphological characters, *T. liliputianus* (Preston, 1909) should be included in the genus *Scabrina* Blanford, 1863 rather than in *Theobaldius*; similarly, *T. oakesi* Godwin-Austen, 1915 should be moved to the genus *Lagocheilus* Blanford, 1864. With the exclusion of these taxa, *Theobaldius* currently numbers 20 species; these are distributed in India (nine species), Sri Lanka (11 species) and Sumatra (one species). Among the Indian species, two: *T. nivicola* (Godwin-Austen, 1876), and *T. orites* (G. Nevill, 1878) are known only from north-east India (Gude 1921; Ramakrishna et al. 2010; Tripathy et al 2018). Based on the available data, six of the seven remaining Indian species, *T. anguis* (Hanley & Theobald, 1874), *T. deplanatus* (L. Pfeiffer, 1855), *T. maculosus* (G.B. Sowerby I, 1843), *T. ravidus* (Benson, 1851), *T. stenostoma* (G.B. Sowerby I, 1843), and *T.*? *tristis* (Blanford, 1869), are endemic to the Western Ghats (Kobelt 1902; Gude 1921; Raheem et al. 2014; MolluscaBase 2024); the seventh species, *T. annulatus*, occurs in both Sri Lanka and the Western Ghats (Gude 1921; Raheem et al. 2014). All the Western Ghats species were thought to be restricted to the central and southern Western Ghats (Raheem et al. 2014), but *T.*?

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Figure 1. A, Distribution of the genus *Theobaldius* in South and Southeast Asia (brown shading) (sources: Nevill 1878; Kobelt and Möllendorff 1897; Gude 1921; Raheem et al. 2014; MolluscaBase 2024); **B,** distribution of the genus *Theobaldius* in the northern Western Ghats. Brown shading indicates the Western Ghats and the black line indicates the border between Maharashtra and Karnataka states. Distributional records of *T.*? *konkanensis* n. sp. are shown by the red star (type locality) and green filled circles, and those of *T.*? *tristis* by the blue filled circle (the type locality of this species is to the south of this site, in the central Western Ghats).

tristis has recently been recorded from Radhanagari and Amba, Maharashtra, in the northern Western Ghats (Bhosale et al. 2016).

As part of ongoing research on the diversity and taxonomy of the land snail fauna of the northern Western Ghats, we have carried out surveys of the lower elevational forests in this region and the adjacent lowlands and of scattered forest patches in coastal areas of Maharashtra. These surveys have yielded specimens and distributional records of a new species of cyclophorid that is provisionally placed in the genus *Theobaldius*. However, this placement is uncertain because unlike *Theobaldius sensu stricto* the new species, like *T.*? *tristis*, has a notch with an overhanging fold on the apertural margin. Although initially identified as *T.*? *tristis*, a detailed comparison of its shell morphology with images of the type material of *T.*? *tristis* and examples of *T.*? *tristis* from Dajipur (near Radhanagari), Maharashtra, has revealed that the new species shows consistent differences from *T.*? *tristis*. We here describe this species as *T.*? *konkanesis* n. sp., giving a detailed account of the shell, operculum, jaw and radula and of the external morphology of the living animal. We

provide an overview of the current distribution of *T.*? *konkanesis* n. sp. based on recently collected data, and compare it with *T.*? *tristis* and other members of the genus *Theobaldius* and other cyclophorid genera.

Materials and methods

Living snails and shells of the new species of *Theobaldius* were collected from two localities and observed at two other localities in Maharashtra State, India (Figure 1B). Of the four localities, three are located in the lower elevational forests of the northern Western Ghats and one in a forest patch in the coastal area of Maharashtra. Live samples were photographed during or soon after collection. They were then euthanased, following the guidelines of the American Veterinary Medical Association (2020), and preserved in 80% ethanol for anatomical study. The shells of the new species were compared with images of the types of *Theobaldius* species from the Mollusca collection of the Natural History Museum, London (NHMUK), the University Museum of Zoology, Cambridge (UMZC) and samples of *T.*? *tristis* collected from Dajipur. Shell morphological terminology follows Cox (1960). Whorls were counted following Kerney and Cameron (1979). Five shell measurements were taken, as shown in Figure 2: shell height (SH), shell width (SW), fold height (FH), fold length (FL) and fold width (FW). Radulae were prepared following Geiger et al. (2007) and opercula were cleaned with a watercolour brush and stored in 80% ethanol; images were taken on a Tescan Vega3 scanning electron microscope (SEM). The type material of the new species has been deposited in the museum and research collection facility at the National Centre for Biological Sciences, Bengaluru (NRC-AA); the Bombay Natural History Museum (BNHS), Mumbai; and in the Zoological Survey of India, Western Regional Centre (ZSI/WRC) in Pune.

Systematics

Subclass Caenogastropoda Cox, 1960

Superfamily Cyclophoroidea Gray, 1847
Family Cyclophoridae Gray, 1847

Genus *Theobaldius* Nevill, 1878

Type species

Theobaldius annulatus (Pfeiffer, 1852) by original designation (Nevill 1878, p. 275).

Revised diagnosis

Shell discoid or conoidally depressed, widely umbilicated, varying from pale or dull yellow through to dark brown, often variously streaked and/or spotted; sometimes with diffuse peripheral or sub-peripheral band. Apertural margin expanded and thickened to form a noticeable 'double' lip with inner and outer layers; margin of lip usually straight, lacking notch at suture and overhanging fold. Operculum proteinaceous, not calcified; robust and corneous; ranging from thin and flat to strongly thickened, with edges of whorls on outer surface of the operculum, correspondingly slightly raised, or moderately or strongly raised; inner surface glossy, smooth, usually flat but sometimes mildly convex, slightly conical or even faintly concave, with infrequent nipple-shaped mamilla.

Remarks

Theobaldius is distinguished from the South Asian cyclophorids such as *Pterocyclos* Benson, 1832 (tribe Pterocyclini, Kobelt & Möllendorff, 1897), *Rhiostoma* Benson, 1860 (Pterocyclini), *Spiraculum* Pearson, 1833 (Pterocyclini) and *Cyclotus* Swainson, 1840 (tribe Cyclotini Pfeiffer, 1853) by its flat, non-calcified operculum and shell with a straight upper apertural margin lacking notches and/or folds/wings (Benson 1832, 1860; Pearson 1833; Gude 1921; Sutcharit et al. 2014, 2019; Tripathy et al. 2021; Tongkerd et al. 2023).

The generic placement of *T.*? *tristis* and *T.*? *konkanensis* n. sp. is uncertain (see Remarks under the relevant species' entries); the two species may belong to a genus distinct from *Theobaldius* and new to science, but this requires further study using DNA sequence data. The generic placement of the species *T.*? *dautzenbergi* (Fulton, 1907) also raises questions because apart from *T.*? *tristis* and *T.*? *konkanensis* n. sp., with their distinctive shell and opercular morphology, none of the other *Theobaldius* species have spines on the outer surface of the operculum; *T.*? *dautzenbergi* is also the only species in the genus to have a shallowly convex profile to the inner surface of the operculum (Figure 5I). Nonetheless, in terms of other shell characters, such as shell shape (e.g., cf. *T. anguis*, *T. annulatus*, *T. cratera* [Benson, 1856] and *T. orites*; Figure 4; Preece et al. 2022, fig. 26; https://zsicollections.in/search/ZSI0000003390) and sculpture (e.g., *T. layardi* [H. Adams, 1868] and *T. subplicatus* [Beddome, 1875]; Figure 4) the placement in *Theobaldius* is justified. We note that Fulton remarked on the similarity of *T.*? *dautzenbergi* to *T. layardi* in his description of the former (Fulton, 1907, p. 156). So, for the time being we suggest retaining *T.*? *dautzenbergi*, *T.*? *tristis* and *T.*? *konkanensis* n. sp. in *Theobaldius*.

Theobaldius? tristis (Blanford, 1869)

(Figures 3A–I, 4U, V, 5G, 6A, B, E, G, I, 7A, 8A–C; Table 1)

Pterocyclos? *tristis* Blanford 1869: 134, pl. 16, fig. 9.

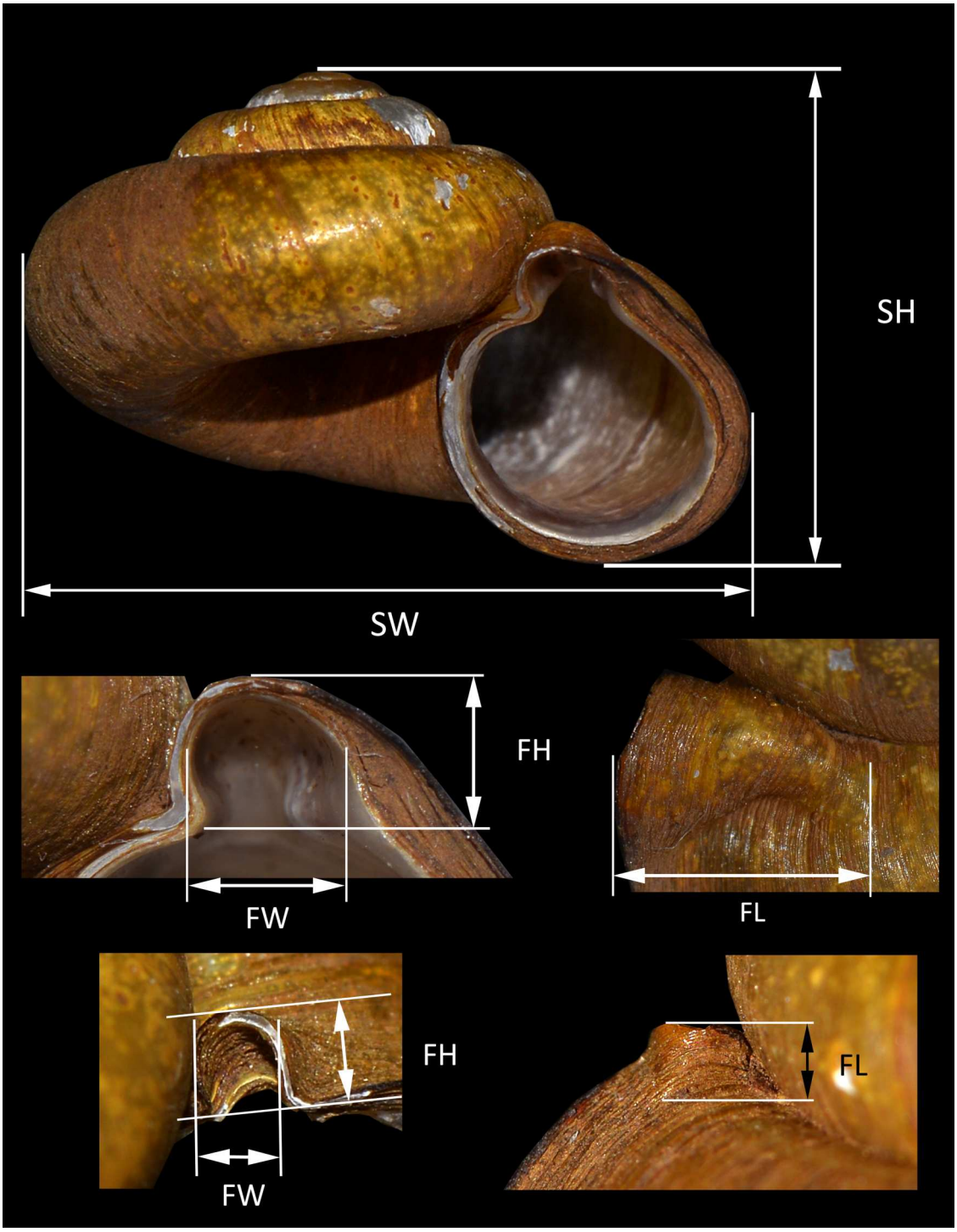

Figure 2. Shell measurements used in the description of *Theobaldius*? *konkanensis* n. sp. and *T.*? *tristis*. **Abbreviations**: **SH**—shell height; **SW**—shell width; **FH**—fold height; **FL**—fold length; **FW**—fold width.

Cyclophorus tristis.—Hanley and Theobald 1876: 57, pl. 143, figs 5, 6.

Cyclophorus (*Theobaldius*) *tristis*.—Nevill 1878: 276.

Theobaldius tristis.—Kobelt 1902: 96; Gude 1921: 44.

Material examined. Ugwai Devi Temple, Dajipur, Radhanagari Wildlife Sanctuary, Kolhapur District, Maharashtra State, India (16°22′21.4″N, 73°51′51.1″E), ca. 650 m a.s.l., coll. S. Pawar, 14 July 2022, ZSI-WRC Moll./3115/1-3(1♀, 2♂). Four specimens from the same locality, coll. A.R. Bhosale, 23 August 2022, BNHS GAS 202–205 (1♀, 3♂).

Description. Shell thin, conoidally depressed, with 4¾ regularly increasing whorls and wide umbilicus; colour dark corneous yellow with brown periostracum, closely collabrally striated and wearing away in patches (Figure 4A–H). Spire convex, apex slightly raised, suture deep. Body whorl stout, rounded at periphery, cylindrical and slightly descending at aperture. Aperture oblique, circular, lip double, inner lip white and outer lip brown,

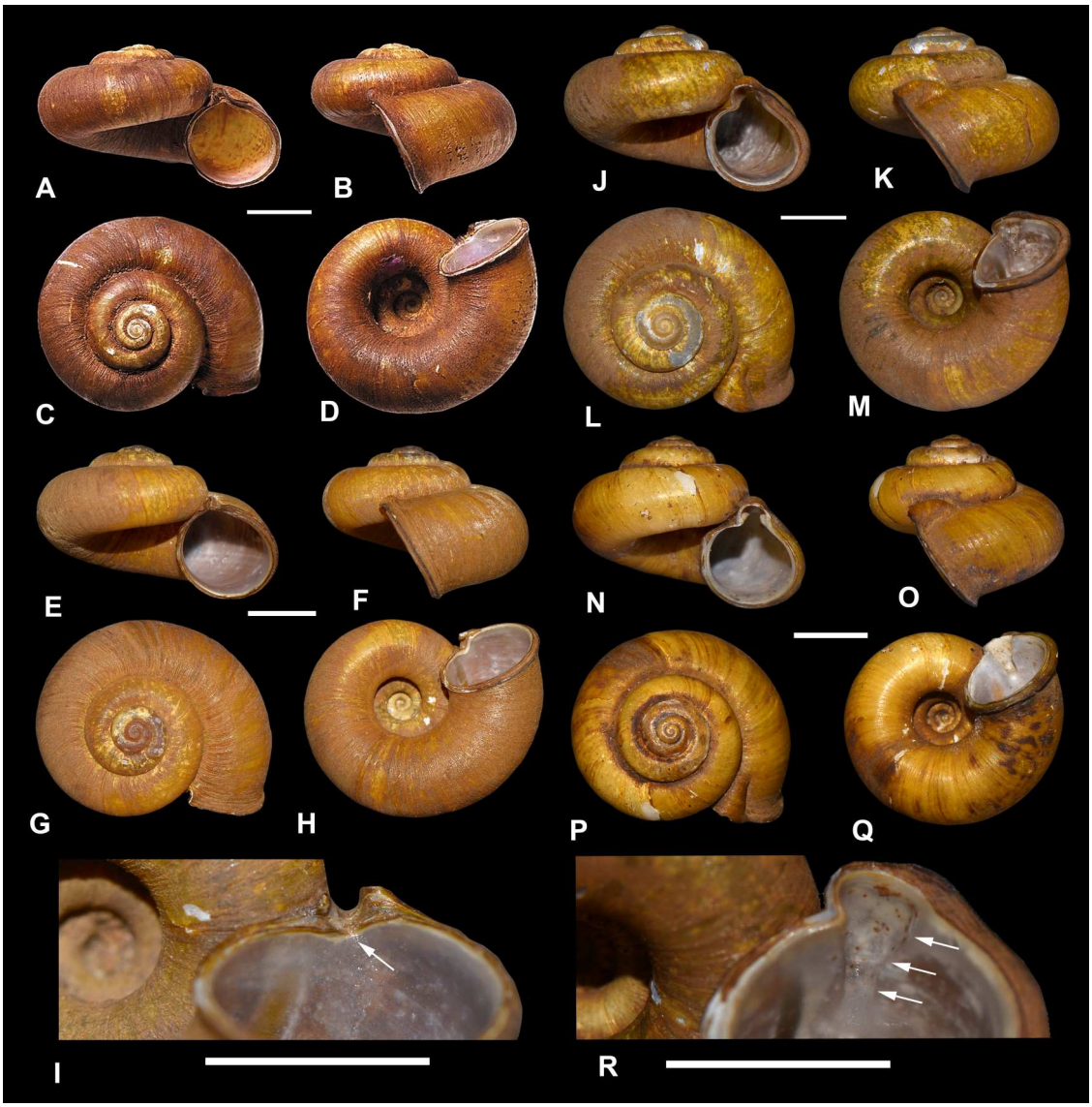

Figure 3. Shell morphology of *Theobaldius* species. **A–I,** *T.*? *tristis*. **A–D**, lectotype (NHMUK 1906.05.05.54/1); **E–I**, specimen from Ugwai Devi Temple, Dajipur (E–H, ZSI-WRC Moll./3116/2; I, BNHS GAS 203). **J–R,** *T.*? *konkanensis* n. sp.; **J–M, R,** holotype (NRC-AA-8426); **N–Q,** paratype (BNHS GAS 191). The white arrows indicate the inner peristome. Scale bars = 5 mm.

multi-layered and slightly expanded. Small notch (sinus) present on the upper edge of the inner lip near the suture (Figure 3I); outer lip expanded to form raised fold (wing) over the notch and near the suture, with fold sometimes touching penultimate whorl. Operculum corneous, thick, circular with outer surface having strongly raised edges ornamented with elongated/long and angled spines (Figure 6A, B, E, G, I), inner surface rather flat (Figure 7G). Radula taenioglossate with each row comprising seven teeth; rachidian tooth pentacuspid, lateral tooth tetracuspid, inner and outer marginal teeth tricuspid (sometimes tetracuspid; Figure 8A). Jaw simple, having serrated edge with two moderately to strongly pointed projections in central region (Figure 8B), and sculpture with irregular rectangular plates (Figure 8C).

Remarks. Blanford (1869) was doubtful of the generic status of this species (he had not seen the operculum) and provisionally placed it in the genus *Pterocyclos*. Hanley and Theobald (1876), who examined the operculum of this species, assigned it to *Cyclophorus*. Subsequently, Nevill (1878, pp. 275, 276) placed this species in *Theobaldius*, a subgenus of *Cyclophorus*, which he erected without a description. While the operculum bears some similarity to *Theobaldius* species with strongly raised edges to the whorls of the operculum (e.g., *T. deplanatus* and *T. nivicola*), the apertural notch and overhanging fold shows some similarity to the notch-fold/wing systems found in genera such as *Pterocyclos*, *Spiraculum* and *Cyclotus* (see Sutcharit et al. 2019). However, like other *Theobaldius* species and several other cyclophorid genera (e.g., *Cyclophorus*, *Aulopoma* Troschel, 1847 and *Scabrina*), *T.*? *tristis* has a non-calcified operculum, whereas in taxa such as *Cyclotus*, *Pterocyclos*, *Rhiostoma* and *Spiraculum* the operculum is strongly calcified. We therefore treat the placement of *T.*? *tristis* in the genus *Theobaldius* as provisional.

Figure 4. Morphology of the shell in the genus *Theobaldius*. **A, B,** *T. annulatus*, possible syntype (NHMUK 20200334/1); **C, D,** *T. parma*, syntype (NHMUK 1912.8.16.321-2); **E, F,** *T. dautzenbergi*, syntype (NHMUK 1907.5.3.128); **G, H,** *T. stenostoma*, lectotype (NHMUK 1843.10.02.117). **I, J,** *T. nivicola*, syntype (NHMUK 1903.7.1.511/1). **K, L,** *T. deplanatus*, lectotype (NHMUK 20110215/1); **M, N,** *T. anguis* (UMZC IDN Moll.5115/1); **O, P,** *T. bairdi*, syntype (NHMUK 20210186/1); **Q, R,** *T. subplicatus* (NHMUK 1875.3.6.60); **S, T,** *T. ravidus*, holotype (UMZC I.103670); **U, V,** *T.? tristis*, lectotype (NHMUK 1906.05.05.54/1); **W, X,** *T.? konkanensis* n. sp., holotype (NRC-AA-8426).

Theobaldius? konkanensis n. sp.

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(Figures 3J–R, 4W, X, 5H, 6C, D, F, H, J, 7B, 8D–F; Table 1)

Type material

Holotype. Dev Gireshwar Temple, Ansure, Ratnagiri District, Maharashtra State, India (16.562750°N, 73.378389°E), ca. 80 m a.s.l., coll. A.R. Bhosale, 18 June 2021, NRC-AA-8426 ♀ (SH = 12.63 mm, SW = 18.71, FH = 2.02, FW = 1.86, FL = 4.03).

Paratypes. Same as holotype, 18 June 2021, NRC-AA-8427–8431 (2 ♀, 3 ♂), 10 July 2021, NRC-AA-8432–8435, ZSI-WRC Moll./3116/1-3 (7 ♂), 2 November 2021, BNHS GAS 190–193 (4 shells).

Other material examined. Uttamrao Patil Biodiversity Garden, Chikhali, Guhagar Chiplun Road, Maharashtra

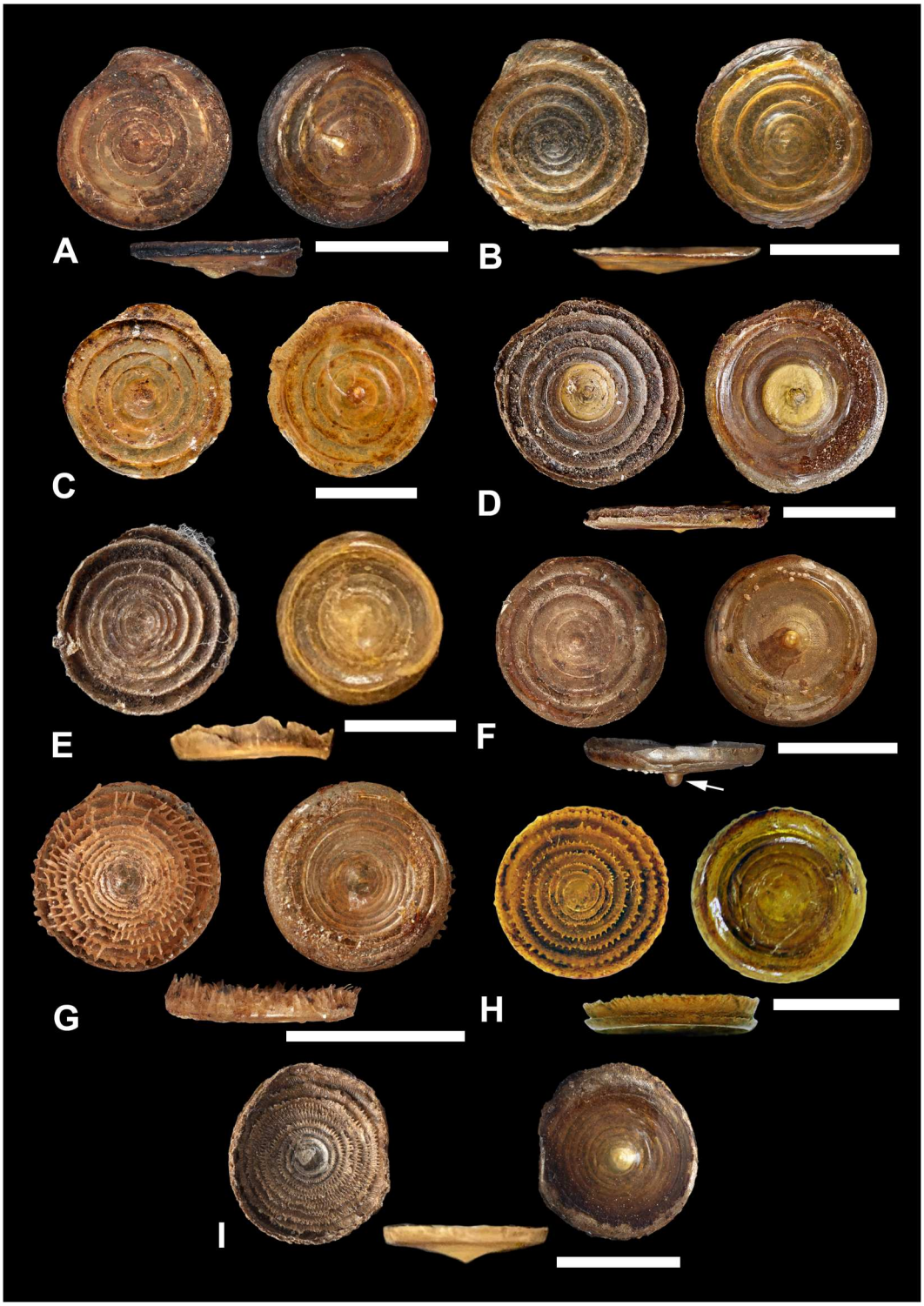

Figure 5. Opercula of species in the genus *Theobaldius*. Views of the outer (left) and inner (right) surfaces of the operculum are shown for all species; a lateral view is also shown for some species. **A,** *T. annulatus*, possible syntype (NHMUK 20200334/1); **B,** *T. cratera*, syntype (NHMUK 1912.8.16.319); **C,** *T. subplicatus* (NHMUK 1875.3.6.60); **D,** *T. nivicola*, syntype (NHMUK 1903.7.1.511/1; operculum is still attached to a dried fragment of foot tissue and this was edited out from the image of the lateral view); **E,** *T. deplanatus* (Beddome collection NHMUK 1912.4.16.573); **F,** *T. anguis*, neotype (NHMUK 20110218/1); **G,** *T.*? *tristis* (NHMUK 1912.4.16.586); **H,** *T.*? *konkanensis* n. sp., holotype (NRC-AA-8426); **I,** *T. dautzenbergi*, syntype (NHMUK 1907.5.3.128). Scale bars = 5 mm.

State, India (17°29′37.9″N, 73°17′28.1″E), ca. 180 m a.s.l., coll. A.R. Bhosale, 2 Nov. 2021, BNHS GAS 194–199 (1 ♀, 5 ♂), 15 June 2022, BNHS GAS 200, BNHS GAS 201, ZSI-WRC Moll./3117/1–4 (3 ♀, 3 ♂).

Etymology. The specific epithet is a toponym referring to South India's Konkan region (coastal regions of the states of Goa, Maharashtra and Karnataka), where the species is distributed.

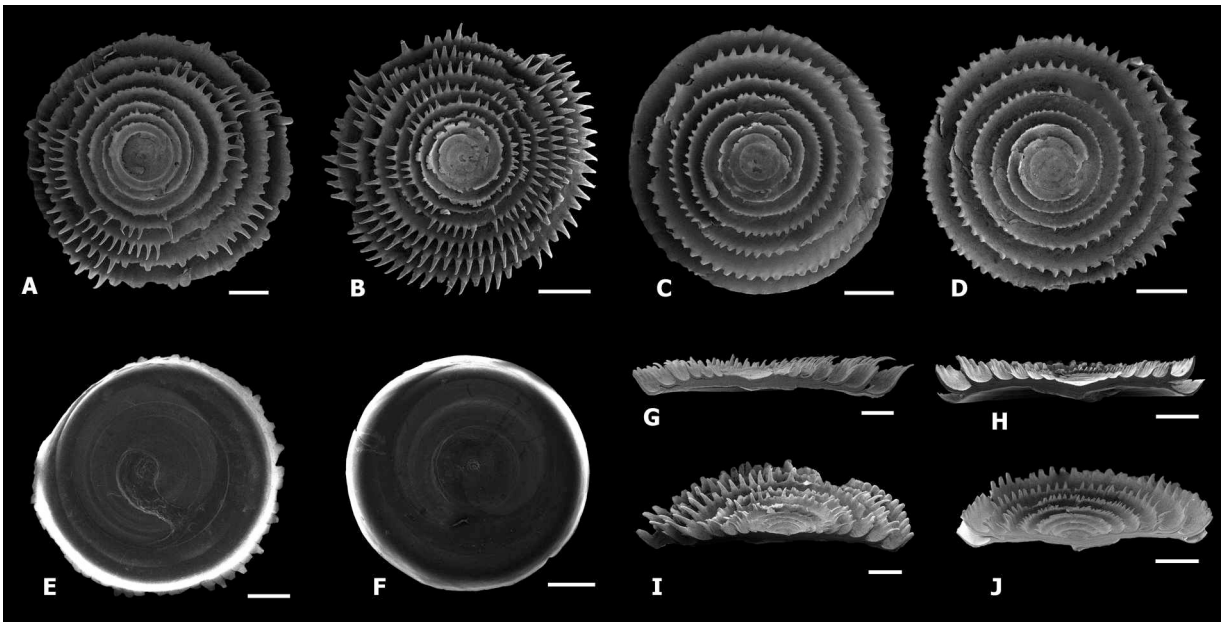

Figure 6. Scanning electron microscopy images of the operculum of *Theobaldius* species from the northern Western Ghats. **A, B, E, G, I,** *T.*? *tristis*. **A, B,** Outer surface (**A**, BNHS GAS 204; **B**, BNHS GAS 202); **E,** inner surface (ZSI-WRC Moll./3115/3); **G,** lateral view of cross-section (BNHS GAS 203); **I,** superolateral view of cross-section (BNHS GAS 203). **C, D, F, H, J,** *T.*? *konkanensis* n. sp. **C, D,** Outer surface (**C**, NRC-AA-8431; **D**, BNHS GAS 193); **F,** inner surface (NRC-AA-8428); **H,** lateral view of cross-section (NRC-AA-8429); **J,** superolateral view of cross-section (NRC-AA-8429). Scale bars = 1 mm.

Diagnosis. The new species differs from all other Indian *Theobaldius* species in having a deep triangular apertural notch overhung by a prominent, raised fold or wing and an operculum with whorl edges strongly raised and ornamented with short spines. This species also tends to have a more elevated spire than other *Theobaldius* species.

Figure 7. A, *Theobaldius*? *tristis* in life from the Ugwai Devi Temple, Dajipur, Radhanagari Wildlife Sanctuary, Kolhapur District, Maharashtra; **B,** *T.*? *konkanensis* n. sp. in life from the Uttamrao Patil Biodiversity Garden, Chikhali, Chiplun Guhagar Road, Ratnagiri District, Maharashtra.

Description

Shell. Adult shell thick, conoidally depressed, widely umbilicated with ca 4½–5 regularly increasing whorls, colour corneous yellow with brown, collabrally striated periostracum that wears off in patches (Figure 3J–Q). Spire raised, obtuse apex with deep suture (sometimes soil fills the suture and conceals it or forms a compacted layer over the shell surface). Body whorl stout, rounded at periphery and gradually descending. Aperture round with double lip; inner lip white, outer lip brown, multi-layered, and slightly expanded. At upper edge of lip near the suture, prominent raised fold that narrows posteriorly (when viewed from above; Figure 3L, P) with corresponding deep V-shaped notch on inner side of lip (Figure 3J, M, N, Q, R). Outer surface of fold touches penultimate whorl along the suture. Shell surface with fine growth lines; under stereomicroscope, close striae visible on teleoconch but protoconch (first 1¼ to 2 whorls) smooth and usually eroded. In some specimens, first 3½ shell whorls sometimes eroded. Operculum thick, corneous, multispiral with raised/slightly angled spinose edges on outer surface (Figure 5C–D, H, J); sometimes central area or spines on the raised edges are missing, most likely due to wear. Inner surface of operculum with horny nucleus at centre; slightly concave with area around nucleus faintly conical (Figure 6H). Small gap evident between edge of operculum

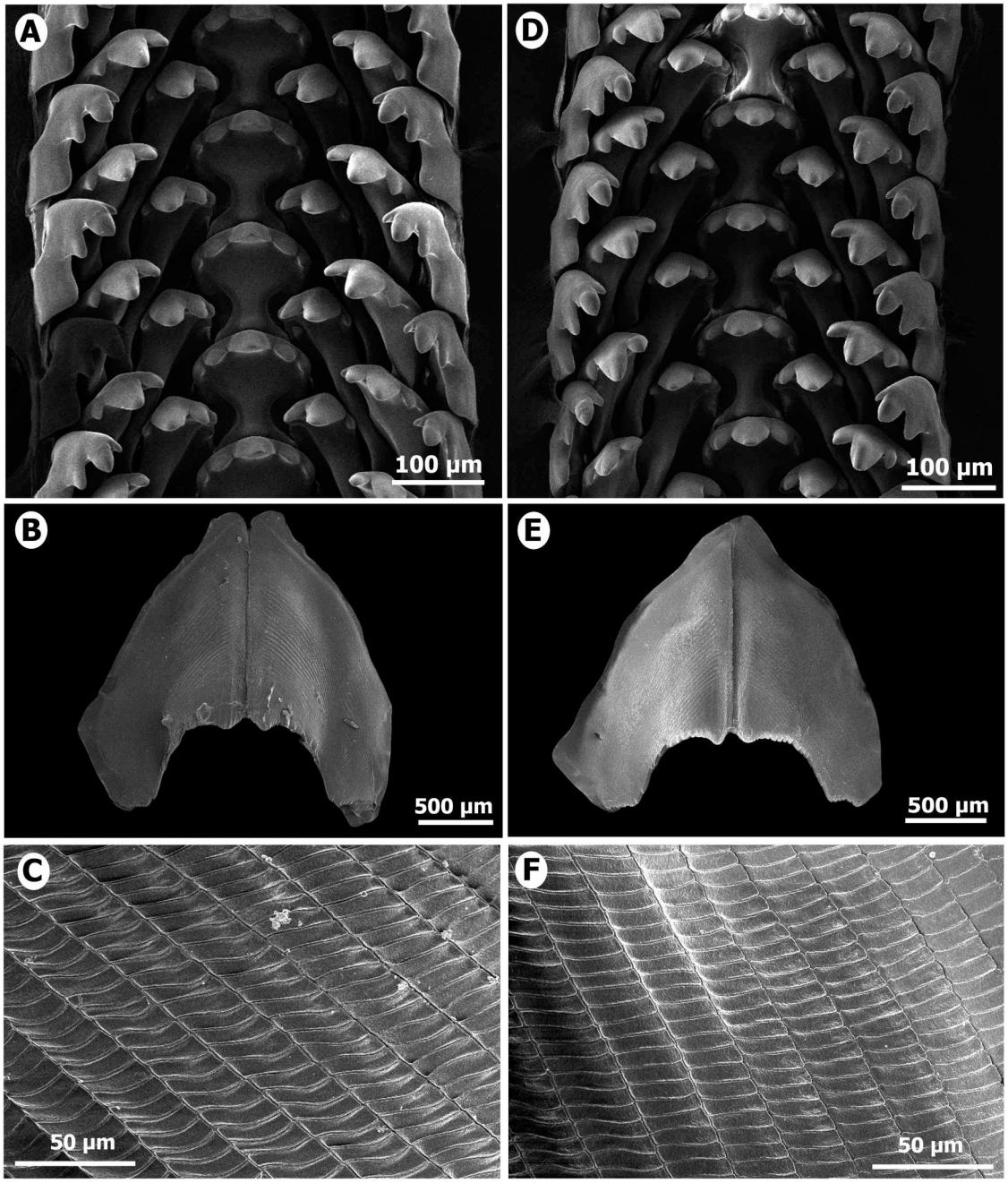

Figure 8. Scanning electron microscopy images of the radula and jaw of *Theobaldius* species from the northern Western Ghats. **A–C,** *T.*? *tristis* (ZSI-WRC Moll./3115/3). **A,** Radula; **B,** jaw; **C,** detail of sculpture on jaw. **D–F,** *T.*? *konkanensis* n. sp. (NRC-AA-8431). **D,** Radula; **E,** jaw; **F,** details of sculpture on jaw.

(when in situ) and upper margin of apertural fold; whether this fold thus functions as a 'breathing device' *sensu* Rees (1964) is unclear.

External morphology of living animal. Greyish black to dark grey body with short, pointed tail and operculum attached to dorsal surface of foot. Head with single long pair of tentacles with eyespots at outer bases. Penis narrow and elongate with tip paler than base; located behind right eye (Figure 7B).

Radula. Taenioglossate with each row comprising seven teeth. Rachidian tooth pentacuspid; central cusp well developed with two smaller cusps on either side (Figure 8D). Lateral tooth tetracuspid; inner two cusps and outermost cusp smaller than the remaining cusp. Inner and outer marginal teeth tricuspid with central cusp larger than two outer cusps. Jaw simple, having serrated edge with two obtuse or pointed projections centrally (Figure 8E) and sculpture with irregular rectangular plates (Figure 8F).

Remarks. Like *T.*? *tristis*, the new species has the combination of an apertural fold similar to cyclophorids such as *Pterocyclos*, *Rhiostoma* and *Cyclotus* and a non-calcified operculum (as found in *Theobaldius* and some other cyclophorids), so its placement in the genus *Theobaldius* is provisional.

Table 1. Variation in shell measurements in *Theobaldius*? *tristis* and *T.*? *konkanensis* n. sp.

Species and locality	No. of specimens	Sex	Shell measurements (mm) (Ranges, mean ± SD) SH	SW	FH	FW	FL	No. of whorls
Theobaldius? *Tristis*								
1. Ugwai Devi Temple, Dajipur,	7	Male ($n = 5$)	9.97–11.5	14.92–18.09	1.12–1.26	0.79–0.99	1.27–1.37	4 ¾–5
Radhanagari Wildlife			11.12 ± 0.61	17.12 ± 1.31	0.94 ± 0.53	0.71 ± 0.40	1.07 ± 0.59	
Sanctuary, Kolhapur District,		Female ($n = 2$)	11.74–12.2	18.49–18.79	1.30–1.31	0.92–1.06	1.41–1.44	5
Maharashtra State, India			11.97 ± 0.32	18.64 ± 0.21	1.29 ± 0.01	0.99 ± 0.09	1.42 ± 0.02	
Theobaldius? *konkanensis* n. sp.								
2. Dev Gireshwar Temple,	17	Male ($n = 9$)	10.6–11.55	15.19–17.3	1.76–2.15	1.54–2.52	3.52–3.98	4 ½–5
Ansure, Ratnagiri District,			11.07 ± 0.38	16.21 ± 0.63	1.92 ± 0.14	2.10 ± 0.26	3.74 ± 0.16	
Maharashtra State, India		Female ($n = 3$)	11.69–12.63	17.29–18.71	1.89–2.07	1.58–2.14	3.64–4.03	4 ¾–5
			12.17 ± 0.47	17.94 ± 0.71	1.99 ± 0.09	1.86 ± 0.28	3.85 ± 0.19	
		Shell ($n = 5$)	9.81–12.29	14.56–16.84	1.52–1.93	1.72 –2.06	2.95–3.91	4 ¾–5
			11.34 ± 0.93	15.67 ± 0.85	1.67 ± 0.19	1.87 ± 0.14	3.43 ± 0.42	
3. Uttamrao Patil Biodiversity	12	Male ($n = 8$)	12.38–14.44	17.19–19.74	2.15–2.72	2.32–3.36	3.28–6.1	4 ¾–5
Garden, Chikhali,			13.1 ± 0.65	18.57 ± 0.76	2.50 ± 0.18	2.84 ± 0.35	4.65 ± 0.86	
Maharashtra State, India		Female ($n = 4$)	13.86–14.47	18.31–19.89	2.43–2.76	2.5–3.33	4.69–5.82	5
			14.17 ± 0.26	19.28 ± 0.70	2.53 ± 0.15	2.72 ± 0.40	5.10 ± 0.53	

Abbreviations: **SD**—standard deviation; **SH**—shell height; **SW**—shell width; **FH**—fold height; **FL**—fold length; F**W**—fold width.

Distribution and natural history. *Theobaldius*? *konkanensis* n. sp. is endemic to the northern Western Ghats, where it occurs in the coastal and lowland areas of Maharashtra. It is currently known from only four localities. The species has been collected from two of these sites: Dev Gireshwar Temple, Ansure, Ratnagiri District; and Uttamrao Patil Biodiversity Garden, Chikhali, Chiplun Guhagar Road, Ratnagiri District. It has been observed at but not collected from two other localities: Kesharnath Vishnu Temple, Shedawai, Ratnagiri District (17°55′24.4″N, 73°15′38.7″E, ca. 190 m a.s.l.); and Supegaon Phansad Wildlife Sanctuary, Raigad District (18° 25′30.3″N, 72°56′58.1″E, ca. 240 m a.s.l.).

The four known localities are distributed along a 210 km-long tract extending from Supegaon in Raigad district in the north to Ansure in Ratnagiri District in southern Maharashtra. The species was found to be fairly common at all four localities at elevations ranging from 80 to 240 m a.s.l. The species is principally found in tropical evergreen and semi-evergreen forests; live specimens were found on the forest floor in leaf litter and on damp fallen branches. Live individuals were seen only from June to September and at other times of the year only shells were observed. This species is active during both day and night, with live individuals being easily found in the afternoon in well-shaded places under the forest canopy. This species co-occurs with other ground-living land-snail genera such as *Ariophanta* Desmoulins, 1829, *Cyclophorus*, *Eurychlamys* Godwin-Austen, 1899 and *Glessula* von Martens, 1860.

Discussion

The new species is morphologically distinct from all other Indian *Theobaldius sensu lato* due to the presence of two key taxonomic characters: a prominent apertural fold and a non-calcified operculum with the edges of the whorls well raised and bearing numerous short spines. *Theobaldius*? *tristis*, the only other *Theobaldius* species known from the northern Western Ghats, is superficially similar but its inner lip has a small apertural notch with the outer lip forming a small fold overhanging it, and the spines on the raised edges of the whorls of the operculum are long. The two species also apparently differ in shell shape: the new species tends to have a more raised profile, whereas *T.*? *tristis* is more depressed.

None of the other *Theobaldius* species has a notch or overhanging fold on the aperture or the more raised and tightly wound shell of *T.*? *tristis* and *T.*? *konkanensis* n. sp.; in the other species the shell is more depressed (e.g., *T.*? *dautzenbergi*, *T. stenostoma*, *T. nivicola*, *T. deplanatus*, *T. anguis*, *T. bairdi* [Pfeiffer, 1862], *T. subplicatus* and *T. ravidus*) or flat and disc-shaped (e.g., *T. annulatus* and *T. parma* [W.H. Benson, 1856]).

With the edges of the whorls strongly raised and bearing spines, the operculum of *T.*? *dautzenbergi* is strikingly similar to the opercula of *T.*? *tristis* and *T.*? *konkanensis* n. sp. Species such as *T. deplanatus* and *T. anguis* have opercula with the edges of the whorls strongly raised, as do *T.*? *dautzenbergi*, *T.*? *tristis* and *T.*? *konkanensis* n. sp.; however, like other species of *Theobaldius*, the first two species lack spiny ornamentation. The considerable variation in the height of the raised edges of the whorls and the corresponding thickness of the operculum is notable. This ranges from the thin opercula of *T. annulatus*, *T. cadiscus* (Benson, 1860), *T. cratera*, *T. cytopoma* (Benson, 1860), *T. loxostoma* (Pfeiffer, 1854), *T. parapsis* (Benson, 1853), *T. thwaitesi* (Pfeiffer, 1855), *T. bairdi*, *T. layardi* and *T. subplicatus* to the moderately thick opercula of *T. nivicola* and *T. parma* (in these species the edges of the whorls are noticeably raised) and the strongly thickened opercula of *T.*? *dautzenbergi*, *T.*? *tristis* and *T.*? *konkanensis* n. sp. The raised edges of

the opercula of *T. anguis*, *T. ravidus* and *T. stenostoma* are more well defined than in *T. annulatus* but not as strongly raised as in *T. deplanatus*; *T. anguis*, *T. ravidus* and *T. stenostoma* have a distinctive nipple-shaped mamilla on the centre of the inner surface of the operculum, which is not found in other *Theobaldius* (but see *T.*? *dautzenbergi*: Figure 5I) but occurs in other cyclophorids (e.g., *Myxostoma petiverianum* [Wood, 1828]; Foon 2016), as well as in other cylophoroidean genera (e.g., *Alycaeus* Blanford, 1864; *Ostodes* Gould, 1862; Girardi 1978; Foon and Liew 2017).

The operculum has traditionally been used as a genus-level taxonomic character in the Cyclophoridae as in other cyclophoroidean groups (e.g., Kobelt 1902; Gude 1921; Torre et al. 1942; Clench 1949), although the monophyly of taxa has generally not been tested using molecular phylogenetic data (exceptions include cyclophorids such as *Rhiostoma* and the African genus *Chondrocyclus* Ancey, 1898; Cole 2019; Tongkerd et al. 2023). The substantial variation in the structure of the operculum in *Theobaldius* is difficult to interpret given the current paucity of molecular systematic data on the relationships of the Cyclophoridae and more broadly of the Cyclophoroidea (but see the Diplommatinidae; Webster et al. 2012; Köhler 2024). One possibility is that *Theobaldius* is monophyletic and comprises distinct clades that are each associated with a particular type of operculum. Alternatively, *Theobaldius* may be non-monophyletic, comprising two or more molecularly and morphologically distinct genus-level clades. These and other hypotheses should be investigated using DNA sequence data to infer phylogenetic relationships within *Theobaldius* and between it and other cyclophorids.

As stated earlier, the placement of *T.*? *tristis* and *T.*? *konkanensis* n. sp. in the genus *Theobaldius* is uncertain, with the two species sharing a few key characters of *Theobaldius* on the one hand and of genera such as *Pterocyclos* on the other. While the operculum resembles *Theobaldius* in being non-calcified and flat when viewed laterally (the operculum in *Pterocyclos* is calcified, with the profile of the outer surface being strongly convex), *T.*? *tristis* and *T.*? *konkanensis* n. sp. have an apertural notch and overhanging fold (these apertural characters are lacking in all other members of the genus *Theobaldius*) that is superficially similar to the apertural notch–fold/wing system of genera such as *Pterocyclos* and *Cyclotus* (see Sutcharit et al. 2014, 2019; Tongkerd et al. 2023). Studies that combine detailed analysis of shell morphology with DNA-sequence-based analyses are required to understand the taxonomic relationships between the new species, *T.*? *tristis*, and other *Theobaldius* spp.

As in a number of other cyclophoroideans, the apertural notch-fold system of *T.*? *tristis* and *T.*? *konkanensis* n. sp. probably represents a modification of the shell to facilitate gas exchange. Such 'breathing devices' have been reported from a range of cyclophoroideans including the cyclophorid genera *Pterocyclos* and *Rhiostoma*, the family Alycaeidae Blanford, 1864 and the pupinid genera *Rhaphaulus* Pfeiffer, 1856, *Streptaulus* Benson, 1857 and *Tortulosa* Gray, 1847 (Kobelt 1902; Rees 1964; Páll-Gergely et al. 2014, 2015, 2016, 2017). Though structurally very varied, these breathing devices usually consist of a tube or channel that opens on the apertural margin and extends into the shell, permitting gas exchange when the aperture is tightly sealed by the operculum (Rees 1964; Subba Rao et al. 1987; Páll-Gergely et al. 2016). It is not clear how the operculum of *T.*? *tristis* and *T.*? *konkanesis* n. sp. is positioned when the animal retracts into the shell for protection or during aestivation; this must be clarified to understand the function of the apertural notch–fold/wing system in these species.

This study shows that the radula and jaw of the new species and *T.*? *tristis* are taenioglossate with seven teeth in each row (a pentacuspid rhachidian tooth, a tetracuspid lateral tooth and tricuspid inner and outer marginals). This agrees with the data published to date for other cyclophorids (e.g., *Cyclophorus*, *Pterocyclos*, *Rhiostoma*, *Spiraculum* and the African genus *Chondrocyclus*; Nantarat et al. 2014, 2019; Sutcharit et al. 2014; Cole 2019; Tripathy et al. 2021; Tongkerd et al. 2023) and for some other cyclophoroideans, for example *Cytora* Kobelt and Möllendorff, 1897 (Pupinidae) (Marshall and Barker 2007) and some Diplommatinidae Pfeiffer, 1856 (Yamazaki et al. 2015). The jaw of *T.*? *tristis* and *T.*? *konkanensis* n. sp. is characterised by irregular rectangular plates, a character shared by some Thai *Cyclophorus* (Nantarat et al. 2014, 2019).

Preliminary sampling efforts in the northern Western Ghats suggest that the new species occurs only at lower elevations (80–240 m a.s.l.), whereas *T.*? *tristis* is known from mid to high elevations (652–822 m a.s.l.). It is possible that these and other species have species-specific elevation ranges—this is certainly the case for some Sri Lankan *Theobaldius* (Raheem et al. 2009; D. Raheem, unpublished data). However, we lack detailed data on the geographical and elevation distributions of most of the known Indian *Theobaldius* species, and this needs to be addressed through extensive field surveys.

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