

High diversity of *Endothyrella* (Gastropoda, Pulmonata, Plectopylidae) in Bhutan, with a description of four new species

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Abstract

Recent fieldwork in Bhutan resulted in the discovery of 4 endemic species of *Endothyrella* that are described as new to science, viz. *E. barnai* Gittenberger & Sherub, *E. manasensis* Gittenberger & Sherub, *E. pterocallus* Gittenberger, Gyeltshen & Tobgay, and *E. trimagnipili* Gittenberger, Gyeltshen & Tobgay. This results in a total of 9 *Endothyrella* species for Bhutan, 7 of which are not known from elsewhere. The new species are described and additional data are presented for the *Endothyrella* species dealt with in an earlier paper. A revised identification key for the Bhutanese species, based on shell characters, is added. The diversity in shell size and structure is discussed and 4 species groups are provisionally distinguished on the basis of the structure of the genital tracts.

Key words. Gastropoda, Plectopylidae, *Endothyrella*, new species, North-East India, Nepal, Bhutan

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Introduction

From 2012 on molluscs were collected in Bhutan within the scope of the Bhutan Evertebrata Inventory Project of the National Biodiversity Centre (Serbithang, Thimphu,

Bhutan), the Ugyen Wangchuck Institute for Conservation and Environmental Research (Bumthang, Bhutan), and Naturalis Biodiversity Center (Leiden, the Netherlands). A series of publications reporting the results of this project started with Gittenberger et al. (2013). A preliminary field guide of the common molluscs of Bhutan, including two unidentified *Endothyrella* species followed (Gittenberger et al., 2017). Since the review of the genus *Endothyrella* Zilch, 1960 by Páll-Gergely et al. (2015, 2017), additional data have been published for the species known from Bhutan by Gittenberger et al. (2018). Ongoing research resulted in more Bhutanese records for the genus and the discovery of four new species that are described in this article. It brings the total of *Endothyrella* species to 30, 26 of which are sinistral and 4 dextral. Since the differences in chirality are associated with differences in other characters, coiling direction is considered species specific. All 9 *Endothyrella* species that are known from Bhutan are sinistral. Based on current records, seven of these species are endemic.

For a general introduction to the taxonomy of *Endothyrella* and the other genera classified in the Plectopylidae, we refer to Páll-Gergely et al. (2015, 2017). Since there are no molecular data for *Endothyrella*, the classification is based on morphological data only. The genus is known from Nepal, Bhutan, and North-East India, with isolated records in southern Myanmar and the province of Sichuan in China (Páll-Gergely et al., 2015: 14, fig. 3; 2017: 137, fig. 3).

Materials and Methods

The specimens were collected by sieving soil samples or by eye, without any standardization. Therefore, sample size

cannot be used as a measure of local abundance. The material is kept in the National Biodiversity Centre, Serbithang, Thimphu, Bhutan (NBCB), with some duplicate specimens in Naturalis Biodiversity Center, Leiden, the Netherlands. The number of specimens is indicated after a forward slash.

The whorls were counted following Kerney & Cameron (1979: 13) and Gittenberger et al. (2018), with an element of subjectivity regarding the exact location of the apical semi-circle. The curved lowest part of the last whorl is referred to as “umbilical bend”. The terminology used for the apertural barriers follows Gittenberger et al. (2018). These structures were studied in damaged shells and, in some cases, by artificially removing parts of the shell wall before and behind the apertural constriction.

Few specimens in ethanol 70% were available for dissection. See Gittenberger et al. (2021: 70) for the terminology used here and for the procedure followed to prepare permanent microscopic slides. As before, the terms proximal and distal are used in relation to the body wall; nearer the genital orifice is considered proximal.

For species that are dealt with by Gittenberger et al. (2018), only additional records and, whenever relevant, an adapted diagnosis is given.

Abbreviations. H = shell height; *n* = number of specimens; NBCB = National Biodiversity Centre, Serbithang, Thimphu, Bhutan; PWh = number of whorls of the protoconch; RMNH.MOL = National Biodiversity Center Naturalis, Leiden, the Netherlands; RMNH.MOL.G = ditto, genital slides collection; U = umbilical width, i.e. the distance between the suture just behind the peristome and the suture at the opposite side of the umbilicus; W = shell width; Wh = number of whorls.

Identification Key to Fully Grown Shells of Bhutanese *Endothyrella* Species

- | | | |
|----|---|------------------------|
| 1a | Shell with 5 or 6 undivided palatal plicae | 6 |
| 1b | Shell with 4 or more bipartite palatal plicae | 2 |
| 2a | W < 1 cm; more than 3 rows of hairs | 3 |
| 2b | W > 1 cm; 3 rows of thick hairs | <i>E. trimagnipili</i> |
| 3a | 7–10 rows of hairs | 4 |
| 3b | 5–7 rows of hairs | 5 |
| 4a | U 27–31% W, with 7–10 rows of ca 0.5 mm long hairs | <i>E. blanda</i> |
| 4b | U 29–36% W, with 10–13 rows of ca 0.3 mm long hairs | <i>E. bhutanensis</i> |
| 5a | Two denticles posterior of the parietal lamella and a prominent main plica; 5 rows of up to 0.9 mm long hairs | <i>E. plectostoma</i> |
| 5b | Wing-like callosities posterior of the parietal lamella and no main plica; 6 or 7 rows of up to 0.5 mm long hairs | <i>E. pterocallus</i> |
-
- | | | |
|----|---|------------------------|
| 6a | W > 1 cm | 7 |
| 6b | W < 1 cm | <i>E. spirostriata</i> |
| 7a | U = 40% W; spire low conical; W < 18 mm | 8 |
| 7b | U > 40% W; spire very low; W > 18 mm | <i>E. pemagatshel</i> |
| 8a | With broadly curved shoulder and slightly convex sides; aperture ca 40% W in basal view | <i>E. barnai</i> |
| 8b | With narrowly curved shoulder and straight sides; aperture ca 35% W in basal view | <i>E. manasensis</i> |

Systematic Part

Superfamily Plectopyloidea Möllendorff, 1898

Family Plectopylidae Möllendorff, 1898

Genus *Endothyrella* Zilch, 1960 (feminine)

Type species. *Helix plectostoma* Benson, 1836, by original designation.

Description. The shell is dextral or sinistral and broader than high, with a more or less depressed conical to slightly concave spire. Its width is 4–20 mm. There is a funnel-shaped umbilicus. The surface is uniform greyish or yellowish brown, or there is a colour pattern with regularly spaced, reddish, relatively dark blotches or broad stripes. The first whorl of the domed protoconch is nearly smooth, provided with irregular wrinkles or increasingly prominent radial riblets, continuing on the adjoining whorls, where spiral lines may be added, most of which are covered by the teleoconch in fully grown shells (Figs 1, 2). The teleoconch is variously sculptured with radial and spiral riblets. The outer lip of the aperture is surrounded by a thickened, reflected border; the inner lip is formed by a more or less prominent, callous ridge. There is no parietal fold. Inside fully grown shells, from the aperture about a quarter to a half whorl deep inside the last whorl, there are vertical parietal lamellae, sometimes with posterior denticles or ridges, and one or two plicae; at the opposite side there are six palatal plicae that may be either undivided or bipartite. The palatal plicae may have conspicuously different anterior versus posterior parts; they are called “bipartite” when these parts are in line but not connected. The obstructing callosities may develop several times during shell growth and thus can also be studied in juvenile shells. Apparently, they are secondarily resorbed, so that only a single set of obstructive lamella and plicae is present in fully grown shells (see the notes with *E. pemagatshel* and *E. plectostoma*).

The periostracum may be dull and felty (Fig. 32) or forming a dense pattern of low fringes on the radial riblets (Fig. 12a–d). The fringes may be wrapped as “hair-like folds” (Páll-Gergely et al., 2015: 12; 2017: 135; fig. 12d), here referred to as “hairs”, since these structures cannot always be distinguished from the solid hairs that can be recognized



Figures 1–4. SEM images of protoconchs with initial teleoconch whorls. **1, 2.** *E. bhutanensis* Gittenberger, Leda, Sherub & Páll-Gergely, 2018, 21 km SW of Pemagatshel (NBCB1262). **3.** *E. pemagatshel* Gittenberger, Leda, Sherub & Páll-Gergely, 2018, NW side of Pemagatshel (NBCB1237). **4.** *E. plectostoma* (Benson, 1836), 4 km NW of Samdrup Jongkhar (NBCB1270). Scale bar: 1 mm.

more or less clearly in most *Endothyrella* species (Figs 1, 4, 17). The hairs may vary considerably in length (Figs 2, 4), and they are arranged in 3–12 spiral rows (Figs 12c, 13a). In species with 6 or more rows, the number of rows may vary.

The structure of the penial caecum and its position relative to the attachment of the penial retractor muscle are quite diverse (Figs 23–26). However, since anatomical details are known for only very few species and specimens, their taxonomic relevance remains unclear.

***Endothyrella blanda* (Gude, 1898)**

Figures 5, 14–16

Plectopylis blanda Gude, 1898: 264, fig. 70a–f (“Naga Hills, Assam”).

Endothyrella blanda—Páll-Gergely et al., 2015: 32, figs 17B (holotype), C, 18, 19A–B, 20A–C; 2017: 153, figs 17B–C, 18, 19A–B, 20A–C; Gittenberger et al., 2018: 204, figs 1, 3, 7A–E.

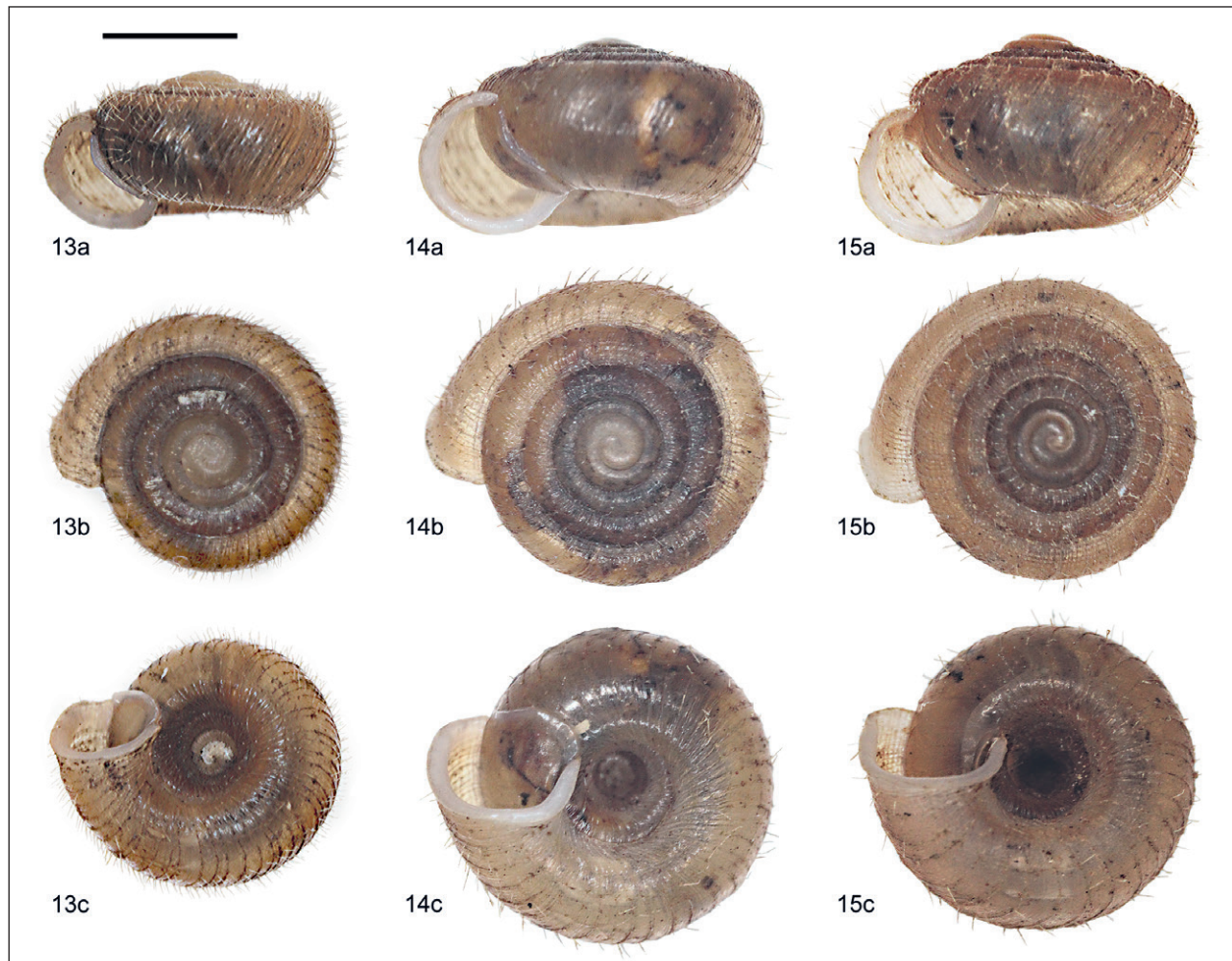
Endothyrella spec. 1—Gittenberger et al., 2017: 74, fig. 66a–d.

Additional records. District Haa, Gakiling: 27°07′N 89°08′E, 896 m a.s.l., Choki Gyeltshen, Kezang Tobgay, Nima Gyeltshen & Pem Zam leg. 20.iv.2021 (NBCB1260/5; RMNH.MOL.507899/1); 27°06′N 89°08′E, 812 m a.s.l., Choki Gyeltshen, Kezang Tobgay, Nima Gyeltshen & Pem Zam leg. 21.iv.2021 (NBCB1261/9; RMNH.MOL.507900/3); 27°07′N 89°09′E, 1260 m a.s.l., Choki Gyeltshen, Kezang Tobgay, Nima Gyeltshen & Pem Zam leg. 20.iv.2021 (NBCB 1259/2); 27°05′N 89°09′E, 890 m a.s.l., Choki Gyeltshen, Kezang Tobgay, Nima Gyeltshen & Pem Zam leg. 20.iv.2021 (NBCB1258/8).

Adapted diagnosis. Spire low conical, W 4.8–5.7 mm, H 3.0–3.6 mm, U < 31% W, Wh 4½–5¾, PWh 2–2½, peristome broadened and reflected, with 7–10 rows of ca 0.5 mm long hairs; with 4 bipartite palatal plicae.

Supplementary description. Four samples of *Endothyrella* from the district of Haa are classified as *E. blanda* with some doubt. The shells from Haa ($n = 28$) are similar to *E. blanda* from the district of Chhukha ($n = 19$) in shell height, measuring 3.0–3.5 mm (versus 3.3–3.6 mm)





Figures 13–15. *Endothyrella* spec. 13. *E. bhutanensis* Gittenberger, Leda, Sherub & Páll-Gergely, 2018, 8 km NNW of Samdrup Jongkhar (NBCB1256). 14, 15. *E. blanda* (Gude, 1898): (14) Gakiling, 896 m a.s.l. (NBCB1260); (15) 2.5 km SE of Phuentsholing (NBCB1336). Scale bar 2 mm.

and relative umbilical width, i.e. 27–31% W (versus 28–30% W), but have only $4\frac{1}{2}$ – $5\frac{1}{4}$ whorls instead of $5\frac{1}{4}$ – $5\frac{3}{4}$ in *E. blanda* from Chhukha. In *E. bhutanensis*, the shells have $4\frac{1}{2}$ – $5\frac{1}{2}$ whorls and are about as broad as the Haa shells, i.e. 4.6–5.7 mm (versus 4.8–5.7 mm), but less high, i.e. 2.6–3.2 mm. Thus in *E. bhutanensis* the spire is more depressed. The only fresh specimen from Haa has 10 rows with hairs, whereas 7–9 rows are indicated for *E. blanda*; the hairs of this shell are up to 0.45 mm long, however, whereas ca 0.3 mm is indicated for *E. bhutanensis*.

Distribution. *Endothyrella blanda* might be a widespread species with large disjunctions in its range (Páll-Gergely et al., 2015: 34; 2017: 154; Gittenberger et al., 2018: 204), but recently collected material is from Nepal and Bhutan only.

Notes. *Endothyrella blanda* maybe a polytypic species. This should be investigated where the ranges of *E. blanda* and *E. bhutanensis* are in contact or nearly so. The structure of the genitalia exhibits differences. According to Páll-Gergely et al. (2015: 32, 34 fig. 18; 2017: 153, 156 fig. 18), there is only an indistinct penial caecum in *E. blanda*, whereas it is prominent in *E. bhutanensis* (see below).

***Endothyrella bhutanensis* Gittenberger, Leda, Sherub & Páll-Gergely, 2018**

Figures 1, 2, 13, 16, 25

Endothyrella bhutanensis Gittenberger, Leda, Sherub & Páll-Gergely, 2018: 204, figs 1, 4, 7F–K, 9B, 10 (“district

◀ **Figures 5–11.** Protoconchs of *Endothyrella* spec. 5. *E. blanda* (Gude, 1898), 2.5 km SE of Phuentsholing (NBCB1336). 6, 7. *E. pterocallus* Gittenberger, Gyeltshen & Tobgay, spec. nov., paratypes, 35 km ENE of Mongar: (6) NBCB1282; (7) RMNH.MOL.507912. 8. *E. spirostriata* Gittenberger, Leda, Sherub & Páll-Gergely, 2018, 7 km E of Pemagatshel (NBCB26). 9. *E. manasensis* Gittenberger & Sherub, spec. nov., holotype (NBCB1243), Manas. 10. *E. trimagnipili* Gittenberger, Gyeltshen & Tobgay, spec. nov., holotype (NBCB1251), 20 km N of Samdrup Jongkhar. 11. *E. barnai* Gittenberger & Sherub, spec. nov., paratype, 9 km N of Samdrup Jongkhar (NBCB1252).

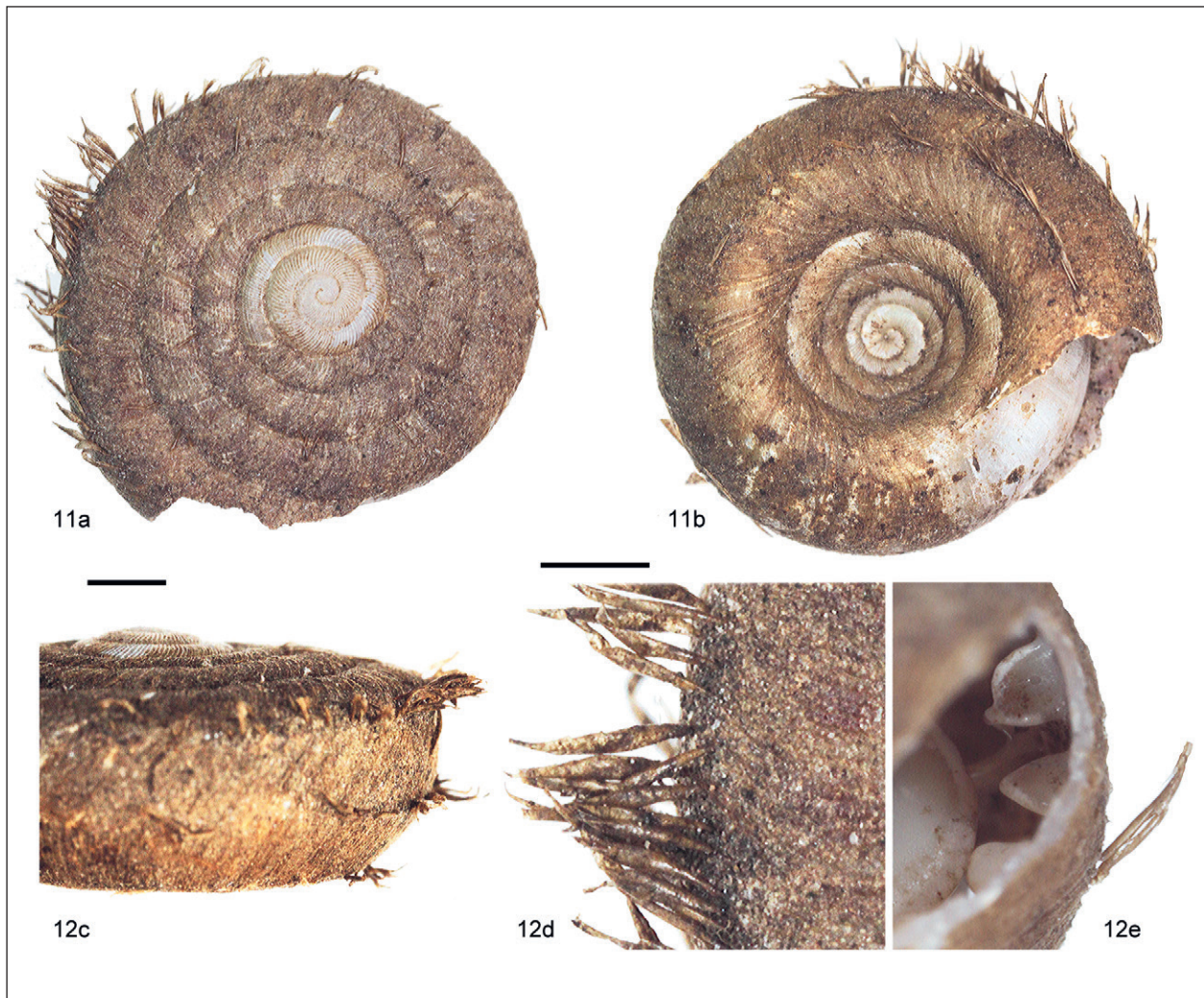


Figure 12. *Endothyrella trimagnipili* Gittenberger, Gyeltshen & Tobgay, spec. nov., holotype (NBCB1251), 20 km N of Samdrup Jongkhar: (a) apical view; (b) umbilical view; (c) lateral view; (d) periostracal “roll up” hairs; (e) posterior side of suprapalatalis (s), upper palatalis (u), and lower palatalis (l). Scale bars: 1 mm.

Tsirang, 35 km WNW of Gelephu, 1050 m a.s.l., 27°01'N 90°08'E”).

Additional records. District Pemagatshel: 21 km SW of Pemagatshel, 460 m a.s.l., 26°56'N 91°12'E, E. Gittenberger, Choki Gyeltshen & Kezang Tobgay leg. 27.ix.2019 (NBCB1262/3; RMNH.MOL.507901/1). District Samdrup Jongkhar: 4 km NW of Samdrup Jongkhar, 260 m a.s.l., 26°49'N 91°28'E, E. Gittenberger, Choki Gyeltshen & Kezang Tobgay leg. 29.ix.2019 (NBCB1257/3; RMNH.MOL.507902/1); 8 km NNW of Samdrup Jongkhar, 815 m a.s.l., 26°52'N 91°28'E; E. Gittenberger, Choki Gyeltshen & Kezang Tobgay leg. 29.ix.2019 (NBCB1256/1); 9 km N of Samdrup Jongkhar, 986 m a.s.l., subtropical broadleaf forest; 26°52'44"N 91°29'25"E; Sherub & Ugyen Tenzin leg. i.2020 (NBCB1255/2); 9 km N of Samdrup Jongkhar, 1008 m a.s.l., warm broadleaf forest, 26°52'N 91°29'E, Sherub & Ugyen Tenzin leg. i.2020 (NBCB1265/2); 7 km NNW of Jomotshangkha, Toka Phu, 940 m a.s.l., 26°57'N 92°04'E,

Sherub leg. 15.vi.2019 (NBCB1263/2). District Zhemgang: ENE of Panbang, 260 m a.s.l., ca 26°52'N 91°00'E, E. Gittenberger, Choki Gyeltshen & Kezang Tobgay leg. 26.ix.2019 (NBCB1264/3; RMNH.MOL.507903/1).

Adapted diagnosis. Spire depressed conical, $W > 4.5$ mm, $U > 29\%$ W, $Wh\ 4\frac{1}{2}-5\frac{1}{2}$, $PWh\ 2\frac{1}{8}-2\frac{1}{4}$, peristome broadened and little reflected adapically, with 10–13 rows of ca 0.3 mm long hairs; with 4 bipartite palatal plicae.

Supplementary description ($n = 59$). The umbilicus is relatively wide, measuring 29–36% W. Shell measurements are $W\ 4.6-5.7$ mm, $H\ 2.6-3.2$ mm. The protoconch (Figs 1, 2) can be described after a newly hatched snail. Its initial whorl is nearly smooth; further on irregular radial riblets and >10 spiral lines are present between the suture and the umbilical bend. In larger shells only one or two of the spiral lines remain uncovered by the adjoining teleoconch whorl.

Genitalia. Anatomical details of this species were described and illustrated from a single specimen (Gittenberger

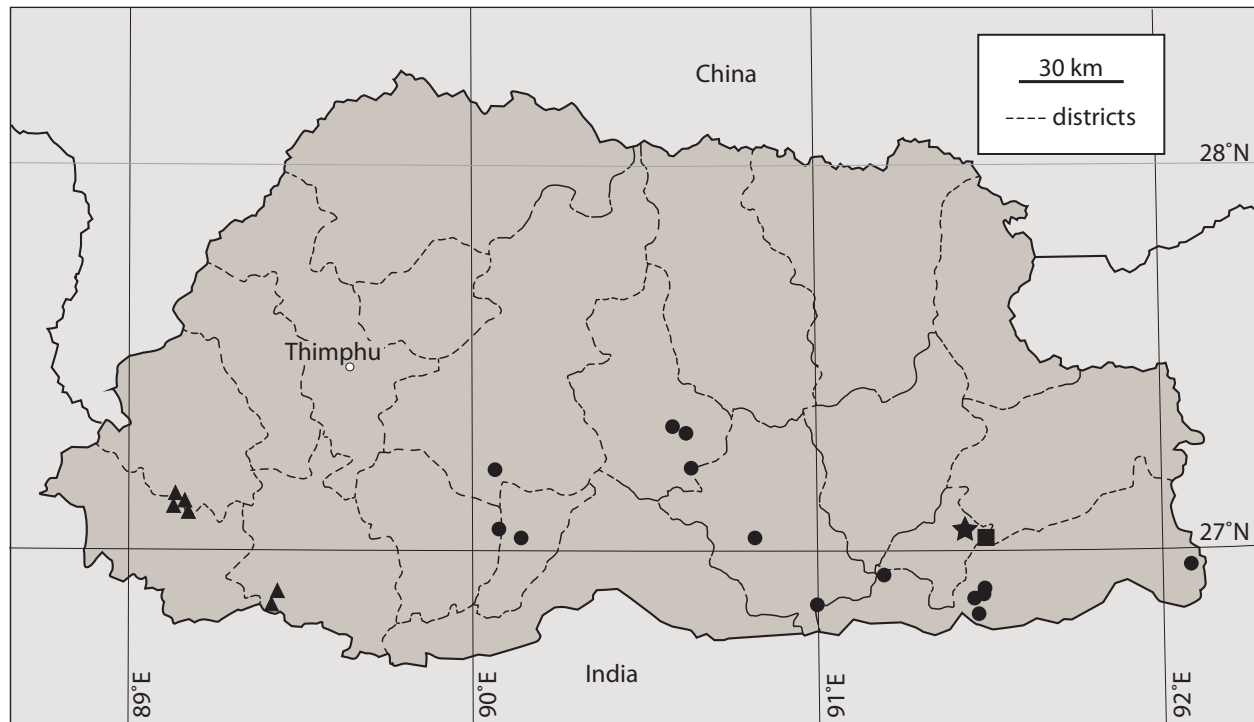


Figure 16. Records of *E. bhutanensis* Gittenberger, Leda, Sherub & Páll-Gergely, 2018 (●), *E. blanda* (Gude, 1898) (▲), *E. pemagatshel* Gittenberger, Leda, Sherub & Páll-Gergely, 2018 (★) and *E. spirostriata* Gittenberger, Leda, Sherub & Páll-Gergely, 2018 (■).

et al., 2018: 206, 211 fig. 9B). In a second dissected specimen, the male part is similar with the presence of a prominent penial caecum while differing by a relatively broader proximal part (Fig. 25).

Distribution. This species is known now from 14 localities ($n = 51$) in central and eastern Bhutan (Fig. 16), at 260–1085 m a.s.l.

Notes. *Endothyrella bhutanensis* is most similar to *E. blanda*, at least in shell characters. See also the notes with that species.

***Endothyrella trimagnipili* Gittenberger,**

Gyeltshen & Tobgay, spec. nov.

Figures 10, 12, 28

ZooBank registration. urn:lsid:zoobank.org:act:FCFF85A8-05E2-4509-AD98-2319487B0896

Type series. Holotype (NBCB1251), Bhutan, district Samdrup Jongkhar, 20 km N of Samdrup Jongkhar, 1680 m a.s.l., 26°59'N 91°31'E, E. Gittenberger, Choki Gyeltshen & Kezang Tobgay leg. 29.ix.2019.

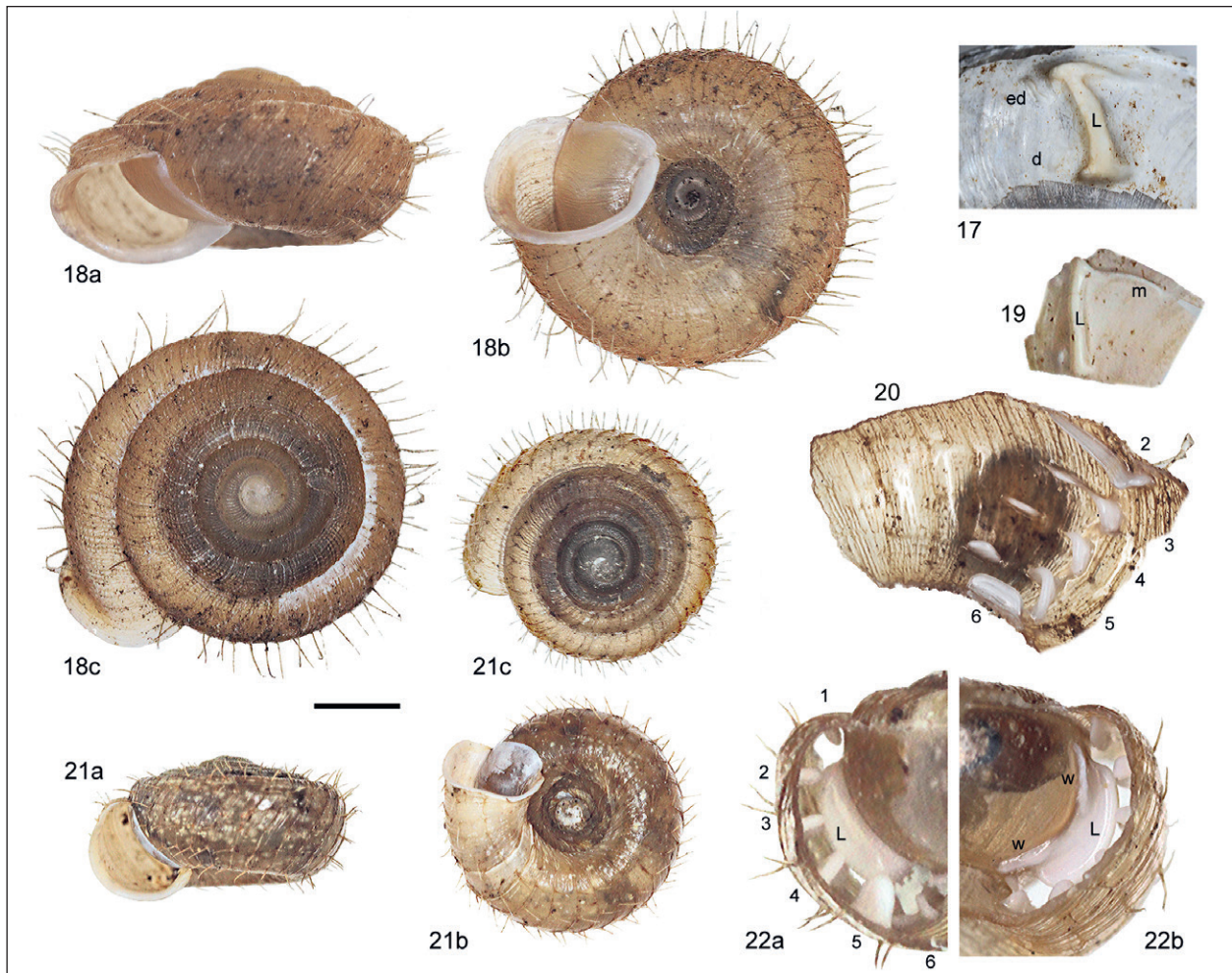
Diagnosis. Spire depressed conical, U ca 44%, Wh ?, PWh 3, with 3 rows of up to 1.7 mm long hairs; with 3 palatal bipartite plicae.

Description. Only a single, damaged shell with 6 moderately convex whorls, without the apertural part, is available.

The apical and the basal parts of the discoidal shell pass into the side by rounded angles, accompanied by an upper and a lower spiral row of prominent hairs that are up to 1.7 mm long. The side has a vertical upper part and an oblique lower part, slightly sloping towards the umbilicus; these parts are separated by a wide angle, marked by a middle row of hairs. The upper row of hairs is still visible on the spire, where the hairs are attached near the suture, resting on the next whorl while pointing to the periphery. The umbilicus measures $> \frac{1}{3} W$.

The protoconch has 3 whorls, sculptured by radial riblets with interspaces wider than their width and, additionally, on the final quarter, there are up to 10 increasingly clear spiral lines. The teleoconch is covered by a felty, rough periostracum; on the first teleoconch whorl, regular radial riblets are most prominent, changing into a regular, reticulate sculpture on the following whorl, whereas from the third teleoconch whorl on, an irregular sculpture of fine periostracal ridges becomes most conspicuous. On the sides of the shell, a dense pattern of fine spiral lines is largely covered by the thick periostracum with dense, radial ridges. Towards and inside the umbilicus, from the lower row of hairs on, more regular, oblique, dense, periostracal ridges are crossed by fine, dense, spiral lines.

The parietal lamella is nearly symmetrical, regularly curved and only at the basal side little higher than adapically; at both sides it reaches nearly as far anteriorly as the



Figures 17–22. *Endothyrella* spec., shells and apertural callosities. **17.** *E. barnai* Gittenberger & Sherub, spec. nov., paratype, Nganglam (RMNH.MOL.507906), parietal lamella (L) with denticle (d) and elongated “denticle” (ed). **18–20.** *E. plectostoma* (Benson, 1836), 4 km NW of Samdrup Jongkhar (NBCB1270): **(18)** shell; **(19)** parietal lamella (L) and main plica (m); **(20)** palatal plicae, viz. suprapalatalis (2), upper palatalis (3), lower palatalis (4), infrapalatalis (5), and basalis (6). **21, 22.** *E. pterocallus* Gittenberger, Gyeltshen & Tobgay, spec. nov., holotype, 35 km ENE of Mongar: **(21)** shell (NBCB1266); **(22)** apertural callosities (NBCB1282), numbered as in (20) with suturalis (1) added, **(a)** anterior and **(b)** posterior side with parietal lamella (L) and wing-like plicae (w). Scale bar (Figs 18, 21): 1 mm.

prominent lower parietal plica. It has 2 posterior denticles, with the adapical one most prominent and less closely connected with the lamella than the basal one. An upper parietal plica is lacking.

The palatal wall has (1) a short simple suturalis, (2) a long suprapalatalis with a somewhat oblique, straight, anterior part, connected with a conspicuous, posterior bifurcation after a deep concave lowering opposite the parietal lamella, (3–5) 3 bipartite palatal plicae with parallel, anterior, lamella-like parts and thickened, nearly radially oriented, posterior parts, (6) a simple basalis, about as long as the lower parietal plica, with a long anterior and a short posterior part.

Measurements. The measurements of the incomplete shell, lacking the apertural part, are W 12.8 mm, H 5.3 mm.

Differentiation. *Endothyrella trimagnipili* is reminiscent of *E. babbagei* (Gude, 1915) by the relatively large size (W 14 mm) and the presence of three rows of hairs. Apart

from being dextral, the latter species also differs by the simple palatal plicae and a slightly concave spire. *Endothyrella aborensis* (Gude, 1915) is equally large and sinistral, but it is hairless and has a very wide umbilicus, measuring half the shell width. The sinistral *Endothyrella* species have either more than three rows of hairs or none. Similarly sized (W > 1 cm) species differ also in other characters, i.e. *E. fultoni* (Godwin-Austen, 1892) by much more oblique sides, *E. miriensis* (Gude, 1915) by the conspicuous spiral sculpture, *E. pemagatshel* by the fine felty periostracum and an asymmetrical parietal lamella, and *E. nepalica* Budha & Páll-Gergely in Páll-Gergely et al., 2015, *E. oakesi* (Gude, 1915), and *E. pinacis* (Benson, 1859) by different posterior parts of the palatal plicae.

Etymology. The epithet *trimagnipili* refers to the presence of three rows of large hairs (L *tri* after *tres* = three; L *magni* after *magnus* = large; L *pili* = hairs).



Figures 23–26. Parts of genital tracts of *Endothyrella*. **24.** *E. plectostoma* (Benson, 1836), 4 km NW of Samdrup Jongkhar (RMNH.MOL.G1191). **24.** *E. pterocallus* Gittenberger, Gyeltshen & Tobgay, spec. nov., paratype (RMNH.MOL.G1192), 35 km ENE of Mongar. **25.** *E. bhutanensis* Gittenberger, Leda, Sherub & Páll-Gergely, 2018 (RMNH.MOL.G1193). **26.** *E. spirostriata* Gittenberger, Leda, Sherub & Páll-Gergely, 2018 (RMNH.MOL.G1176). Abbreviations: b = bursa copulatrix, c = penial caecum, d = diverticulum, dh = ductus hermaphroditicus, e = epiphallus, ga = glandula albuminifera, p = penis, pr = prostate, rm = penial retractor muscle, u = uterus, v = vagina, vd = vas deferens. Scale bar: 1 mm.

***Endothyrella spirostriata* Gittenberger, Leda,
Sherub & Páll-Gergely, 2018**

Figures 8, 16, 26, 29, 30

Endothyrella spirostriata Gittenberger, Leda, Sherub & Páll-Gergely, 2018: 207, figs 1, 5, 7L–N, 9A (“Pemagatshel district, 7 km E of village of Pemagatshel, 2300 m a.s.l., 27°01′N 91°29′E”).

Diagnosis ($n = 4$). Spire very low, $W > 7$ mm, U 38–40% W, Wh 5, PWh $2\frac{1}{2}$, with 4 rows of hairs; palatal plicae, except for basalis, undivided.

Note. For this species no new data are available.

***Endothyrella pemagatshel* Gittenberger, Leda,
Sherub & Páll-Gergely, 2018**

Figures 3, 16, 31, 32

Endothyrella pemagatshel Gittenberger, Leda, Sherub & Páll-Gergely, 2018: 209, figs 6, 7O–Q (“Pemagatshel district, NW side of village of Pemagatshel, 1750 m a.s.l., 27°02′N, 91°25′E”).

Additional material. Type locality, E. Gittenberger, C. Gyeltshen & K. Tobgay leg. 28.ix.2019 (NBCB12377/1, 6 juveniles; RMNH.MOL.507904/2 juveniles, 1 fragment).

Adapted diagnosis. Spire very low, $W > 18$ mm, without

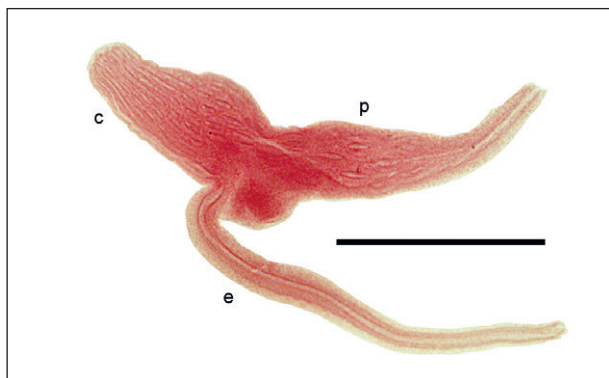


Figure 27. Distal part of penis with caecum and epiphallus in *Endothyrella pterocallus* Gittenberger, Gyeltshen & Tobgay, spec. nov., 35 km ENE of Mongar (RMNH.MOL.G1192). The proximal part of the penis, a penial retractor muscle, and the transition of the epiphallus to the vas deferens are lacking. Abbreviations: c = caecum; e = epiphallus; p = penis. Scale bar: 1 mm.

hairs; palatal plicae undivided.

Adapted description. This species was described after a fully grown shell without the periostracum and 2 damaged shells with incomplete remains of the periostracum. Additional material from the type locality—a fully grown shell, 8 juvenile shells, and a fragment of a fully grown shell with the aperture, the final half whorl and the internal part of the columella—enable an improved description.

The discoidal shell has ca $6\frac{1}{4}$ whorls and a hardly elevated spire. It is yellowish brown, with regular, reddish brown radial stripes, which are most clearly seen at the smooth parietal side of the aperture and, as blotches, on the spire; elsewhere the colour pattern is covered by the periostracum. The final part of the body whorl descends to about the upper quarter of the penultimate whorl. The outer lip is reflected and more prominently thickened than the low parietal callus. There is a wide, funnel-shaped umbilicus.

The protoconch has $3\frac{1}{8}$ – $3\frac{1}{4}$ whorls; it has dense radial riblets that become somewhat irregularly wrinkly towards the outer suture and spiral lines after about the first whorl. The adjoining teleoconch whorls are more convex; they have a finely reticulate sculpture on the spire, very fine, dense, spiral lines at the sides and a more prominent spiral sculpture near the umbilical bend and inside the umbilicus. The felty periostracum, with very oblique, dense, micro-ridges, obscures the underlying sculpture.

The parietal lamella is asymmetrical; at the basal side it is higher than apically, where two slightly concave parts correspond with the positions of the suprapalatalis and the upper palatalis. At the basal side it is elongated anteriorly as far as the anterior end of the bipartite lower plica. Behind the lamella, there are a very short plica-like upper denticle and a less prominent lower denticle next to the short, low, posterior part of the lower plica. The suturalis is much shorter than the other palatal plicae, whereas the much

longer basalis may end anteriorly next to the end of the protruding part of the lamella. The suprapalatalis has a long, lamella-like anterior part and a much shorter, thickened posterior part with a more or less clearly developed bifurcation. The anterior part of the upper palatalis is shorter than that of the suprapalatalis; a comparable part is lacking in both the thick lower palatalis and the most prominent, very obliquely thickened infrapalatalis. The lamella-like basalis is 2–3 times longer than the suturalis. The most prominent, posterior parts of central palatal folds are interconnected by a narrow, low callous ridge.

Measurements. W 18.1–18.3 mm, H 7.1–7.6 mm, U 45% W.

Notes. In a juvenile shells of $3\frac{1}{8}$ whorls, there is an apertural barrier at $2\frac{7}{8}$ whorls from the apex. In a juvenile shell of $3\frac{1}{4}$ whorls there is a barrier at $2\frac{3}{4}$ whorls, and in an equally large shell there are two barriers close to one another, at 3 and $3\frac{1}{4}$ whorls, respectively. Apparently, a barrier is already formed in the final part of the protoconch. It has to be investigated whether this happens before the beginning of the formation of the teleoconch. In a fragment of a fully grown shell there is only a barrier about half a whorl before the apertural lip. Apparently, barriers in earlier whorls have been secondarily resorbed.

***Endothyrella manasensis* Gittenberger & Sherub, spec. nov.**

Figures 9, 33, 34

ZooBank registration. urn:lsid:zoobank.org:act:6289A9FE-AF7C-412D-8797-1296DC7B34C4

Type series. District Zhemgang, Manas, 132 m a.s.l., $27^{\circ}02'N$ $90^{\circ}48'E$, Chimi Yuden, Pema Yangzom, Ugyen Tenzin & Sherub leg. 11-12-2018 (NBCB1243/holotype, 1244/paratype; RMNH.MOL.507905/paratype). District Sarpang, Royal Manas National Park, 310 m a.s.l., $26^{\circ}53'N$ $90^{\circ}54'E$, Sherub leg. 05-02-2020 (NBCB1253/2 fragments, paratypes).

Diagnosis. Shell with oblique, nearly straight sides, a prominent keel, and a low conical spire, W < 13 mm, H ca 6 mm, with at least one row of hairs; palatal plicae undivided.

Description ($n = 3 + 2$ fragments). The shell has $6\frac{1}{4}$ – $6\frac{1}{2}$ whorls and a low, conical spire, bordered by a prominent keel with a narrow furrow that remains visible on the entire teleoconch. The sides of the shell are oblique and nearly straight. The final part of the body whorl descends to about the upper third of the penultimate whorl. The umbilicus is moderately wide. Since the shells are heavily worn, the colour of fresh specimens remains unknown; there is a vague pattern of dark blotches, similar to that exhibited in *E. barnai* and *E. pemagatshel*.

The protoconch has $2\frac{7}{8}$ – $3\frac{1}{4}$ whorls; after the first whorl, which may be nearly smooth, dense radial riblets are seen and additionally some spiral lines close to the beginning of the teleoconch. The adjoining teleoconch whorls are nearly

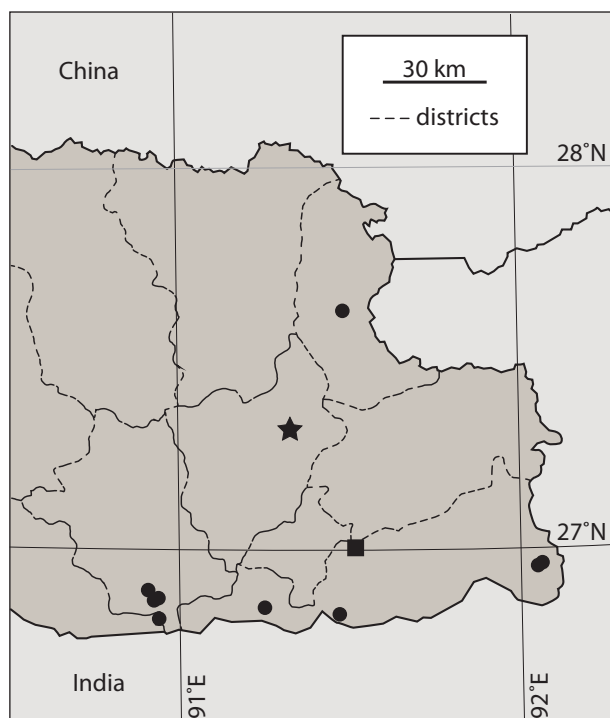


Figure 28. Records of *Endothyrella plectostoma* (Benson, 1836) (●), *E. pterocallus* Gittenberger, Gyeltshen & Tobgay, spec. nov. (★) and *E. trimagnipili* Gittenberger, Gyeltshen & Tobgay, spec. nov. (■).

flat; they have 6 or 7 rather coarse spiral ridges, crossed by more narrowly spaced and little less prominent radial ridges. The sides of the shell have dense oblique growth lines and a vague pattern of spiral lirae, which are more prominent at the umbilical bend and inside the umbilicus. The three shells that are available are heavily worn, with only fragments of a very coarse periostracum left; just below the teleoconch keel, attached to the short vertical part of the wall, there is a row of single hairs, 0.5–0.6 mm long, resting on the next whorl while pointing to the periphery. The hairs may be longer on the last whorl, and there might be more rows of hairs.

The thick parietal lamella is about symmetrical; adapically an inconspicuous extension points anteriorly. The anterior part of the bipartite lower plica runs next to the lamella; its inconspicuous, short, posterior part is situated deeper inside the shell. In the 2 specimens studied, the lamella has 2 posterior thickenings, but no separate denticles. The minute suturalis is much shorter than the other palatal lamellae. The basalis is as prominent as the other palatal folds; it ends posteriorly next to the short and inconspicuous posterior part of the parietal lower plica and anteriorly it reaches little further than the lamella. The suprapalatalis has a long straight lamella-like anterior part; it ends posteriorly with an S-like twist. The anterior parts of the upper palatalis, lower palatalis, and infrapalatalis are increasingly shorter and about equally strong thickened posteriorly. The thickened posterior part of the

infrapalatalis is obliquely extended towards the basalis. The most prominent, posterior parts of the central palatal folds are interconnected by a narrow, low callous ridge.

Measurements. W 11.9–12.9 mm, H 5.6–6.3 mm, U 37–38% W. Holotype: 12.9 × 6.1 mm.

Differentiation. *Endothyrella manasensis* is most similar to *E. barnai*, while differing by being slightly smaller, with straight sides, a wider umbilicus and a relatively small aperture, measuring ca 35%W instead of ca 40% seen from below.

Note. According to the structure of the apertural lamella and the plicae *E. manasensis* is most closely related to *E. barnai*.

Etymology. The epithet *manasensis* refers to the location of type locality inside Royal Manas National Park.

***Endothyrella barnai* Gittenberger & Sherub,
spec. nov.**

Figures 11, 17, 33, 35–38

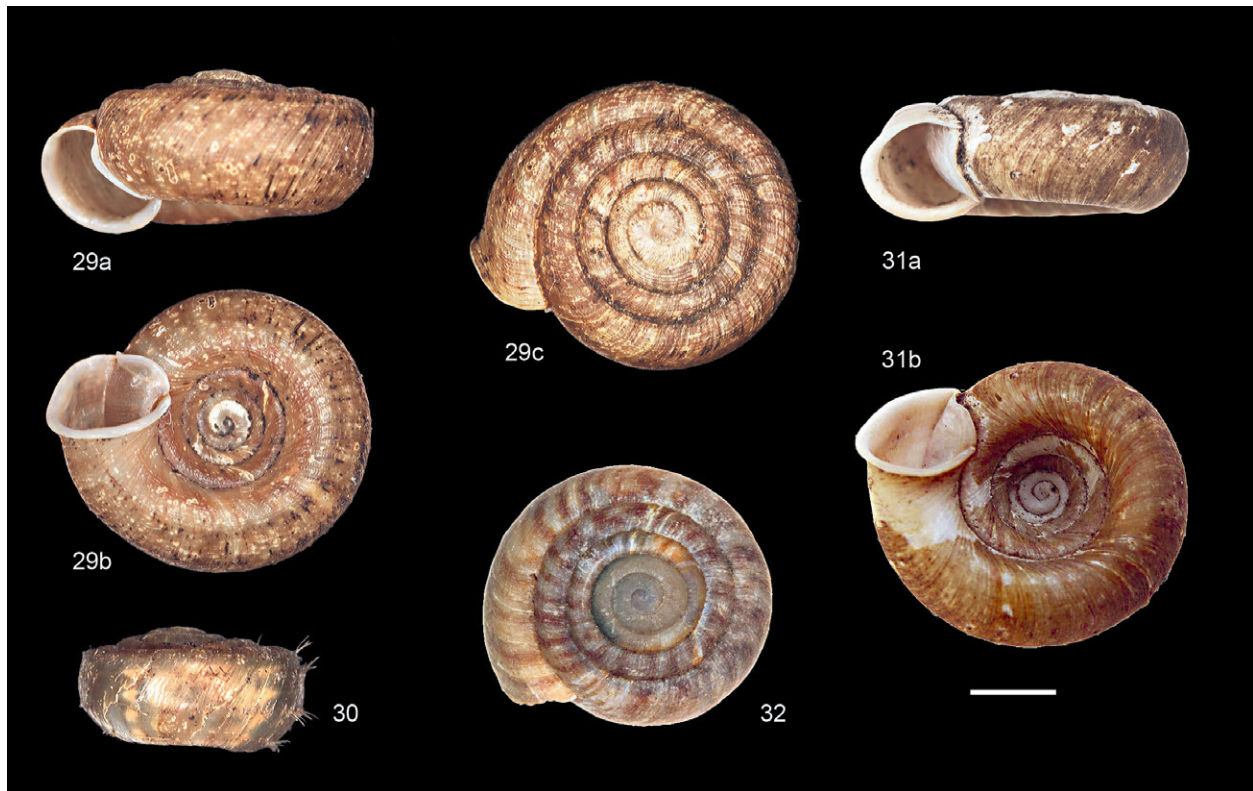
ZooBank registration. urn:lsid:zoobank.org:act:B05BE0A4-D2FE-4899-9DEC-6BCB680C844F

Type series. District Pemagatshel, Nganglam, ca 500 m a.s.l., 26°50'N 91°15'E, Sherub leg. 6/8-11-2018 (NBCB1245/ holotype, 1246/7 paratypes; RMNH.MOL.507906/3 paratypes). District Samdrup Jongkhar, 9 km N of Samdrup Jongkhar, 1094 m a.s.l., warm broadleaf forest, 26°52'N 91°30'E, Sherub & Ugyen Tenzin leg. i.2020 (NBCB1252/2 paratypes).

Diagnosis. Shell with slightly curved sides, a moderately prominent keel, and a low conical spire, W > 14 mm, H > 7 mm, hairs unknown; palatal plicae undivided.

Description ($n = 13$). The shell has $6\frac{1}{2}$ – $7\frac{1}{4}$ whorls and a low, conical spire, bordered by a moderately prominent keel with a narrow furrow that remains visible on the entire teleoconch. The sides are oblique and only little convex. The final part of the body whorl descends to about the upper third of the penultimate whorl. It has regularly spaced, dark reddish blotches on top and corresponding stripes on the sides. The umbilicus is moderately wide.

The protoconch has 3 – $3\frac{1}{4}$ whorls; after the first whorl, that is more or less worn in all shells, there are only rather coarse, radial riblets, more widely spaced than their own width. The adjoining teleoconch whorls are fairly convex; they have 6 or 7 rather coarse spiral ridges, crossed by similarly widely spaced, equally prominent radial ridges, resulting in a squarish sculpture. The sides of the shell have dense oblique growth lines and a vague pattern of spiral lirae, which are more prominent at the umbilical bend and inside the umbilicus, where a reticulate pattern is more or less clearly developed. Remains of a thick, light brown, felty periostracum are present on some shells; in the holotype there is a short row of hair-stumps, attached to the narrow furrow on the spire.



Figures 29–32. *Endothyrella* spec. **29, 30.** *E. spirostriata* Gittenberger, Leda, Sherub & Páll-Gergely, 2018, 7 km E of Pemagatshel, fully grown shell, holotype (NBCB26) (**29**) and paratype, juvenile (NBCB27) (**30**) with 4 rows of hairs. **31, 32.** *E. pemagatshel* Gittenberger, Leda, Sherub & Páll-Gergely, 2018, fully grown shell (NBCB1237) (**31**) and subadult (**32**) showing the periostracum and colour pattern (RMNH.MOL.507904). Scale bars: 0.5 cm (**29, 30**) and 1.0 cm (**31, 32**).

The parietal lamella is asymmetrical; adapically, after an indentation, it forms a short, lamella-like extension pointing anteriorly, and basally it is slightly thickened in the same direction. The anterior part of the bipartite lower plica runs next to the lamella; it is inconspicuous, short, and the posterior part is situated deeper inside the shell. The lamella is accompanied posteriorly by a separate basal denticle and an elongated, upper “denticle” (Fig. 17). The suturalis is much shorter and thinner than the other palatal lamellae, apart from an even smaller accessory plica. The suprapalatalis has a long, straight, lamella-like anterior part; it ends posteriorly with a wide S-like curve. The anterior part of the upper palatalis is clearly shorter than that of the lower palatalis; it is lacking in the infrapalatalis, which is thickened obliquely towards the basalis. The basalis is as prominent as the other palatal folds; it ends posteriorly next to the short and inconspicuous posterior part of the parietal lower plica and anteriorly it reaches clearly further than the lamella. The most prominent, posterior parts of the central palatal folds are interconnected by a narrow, low callous ridge.

Measurements. The shells from the type locality ($n = 8$) have 7–7¼ whorls and measure W 14.5–15.9 mm, H 8.0–8.9 mm. The shells from north of Samdrup Jongkhar ($n = 2$)

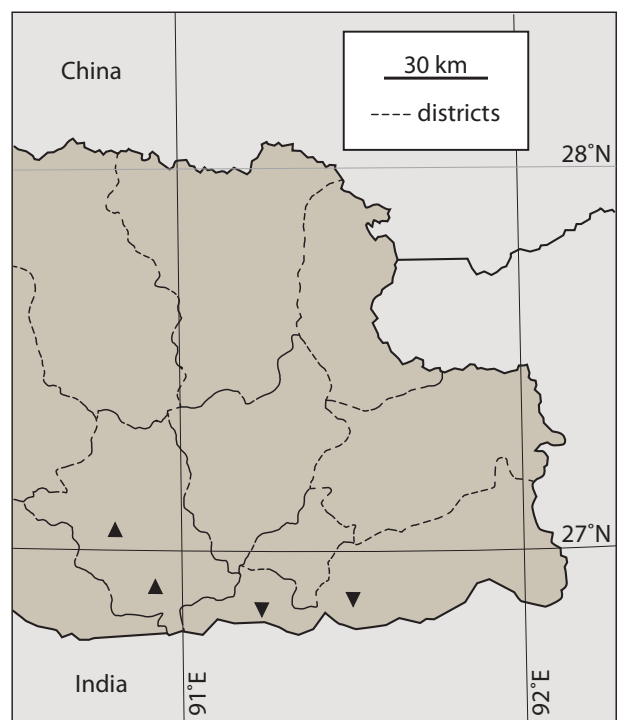
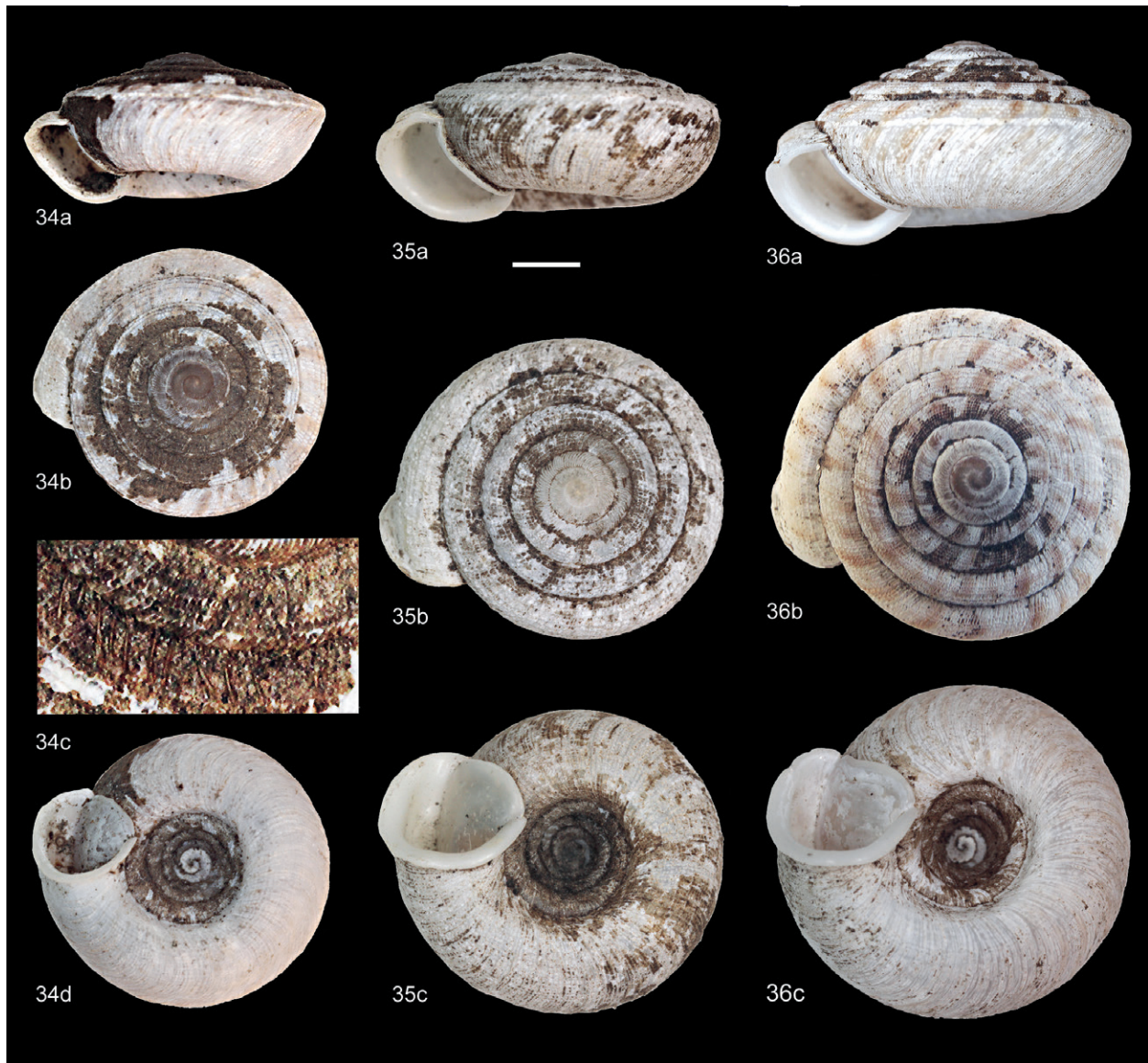


Figure 33. Records of *Endothyrella barnai* Gittenberger & Sherub, spec. nov. (▼) and *E. manasensis* Gittenberger & Sherub, spec. nov. (▲).



Figures 34–36. *Endothyrella* spec. **34.** *E. manasensis* Gittenberger & Sherub, spec. nov., holotype (NBCB1243), Manas: (c) detail of periostracum and hairs. **35, 36.** *E. barnai* Gittenberger & Sherub, spec. nov.: (35) paratype (NBCB1252), 9 km N of Samdrup Jongkhar; (36) holotype (NBCB1245), Nganglam.

have 6½ whorls and measure W 15.0, H 7.6 mm, and W 14.8, H 7.4 mm. Holotype: 15.9 × 8.7 mm. U 35–36% W.

Differentiation. *Endothyrella barnai* is most similar to *E. manasensis*, while differing by being slightly larger, with less straight sides, a narrower umbilicus, and a larger aperture.

Etymology. The epithet *barnai* refers to Barna Páll-Gergely, the first author of a fundamental article about *Endothyrella*.

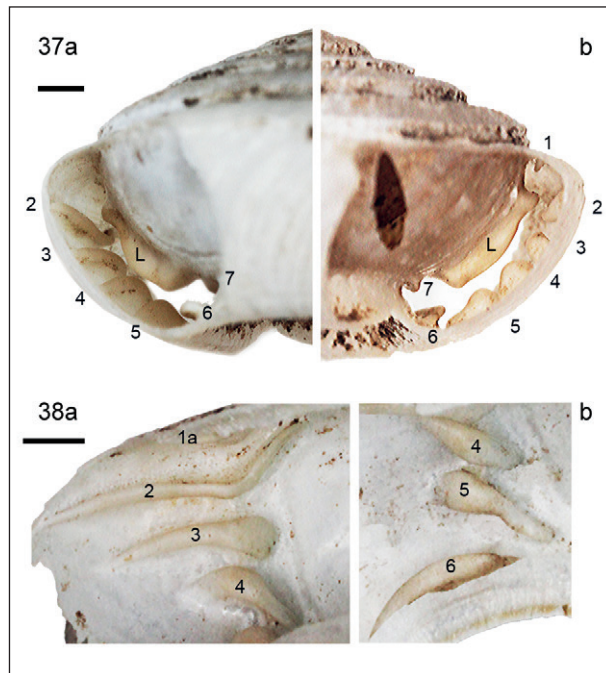
***Endothyrella plectostoma* (Benson, 1836)**

Figures 4, 18–20, 23, 28

Helix plectostoma Benson, 1836: 351 (p. 350: “North-East frontier of Bengal”).

Endothyrella plectostoma—Páll-Gergely et al., 2015: 54, figs 6D, 13A, B, 19E, F, 20 D, E, 22A, D–F, 26.; 2017: 174, figs 6D, 13A, B, 19E, F, 20 D, E, 22A, D–F, 26.

Material. District Pemagatshel: Nganglam, ca 500 m a.s.l., 26°50′N 91°15′E, Sherub leg. 6/8-11-2018 (NBCB 1271/4). District Samdrup Jongkhar: 4 km NW of Samdrup Jongkhar, 260 m a.s.l., 26°49′N 91°28′E, E. Gittenberger, Choki Gyeltshen & Kezang Tobgay leg. 29.ix.2019 (NBCB 1270/8; RMNH.MOL.507907/2); N of Bangtar, Phuntshothang, 26°53′N 91°42′E, 375 m a.s.l., Choki Gyeltshen & Mani Prasad Nirola leg. 23.i.2022 (NBCB1334/4); Bangtar, 26°53′N 91°43′E, 386 m a.s.l., Choki Gyeltshen & Mani Prasad Nirola leg. 25.i.2022 (NBCB1333/15); 7 km NNW of Jomotshangkha, Toka Phu, 940 m a.s.l., 26°57′N 92°04′E,



Figures 37, 38. *Endothyrella barnai* Gittenberger & Sherub, spec. nov., 9 km N of Samdrup Jongkhar, paratypes. **37.** Apertural callosities (NBCB1246): (a) anterior side; (b) posterior. **38.** Palatal callosities (RMNH.MOL.507906). Abbreviation: L = parietal lamella. The plicae are numbered: 1 = suturalis, 1a = accessory plica, 2 = suprapalatalis 3 = upper palatalis, 4 = lower palatalis, 5 = infrapalatalis, 6 = basalis, 7 = lower parietal plica. Scale bars: 1 mm.

Sherub leg. 15.vi.2019 (NBCB1268/2). District Sarpang; Royal Manas National Park, 26°53'N 90°54'E, 310 m a.s.l.; Sherub leg. 05.ii.2020 (NBCB1254/2). District Trashiyangtse, Trashiyangtse, 27°37'N 91°29'E, 1765 m a.s.l., Choki Gyeltshen leg. 2022 NBCB1332/10; RMNH.MOL.507909/2). District Zhemgang: ca 7 km S of Panbang, 157 m a.s.l., 26°49'N 90°56'E, Choki Gyeltshen & Nima Gyeltshen leg. 09.ii.2018 (NBCB1269/8; RMNH.MOL.507910/4); 2.5 km NW of Panbang, roadside, 180 m a.s.l., 26°52'N 90°56'E, E. Gittenberger, Choki Gyeltshen & Pema Leda leg. 24.x.2018 (NBCB1267/8; RMNH.MOL.507911/2).

Diagnosis. Spire low conical; with 5 rows of hairs; upper part of the parietal lamella connected to a long main plica, 2 or 3 bipartite palatal plicae.

Description ($n = 40$). The yellowish-brown shell has 5½–6 whorls, a low conical spire and slightly angular sides in accordance with the arrangement of the 5 rows of up to 0.9 mm long hairs. The upper 2 rows are closest and separated from the lower 3 rows by a straight, relatively long part of the shell wall. The final part of the body whorl descends to about halfway the penultimate whorl. The umbilicus comprises about a quarter of the total width.

The protoconch has 2½–2¾ whorls; from the apex on there are increasingly prominent, dense, radial riblets and on its final half 1 or 2 spiral ridges next to the suture. The

teleoconch whorls have sharp radial ridges, that are initially more prominent than the spiral lines. On the penultimate whorl there is a delicate, reticulate sculpture with 8–12 spiral lines between the sutures; additionally, the last whorl has more widely spaced radial riblets with periostracal fringes and hairs. The spiral sculpture may become obsolete on the sides of the shell; inside the umbilicus there are sharp oblique radial ridges.

The apertural lip is broadly reflected but little thickened; the parietal callus is moderately strong. There is a symmetrical lamella connected with its upper part to a long main plica (Fig. 19). The anterior part of the bipartite lower plica reaches less far forwards than the main plica; the obsolete posterior part of the lower plica is hardly a denticle, situated somewhat deeper inside the whorl than the two denticles behind the lamella. There is a short suturalis. The suprapalatalis has a long, straight anterior part, ending posteriorly with a conspicuous S-like twist. The upper palatalis has a shorter anterior part, still weakly connected with a thicker, oblique posterior part. The lower palatalis and the infrapalatalis are widely bipartite, with a short, spiral, anterior part and a much thicker, oblique posterior part. The uniform basalis is relatively high and short; it is situated opposite the middle of the main palatal folds, which are connected by a conspicuous callous ridge.

Measurements. W 7.7–9.3 mm, H 4.4–5.4 mm, U 23.5–27.0% W.

Genitalia. The genital anatomy of this species was described by Páll-Gergely et al. (2015: 56, 57, fig. 26; 2017: 176, 177, fig. 26). The genitalia of a specimen from 4 km NW of Samdrup Jongkhar are very similar. The penis increases in width from the proximal part to the distal part, which has a slight swelling. The prominent, slender caecum is about half as broad as the proximal penis; the penial retractor muscle inserts at its end. The lumen of the caecum has ca 7 nearly parallel ridges, which become interconnected in the adjoining part of the penis. The bursa copulatrix is longer than the smaller diverticulum. The vagina is as long as the penis and equally broad over its entire length.

Distribution. According to Páll-Gergely et al. (2015: 58; 2017: 176), *E. plectostoma* is widespread in North-East India, Bangladesh, Myanmar, and maybe Thailand. In Bhutan it is known from the south-east part of the country, at 157–1765 m a.s.l.

Notes. In 2 juvenile shells of 3½ and 3¾ whorls, apertural barriers are situated ¼ whorl from the apertural border.

***Endothyrella pterocallus* Gittenberger, Gyeltshen & Tobgay, spec. nov.**

Figures 6, 7, 21, 22, 24, 27, 28

ZooBank registration. urn:lsid:zoobank.org:act:779D9E73-94D8-4D1D-B55A-6A2DB4893936

Type series. District Mongar, 35 km ENE of Mongar, 2100 m a.s.l., 27°18'N 91°19'E, E. Gittenberger, Choki Gyeltsen & Kezang Tobgay leg. 30.ix.2019 (NBCB1266/holo-type, 1282/3 paratypes; RMNH.MOL.507912/2 paratypes).

Diagnosis. Spire low conical, with 6 or 7 rows of hairs; parietal lamella accompanied by wing-like callosities posteriorly; 4 middle palatal plicae bipartite.

Description ($n = 6$). The transparent, fragile shell is light brown with irregular whitish spots; it has a low conical spire, $4\frac{7}{8}$ – $5\frac{1}{4}$ shouldered whorls separated by a deeply incised suture, and regularly curved sides. The final part of the body whorl descends to about the upper third of the penultimate whorl. The umbilicus comprises about a third of the total width.

The protoconch has 2 – $2\frac{1}{4}$ whorls; from the apex on there are dense radial riblets, after $1\frac{1}{8}$ – $1\frac{1}{4}$ whorl accompanied by a prominent spiral ridge about halfway the whorl. The initial teleoconch whorls have dense, blunt radial riblets crossed by equally blunt spiral ridges; there are ca 6 vague spiral ridges between the sutures on the penultimate whorl and ca 4 next to the suture on the shoulder. The sides of the shell have irregular growth lines and radial periostracal ridges; inside the umbilicus there are dense, oblique, sharp ridges only. On the penultimate whorl there is a single row of hairs; the last whorl has 6 ($n = 5$) or 7 ($n = 1$) spiral rows of hairs that are up to 0.5 mm long

The apertural lip is reflected; the parietal callus is only slightly protruding. The lamella is regularly curved and symmetrical apart from being slightly lower adapically; it has no protruding parts. At the posterior side the lamella is connected to two symmetrically diverging plicae. The uniform lower plica has a blunt ending next to the lamella; gradually lowering it reaches little further than the basalis towards the aperture. The thin suturalis is shorter than the broader basalis that has a faint indentation halfway. The four central palatal plicae are bipartite, with short but high, lamella-like anterior parts and broadened, more denticle-like posterior parts. Only in the suprapalatalis and the upper palatalis the two parts are weakly connected. In between the infrapalatalis, the most prominent of the plicae, and the basalis, there is a short, transverse plica.

Measurements ($n = 2$). W 5.6–5.8 mm, H 3.3–3.4 mm, U ca 33% W. Holotype: 5.8×3.3 mm.

Differentiation. Nearly all other *Endothyrella* species differ by another number of spiral rows of hairs. In *E. blanda* there may be 7 rows as in one of the 6 shells known of *E. pterocallus*; the former species differs by the presence of denticles posterior of the parietal lamella, a less prominently sculptured protoconch and a much less prominent penial caecum.

Genitalia. While trying to remove the body from the only specimen collected alive, the genital tract was broken. Apart from the entire vagina, an important part of the male genitalia was also recovered (Fig. 27). The penis has

a narrow proximal part with a straight, simple lumen. In the much broader distal part, there is an irregular pattern of ridges on the luminal wall, with several spindle-shaped granules; near the insertion of the vas deferens there is a prominent penial thickening. The lumen of the broad basal half of the caecum has a pattern of interconnected ridges with several spindle-shaped granules in between, changing into ca 10 parallel ridges in its narrower distal half. A penial retractor muscle left no traces. The available part of the epiphallus has a simple lumen. The vagina has a spindle-shaped broadening in the distal third, narrowing again before the attachment of the pedunculus of the bursa copulatrix, which is about as broad as the spermoviductus there.

Etymology. The epithet *pterocallus* refers to the wing-like callus formation posterior of the lamella (*G ptero* after pteryx = wing; *L callus* = callus).

Discussion

We accept the classification of *Endothyrella* as proposed by Páll-Gergely et al. (2015, 2017), which is based nearly exclusively on shell morphology. There are conspicuous differences in dimensions among the species. Shell width varies from 4 mm in *E. minor* (Godwin-Austen, 1879) (Páll-Gergely et al., 2015: 46, 2017: 166) to 20.3 mm in *E. fultoni* (Godwin-Austen, 1892) (Páll-Gergely et al., 2015: 39; 2017: 160). The species are either sinistral or dextral. We are not aware of character states supporting a subdivision of *Endothyrella* based on coiling direction.

Mixed chirality is known for *E. nepalica*, but only from a single population in Nepal. A dextral shell of that species, accompanied by 5 sinistral ones, is present in the collection of the late W.J.M. Maassen (now RMNH). The shells were found by A.G. Kuznetsov, according to the original label at the “NW end of Kathmandu, middle part of S slope of Swayambhunath hill”, at “1500 m”. The dextral shell had a separate label with “f. dextrorsa”, “extrem. rare”, suggesting that it is not a unique dextral shell that was donated to Mr Maassen.

The differences in apertural callosities, e.g. the presence of bipartite versus single plicae, cannot be correlated with other character states. *Endothyrella blanda* and *E. bhutanensis* are similar in shell characters and might be closely related, if not sister-species, like *E. manasensis* and *E. barnai*, but the similarities of the other Bhutanese species are less easily interpreted.

Details regarding the structure of the genitalia are known for only 8 *Endothyrella* species.

The structure of the penial caecum varies considerably so that 4 groups are distinguished provisionally. In group 1, *E. blanda* there is hardly any caecum (Páll-Gergely et al., 2015: 32, 34, fig. 18; 2017: 153, 156, fig. 18). In group 2, including *E. bhutanensis* (Fig. 25), the penial retractor



Figure 39. The roadside NW of Pemagatshel, type locality of *E. pemagatshel*, where one of these children may have collected the holotype, 16.iv.2015. With Pema Leda at the left, participant in the molluscan inventory team since 2013, and our driver at the right. Photograph by Adriana C. Gittenberger-de Groot.

muscle inserts next to the basis of a prominent caecum with a rounded tip, thick walls and a simple lumen. In group 3, including *E. spirostriata* (Fig. 26), the vas deferens and the pointed distal end of the penis are grown together; the retractor muscle inserts at the tip of this structure. The remaining 5 species form group 4, characterized by a prominent caecum with the penial retractor inserting at its top (Figs 23, 24?). These groups cannot be characterized by shell morphology. In *E. fultoni* (Páll-Gergely et al., 2015: 39, 40, fig. 21; 2017: 160, 161, fig. 21) and maybe also in *E. pterocallus* the retractor muscle inserts near a globular, penial thickening at the rounded end of a prominent, broad caecum with several, parallel, longitudinal ridges in the lumen. A retractor muscle inserted on a similar but smaller caecum (its lumen is not mentioned) is described for *E. nepalica* (Páll-Gergely et al., 2015: 49, 53, fig. 25; 2017: 169, 173, fig. 25). In *E. plectostoma* (Fig. 23; Páll-Gergely et al., 2015: 56, 57, fig. 26; 2017: 177, 178, fig. 26) the lumen of the caecum is narrowed by several parallel ridges as in *E. fultoni* and *E. pterocallus*. A narrow retractor muscle inserted at a much broader penial caecum, with the vas deferens inserting more proximally, was illustrated by Godwin-Austen (1907: pl. 114 fig. 2a) for *E. pinacis* (Benson, 1859).

Nearly a third of all *Endothyrella* species known, i.e., 9 of 30, occur in Bhutan. Only 2 of these species are also known from elsewhere.

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