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Ptychotrema (Gastropoda: Streptaxidae) in north-east Africa: thirteen new species from Ethiopia reveal the presence of a diverse but little-known fauna

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Abstract. This paper reports on the *Ptychotrema* fauna of Ethiopia and other countries of north-east Africa (Somalia, Eritrea, Djibouti). It describes 13 new species that were collected during two short visits to Ethiopia in 2015 and reviews and figures the other species that have been attributed to *Ptychotrema* from the region. It provides an identification key based on adult shell characters. The new species are assigned to subgenus *Parennea* (five species) or subgenus *Ennea* (eight species) based on apertural dentition. These subgenera are adopted for pragmatic reasons, and it is recognised that they are almost certainly artificial categories. The introduced species are *Ptychotrema* (*Parennea*) *bishanwakaense* sp. nov., *P.* (*Pa.*) *dolfi* sp. nov., *P.* (*Pa.*) *wondogenetense* sp. nov., *P.* (*Pa.*) *keffaense* sp. nov., *P.* (*Pa.*) *gaysayense* sp. nov. and *Ptychotrema* (*Ennea*) *aethiops* sp. nov., *P.* (*E.*) *unumiugum* sp. nov., *P.* (*E.*) *harennae* sp. nov., *P.* (*E.*) *canaliculatum* sp. nov., *P.* (*E.*) *balenense* sp. nov., *P.* (*E.*) *epicratis* sp. nov., *P.* (*E.*) *wiersbowskyi* sp. nov., and *P.* (*E.*) *propenanum* sp. nov. The identification of so many undescribed species, following such a short period of fieldwork, highlights just how poorly the Ethiopian streptaxid fauna is known. They increase the number of streptaxid species known from Ethiopia and Eritrea by about 50%, and the number of *Ptychotrema* reported from the "Horn of Africa" from seven to 20. The ecological and biogeographical implications are discussed.

Key words. *Parennea*, *Ennea*, Afromontane, biogeography, refugia, land snail

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Introduction

In 2015, I participated in two expeditions to southern Ethiopia. My involvement concerned the collection of land-snail material, although the expeditions were conducted with entomologists under the auspices of the Ethiopia Insects Project, which was established in 2013 by the Ethiopian Wildlife Conservation Authority, the Bavarian State Collection of Zoology (Germany), and the Thomas Witt Foundation (Germany). The two areas visited were centred on the Kafa Biosphere Reserve and the Bale Mountains National Park, although several sites outside these protected areas were also sampled. These two areas lie to the west and east of the African Great Rift Valley, respectively.

This paper deals with species attributed to *Ptychotrema* hitherto reported from north-east Africa, including several that are probably better classified in other genera. It introduces several further species from Ethiopia that are all assigned to *Parennea* or *Ennea*, which are here treated as subgenera of *Ptychotrema*, as proposed by Pilsbry (1919) and subsequently maintained by various authors including Adam and Van Goethem (1978), van Bruggen (1989), and Adam *et al.* (1994). Pilsbry's (1919) subgenera were based entirely on apertural dentition, with *Parennea* and *Ennea* being characterised, respectively, by the presence of either one or two entering palatal folds with corresponding dorsal furrows on the back of the last whorl. However, in some species the lower palatal fold and external furrow are poorly developed, and the distinction between the two subgenera may be unclear. De Winter & de Gier (2019: 23) commented that "some species now attributed to *Parennea* may be more related to some *Ennea* species and vice versa", and Adam & Van Goethem (1978) and van Bruggen (1989) gave examples of species with characters that are intermediate between *Parennea* and *Ennea*.

The taxonomic status of *Parennea* and *Ennea* as subgenera is by no means clear. Some authors have raised them to generic rank (e.g. Zilch 1960; Schileyko 2000) or provisionally to generic rank (de Winter 2008; de Winter & de Gier 2019), whereas MolluscaBase (MolluscaBase Eds 2024a) prefers not to accept either *Ennea* or *Parennea* as subgenera, assigning all species to genus *Ptychotrema*. Rowson (2010: 232) used morphological and molecular characters to identify a well-supported clade to which he considered the name *Ptychotrema* applicable, and he also confirmed that it contained species referred to subgenus *Ennea.* Rowson (2010: 221) did not provide molecular data for *Parennea* but commented that his analysis "does little to challenge the classification" of other subgenera, including *Parennea*. De Winter & de Gier (2019) questioned whether either were likely to be monophyletic groups. They noted significant differences in the shells of species attributed to *Parennea* and of most *Ennea* to those of *Ptychotrema*, so preferred "not to treat these taxa as subgenera of *Ptychotrema*, which would imply a close relationship between them, which in our opinion is very unlikely". Evidently, further revision will be needed to clarify this situation, so in the meantime I prefer to adopt Pilsbry's (1919) original classification, albeit largely for pragmatic reasons.

Adam and Van Goethem (1978) and van Bruggen (1989) provided detailed reviews of *Parennea,* with van Bruggen's contribution also including information on distribution and ecology. Since these papers, further distributional information has been provided by Wronski & Hausdorf (2009), and de Winter (2008) and Tattersfield (1998) have described new *Parennea* species from West Africa and Tanzania, respectively. *Ennea* has not been subject to such comprehensive examination, although Pilsbry (1919), Adam *et al.* (1994), and de Winter & de Gier (2019) have made significant contributions to its study.

The land-snail fauna of north-east Africa (Ethiopia, Eritrea, Somalia, and Djibouti) is rather poorly known compared with the countries to the south (especially Kenya, Tanzania, and Uganda). Most information derives from collections made between 1870 and 1905 by O. Antinori, O. Beccari, A. Issel, Carl Jickeli, Carlo von Erlanger, Oscar Neumann, M. Raffray, Maurice de Rothschild, and others. These collectors' specimens were described by Morelet (1872), Jickeli (1873, 1874, 1875, 1881), Bourguignat (1883), Kobelt (1909, with corrections and additions by Haas 1932), Thiele (1933), Simroth (1904), and Neuville & Anthony (1908). Further species were added by Preston (1910) and Connolly (1928) in the first half of the 20th century, and more recently, Bernard Verdcourt published a review of eastern African *Ptychotrema* (Verdcourt, 1961), and on material collected by Hugh Scott (Verdcourt 1976, 1980) and David S. Brown (Verdcourt 1990). Geertz (2017) has most recently surveyed land snails in the Keffa (= Kaffa or Kafa) Region. Bourguignat (1883) attempted to compile the first list of species from Abyssinia, or Ethiopia, and this was updated by Connolly (1928) and Bacci (1951).

Nine species classified in *Ptychotrema* have hitherto been reported from north-east Africa, and of these, two have been assigned to *Parennea*, four to *Ennea*, and one to *Ptychotrema*. These are *P.* (*Parennea*) *tshibindanum septentrionale* Verdcourt, 1985, *P.* (*Parennea*) *somaliense* Verdcourt, 1961, *P.* (*Ennea*) *hyalinum* Thiele, 1933, *P.* (*Ennea*) *laeve* Thiele, 1933, *P.* (*Ennea*) *massauense* Thiele, 1933 and *P.* (*Ennea*) *denticulatum* Morelet, 1872 (including varieties *nana* Connolly, 1928, *hamacenica* (Bourguignat, 1883), *hildebrandti* (Jickeli, 1874), and *papilliferum* (Jickeli, 1873) (= *quinqueplicatum* (Bourguignat, 1883)), and *Ptychotrema gratum* Thiele, 1933 (although see below for discussion of the classification of *P. gratum*). The two remaining species, *P. roberti* (Preston, 1910) and *P. raffrayi* (Bourguignat, 1883), are more appropriately assigned to other genera.

This paper provides photographs and an identification key to the adult shells of species attributed to *Ptychotrema* reported from north-east Africa and introduces a further 13 species.

Materials and Methods

Study Areas

Molluscs were sampled in 2015 in forest and woodland habitats in south-west Ethiopia, in the Bale Mountains and at one site near the town of in Wondo Genet (Fig. 1, Tables 1, 2). These areas are all within the Eastern Afromontane Biodiversity Hotspot (Mittermeier *et al.* 2004).

South-west Ethiopia. Fourteen forest and woodland sites ranging from 1388 m to 2486 m in elevation were sampled in south-west Ethiopia to the west of the Great Rift Valley. Most of the sites contained Afromontane rainforest, which, according to Friis (1992), lies between 1500 and 2600 m, but the sites in the west of the study area (especially Bishan Waka Lake (1388 m) but also Sheko (1564–1567 m) and Dembi Forests (1400 m)) had affinities with Transitional rain forest (Friis 1992). The highest site, Boka Forest (2479 m) was rather distinctive because of the presence of the upland tree *Hagenia abyssinica* (Bruce) J.F. Gmel., and stands of bamboo, which are both characteristic of high-elevation areas in eastern Africa.

All sites were in or near the Kafa Biosphere Reserve (Table 1, Fig. 1), which lies about 460 km to the south-west

SW Ethiopia – Kafa Biosphere Reserve

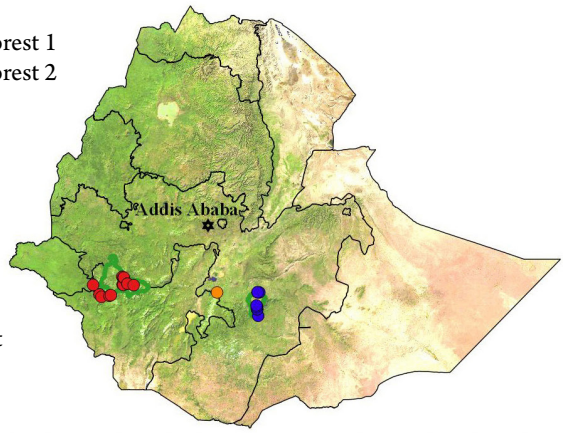
1 Sheko Forest 1
2 Sheko Forest 2
3 Dembi Forest
4 Wacha Maji
5 Boka Forest (Mizan Teferi)
6 Bishan Waka Lake
7 Komba Forest 1
8 Komba Forest 2
9 Bodinga Forest 1
10 Bodinga Forest 2
11 Bodinga Forest 3
12 Shorori wetland forest 1
13 Shorori wetland forest 2
14 Boka Forest (Bonga FR)

Bale Mountains

15 Dinsho
16 Gaysay grasslands forest 1
17 Gaysay grasslands forest 2
18 Harenna Forest 1
19 Harenna Forest 2
20 Harenna Forest 3
21 Harenna Forest 4
22 Harenna Forest 5
23 Harenna Forest 6

Wondo Genet

24 Wondo Genet forest



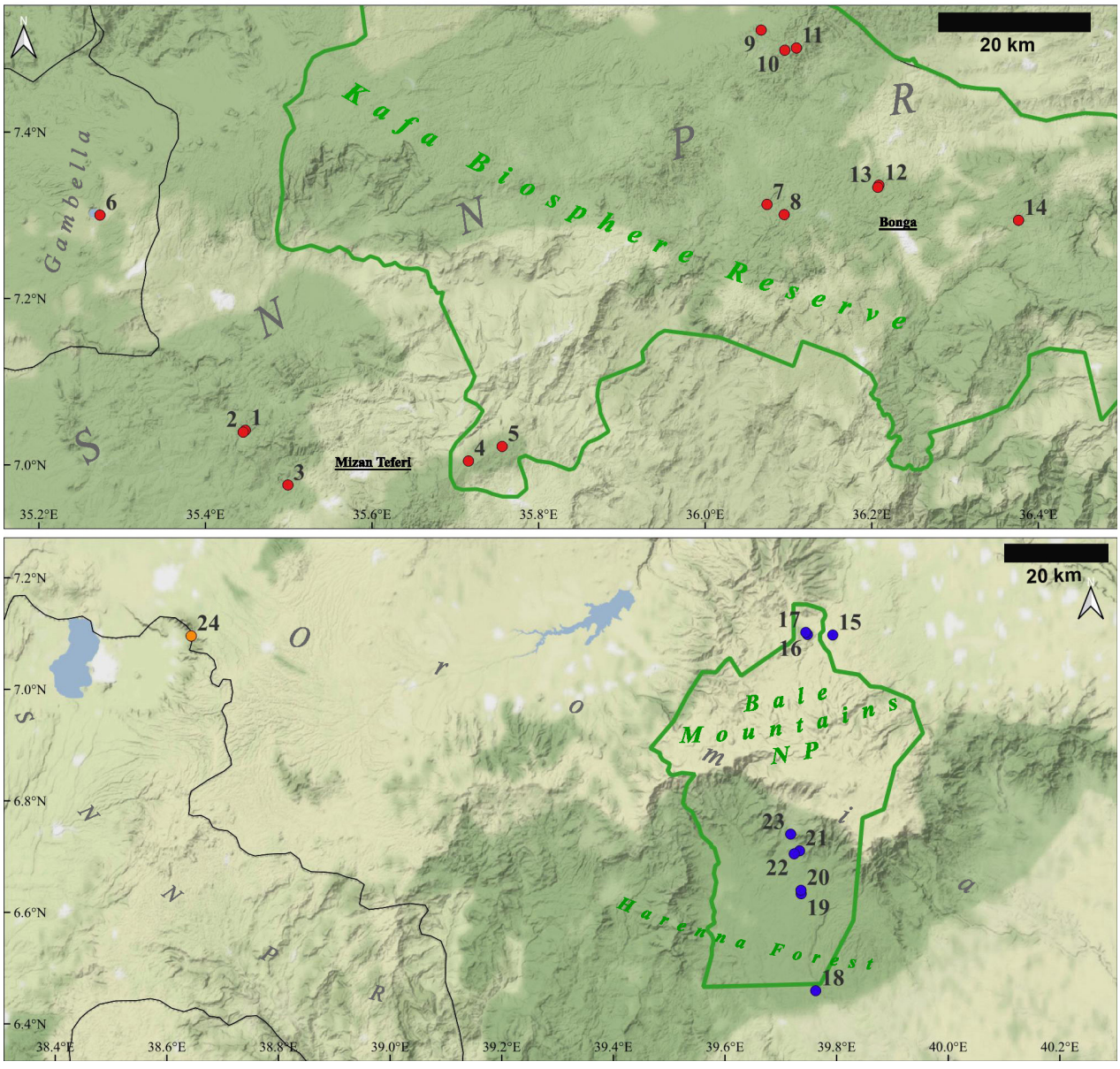


Figure 1. Locations of the 2015 sampling sites in and around the Kafa Biosphere Reserve, Bale Mountains National Park and at Wondo Genet, Ethiopia.

Table 1. Site names, geographic coordinates, altitudes, and other locality information for 24 collecting sites in and around Kafa Biosphere Reserve, the Bale Mountains National Park and at Wondo Genet, Ethiopia, in 2015. See Table 2 for descriptions of habitats at these sites.

Site	Site name	Survey date	Region	Zone	Woreda	Latitude (°N)	Longitude (°E)	Altitude (m)
SW Ethiopia: Kafa Biosphere Reserve								
1	Sheko Forest 1	13-04-2015	SNNPR	Bench Maji	Sheko	07.042	035.448	1567
2	Sheko Forest 2	13-04-2015	SNNPR	Bench Maji	Sheko	07.039	035.445	1564
3	Dembi Forest	14-04-2015	SNNPR	Bench Maji	Dehub Bench	06.976	035.499	1400
4	Wacha Maji	15-04-2015	SNNPR	Keffa	Chena	07.005	035.716	2342
5	Boka Forest (Mizan Teferi)	15-04-2015	SNNPR	Bench Maji	Shay Bench	07.022	035.756	2486
6	Bishan Waka Lake	16-04-2015	Gambela	Majang	Mengesh	07.300	035.273	1388
7	Komba Forest 1	19-04-2015	SNNPR	Keffa	Gimbo	07.313	036.074	1930
8	Komba Forest 2	19-04-2015	SNNPR	Keffa	Gimbo	07.301	036.095	1998
9	Bodinga Forest 1	20-04-2015	SNNPR	Keffa	Gewata	07.523	036.067	1710
10	Bodinga Forest 2	20-04-2015	SNNPR	Keffa	Gewata	07.498	036.096	2163
11	Bodinga Forest 3	20-04-2015	SNNPR	Keffa	Gewata	07.501	036.110	2121
12	Shorori wetland Forest 1	22-04-2015	SNNPR	Keffa	Gimbo	07.336	036.208	1623
13	Shorori wetland Forest 2	22-04-2015	SNNPR	Keffa	Gimbo	07.334	036.207	1604
14	Boka Forest (Bonga FR)	23-04-2015	SNNPR	Keffa	Menjiwo	07.294	036.376	2479
Bale Mountains								
15	Dinsho	08-12-2015	Oromia	Bale	Dinsho	07.097	039.793	3200
16	Gaysay grasslands Forest 1	09-12-2015	Oromia	Bale	Dinsho	07.098	039.748	3173
17	Gaysay grasslands Forest 2	09-12-2015	Oromia	Bale	Dinsho	07.102	039.745	3219
18	Harenna Forest 1	13-12-2015	Oromia	Bale	Goba	06.459	039.762	1487
19	Harenna Forest 2	13-12-2015	Oromia	Bale	Goba	06.633	039.736	1894
20	Harenna Forest 3	13-12-2015	Oromia	Bale	Goba	06.640	039.736	1904
21	Harenna Forest 4	12-12-2015	Oromia	Bale	Goba	06.710	039.734	2360
22	Harenna Forest 5	12-12-2015	Oromia	Bale	Goba	06.705	039.724	2420
23	Harenna Forest 6	15-12-2015	Oromia	Bale	Goba	06.740	039.718	2665
Wondo Genet								
24	Wondo Genet Forest	17-12-2015	SNNPR	Sidama	Wondo Genet	07.096	038.644	1950

of Addis Ababa. The Biosphere Reserve has high biodiversity importance (NABU 2017) and is the centre of origin and a key locality of genetic diversity of *Coffea arabica* L. According to NABU (2017) about 47% of the Biosphere Reserve supports natural cloud- and rainforest communities, and it also contains areas of bamboo forest, grasslands, shrublands, and some quite extensive wetlands. The area experiences a bimodal rainfall pattern, with the main rainy season between June and September and a short rainy period from February to April. It is the most humid part of Ethiopia, with only 2–4 dry months in the year (NABU 2017). Mean annual rainfall ranges from 1500 mm in the lowlands up to 2000 mm at the highest elevations (NABU 2017; EWNHS 2008), although there is considerable local variation, and, according to Gamachu (1977), annual temperatures vary between 15 and 24 °C. These ranges are consistent with figures obtained by interrogation of the Worldclim climate layers datatset (30 second of arc resolution) (Fick and Hijmans 2017) that returned ranges for mean annual rainfall and mean annual temperature of 1436–1920 mm per year and 15.5–20.9 °C, respectively, across the 14 sites.

Bale Mountains. Molluscs were sampled at nine forest sites in and around the Bale Mountains National Park, to the east of the Great Rift Valley (Table 1, Fig. 1). Three sites were at high elevations (3173–3219 m) on the north side of the Bale massif around the town of Dinsho. Their structure was open, with extensive grassy areas and characteristic high-elevation plants including *Hagenia abyssinica* and *Hypericum revolutum* Vahl. The other six sites were taken at various elevations in Harenna Forest, which dominates the southern slopes of the Bale massif and is the largest continuous forest block in Ethi-

Table 2. Descriptions of habitats at mollusc sampling sites in south-west Ethiopia, Bale Mountains and at Wondo Genet. Table 1 provides geographical information of these sites.

Site	Site Name	Description
SW Ethiopia: Kafa Biosphere Reserve		
1	Sheko Forest 1	Forest with broken canopy (*c.* 35 m) and a few large buttress-rooted emergents to about 35 m; fallen trees. Understorey shrubs largely cleared apart from cultivated coffee; herbaceous plants abundant in field layer.
2	Sheko Forest 2	Similar to Sheko Forest 1 but with a denser understorey and lower herb cover; on a steep slope
3	Dembi Forest	Forest in steep valley in spray zone of waterfall, with dripping mossy/*Selaginella*- and *Impatiens*-dominated banks. Sample also taken from a close by area of scrubby disturbed woodland, with a low shrub canopy (*c.* 10–15m) and grasses and other herbs in field layer.
4	Wacha Maji	Disturbed forest with very broken canopy and dense shrub layer; steep slope, small streams.
5	Boka Forest (Mizan Teferi)	Largely cleared forest with a few remaining trees; dense scrubby understorey, on flat plateau on top of ridge
6	Bishan Waka Lake	Narrow belt of Afromontane/Transitional forest (*c.* 100–150 m wide) on slopes around Bishan Waka Lake. Disturbed by human use, especially grazing.
7	Komba Forest 1	Forest, intact (60–80% tree canopy cover, 45 m tall) plus emergents to 50 m. Dense understorey. Abundant *Dracena.* Fallen tree with ferns on trunk. Little human disturbance apart from weak paths.
8	Komba Forest 2	Dense, tall forest with tree ferns, lianes, *Impatiens*. Steeply incised small stream valley. Few large trees, but one fallen tree acrosss stream.
9	Bodinga Forest 1	Mature forest (*c.* 45 m canopy height and 40–60% canopy cover) with large trees and coffee-dominated understorey. Steep valley side. Lianes very abundant.
10	Bodinga Forest 2	Forest, grazed and disturbed with rather broken canopy (*c.* 35m) and dense shrub layer. Grasses and other herbs abundant. Evidence of timber cutting.
11	Bodinga Forest 3	Degraded, scrubby forest/woodland, with broken canopy (20–30 m tall), along valley bottom. Abundant grasses and shrubs.
12	Shorori wetland forest 1	Very disturbed forest on the lower sides of a valley, sloping down to a flat open wetland swamp. Intensive cattle grazing causing poaching and tracks; also tree cutting and fires. Low canopy cover (20–40%) and dense shrub layer.
13	Shorori wetland forest 2	Very disturbed forest on the lower sides of a valley, sloping down to a flat open wetland swamp. Less disturbed than Shorori wetland forest 1. Intensive cattle grazing; ground poached; tree cutting and fires. Includes area of *Phoenix* palm-swamp forest.
14	Boka Forest (Bonga FR)	Upper afromontane forest. Structurally diverse with large trees and abundant epiphytic ferns. More or less complete canopy, but floor is grass dominated. Abundant low shrubs, patches of bamboo. *Hagenia* at edge of forest.
Bale Mountains		
15	Dinsho	Widely spaced juniper/*Hagenia abyssinica* woodland with low canopy (*c.* 15–20 m) on grass-dominated slope. Sparse understorey. Accumulations of leaf litter in branch axils and on rocks.
16	Gaysay grasslands forest 1	Woodland with juniper, occasional *Hagenia* and *Hypericum revolutum*. Dry valley with grass-dominated field layer. Low canopy (15–20 m). Large boulders covered in herbs, grasses, ferns, and bryophytes.
17	Gaysay grasslands forest 2	Woodland in valley with small flowing stream. Large *Hagenia* and smaller juniper trees. Grass-dominated field layer.
18	Harenna Forest 1	Frequent large *Podocarpus* trees in mixed forest community. Coffee crop being promoted by clearance of other understorey shrubs. Evidence of cattle (dung), wood cutting, and coffee production.
19	Harenna Forest 2	Flat, small area of severely fragmented forest, with isolated trees interspersed with tall herbs and shrubs. No continuous canopy. Shrub layer forms canopy at 12 m.
20	Harenna Forest 3	Mature forest with widely spaced buttress-root emergents (50 m) and broken lower canopy at about 30 m. Understorey (8–10 m). Field layer with a sparse grass plus other herbs, including stinging nettle in well-illuminated areas.

Table 2. Continued.

Site	Site Name	Description
21	Harenna Forest 4	Rather fragmented mature forest, with a canopy at about 25 m and occasional large emergent trees (35 m), in the valley of a small stream. Moss covered lianes and complex structure.
22	Harenna Forest 5	Mature closed forest with dense canopy (*c.* 30 m); complex structure with several very large trees (40 m), abundant lianes, bushes, and patches of bamboo.
23	Harenna Forest 6	Very disturbed *Hagenia*-dominated woodland with abundant dead wood (from cutting). Ground cover of *Alchemilla, Trifolium*, and short grasses.
Wondo Genet		
24	Wondo Genet	Small areas of forest in base of shallow stream valley. Scrubby, rather disturbed low forest/woodland. Frequent human pathways.

opia. Harenna Forest contains a wide range of Afromontane forest types and the mollusc sampling sites, which extended across an elevational range of 1178 m, were selected to span much of this variation. Bussman (1997) described Harenna Forest as containing open-canopy dry forest types at about 1500 m, changing through forests dominated by *Podocarpus* L'Hér ex Pers. in the submontane zone (1450–1900 m) to mixed broadleaved forest types in the lower (1900–2300 m) and middle (2300–2800m) zones. The upper montane zone (2800–3250 m) contains patches of bamboo and stands of woodland and forest with *H. abyssinica*. Trees disappear in the subalpine zone, above about 3250 m, where tree heather *Erica arborea* L. dominates.

The Bale massif was formed by outpourings of lava during the Miocene and Oligocene and holds very high biodiversity value. It harbours an exceptionally high number of species endemic to Ethiopia, including molluscs (e.g. Pfarrer *et al.* 2021). It lies about 400 km to the south-east of Addis Ababa and rises from a plateau of about 2500 m elevation to the west, north, and east, with the southern slopes firstly dropping sharply from 3800 m to 2800 m and then more gradually to 1500 m. It includes the Sanetti Plateau, Africa's largest alpine plateau above 3000 m, which displays signs of former glaciation (Osmaston and Harrison 2005).

The Bale Mountains receive considerably less precipitation than the south-west Ethiopian study area. About 600–1000 mm falls annually in the lower altitude areas, increasing to 1000–1400 mm at higher altitudes, although there is considerable orographic variation and occult precipitation from mist probably also makes a significant contribution between about 2300 m and 3000 m elevation, especially during the wet season (Bussmann 1997). Rainfall is slightly bimodal, with a peak in July to October and a smaller peak in March to June. Interrogation of the Worldclim climate layers datatset (30 second of arc resolution) (Fick and Hijmans 2017) for the nine sampling sites returned values of mean annual rainfall and mean annual temperature of 885–1132 mm per year and 9.6–20.6 °C, respectively.

Wondo Genet. A single area of disturbed forest was sampled on 17 December 2015 near the town of Wondo Genet on the eastern escarpment of the Rift Valley. This site lies about 120 km to the west of the Bale Mountain sites and about 250 km to the east of Kafa Biosphere Reserve. Worldclim climate layers (Fick and Hijmans 2017) returned a mean annual rainfall of 1115 mm per year and a mean annual temperature of 16.9 °C.

Mollusc Sampling

The fieldwork was undertaken by the author and trained local assistants in April (south-west Ethiopia) and December 2015 (Bale Mountains and Wondo Genet). Molluscs were sampled by direct searching and by extracting specimens from samples of dried and sieved forest-floor leaf litter and soil. In total about 110 person hours of direct searching were completed on the 24 sites over the course of the two expeditions, and about 520 L of leaf litter were sieved and searched. Direct searching involved collecting molluscs from microhabitats such as forest floor leaf litter, on and around dead wood, on rock surfaces, and in poorly drained areas. Arboreal species were sampled by beating bushes and lower tree branches and collecting the arisings in an inverted umbrella for latter detailed study. Litter samples (typically about 20 L per site; range: 4.5–45 L) were collected in plastic bags and removed for drying, where necessary, and sieving through a stack of three sieves (minimum mesh size 0.5 mm). Each fraction was then carefully examined under sufficient lighting and all molluscs extracted.

Curation, Identification, and Description

Mollusc material was either stored dry or drowned and then preserved in 70% ethanol. It was sorted and identified using

shell characters using the taxonomic literature and museum collections. Intact adult shells were measured using vernier callipers (larger species) or a micrometer eyepiece mounted on a Meiji EMZ zoom microscope at magnification ×7–45. Shell photographs were taken in apertural, lateral, and dorsal views, with several images stacked using Helicon Focus v. 8.2.2 (Helicon Soft Ltd 2000) to increase depth of field. The number of whorls was counted in apical view under the microscope using the method given by Herbert & Kilburn (2004).

Some adaptation has been necessary, but terminology used in shell description has generally followed Herbert & Kilburn (2004); this applies in particular to the description of shell shape, shell sculpture, and whorl shape and profile.

The following abbreviations are used: H = shell height, D = shell width; h = aperture height, d = aperture width, a.s.l. = above sea level, DRC = Democratic Republic of the Congo, SNNPR = Southern Nations, Nationalities, and Peoples' Region of Ethiopia.

The following shell size categories (Herbert & Kilburn 2004) are used: minute <3 mm, very small 3–5 mm, small 5–10 mm, and moderate 10–25 mm.

Museum acronyms: MSNG = Museo Civico di Storia Naturale "G. Doria" (Genoa), NHMUK = Natural History Museum (London), NMW = National Museum of Wales (Cardiff), RBINS = Royal Belgian Institute of Natural Sciences (Brussels) RBINS, SMF = Senckenberg Research Institute (Frankfurt am Main), SMNH = Swedish Museum of Natural History (Stockholm), ZMB = Museum für Naturkunde (Berlin).

Systematics

Superfamily Streptaxoidea

Family Streptaxidae

Genus *Ptychotrema* L. Pfeiffer, 1853

Subgenus *Parennea* Pilsbry 1919

***Ptychotrema* (*Parennea*) *bishanwakaense* sp. nov.**
Figure 2A, Table 3

ZooBank identifier. urn:lsid:zoobank.org:act:63689998-7C1A-4DFE-8840-6595EEEC45F4

Type material. Holotype: NMW.Z.2025.002.01. Paratypes: 4 adults, 2 juveniles, NMW.Z.2025.002.02, data as holotype.

Type locality. SW Ethiopia: Gambela Region: Majang Zone: Mengesh Woreda: Bishan Waka Lake; 07.300°N, 035.273°E, 1388 m a.s.l. (Site 6; Fig. 1, Table 1).

Diagnosis. The strongly ribbed shell, its minute size, open umbilicus, bifid columella process, and the relatively short palatal fold and external furrow, serve to separate this species from other *Parennea*.

Description. The shell (Fig. 2A, Table 3) is minute (H: 2.1–2.6 mm; D: 1.2–1.3 mm), pupiform-cylindrical, and with an apex obtuse. Shell glassy and translucent when fresh, but old shells are opaque white. The protoconch has 2½ slightly shouldered whorls and a simple suture, with very fine spiral microsculpture, which is just visible in fresh shells at ×45 magnification. The teleoconch has strong, slightly prosocline axial ribs, which are weakly sigmoidal on the central whorls; there are about 15–19 ribs visible on the face of the body whorl. In adults the shell has 7–7¾ convex whorls separated by a moderately impressed suture. The suture is strongly crenellated by axial ribs. The umbilicus is clearly open but narrow, about 1/10 of the shell diameter. The aperture is broadly heart-shaped, with rounded basal and columellar margins. The peristome is complete; the parietal margin has a thin, transparent callus in fresh shells but is thickened in old shells; the lip is reflected and slightly thickened. The apertural profile is curved in lateral view, with its lower half reflexed back from about the midpoint. The aperture bears three major processes. The parietal lamella, which is slightly curved and extends from the peristome for about ⅓ whorl into shell. In

Table 3. Shell dimensions of *Ptychotrema* (*Parennea*) *bishanwakaense* sp. nov. See Tables 1 and 2 for information on the collecting sites.

Site	Type	H	D	h	d	Whorls	Notes
6	Holotype	2.2	1.2	0.7	0.8	7	
6	Paratype 1	2.1	1.3	0.7	0.7	7	Adult; second parietal nodule
6	Paratype 2	2.6	1.3	0.7	0.8	7¾	Peristome broken; spiral apical sculpture visible
6	Paratype 3	1.7	1.3	0.5	0.7	6	Juvenile; peristome broken
6	Paratype 4	2.5	1.3	0.7	0.8	7½	Adult; second parietal nodule
6	Paratype 5	2.4	1.3	0.7	0.7	7¼	Adult
6	Paratype 6	1.6	1.3	0.4	0.7	5⅞	Juvenile

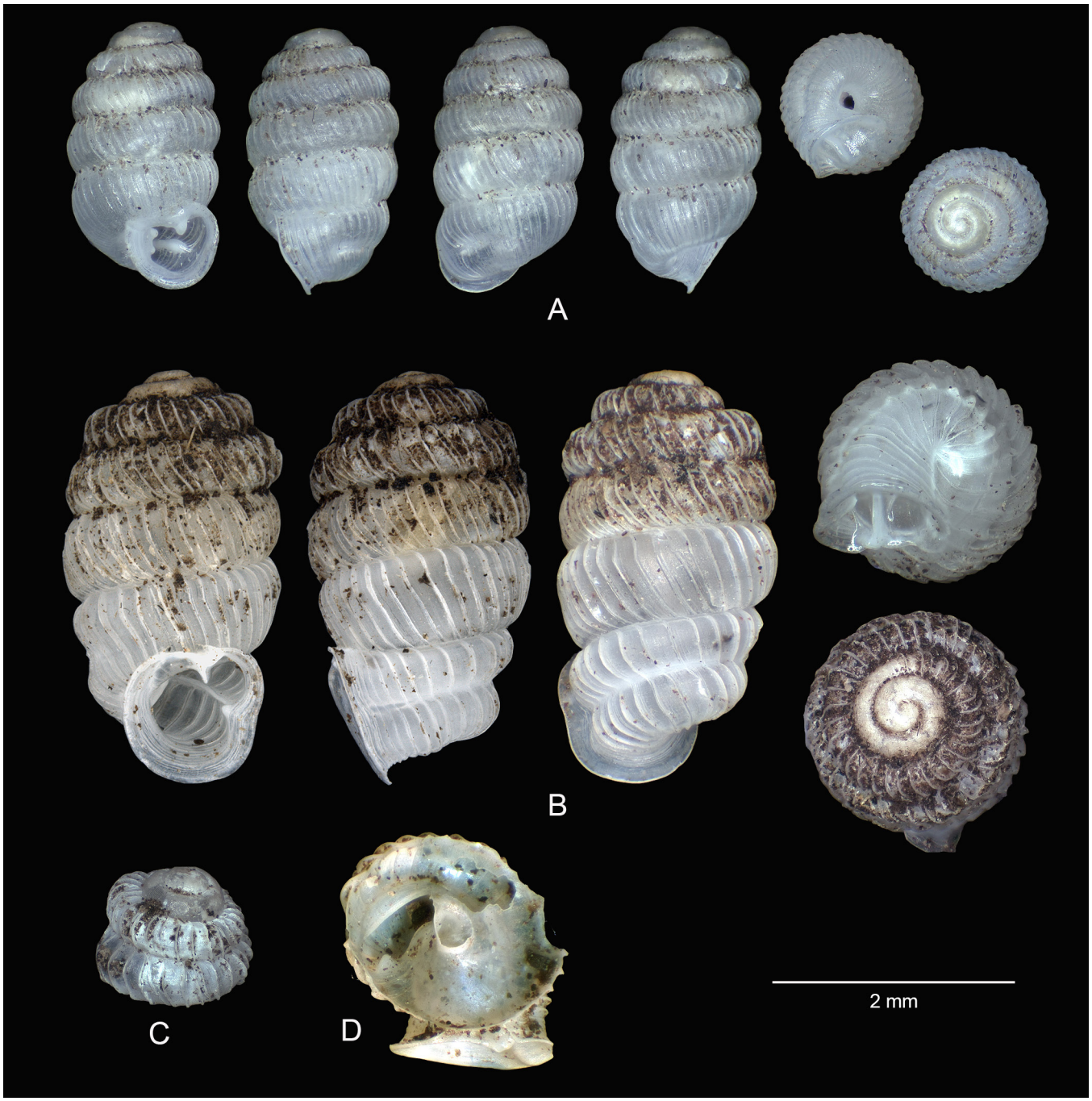


Figure 2. Ethiopian *Ptychotrema* species. **A**, *P.* (*Parennea*) *bishanwakaense* sp. nov., holotype. **B**–**D**, *P.* (*Pa.*) *dolfi* sp. nov.: (**B**) holotype; (**C**) paratype #2 showing apical microsculpture; (**D**) paratype #4 showing deep basal denticle.

some shells (Table 3), there is an additional small parietal nodule to the left of the parietal lamella, as viewed looking into the aperture. The single palatal fold starts about 0.5 mm from the lip and is in-running for about ⅓ whorl; it has a corresponding rather short external furrow. The columellar process is bifid, with the upper lobe strongest. There is weak thickening just inside the aperture at the basal-columellar junction, and, in some specimens, on the outer lip where it forms a very weak lip tooth. Juvenile shells are edentate.

Distribution and habitat. Known only from the type locality in Transitional rain forest at an altitude of 1388 m (Table 2). Sieved from leaf litter.

Differentiation. The only species of *Parennea* hitherto reported from Ethiopia is *Ptychotrema* (*Pa.*) *tshibindanum*

septentrionale Verdcourt, 1985, but that species differs from *P. bishanwakaense* in its larger shell size (2.8 mm), closed umbilicus, much weaker shell sculpture and apertural dentition (Fig. 4B). In particular, the palatal fold in *P. tshibindanum septentrionale* extends to the outer lip, expanding there to form a large lip tooth, whereas this in this species it terminates before reaching the lip. In Adam & van Goethem's (1978) monograph on *Parennea*, *P. bishanwakaense* bears some similarities with *P.* (*Pa.*) *wittei* Adam & Van Goethem, 1978 and *P.* (*Pa.*) *splendens* Adam & Van Goethem, 1978, but both are larger (shell height *c.* 3 mm) and the former has a bilobed angular lamella and trellised apical microsculpture, while the latter has fine axial striation on the protoconch, lacks any folds or teeth on its columella, and has an almost closed umbilicus. *Ptychotrema bishanwakaense* does not appear to match any species described by van Bruggen (1989), Pilsbry (1919), or de Winter (2008). In terms of size and ribbed sculpture, *P. bishanwakaense* is superficially close to a single shell (Peter Tattersfield manuscript name: Strep_6) collected by the author from Sheko Forest, Sanka Ber, Ethiopia in April 2015. Its shell shape and aperture shape differ from *P.* (*Pa.*) *bishanwakaense*, and it also has a palatal lip tooth that is lacking in *P. bishanwakaense*. Unfortunately, Strep_6 has a damaged aperture so it cannot be adequately assessed, and it is not included in this paper.

Remarks. Assignment of this species to *Ptychotrema* is provisional because its palatal fold and corresponding external furrow are short, and they do not extend around the body whorl as in other *Ptychotrema* species. Consideration has been given to its inclusion in *Gulella sensu lato*, but the new species does not resemble any species known to me and its form is not easily assigned to any of the (mainly artificial) groups in Verdcourt's (1962) key to East African *Gulella* species.

Etymology. From Bishan Waka Lake, the only known locality.

***Ptychotrema* (*Parennea*) *dolfi* sp. nov.**

Figure 2B–D, Table 4

ZooBankidentifier.urn:lsid:zoobank.org:act:599D2A04-C331-44F3-AF2B-6F447430805D

Type material. Holotype: NMW.Z.2025.002.03. Paratypes: 2 adults, 2 juveniles NMW.Z.2025.002.04, data as holotype.

Type locality. SW Ethiopia: Gambela Region: Majang Zone: Mengesh Woreda: Bishan Waka Lake; 07.300°N, 035.273°E, 1388 m a.s.l. (Site 6; Fig. 1, Table 1).

Diagnosis. The rather squat and less elongated shell of *P.* (*Pa.*) *dolfi*, its broadly domed apex, strong and sharp ribs, very convex whorls, and unusually deep palatal furrow that constricts the body whorl separate this species from other *Parennea* species.

Description. The shell (Fig. 2B–D, Table 4) is very small (H: 3.4–3.55 mm; D: 1.85 mm), shortly and irregularly cylindrical, with the central whorls widest. The spire is low, and the obtuse apex is well defined because it is distinctly narrower than the following whorls (*c.* 56% of the width of whorl 3). Fresh shells are translucent white. The protoconch consists of about 2⅓ whorls and has fine spiral threadlets (Fig. 2C). The teleoconch has very strong, prosocline, thin ribs, almost lamellae; there are about 13 visible ribs on the face of the body whorl, and there is no trace of spiral sculpture. The shell between the ribs is mostly smooth and with a silky texture. The adult shell has about 7 very convex whorls which are separated by a deeply impressed suture. Whorl 3 is slightly shouldered, perhaps emphasised by the pronounced ribs. Whorls 4 and 5 are wider than whorl 6 and the body whorl (whorl 7), which is constricted by the unusually deep, long palatal fold. The umbilicus is closed in adult shells but minutely open and circular in juveniles (*c.* 5% of shell diameter in a juvenile with 5¾ whorls). The peristome is continuous and detached from the previous whorl across the parietal zone. It is strongly flared into a wide rim. The lip is thin, especially around the columellar, basal, and palatal margins. The aperture is round but with flattened palatal and parietal margins. The apertural dentition has two strong in-running lamellae. The palatal fold extends almost from a weak lip tooth on the peristome to about ¾ whorl into the shell and has a corresponding very deep external furrow, strongly constricting the body whorl. A strong parietal lamella forms a thickened, triangular angular denticle that

Table 4. Shell dimensions of *Ptychotrema* (*Parennea*) *dolfi* sp. nov. See Tables 1 and 2 for information on the collecting sites.

Site	Type	H	D	h	d	Whorls	Notes
6	Holotype	3.40	1.85	1.15	1.20	7	D measured across whorl 4
6	Paratype 1	3.55	1.85	1.10	1.10	7⅓	D measured across whorl 4
6	Paratype 2	1.75	1.25	0.55	0.70	4½	Juvenile
6	Paratype 3	2.20	1.80	0.70	0.90	5¾	Juvenile
6	Paratype 4	—	—	1.10	1.15	—	Broken shell; aperture only

slightly projects beyond the previous whorl where is meets the peristome. Internally, the parietal lamella is interrupted about 0.6 mm into the aperture, its inward continuation represented by a short lamella-like denticle. The angular denticle is detached from the section of peristome on the right side of the shell. The palatal and parietal lamellae define an open circular sinus in the upper right section of the aperture. The columella has a lamella-like thickening, which is weakly linked to a small basal denticle deeper within the body whorl, and that is only visible in the broken shell of paratype #4 (Fig. 2D) and through the translucent shell of the holotype. Juvenile shells are edentate.

Distribution and habitat. Known only from the type locality in Transitional rain forest at an altitude of 1388 m (Table 2). Sieved from leaf litter.

Differentiation. This species does not match either of the *Parennea* previously reported from north-east Africa (*P. tshibindanum septentrionale* and *P.* (*Pa.*) *somaliense* Verdcourt, 1961, see Fig. 4), or any of the species reviewed by Adam & Van Goethem (1978) or van Bruggen (1989). In terms of other *Parennea* described in this paper, *P. dolfi* is larger and broader than *P.* (*Pa.*) *wondogenetense* sp. nov., and its spire is much lower. Its sculpture is stronger than *P. wondogenetense*, *P.* (*Pa.*) *keffaense* sp. nov., and *P.* (*Pa.*) *gaysayense* sp. nov., and its shell shape is also very different. *Parennea dolfi* has some similarities to *P. bishanwakaense* in terms of its general shell shape, but it is larger, the form of the ribbing is very different, and its palatal fold is much stronger and longer.

Etymology. Named in appreciation of the great contribution made to the study of African land snails by the late Dr A. C. (Dolf) van Bruggen (Leiden), and for his help and encouragement that he provided to me over many years.

***Ptychotrema* (*Parennea*) *wondogenetense* sp. nov.**
Figure 3A, Table 5

ZooBank identifier. urn:lsid:zoobank.org:act:6BD599EA-483E-49E7-BD93-5F8A6783868A

Type material. Holotype: NMW.Z.2025.002.05. Paratypes: 2 adults, NMW.Z.2025.002.06, data as holotype.

Type locality. Eithiopia: Southern Nations, Nationalities, and Peoples' Region: Sidama Zone: Wondo Genet Woreda: Near Wondo Genet town: Wondo Genet forest; 7.096°N, 38.644°E, 1950 m a.s.l. (Site 24; Fig. 1, Table 1).

Diagnosis. The diagnostic characters of *P. wondogenetense* are its minute size and strongly ribbed shell, the presence of a strong lip tooth, the very narrow pyriform umbilical opening, the absence of both apical microsculpture, and an entire to weakly bilobed columellar process.

Description. The shell (Fig. 3A, Table 5) is minute (H: 2.55–2.70 mm; D: 1.20 mm), weakly biconical, with an obtuse apex, and translucent when fresh. The protoconch has 2–2½ whorls and with a simple suture; it is smooth, with no evidence of spiral sculpture. The teleoconch has strong, regular, slightly prosocline axial ribs, which are weaker and less regular on the upper whorls; there are about 18 ribs visible on the face of the body whorl, approximately 13 per mm. The adult shell has about seven convex whorls separated by a moderately impressed suture, which is strongly crenellated by the ribbing. The umbilicus is minute and pyriform. The dentition comprises a strong, deeply in-running palatal fold which is detached from a small mid-palatal lip tooth situated approximately opposite the deeply in-running angular lamella, and there is a very weakly bilobed (almost entire in some specimens) columellar lamella. The palatal fold is marked externally by a furrow which extends for about ½ whorl, and there is a small external depression in the labrum behind the denticle. The aperture is rounded-triangular, and the peristome is thickened and weakly reflected, especially on the columellar margin.

Distribution and habitat. Only known from the type locality in disturbed Afromontane forest at (Table 2). Sieved from forest-floor leaf litter.

Differentiation. *Ptychotrema wondogenetense* is smaller and narrower than *P. dolfi*, its shell has a uniform rather than irregular outline and its axial ribbing differs in form and strength. *Ptychotrema wondogenetense* also lacks apical spiral microsculpture, has a more highly domed apex and a strong palatal lip denticle. The shell of *P. wondogenetense* is smaller and less cylindrical than *P. tshibindanum sepentrionale*; its apertural dentition is similar although *sepentrionale*'s palatal fold extends to the peristome whereas it is interrupted in *P. wondogenetense*. In comparison with *P. bishanwakaense*, *P. wondogenetense* has more complete axial ribbing and a much narrower umbilical opening, and it lacks the additional parietal nodule/lamella and the strongly bifid columellar

Table 5. Shell dimensions of *Ptychotrema* (*Parennea*) *wondogenetense* sp. nov. See Tables 1 and 2 for information on the collecting sites.

Site	Type	H	D	h	d	Whorls
24	Holotype	2.6	1.2	0.7	0.8	7½
24	Paratype 1	2.55	1.2	0.7	0.6	7⅓
24	Paratype 2	2.7	1.2	0.7	0.8	7¾

Figure 3. Ethiopian *Ptychotrema* species. **A**, *P.* (*Parennea*) *wondogenetense* sp. nov., holotype. **B**, *P.* (*Pa.*) *keffaense* sp. nov., holotype. **C**, **D**, *P.* (*Pa.*) *gaysayense* sp. nov: (**C**) holotype; (**D**) larger shell of paratype #1.

process. This species' size and general shape is similar to *P. keffaense*, but *P. wondogenetense* has much stronger ribbing and lacks or has only a very weakly bilobed columellar process. The general shell shape and ribbed sculpture of *P. wondogenetense* are similar to *P. wittei* and *P.* (*Pa.*) *subaequatoriale* Adam & Van Goethem, 1978 (both described from the DRC), but both are larger, especially the latter (H: 4.4 mm). Also, unlike the smooth protoconch *of P. wondogenetense*, *P. wittei* is ornamented with "très fine striation trellisée" (Adam & van Goethem 1978: 33). *Ptychotrema wondogenetense* is similar to *P.* (*E.*) *canaliculatum* sp. nov. and *P.* (*E.*) *balenense* sp. nov. in terms of shell shape and ribbing, but it

is much smaller, and it lacks the lower palatal furrows that assign these two species to *Ennea*.

Etymology. From the town of Wondo Genet, the type and only known locality.

***Ptychotrema* (*Parennea*) *keffaense* sp. nov.**
Figure 3B; Table 6

ZooBank identifier. urn:lsid:zoobank.org:act:D196E295-3C40-4B4D-BAF4-D9556FB41D92

Type material. Holotype: NMW.Z.2025.002.07. Paratypes: 1 adult, 1 juvenile, NMW.Z.2025.002.08, from Site 9; 1 subadult with incomplete dentition, NMW.Z.2025.002.09, from Site 11 (Fig. 1, Table 1).

Type locality. SW Ethiopia: Southern Nations, Nationalities, and Peoples' Region: Keffa Zone: Gimbo Woreda: Kafa Biosphere Reserve: Komba Forest 1; 07.313°N, 036.074°E, 1930 m a.s.l. (Site 7; Fig. 1, Table 1).

Diagnosis. The characteristic features of this species are its minute size, the absence of strong axial ribbing, the round and conspicuously open umbilicus and the strongly bifid columellar process.

Description. The shell (Fig. 3B, Table 6) is minute, weakly biconical-subcylindrical (H: 2.5–2.8 mm; D: 1.15–1.3 mm), although Paratype 2 appears atypical in being irregularly shaped with whorl 5 narrower than whorls 4 and 6. The shell is translucent when fresh. The apex is obtuse, and the protoconch consists of 2½ whorls, with extremely fine and very closely set spiral lines and axial riblets which are only and barely visible in the fresh subadult shell of Paratype 2 at ×45 magnification. The teleoconch whorls lack strong ribbing but have variable and typically weak and irregular axial ribs, which are strongest on whorls 3 and 4. The suture is moderately impressed and crenellated, especially on the body and lower spire whorls. The body whorl is smooth, apart from the crenellated suture. The adult shell consists of 7–7¼ convex whorls. The umbilicus is narrow (*c.* 1/10 of the diameter of the shell) but conspicuously open and rounded. The aperture is triangular, with rounded basal and columellar margins. The peristome continuous and reflexed. The apertural dentition is 4-fold, comprising an in-running palatal fold externally marked by a corresponding external furrow, a very weak palatal lip tooth which is detached from the deeper palatal fold, a strong in-running parietal lamella forming a sharp angular denticle where it meets the peristome, and a strongly bifid columellar process. The juvenile Paratype 3 is edentate, has an open, narrow umbilicus, and very fine, close, regular axial microsculpture on whorl 4. The apertural dentition is incompletely developed in the subadult shell of Paratype 2.

Distribution and habitat. Known only from leaf litter in Afromontane forest, in Bodinga and Komba Forests at 1710 m and 1930 m elevation (Table 2). Sieved from forest floor leaf litter.

Differentiation. The shape and size are similar to *P. wondogenetense*, but that species has much stronger axial ribs, lacks or has only a very weakly bilobed columellar process, and has a smooth protoconch. Shell shape is similar to *Parennea* (*Pa.*) *kigeziense* (Preston, 1913), but *P. keffaense* has a bifid rather than trifid columella process, and it also lacks the large palatal denticle present in *P. kigeziense* (*P. keffaense* has weak thickening only). The species can be separated separated from the rather similarly shaped *P. harennae* sp. nov., *P. canaliculatum*, and *P. balaensis*, which have been placed in *Ennea*, by the absence of a second palatal fold/furrow. *Ptychotrema harennae* is also larger and has strong axial ribs, whereas *P. keffaense* has a smoother shell. *P. canaliculatum* and *balaensis* are larger and have stronger axial ribbing.

Etymology. From the Keffa zone in the SPPR where the specimens were collected.

***Ptychotrema* (*Parennea*) *gaysayense* sp. nov.**
Figure 3C, D, Table 7

ZooBank identifier. urn:lsid:zoobank.org:act:EF7DD660-9753-47AC-8B30-3F6E9CADBC2B

Type material. Holotype: NMW.Z.2025.002.10. Paratypes: 4 old and worn shells, NMW.Z.2025.002.11, from Site 16. One fresh but damaged juvenile shell, 9 old and worn adult shells, NMW.Z.2025.002.12, from Site 17 (Fig. 1, Table 1).

Table 6. Shell dimensions of *Ptychotrema* (*Parennea*) *keffaense* sp. nov. See Tables 1 and 2 for information on the collecting sites.

Site	Type	H	D	h	d	Whorls	Notes
7	Holotype	2.70	1.20	0.80	0.70	7¾	
9	Paratype 1	2.70	1.25	0.75	0.75	7½	
11	Paratype 2	2.50	1.10	0.70	0.70	7½	
9	Paratype 3	1.60	1.15	0.50	0.60	6	Juvenile

Table 7. Shell dimensions of *Ptychotrema* (*Parennea*) *gaysayense* sp. nov. See Tables 1 and 2 for information on the collecting sites.

Site	Type	H	D	h	d	Whorls	Notes
17	Holotype	3.4	1.5	0.9	1.0	7½	
16	Paratype 1	4.1	1.5	1.0	1.1	9	
16	Paratype 2	3.7	1.6	1.0	1.1	8	
17	Paratype 3	1.55	1.6	0.6	0.8	5	Old juvenile; edentate
17	Paratype 4	1.1	1.4	—	—	4½	Broken juvenile shell; fresh
17	Paratype 5	3.4	1.55	0.9	1.0	7½	
16	Paratype 6	3.7	1.55	0.8	0.95	8	Old shell; peristome damaged
16	Paratype 7	3.75	1.65	1.05	1.0	8	
17	Paratype 8	3.3	1.6	1.0	0.9	7⅓	
17	Paratype 9	3.4	1.4	0.9	0.9	7½	
17	Paratype 10	3.7	1.55	0.9	1.0	—	
17	Paratype 11	3.45	1.55	0.9	1.0	7¾	
17	Paratype 12	2.95	1.55	—	—	7	Old shell; aperture broken
17	Paratype 13	2. 35	1.55	0.8	0.8	6¼	Juvenile; old shell
17	Paratype 14	—	1.55	—	—	—	Broken shell

Type locality. Eithiopia: Oromia Region: Bale Zone: Dinsho Woreda: Bale Mountains National Park: Gaysay grasslands forest 2; 07.102°N, 039.745°E, 3219 m a.s.l. (Site 17; Fig. 1, Table 1).

Diagnosis. The shell is characterised by its evenly cylindrical shape, larger size (in comparison with several other ribbed *Parennea* species), and weak axial ribbing.

Description. The shell (Fig. 3C, D, Table 7) is very small (H: 3.4 mm; D: 1.5 mm), cylindrical, with a domed apex, and translucent when fresh. The protoconch is poorly defined and has 2 whorls which are smooth, with no sign of microsculpture. The teleoconch has weak, evenly and widely spaced prosocline ribs, about 17 ribs visible on the face of the adult body whorl. The ribs are strongest behind the peristome and below the suture, which appears crenellated; they are faint and worn on the face of the body whorl. The adult shell has (7)–7½–(9) weakly convex whorls, and the umbilicus is almost closed (barely open at all in Paratype 1). The aperture is subtriangular. The apertural dentition comprises a strong and deeply in-running angular lamella and a palatal fold. There is a small palatal lip tooth formed by thickening of the peristome, about midpoint on the palatal labrum, and not connected to the internal palatal fold. The palatal fold is marked externally by a deep furrow which extends for about ½ whorl; the end of the furrow corresponding with the free end of the fold forms a pit. The columella is thickened, with the upper part forming a very broad and weak lobe. The parietal lamella extends for about ⅓ whorl and then weakens or terminates in some shells, only to recommence slightly further into the shell (only visible through the aperture in oblique view). The peristome is thickened, strongly flared and reflexed, and continuous across the parietal region as a rather thin transparent membrane in fresh shells. Juvenile shells are edentate.

Distribution and habitat. Known only from leaf litter in Upper Afromontane woodland at an altitude of 3173 m, on the north side of the Bale Mountains. Sieved from leaf litter.

Differentiation. This species appears to be closest to *P. tshibindanum septentrionale* (Fig. 4B), which was described from Shoa, 90 km west of Addis Ababa at 2450 m. However, the shell of *P. gaysayense* is considerably larger and it has a very small umbilicus in contrast to Verdcourt's imperforate species. It is also weakly ribbed, in contrast to the smooth whorls of *P. tshibindanum septentrionale.* In terms of dentition, Verdcourt (1985: 120) described "a deep external furrow running backwards round the body-whorl from the outer lip process", whereas in *P. gaysayense* there is a gap between the end of the external furrow and the lip tooth. The lip tooth and columellar process in *P. gaysayense* also appear to be weaker, with the latter also being rather different in form from that described by Verdcourt. Additionally, the angular lamella of *P. gaysayense* is not bilobed (unless Verdcourt's description of *P. tshibindanum septentrionale* as having a bilobed angular lamella refers to the weakening/interruption of the lamella within the shell as noted in some specimens of *P. gaysayense*; this could, perhaps, be interpreted as a single bilobed structure).

Ptychotrema (*Pa.*) *tshibindanum* Pilsbry & Cockerell, 1933 and *P.* (*Pa.*) *nyangweense* (Putzeys, 1899) are similar in size, and their palatal furrow is separated from the lip tooth as in *P. gaysayense*. Both have cylindrical shells, and the whorls of *P. nyangweense* are rather flattened, as in *P. gaysayense*. However, *P. tshibindanum* has more convex whorls and its overall shape differs, with the authors emphasising that the shell is noticeably wider above, the greatest diameter being the antepenultimate whorl. Both these species have a bilobed angular lamella, which is not present, or very weak, in *P. gaysayense* (but see note above). *Ptychotrema tshibindanum* has a wide, straight and deeply placed lamella on the columella that is not present in *P. gaysayense*, and, judging from Pilsbry's drawing, the lip tooth is also much stronger than in *gaysayense*. *Ptychotrema nyangweense* also differs because its shell has very fine spiral striation, a thick parietal callus and the upper part of the columella has a large obtusely rounded vertical lobe, which, according to Adam & Van Goethem (1978) is never bilobed. Adam & Van Goethem (1978) noted that material identified as *P. nyangweense* from Rutshuru (eastern DRC) belongs to *P. tshibindanum*, which is not a subspecies of *P. nyangweense*.

Remarks. Based on the available material it seems likely that *P. gaysayense* represents a separate species, although examination of additional material from a range of geographical locations would be desirable to confirm this.

Etymology. From the Gaysay Grasslands area, Bale Mountains, where the specimens were collected.

Other North-east African *Parennea*

***Ptychotrema* (*Parennea*) *somaliense* Verdcourt, 1961**
Figure 4A

Verdcourt 1961: 159–160, fig. 5—Adam & Van Goethem 1978: 6, 28; Richardson 1988: 138; Van Bruggen 1989: 33, 39, 45, 47, fig. 36; Brown 2023: 180–181.

Remarks. Verdcourt provided shell measurements of H: 4.0 mm; D: 1.7 mm. Mait-Erigavo escarpment (*c.* 10.75°N 047.25°E) at 5900–6900 ft a.s.l., Somalia, leg. C.F Hemming. Shell oblong-cylindrical, slightly clavate; whorls smooth but suture strongly crenellate.

***Ptychotrema* (*Parennea*) *tschibindanum septentrionale* Verdcourt, 1985**
Figure 4B

Verdcourt 1985: 120–121, fig. 19—van Bruggen 1989 (as *Ptychotrema* (*Parennea*) *tshibindanum* [sic] *septentrionale*): 33, 39, 45, 47, fig. 35; Brown 2023 (as *Ptychotrema* (*Parennea*) *tshibindanum* [sic] *septentrionale*): 185–186.

Remarks. Verdcourt provided shell measurements of H: 2.8 mm; D: 1.27 mm. Shoa, 90 km W of Addis Ababa at 2450 m a.s.l., leg. Åke Holm. *Ptychotrema* (*Pa.*) *tshibindanum* was described from Tshibinda, west of Lake Kivu, DRC. Noting the similarities with that species, Verdcourt (1985) erected a subspecies for the Ethiopian shell, but he also noted the zoogeographical relevance. Van Bruggen (1989: 47) commented that *P. septentrionale* was "a geographically excentric [sic] taxon".

Genus *Ptychotrema* Pfeiffer, 1853

Subgenus Ennea H. Adams & A. Adams, 1855

***Ptychotrema* (*Ennea*) *aethiops* sp. nov.**
Figures 5A, 6, Table 8

ZooBank identifier. urn:lsid:zoobank.org:act:29394C65-674B-453D-B5A6-B21BD6E6E5A3

Type material. Holotype: NMW.Z.2025.002.13. Paratypes: 6 adults, 1 juvenile, all shells in spirit with bodies withdrawn, NMW.Z.2025.002.14, data as holotype; 13 adults, 2 juveniles, including 12 shells in spirit with bodies withdrawn, NMW.Z.2025.002.15, from Site 6 (Fig. 1, Table 1).

Type locality. SW Ethiopia: Southern Nations, Nationalities, and Peoples' Region: Bench Maji Zone: Sheko Woreda: Near Mizan Teferi town: Sheko Forest 1; 07.042°N, 035.448°E, 1567 m a.s.l. (Site 1; Fig. 1, Table 1).

Diagnosis. The main distinguishing characters of this species' shell are its moderately large size (in comparison with other Ethiopian *Ennea*) and ovoid shape, its strongly crenellated suture, closed umbilicus, and the faint, closely spaced axial microsculpture.

Description. The shell (Fig. 5A, 6, Table 8) is of moderate size, elongate-oval (H: 10.0–12.8 mm; D: 4.6–5.7 mm), translucent when fresh but opaque-white in older individuals, and with a rounded apex. The protoconch consists of 2½ whorls, with very fine, weak, and extremely close-set and regular axial wrinkles which are visible in fresh shells under good illumination at ×45 magnification; the junction of the protoconch with the teleoconch is indistinct. The adult shell has 7¾–9¾ convex whorls, and the upper whorls are slightly shouldered. The suture is strongly and quite regularly crenellated, and the crenelations extend onto the shoulder of the whorl, then fade out or cross some or all the whorl as very weak axial, prosocline ribs. In apertural view, the crenelations are about 0.25 mm apart, with about 22 visible on the suture that separates the body whorl and preceding whorl. The face of the body whorl is smooth, apart from the rather regularly crenellated suture.

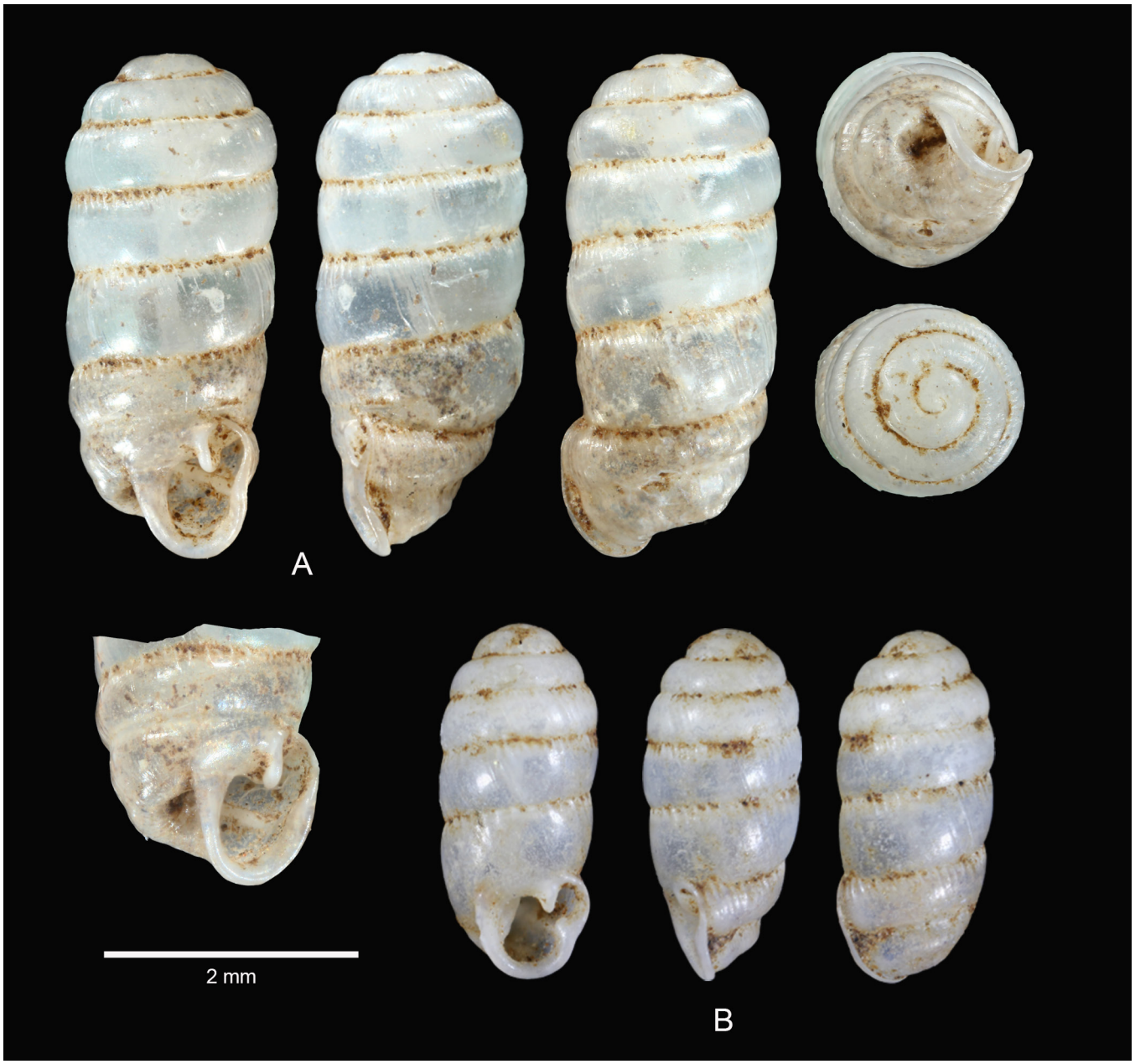


Figure 4. Ethiopian *Ptychotrema* species. **A**, *P.* (*Parennea*) *somaliense* Verdcourt, 1961, holotype (SMF 164300, photograph by Sigrid Hof). **B**, *P.* (*Pa.*) *tschinbindanum septentrionale* Verdcourt, 1985 (SMNH 3698, photograph by Alexander Fedosov).

Some shells also have a few widely and irregularly spaced growth ridges. In addition to the coarse ribbing, the shell has axial microsculpture of fine, faint, closely spaced, and branching etched lines, most readily visible on the middle whorls of fresh shells under good illumination. The umbilicus is closed. The aperture is broadly pyriform. The peristome is continuous, extending as a thin translucent membrane across the parietal section in fresh shells, but white, opaque, and more apparent in older shells. The lip is thickened and strongly reflexed. The apertural dentition is 4-fold, with one deeply in-running parietal lamella (Fig. 5A), two deeply in-running palatal folds, and an elongated columellar process which is distinctly bilobed in some individuals but entire in others. The upper palatal fold, the stronger of the two palatal folds, reaches the lip where it forms an area of thickening or a weak lip tooth. The palatal folds are externally marked by corresponding, rather deep, external furrows, which extend about halfway around the body whorl. Juvenile shells are edentate and have an open umbilicus.

Table 8. Shell dimensions of *Ptychotrema* (*Ennea*) *aethiops* sp. nov. See Tables 1 and 2 for information on the collecting sites.

Site	Shell	Type	H	D	h	d	Whorls	
Sheko Forest								
1	4	Holotype	10.3	4.9	3.5	3.7	8½	
1	22	Paratype 1	10.2	4.8	3.4	3.5	8¾	
1	3	Paratype 2	10.7	4.9	3.6	3.7	9¼	
1	5	Paratype 3	11.1	4.9	3.8	3.8	9¼	
1	6	Paratype 4	4.1	4.6	1.6	2.3	6¼	Juvenile
1	7	Paratype 5	10.2	4.6	3.3	3.6	8¾	
1	8	Paratype 6	10	4.6	3.3	3.3	9	
1	23	Paratype 7	10.8	4.4	3.5	3.3	9	
Bishan Waka Lake								
1	21	Paratype 8	10.5	4.7	3.1	3.6	8¼	
6	16	Paratype 9	11.1	5	3.7	4.2	9½	
6	17	Paratype 10	11.6	4.9	3.6	3.8	9	
6	18	Paratype 11	10.8	4.9	3.4	3.8	9	
6	19	Paratype 12	3	4.5	1.6	2.1	5¼	Juvenile
6	20	Paratype 13	4	5.2	2	2.6	6⅛	Juvenile
6	1	Paratype 14	12.2	5.3	3.9	3.7	9½	
6	2	Paratype 15	11.3	5.3	3.7	3.8	9⅓	
6	9	Paratype 16	11.5	5.35	4	3.8	9¼	
6	10	Paratype 17	12	5.2	4.1	3.8	9¾	
6	11	Paratype 18	10.8	5.1	3.5	3.6	9¼	
6	12	Paratype 19	10.9	5.15	3.8	3.3	9½	
6	13	Paratype 20	10	5.2	4.2	3.5	8¾	
6	14	Paratype 21	11.3	5.5	4	3.6	9⅛	
6	15	Paratype 22	12.6	5.6	4.1	4.1	9¾	

Animal (Fig. 6): body of living animal dorsally pale orange, fading to pale yellow-orange towards the sole. Tentacle retractor muscles pale orange.

Distribution and habitat. Known only from leaf litter collected in Transitional/Afromontane forest habitats, at elevations of 1567 m and 1388 m, in the Gambela and western SNNPR regions of south-west Ethiopia. Sieved from leaf litter collected in disturbed forest habitat.

Etymology. From the Latin "aethipos", Ethiopian.

Differentiation. The suture of *P. unumiugum* sp. nov. is crenellated, but its shell is smaller, and it lacks the lower palatal fold that is present in this species. Four species of *Ennea* have been previously described from north-east Africa (Fig. 8), all of which have smaller shells than *P. aethiops* (Figs 8B–F, 11). *Ptychotrema* (*E.*) *denticulatum* (Morelet, 1872) (including several varieties) has a strongly crenellated suture like *aethiops*, but its cylindrical shell is quite different in form to the more inflated oval shell of *P. aethiops*. *Ptychotrema* (*E.*) *massauense* Thiele, 1933, *P.* (*E.*) *hyalinum* Thiele, 1933 and *P.* (*E.*) *laeve*, Thiele, 1933 do not have strongly crenellated sutures, and they also differ in terms of shell shape and/or size. *Ptychotrema massauense* (H: 6.2mm) (Fig. 8F) is much smaller than *P. aethiops*, and *P. laeve* has a thinner, narrower and much more elongated shell. The shell of *P. hyalinum* (Fig. 8E) has roughly the same proportions as *P. aethiops*, but it is widest above the midpoint rather than close to the centre as in *P. aethiops*; additionally, the two external palatal furrows are much shallower in *P. hyalinum. Ptychotrema aethiops and P. epicratis* sp. nov. have rather similar very fine and branching axial microsculpture, although it is stronger and more readily apparent in *P. epicratis*. However, *aethiops* is a much larger species, it has crenellated suture, lacks a lip tooth, and the ends of the palatal folds are not inflated or only very weakly so.

Outside north-east Africa, *Ptychotrema* (*E.*) *pollonerae* (Preston, 1913), described from Lake Kivu, DRC, has a crenellated suture and it is comparable in size (12 × 6.75 mm, with 6½ whorls) to *P. aethiops*. However, its shell is wider and more cylindrical, with fewer whorls, and it has a

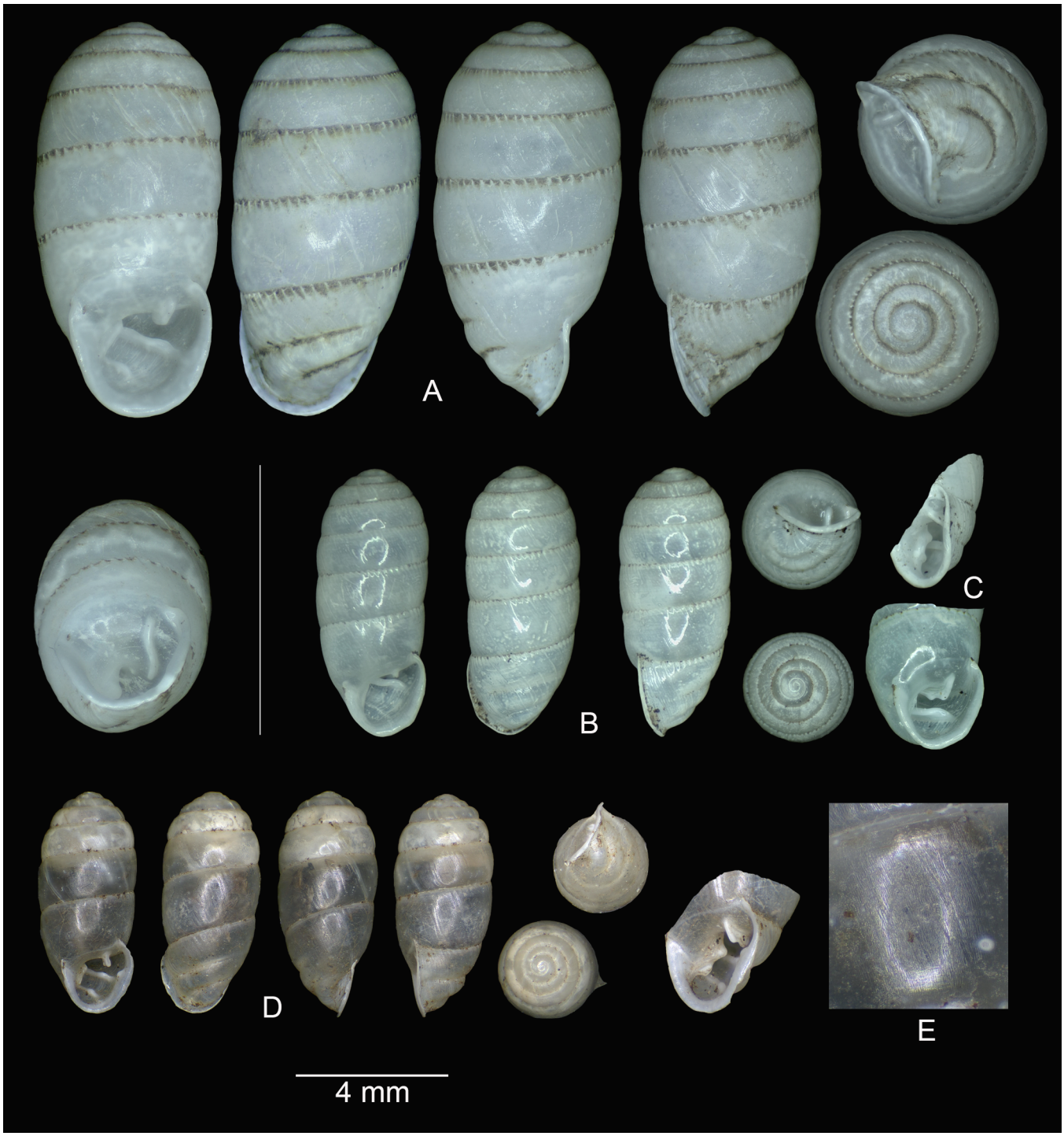


Figure 5. Ethiopian *Ptychotrema* species. **A**, *P.* (*Ennea*) *aethiops* sp. nov., holotype. **B**, **C**, *P.* (*E.*) *unumiugum* sp. nov.: (**B**) holotype; (**C**) paratype #7 showing detail of columellar and parietal dentition (not to scale). **D**, **E**, *P.* (*E.*) *epicratis* sp. nov.: (**D**) holotype (**E**); teleoconch microsculpture (not to scale).

smaller aperture. Several *Ptychotrema* (*Ennea*) with markedly crenulate or denticulate sutures have been described from West Africa, but all are much smaller species. These include *P.* (*E.*) *serratum* (d'Ailly, 1896) (Cameroon: 7.0 × 2.7 mm; H: 2.0, D: 2), which has a more cylindrical shell, *P.* (*E.*) *elegantulum* (L. Pfeiffer, 1846) which is also less ovoid, has a projecting anglular denticle, and is usually smaller (Adam *et al.* (1994) give shell measurements of 6.5-7.3 mm

Figure 6. Living animal of *Ptychotrema* (*Ennea*) *aethiops* sp. nov. Paratype #21, Sheko Forest, Kafa Biosphere Reserve.

for material from Liberia and Côte d'Ivoire), and *P.* (*E.*) *aillyi* Adam, 1981 (Cameroon: 6.1 × 2.9 mm with 8½ whorls) that has a more markedly oval shell. Of West African species, *P.* (*E.*) *thompsonae* Connolly, 1928 best resembles *aethiops* in terms of shape, sculpture and the closed umbilicus, but it is smaller (7.4 mm) and has a tooth-like thickening on the mid-palatal lip.

Remarks. There appears to be some variation in shell form, both within and between populations. The columellar process is variable within populations, ranging from entire to strongly bilobed, so it does not appear to represent a reliable character to separate this species. The upper nodule is the strongest projection on the columellar process. Adult specimens collected from Bishan Waka Lake (Site 6) are significantly larger (*t*-test, $P < 0.01$) and have more whorls ($P < 0.01$) than those collected in Sheko Forest (Site 1). These two sites are separated by 35 km, but apart from this inter-population variation in shell size no other significant differences were identified.

Ptychotrema (*Ennea*) *unumiugum* sp. nov.

Figure 5B, C, Table 9

ZooBank identifier. urn:lsid:zoobank.org:act:30604282-413D-4988-89E2-90440161E0B6

Type material. Holotype: NMW.Z.2025.002.16. Paratypes: 1 adult, NMW.Z.2025.002.17, from Site 4; 9 adults, 1 juvenile, including 9 shells in spirit, NMW.Z.2025.002.18, from Site 10; 4 adults, NMW.Z.2025.002.19, from Site 11; 6 adult shells including 4 in spirit, NMW.Z.2025.002.20, from Site 12 (Fig. 1, Table 1).

Type locality. SW Ethiopia: Southern Nations, Nationalities, and Peoples' Region: Keffa Zone: Gewata Woreda: Kafa Biosphere Reserve: Bodinga Forest 2; 07.498°N, 036.096°E, 2163 m a.s.l. (Site 10; Fig. 1, Table 1).

Diagnosis. *Ptychotrema* (*Ennea*) *unumiugum* is distinguished from other Ethiopian *Ennea* species by the near absence of the lower internal palatal fold, which, in this species is, represented only by a low angled ridge and associated strong external furrow.

Description. The shell (Fig. 5B, C, Table 9) is small, cylindrical (H: 6.3–8.0 mm; D: 2.7–3.1 mm), translucent when fresh but opaque-white in older individuals, glossy, and with a conical apex. The protoconch is about 2½ whorls, smooth, and its junction with the teleoconch is indistinct. The adult shell has 7¾–9 weakly convex whorls. The suture is strongly and quite regularly crenellated, with about 20 crenellations visible on the suture that separates the body whorl and preceding whorl. The face of the whorls is smooth and glossy, with infrequent weak axial growth ridges, apart from immediately behind the peristome where the ribbing is stronger and more regular, and on the upper whorls where the weak but regular ribbing is slightly more pronounced. The umbilicus is closed. The aperture is pyriform. The peristome is weakly continuous, represented by a thin, transparent callus across the parietal in some specimens. The lip is thickened and reflexed. The major apertural dentition is 2-fold, with a deeply in-running upper palatal fold and a bilobed parietal lamella (Fig. 5B). The columella is typically thickened and bilobed (Fig. 5C). The upper palatal fold is slightly curved at the free end, which does not reach the lip. The position typically occupied in many *Ennea* species by a lower palatal fold is marked, in this species, by a weakly angled ridge. However, both this ridge and the upper palatal fold are marked externally by corresponding external furrows that extend about ½ whorl around the body whorl. Juvenile shells are edentate and have an open umbilicus.

Distribution and habitat. Known only from leaf litter collected in Afromontane forest habitats, at elevations between 1710 and 2342 m, in Kafa Biosphere Reserve, south-west Ethiopia.

Differentiation. The near absence of the lower palatal fold, and its replacement with a low ridge, is diagnostic for this species among Ethiopian *Ennea*, although similar morpholo-

gies do occur in some West African species. Compared with other north-east African species, *Ptychotrema unumiugum* is much smaller and more cylindrical than *P. aethiops* and larger than *P.* (*E.*) *denticulatum* var. *nanum* Connolly, 1928 and *P.* (*E.*) *propenanum* sp. nov. (Figs 5, 8, 11). Based on the information and specimens available, *P. laeve* and varieties of *denticulatum* typically have more elongated shells (Fig. 11), although there appears to be some variation. *Ptychotrema denticulatum* is of similar size and (Verdcourt (1961) gave 4.5–9 × 3 mm), but its columella is smooth (although thickened above) and without pronounced folds or teeth, whereas in *P. unumiugum* the columella is clearly bilobed. Several varieties of *denticulatum* have been described, but these all appear to differ from *P. unumiugum*. Variety *hildebrandti* is ribbed and larger (7.3–11.0 × 3.5–4.0 mm, according to Verdcourt (1961)) than both Morelet's *denticulata* and *unumiugum*. Variety *papillifera* (= *quinqueplicata*) has a striate shell and much stronger teeth on the columella, which, judging from Jickeli's drawing (1874: pl. 4 fig. 1a–c), and unlike *P. unumiugum*, are clearly visibly in apertural view. According to Bourguignat (1883), var. *hamacenica* has fewer whorls and a more strongly crenellated columella than Morelet's species. Thiele's *P. hyalinum* and *P. massauense* are comparable in terms of size, but the suture of the former is much less crenellated than *P. unumiugum*, and the latter's is simple. The shell shape of *P. hyalinum* is also distinctive, with the widest part being above the mid-point. The peristome of *P. massauense* is more strongly thickened, and its projecting lip tooth gives it a distinctive profile (Fig. 8F); it also has a strong, somewhat curved parietal lamella which, unlike *P. unumiugum*, is connected to the outer edge of the shell. The form of the columella in these two species seems rather similar to *P. unumiugum*; Thiele (1933) described two nodules ("knoten") on the columella of both *P. hyalinum* and *P. massauense*, with those associated with the latter being described as weak ("schwach").

Table 9. Shell dimensions *Ptychotrema* (*Ennea*) *unumiugum* sp. nov. See Tables 1 and 2 for information on the collecting sites.

Site	Type	H	D	h	d	Whorls	Notes
Shells lacking or with only poorly developed lower palatal lamella							
10	Holotype	7.0	2.9	2.3	2.2	8½	
4	Paratype 1	6.3	2.7	2.1	1.6	8¼	
12	Paratype 2	6.6	2.9	2.3	2.1	8¼	
10	Paratype 3	7.6	2.8	2.4	2.0	8¾	
10	Paratype 4	6.6	3.0	2.4	1.8	—	Apex damaged
12	Paratype 5	8.0	3.0	2.4	2.3	9	
11	Paratype 6	7.0	2.9	2.2	2.1	8	
10	Paratype 7	7.1	2.9	2.3	2.0	8½	
10	Paratype 8	1.2	2.0	0.8	0.8	3½	Juvenile
11	Paratype 9	7.1	3.1	2.25	3.1	8¾	
10	Paratype 10	7.25	2.9	2.3	2.0	7¾	
12	Paratype 11	7.0	3.0			8	
12	Paratype 12	7.6	2.9			8	
12	Paratype 13	6.6	2.9			7¾	
12	Paratype 14	7.0	2.8	2.2	2.1	8½	
11	Paratype 15	7.4	2.8			7¾	
11	Paratype 16	7.5	3.0			7¾	
10	Paratype 17	6.5	2.9	1.9	1.9	8	
10	Paratype 18	6.5	2.8			8	
10	Paratype 19	6.7	2.75	1.9	1.9	7¾	
10	Paratype 20	7.2	3.0	2.3	2.15	7¾	
10	Paratype 21	6.9	3.0	2.2	2.15	8¼	
Shells with prominent lower palatal lamella							
1		8.1	3.3	2.5	2.3	8½	
3			3.35	2.35	2.35		Broken shell

Remarks. Two additional shells (one broken) that are not included in the type series (Table 9) are similar in terms of shell shape and crenellated suture, but they are furnished with a strong lower palatal fold. These were collected from Sheko (Site 1, NMW.Z.2025.002.21) and Dembi (Site 3, NMW.Z.2025.002.22) Forests to the west of the town of Misan Teferi, about 25 km to the west of Wacha Maji (Site 4) where *P. unumiugum* was collected. The intact shell is larger than any of the specimens of *P. unumiugum* (Table 9), and the umbilicus of the broken shell is open, unlike in *P. unumiugum*. These shells are close to *P. hyalinum* in terms of size and dentition, but the available material is unfortunately not sufficient to decide whether they reflect variation within *P. hyalinum* (or *P. unumiugum*) or a further species of *Ennea*. *Ptychotrema hyalinum was* collected by Oscar Neumann in the Kella Mountains, which are less than 50 km from the two sites where these two shells were collected, and less than about 90km from the four *P. unumiugum* sites. *P. hyalinum* has an obovate shell, but these two shells and *P. unumiugum* are more uniformly cylindrical and also have more a strongly crenellated suture.

Etymology. From Latin: "unum", single, and "iugum", ridge, referring to the diagnostic low palatal ridge that replaces the usual stronger lower palatal fold in this species.

***Ptychotrema* (*Ennea*) *epicratis* sp. nov.**
Figure 5D, E, Table 10

ZooBank identifier. urn:lsid:zoobank.org:act:7B573A55-7E95-49A2-86FA-5B9736A71A90

Type material. Holotype: NMW.Z.2025.002.34. Paratypes: 2 adult, both in spirit, NMW.Z.2025.002.37, from Site 19; 10 adults, including 2 shells in spirit, 3 juveniles, NMW.Z.2025.002.35, from Site 21; 4 adults, NMW.Z.2025.002.36, from Site 22 (Fig. 1, Table 1).

Type locality. Eithiopia: Oromia Region: Bale Zone: Goba Woreda: Bale Mountains National Park: Harenna Forest 2; 06.633°N, 039.736°E, 1894 m a.s.l. (Site 19; Fig. 1, Table 1).

Diagnosis. A small, elongate ovoid shell with a silky lustre. Body and lower whorls with very distinctive regular axial reticulation of fine anastomosing incised lines. Apertural dentition with a bicuspid columellar process and two deeply in-running palatal folds with free ends thickened and lobed.

Table 10. Shell dimensions of *Ptychotrema* (*Ennea*) *epicratis* sp. nov. See Tables 1 and 2 for information on the collecting sites.

Site	Type	H	D	h	d	Whorls	Notes
19	Holotype	5.85	2.55	1.9	1.9	7¾	
21	Paratype 1	5.4	2.5	1.7	1.8	7½	
22	Paratype 2	5.4	2.4	1.7	1.6	7	
22	Paratype 3		2.4			—	Old broken shell
22	Paratype 4	5.3	2.4	1.7	1.6	7½	
22	Paratype 5	5.5	2.4	1.6		7½	
21	Paratype 6	5.5	2.4	1.6	1.6	7¾	
21	Paratype 7	5.35	2.5	1.7	1.7	7¼	
21	Paratype 8	5.15	2.4	1.6	1.65	7⅓	Very strong palatal folds, corresponding very strong furrows
21	Paratype 9						Old broken shell
21	Paratype 10	5.6	2.35	1.8	1.7	8¼	
21	Paratype 11	5.2	2.35	1.65	1.6	7¼	
21	Paratype 12	5.7	2.35	1.65	1.7	7½	
21	Paratype 13	2.5	2.3	1.0	1.1	5½	Juvenile
21	Paratype 14	1.35	2	0.8	0.9	4⅓	Juvenile
21	Paratype 15	2.7	2.3	1.0	1.1	5¾	Juvenile
19	Paratype 16	5.6	2.55			—	
19	Paratype 17	5.25	2.4	1.7	1.7	7½	
21	Paratype 18	5.55	2.4	1.7	1.7	7¾	
21	Paratype 19	5.4	2.35	1.7	1.7	7⅔	
21						—	Shell fragment
21						—	Shell fragment
21						—	Shell fragment

Description. The shell (Fig. 5D, E, Table 10) is small, elongate-ovoid (H: 5.2–5.85 mm; D: 2.35–2.55 mm), and with 7–8¼ convex whorls, with the upper whorls slightly shouldered. The shell is glassy and translucent when fresh. The apex is rounded, although it is more conical in some specimens. The protoconch consists of 2 whorls; whorl 1 is smooth and glossy, and whorl 2 is glossy with very fine, close, rather regular axial wrinkles. The teleoconch is silky, with the upper whorls having very close, regular, weak, and fine axial wrinkles. The lower whorls, including the body whorl, have a very distinctive, regular axial reticulation of fine anastomosing incised lines (Fig. 5E). The whorl preceding the body whorl is generally the widest. The suture is simple. The umbilicus is closed. The peristome is continuous, flared, and reflected. The aperture is pyriform; apertural dentition comprises a bicuspid columellar process (Fig. 5D), a rather short, blade-like, bilobed parietal lamella which extends for only about ¼ whorl into the shell, and two deeply in-running palatal folds, their ends closest to the peristome typically being thickened and lobed. Neither of the palatal folds extend to the peristome; the lower varies in strength, but the upper fold is generally the strongest. There is an upper palatal lip tooth, which is externally marked by a shallow depression. The two palatal folds have corresponding strong external spiral furrows that extend for about 1/3 of a whorl. Juvenile shells are edentate. Apertural dentition appears to be very constant among the specimens.

Distribution and habitat. Harenna Forest, Bale Mountains, Ethiopia. Found living in leaf litter in Afromontane forest at elevations of between 1894 and 2420 m.

Differentiation. *Ptychotrema epicratis* lacks the crenellated suture of *P. aethiops*, *P. unumiugum*, *P. propenanum*, and *P. denticulatum* (and varieties). It is also smaller (Figs 5, 11) and has a more strongly developed lip tooth than these species, and there is distinctive microsculpture on the teleoconch. *Ptychotrema aethiops* does have rather similar fine, branching axial microsculpture, but its shell is much larger, has a crenellated suture, lacks a strong lip tooth, and the ends of the palatal folds are not inflated (or only very weakly so) as in *P. epicratis*. It differs from *P. hyalinum* and *P. laeve*, which both have weakly crenellated sutures and rather different shell shapes, lack a lip tooth, and are larger. *Ptychotrema epicratis* has some similarities with *P. massauense,* which has a simple suture and strong palatal lip tooth. However, unlike *P. epicratis*, the parietal lamella in *P. massauense* connects with the outer lip and, in profile, its outer lip projects to a point corresponding with the lip tooth, rather than forming a smooth arc as in *P. epicratis* (Fig. 5D). According to Thiele (1933), *P. massauense* was collected by Hildebrandt at Massaua, Eritrea, which is coastal town on the Red Sea some 950 km to the north of this site. Additionally, Thiele's description of *P. massauense* does not mention any fine microsculpture.

Etymology. From Latin "epi-", over or upon, and "cratis", wicker-work or a hurdle. Pertaining to the fine and distinctive shell microsculpture that bears some resemblance to bundles of wicker-work or hurdle.

***Ptychotrema* (*Ennea*) *harennae* sp. nov.**
Figure 7A, Table 11

ZooBank identifier. urn:lsid:zoobank.org:act:E55B4873-AD66-4E9F-8F9E-228CD9B074EC

Type material. Holotype: NMW.Z.2025.002.23. Paratypes: 15 adults, 3 juveniles, NMW.Z.2025.002.24, from Site 20; 1 adult, NMW.Z.2025.002.25, from Site 19; 2 juveniles, NMW.Z.2025.002.26, from Site 18 (Fig. 1, Table 1).

Type locality. Eithiopia: Oromia Region: Bale Zone: Goba Woreda: Bale Mountains National Park: Harenna Forest 3; 06.640°N, 039.736°E, 1904 m a.s.l. (Site 20; Fig. 1, Table 1).

Diagnosis. Diagnostic characters of this species are the strongly ribbed shell, the basal rather than palatal position of the lower fold, the presence of a second, small, deep and in-running parietal lamella, the open but very narrow umbilicus, the presence of a mamillate nodule on the upper part of the columellar process, and the absence of apertural dentition in juvenile shells.

Description. The shell (Fig. 7A, Table 11) is very small and biconical (H: 3.0–3.5 mm, D: 1.5–1.65 mm), with 7–8¼ rounded whorls. The shell is glassy and translucent when fresh. The apex is rounded. The protoconch consists of 2⅓ whorls and is smooth, with very fine, faint, incised spiral lines which are visible on fresh shells (paratypes 1, 27, 30) at ×40 magnification. The teleoconch has strong, regular, axial ribs that cross and crenellate the suture; these ribs are weakly sigmoid on the upper whorls but more or less straight on the lower ones. There are about (16–)17–19(–22) ribs visible on the face of the adult body whorl. The umbilicus is rimate and very narrowly pyriform. The aperture is broadly heart-shaped. The peristome is reflected, continuous across parietal. The apertural dentition comprises a thickened palatal tooth midpoint on the outer lip, two parietal lamellae, one palatal and one basal fold, and a columellar process. The parietal lamellae consist of a large, in-running angular lamella which extends to and protrudes slightly across the plane to the peristome, and a deeper, much shorter, in-running lamella which runs at an angle to the larger lamella. The larger angular lamella extends strongly for about ⅓ whorl into the shell after which it gradually reduces in height, only

Table 11. Shell dimensions of *Ptychotrema* (*Ennea*) *harennae* sp. nov. See Tables 1 and 2 for information on the collecting sites.

Site	Type	H	D	h	d	Whorls	Notes
20	Holotype	3.25	1.55	0.9	0.9	8⅛	
20	Paratype 1	3.5	1.65	0.9	0.95	8¼	
20	Paratype 2	3.25	1.55	0.9	0.9	7	
20	Paratype 3	3.1	1.55	0.85	0.9	7¾	
20	Paratype 4	3.2	1.6	0.85	0.95	7	
20	Paratype 5	3.35	1.6	0.95	0.9	7⅞	
20	Paratype 6	3.15	1.55	0.9	0.9	7	Old, broken shell
20	Paratype 7	2	1.5	0.6	0.8	6	Juvenile, broken apex. Assigned to *harennae* based on metrics
20	Paratype 8		1.6	0.9	0.9	—	Old shell; apex absent
20	Paratype 9	3.3	1.65	0.9	0.95	7¾	
20	Paratype 10	3.1	1.6	0.9	0.9	7¾	
20	Paratype 11	2.95	1.5	0.85	0.9	7¾	
20	Paratype 12	3.2	1.6	0.85	0.85	7¾	Old worn shell
20	Paratype 13	3.25	1.6	0.9	0.85	8	
20	Paratype 14	3.4	1.6	0.85	0.9	8	
20	Paratype 15	3.25	1.55	0.9	0.9	8	
20	Paratype 16	1.7	1.5	0.6	0.75	5¾	Juvenile shell assigned to *harennae* based on D/whorl metrics
20	Paratype 17					—	Broken ad shell missing peristome
20	Paratype 18	1.65	1.5	0.5	0.75	5¾	Juvenile shell assigned to *harennae* based on D/whorl metrics
19	Paratype 19	3.4	1.6	1	0.9	8	
18	Paratype 20	0.9	1.25	0.5	0.6	3½	Juvenile assigned to *harennae* based on metrics
18	Paratype 21	0.8	1.05	0.4	0.5	3¼	Juvenile assigned to *harennae* based on metrics

to reappear as a stronger lamella about ½ whorl further into the shell. There are strong external furrows in the shell that correspond with the palatal and basal folds. These two folds do not extend to the thickened peristome, the weaker basal fold starting about 0.35 mm from the peristome. The section of shell between these folds and the peristome is inflated. The columellar process consists of an upper mamillate nodule and a lower, larger, rectangular slab which is variously entire to weakly bilobed. Juvenile shells are edentate.

Distribution and habitat. Harenna Forest, Bale Mountains, Ethiopia. Sieved from leaf litter taken from mature Afromontane forest in the submontane zone between 1487 and 1904 m altitude.

Differentiation. Among the described *Ennea* species, the overall shell shape of *P. harennae* most closely resembles that of *P.* (*E.*) *pseudosilvaticum* Adam *et al.* 1994 and *P.* (*E.*) *silvaticum* Pilsbry, 1919. However, *P. pseudosilvaticum* is larger, has strong spiral "costulation" on the protoconch. Its peristome is detached from the body whorl and curved, whereas *harennae*'s is united and more or less straight. In both *P. pseudosilvaticum* and *P. silvaticum*, the lower fold is palatal rather than basal as in *harennae*, the axial ribs are stronger and more widely spaced, and the columellar process is formed of three distinct teeth/tubercles. *Ptychotrema silvaticum* is closer to *P. harennae* in terms of both its shell size and the weaker, fine, spiral threads on the protoconch. However, *P. silvaticum's* upper palatal fold reaches the peristome where it forms a lip tooth, rather than being detached as in *harennae*. Perhaps the difference of greatest significance is that juveniles of *P. silvaticum* are dentate, whereas those of *P. harennae* (and *P.*

Figure 7. Ethiopian *Ptychotrema* species. **A,** *P.* (*Ennea*) *harennae* sp. nov., holotype. **B**, *P.* (*E.*) *canaliculatum* sp. nov. holotype. **C**, *P.* (*E.*) *balenense* sp. nov., holotype. **D, E**, *P.* (*E.*) *wiersbowskyi* sp. nov.: (**D**) holotype; (**E**) detail of aperture (not to scale).

pseudosilvaticum) are not. Finally, consideration must also be given to the possibility that this species has been assigned to *Parennea,* of which Adam & van Goethem's *P. wittei* would appear to bear the strongest similarity. However, *P. harennae* does not have the 'trellised' apical microsculpture of *P. wittei,* or the single external furrow and detached peristome that is curved above the angular denticle of that species. *Ptychotrema harennae* may be separated from *P. canaliculatum* and *P. balenense* by its smaller shell (Fig. 10), the presence of a basal fold rather than a second, lower palatal one, the faint spiral microsculpture on the protoconch, the distinct nodule at the top of the columella and the open umbilicus. Also, the second small, deep parietal lamella of *P. harennae* is not present in *P. balenense*.

Remarks. In this species the lower fold/furrow is in a basal rather than palatal position, so it does not entirely accord with Pilsbry's (1919) description of subgenus *Ennea* as having "deeply entering upper and lower palatal folds, with corresponding spiral furrows". Assignment to subgenus *Ennea* is thus provisional. Juvenile shells of this species are difficult to separate from *P.* (*E.*) *canaliculatum* and *P.* (*E.*) *balenense*. Identification of the two juvenile shells from Site 18 has been based on the diameter of the shell relative to the number of whorls. Sites 18 and 20 are geographically very close to each other.

Etymology. After Harenna Forest on the south side of the Bale Mountains, where the specimens were collected.

***Ptychotrema* (*Ennea*) *canaliculatum* sp. nov.**
Figure 7B; Table 12

ZooBank identifier. urn:lsid:zoobank.org:act:9E27849F-BBBE-4DDA-8C4E-68D1D1EED862

Type material. Holotype: NMW.Z.2025.002.27. Paratypes: 6 adults, 3 juveniles, NMW.Z.2025.002.28, from Site 18; 2 adults, NMW.Z.2025.002.29, from Site 19; 1 adult, 1 juvenile, NMW.Z.2025.002.30, from Site 20 (Fig. 1, Table 1).

Type locality. Eithiopia: Oromia Region: Bale Zone: Goba Woreda: Bale Mountains National Park: Harenna Forest 1; 06.459°N, 039.762°E, 1487 m a.s.l. (Site 18; Fig. 1, Table 1).

Diagnosis. A very small *Ennea* with a strongly thickened white peristome, a constricted aperture and very strong external furrows associated with the palatal folds. An internal 'gutter', between the lower palatal denticle and the columellar wall forms a distinctive is 'J' shape when viewed externally, .

Description. The shell (Fig. 7B, Table 12) is very small and biconical (H: 4–4.6 mm, D: 1.8–2.1 mm), with 7¾–8½ convex whorls. Shells are white to brownish white; fresh shells are translucent and glassy between the axial ribs. The apex is obtuse. The protoconch consists of two whorls, with the suture simple, and is largely smooth, but there are areas of fine, very closely set axial riblets and traces of spiral lines. The boundary of the protoconch with the ribbed teleoconch is distinct. The teleoconch has strong, regular, axial ribs that cross and crenellate the moderately deep suture; there are about 18–20 ribs visible on the face of the adult body whorl. The umbilicus is closed. The peristome is thick, white, very strongly flared, and continuous across the parietal. The aperture is subquadrate and strongly constricted by four major processes: a parietal lamella, a columellar process, and two palatal folds. There is also a second minor and deeper parietal lamella, and areas of thickening on and close to the peristome and on the columella. The upper palatal process is a very strong and in-running fold which extends for about ½ whorl and is detached from a strong, broad lip tooth. The lower palatal process/fold is perhaps best described as an elongated denticle at the junction of the palatal and basal zones; it runs parallel with the upper palatal fold and terminates before an area of basal thickening just inside the lip. These palatal processes are associated with two very strong external furrows. The sections of shell between the furrows, and also the columellar wall, are compressed into cylindrical structures (visible externally) that coil around the axis of the shell for about ½ whorl, with the upper being slightly inflated just behind the aperture. The lower cylindrical structure is J-shaped when viewed externally in basal view (Fig. 7B). Internally it forms a deep gutter between the columellar wall and lower palatal denticle. The strong in-running parietal lamella forms a three-branched angular denticle where it meets the peristome, protruding slightly from the plane to the aperture. A second, deeper, weaker in-running parietal lamella runs parallel with the larger lamella. The columella is thickened, forming an entire, or rarely a very weakly bilobed, process. Juvenile shells are edentate and have an open umbilicus.

Distribution and habitat. Harenna Forest, Bale Mountains, Ethiopia. Living in leaf litter in mature Afromontane forest at lower elevations in the submontane zone between 1487 and 1904 m altitude.

Differentiation. In terms of general shell shape, this biconical species is similar to *P. harennae* and *P. balenense*, which were also collected from Harenna Forest. However, *P. canaliculatum* is significantly larger and its shell is more obese than *P. harennae* (Fig. 10). The strong lower palatal denticle, the second, small and deep parietal denticle and the more or less entire columellar process separate it from *P. balenense*. With respect to other described *Ennea* species, *P. canalicula-*

Table 12. Shell dimensions of *Ptychotrema* (*Ennea*) *canaliculatum* sp. nov. See Tables 1 and 2 for information on the collecting sites.

Site	Type	H	D	h	d	Whorls	Notes
18	Holotype	4.2	2.1	1.3	1.3	8¼	
20	Paratype 1	2.15	1.6	0.6	0.8	6½	Juvenile
18	Paratype 2	1.5	1.7			4¾	Juvenile
18	Paratype 3	4.2	2.0	1.2	1.2	7¾	
20	Paratype 4	4.3	1.9	1.2	1.2	8⅛	
18	Paratype 5	4.5	2.0	1.3	1.2	8½	
18	Paratype 6	4.3	2.1	1.3	1.3	8⅛	
18	Paratype 7	4.5	1.9	1.1	1.2	7⅞	
18	Paratype 8	4.3	2.0	1.2	1.3	8¼	
18	Paratype 9	3.9	2.0	1.3	1.2	7¾	
19	Paratype 10	4.0	1.8	1.1	1.1	8	
19	Paratype 11	4.6	2	1.3	1.2	8½	
18	Paratype 12	0.7	1.8	0.7	0.8	5⅛	Juvenile
18	Paratype 13	2.1	1.9	0.6	0.9	5⅞	Juvenile

tum is perhaps closest to *P. pseudosilvaticum* in terms of general shell shape and size, but that species has strong spiral costulations on the protoconch, and it has axial ribs on the teleoconch that are stronger and much more widely spaced than on *P. canaliculatum*.

Remarks. Juveniles of *P. canaliculatum* and *P. balenense* are difficult to separate. Juvenile specimens assigned to *P. canaliculatum* have been identified using shell dimensions and whorl counts, and because adult shells of *balenense* were not found in Harenna Forest Sites 1–3.**Etymology.** Latin "canaliculatum", channeled. Relating to the canal or gutter-like basal grove in the shell aperture, which helps to distinguish this species.

Ptychotrema (*Ennea*) *balenense* sp. nov.

Figure 7C; Table 13

ZooBank identifier. urn:lsid:zoobank.org:act:A52F919D-B288-4709-B3A6-A70D47796E99

Type material. Holotype: NMW.Z.2025.002.31. Paratypes: 1 adult, NMW.Z.2025.002.32, from Site 21; 2 adults, NMW.Z.2025.002.33, from Site 23 (Fig. 1, Table 1).

Type locality. Eithiopia: Oromia Region: Bale Zone: Goba Woreda: Bale Mountains National Park: Harenna Forest 4; 06.710°N, 039.734°E, 2360 m a.s.l. (Site 21; Fig. 1, Table 1).

Diagnosis. A very small, biconical species with strong, regular, axial ribs. The species is characterised by the near absence of a lower palatal fold, which in this species is represented by an area of weak thickening internally, and a weak external furrow.

Description. The shell (Fig. 7C, Table 13) is very small, biconical (H: 4–4.2 mm, D: 1.8–1.9 mm), with 8–8½ moderately convex whorls and translucent white. The apex is obtuse. The protoconch consists of 2¼ smooth, glossy whorls. The teleoconch has strong, regular, axial ribs which cross and crenellate the suture; there are about 18–21 ribs visible on the face of the adult body whorl. The umbilicus is closed. The aperture is rounded-triangular, with a thickened and weakly flared peristome, which is continuous across parietal. Apertural dentition comprises an in-running upper palatal fold, a parietal lamella, and a broad, rounded outer-lip tooth. The columella is thickened. The palatal fold is detached from the lip tooth and is marked externally by a moderately strong external furrow which extends almost around the body whorl. The free end of the palatal fold is slightly thickened, and there is a small external depression behind the lip tooth. The parietal lamella protrudes slightly from the plane of the aperture, forming an angular denticle that creates an open oval sinus with the lip tooth. There is hint of thickening at the junction of the basal and palatal zones, and this corresponds with a weak external linear furrow. In lateral view, the aperture profile curves back either side of the outer-lip tooth.

Table 13. Shell dimensions of *Ptychotrema* (*Ennea*) *balenense* sp. nov. See Tables 1 and 2 for information on the collecting sites.

Site	Type	H	D	h	d	Whorls
21	Holotype	4.1	1.8	1.2	1.1	8⅛
21	Paratype 1	4	1.8			8½
23	Paratype 2	4.2	1.9	1.1	1.1	8½
23	Paratype 3	4	1.9	1.1	1.2	8

Distribution and habitat. Found living in leaf litter in Harenna Forest, Bale Mountains, Ethiopia. In Afromontane forest and *Hagenia abyssinica* dominated woodland at elevations of between 2360 m and 2665 m. Sieved from leaf litter taken from mature Afromontane forest with large widely spaced emergent trees with buttress roots, a broken lower canopy and a field layer containing grass and other herbs.

Differentiation. The absence of the lower palatal fold and second parietal lamella distinguish this species from *P. canaliculatum*. *Ptychotrema balenense* is almost certainly closely related to *P. canaliculatum* and it is close in terms of shell shape and sculpture, although on average it is slightly smaller (Fig. 8). Both species were collected in Harenna Forest, but *P. balenense* was found at a higher altitude than *P. canaliculatum*.

Etymology. From the Bale Mountains, where the specimens were collected.

***Ptychotrema* (*Ennea*) *wiersbowskyi* sp. nov.**
Figure 7D, E

ZooBank identifier. urn:lsid:zoobank.org:act:0AC19BF8-7074-4C9E-8792-1357DB7E0626

Type material. Holotype: NMW.Z.2025.002.38.

Type locality. SW Ethiopia: Southern Nations, Nationalities, and Peoples' Region: Bench Maji Zone: Sheko Woreda: Near Mizan Teferi town: Sheko Forest 1; 07.042°N, 035.448°E, 1567 m a.s.l. (Site 1; Fig. 1, Table 1).

Diagnosis. Shell very small and cylindrical, with moderately tumid and strongly ribbed convex whorls separated by a deep crenellated suture. Apertural dentition with a large bilobed columellar slab, the lower lobe being largest. The upper palatal fold is strong, but the lower palatal fold is short and associated with a short external furrow.

Description. The shell (Fig. 7D, E) is very small (H: 3.45 mm; D: 1.60 mm; h: 1.0 mm; d: 1.0 mm; 7¼ whorls) and cylindrical. The single old shell is white and opaque, but fresh shells are probably glassy and translucent. It has 7¼ moderately tumid convex whorls separated by a deep, crenellated suture. The apex is rounded. The protoconch has 2½ whorls and is probably smooth, although this is not clear because the single specimen has many corrosion pits; the junction with the teleoconch is indistinct. The aperture is circular. The teleoconch of 4¾ whorls has widely spaced, very strong, axial ribs, with smooth shell between the ribs. About 14 ribs are visible on the face of the body whorl in apertural view. The ribs are very weak immediately above the aperture. The umbilicus is closed or possibly minutely rimate (obscured by debris). The peristome is thickened and weakly reflected, with additional thickening into a rather flattened outer-lip tooth about mid-point on the palatal margin. It is continuous across the parietal as a layer of transparent callus. There are four apertural processes. There is a strong, deeply in-running parietal angular lamella, which connects via a small area of callus to the outer peristome; a strong and in-running upper palatal fold which does not reach the peristome and has a corresponding deeply impressed external furrow which extends about ½ a whorl; a short, weak elongated basal ridge, also not reaching the peristome and also with a corresponding short external basal furrow extending

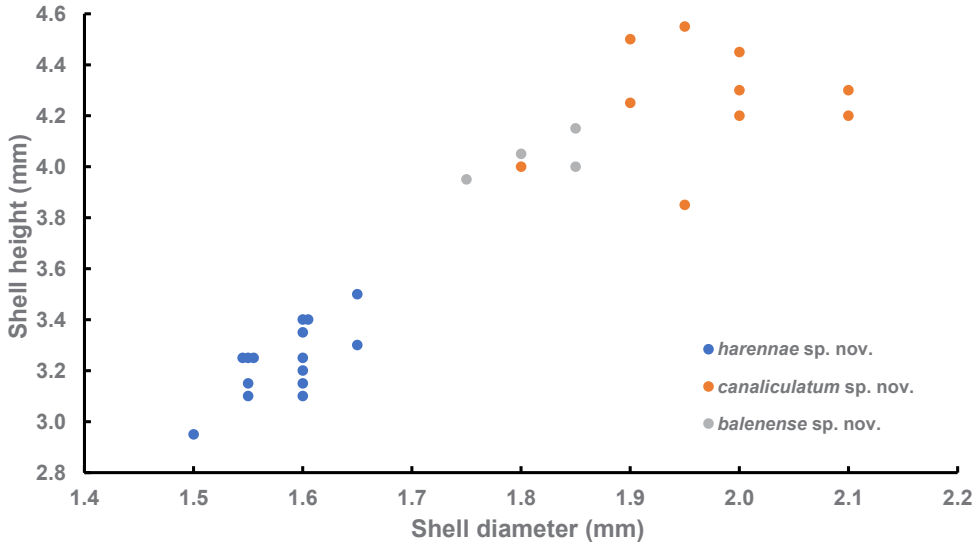


Figure 8. Shell height (H) versus shell diameter (D) for adult shells of *Ptychotrema* (*Ennea*) *harennae, canaliculatum* and *balenense* spp. nov. (note: some data points jittered for clarity).

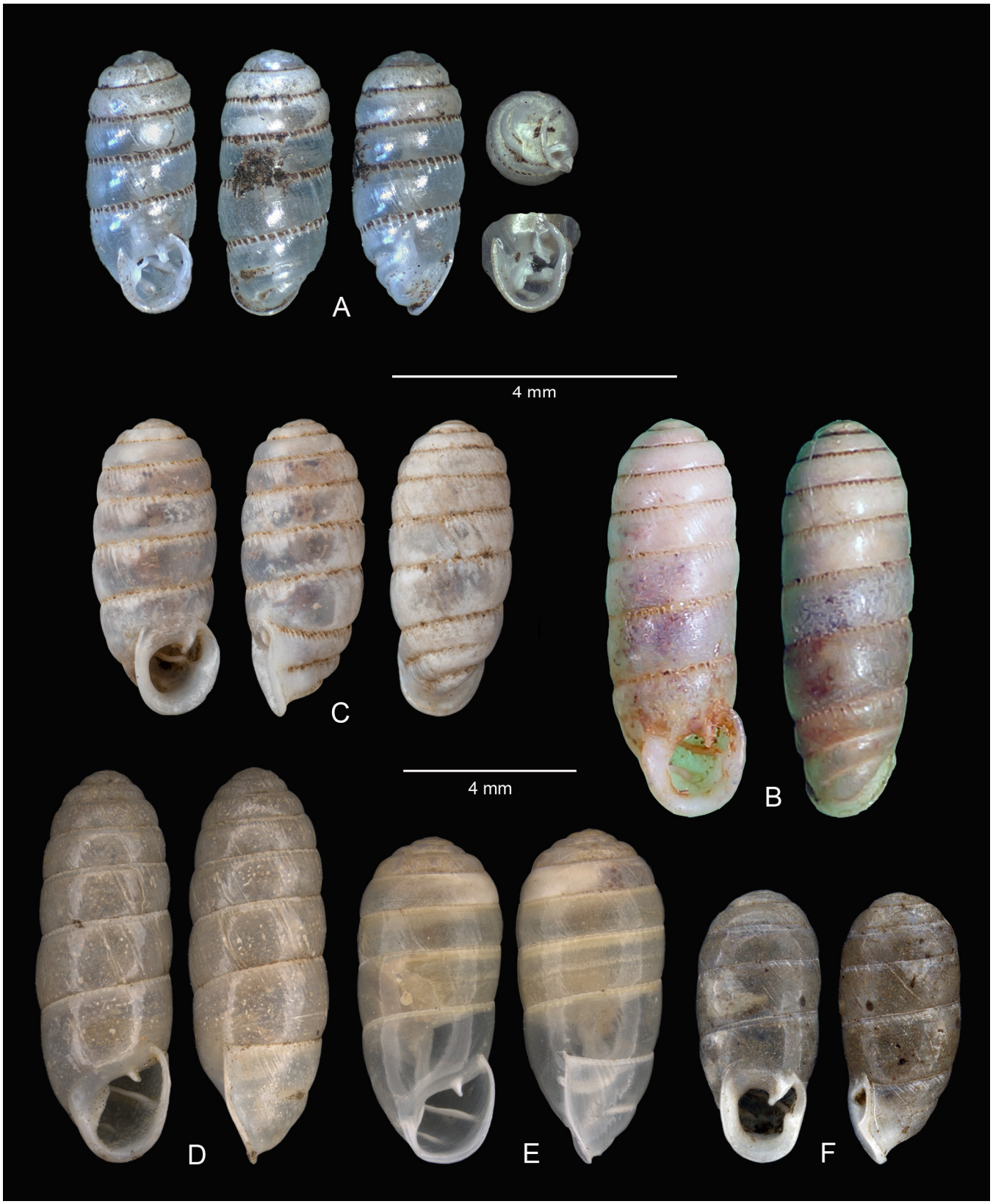


Figure 9. Ethiopian *Ptychotrema* species. **A**, *P.* (*Ennea*) *propenanum* sp. nov. holotype. **B**, **C**, *P.* (*E.*) *denticulatum* (Morelet, 1872): (**B**) syntype MSNG; (**C**) syntype NHMUK 1893.2.4.109. **D**, *P.* (*E.*) *laeve* (Thiele, 1933), holotype ZMB 109975. **E**, *P.* (*E.*) *hyalinum* (Thiele, 1933) holotype ZMB 109976. **F**, *P.* (*E.*) *massauense* (Thiele, 1933) holotype ZMB 37389.

for about ¼ of a whorl; and a large bilobed columellar slab, with the lower lobe largest.

Distribution and habitat. Only known from the type locality of Sheko Forest, near Mizan Teferi in south-west Ethiopia (Table 2). Living in leaf litter in disturbed Afromontane forest.

Differentiation. The general shell shape and sculpture is similar to *P. wondogenetense*, but that species is much smaller, and it is clearly a *Parennea* with a single palatal fold/furrow rather than the two in *wiersbowskyi*. *Ptychotrema* (*E.*) *propenanum* is about same size and shape but only the suture is crenellated, and the whorls are less tumid. *Ptychotrema* (*Ennea*) *bequaerti* Dautzenberg & Germain, 1914 is larger and it is more closely ribbed. *Ptychotrema bishanwakaense* is strongly ribbed like this species, but it has an open umbilicus and is also in *Parennea,* and there is a difference in the spacing of the ribs. This shell does not match any of the figures in the works of Adam *et al.* (1994) or Pilsbry (1919).

Etymology. Named in appreciation of the assistance provided by Daniel Wiersbowsky, who organised and coordinated the field trips in Ethiopia.

***Ptychotrema* (*Ennea*) *propenanum* sp. nov.**
Figure 9A

ZooBank identifier. urn:lsid:zoobank.org:act:EC0BFF3B-1933-4407-AAA4-D0B1709A9325

Type material. Holotype: NMW.Z.2025.002.39.

Type locality. SW Ethiopia: Southern Nations, Nationalities, and Peoples' Region: Keffa Zone: Gimbo Woreda: Kafa Biosphere Reserve: Shorori wetland forest 1; 7.336°N, 36.208°E, 1623 m a.s.l. (Site 12; Fig. 1, Table 1).

Diagnosis. The key characters of this species are its very small shell, its smooth whorls but strongly crenellated suture, the strongly trifid and elongate columellar process, its open umbilicus and the presence of fine spiral microsculpture on the protoconch.

Description. The shell (Fig. 9A) is very small, cylindrical (H: 3.70 mm; D: 1.55 mm; h: 1.2 mm; d: 1.05 mm), with rounded apex and 7¼ convex whorls, and glassy and translucent when fresh. The protoconch, which consists of two whorls, is smooth, with very fine, faint, rather regularly spaced, incised spiral lines visible at high magnification (*c.* ×45). The teleoconch whorls are smooth, with traces of rather irregular, very fine, faint, incised spiral lines, which are especially apparent on the lower whorls, and a few irregularly spaced axial growth lines; the area immediately behind the outer lip is weakly ribbed. The suture is very strongly crenellated, and the crenelations extend for a short distance downward onto the whorl, especially on the central whorls. The aperture is subquadrate. The umbilicus open and very narrow. The peristome is continuous as a thin, transparent callus across the parietal, and the lip is thickened, white, and strongly reflexed, with additional thickening at the midpoint to form a weak lip tooth. Apertural dentition is 4-fold, comprising one deeply in-running angular–parietal lamella; two deeply in-running palatal folds which do not reach the lip (the uppermost one stronger and both with slightly swollen ends), and a trifid, elongate columellar process with its upper two nodules opposite the two palatal folds and constricting entry into the shell. The palatal folds are externally marked by two corresponding external furrows. The section of peristome in front of the upper palatal fold is thickened into a weak lip tooth.

Distribution and habitat. Shorori wetland forest in Kafa Biosphere Reserve, south-west Ethiopia. Sieved from leaf litter taken from disturbed, low, rather scrubby forest along the lower slopes of a valley.

Differentiation. This specimen was initially provisionally identified as *Ptychotrema* (*Ennea*) *denticulatum* var. *nanum* Connolly, 1928 because of its very small size and strongly crenellated suture. *Ptychotrema denticulatum* var. *nanum* was collected by J. Omer-Cooper in Jem Jem Forest, Ethiopia, which is about 300 km north-east of Shorori wetland forest (Site 12). In his short description, Connolly (1928: 164) commented that this form is an "almost exact miniature of" other material identified as *P. denticulatum* collected by Omer-Cooper in Jem Jem Forest and at Zukwala, "but measuring only 3.1 × 1.2 mm", and that "the tubercle on the outer lip is comparatively stronger". It appears that var. *nana* was found living sympatrically in Jem Jem Forest along with larger specimens identified by Connolly as *P. denticulata*. Unfortunately, Connolly did not figure this variety, and the type has not been found in NHMUK (J. Ablett pers. comm.). Although weakly thickened, the outer lip of *P. propenanum* is not furnished with a "tubercle", and Connolly made no reference to a strong columellar process (which is a very distinctive character in *P. propenanum*) or to any apical microsculpture, and from these considerations it seems unlikely that *P. propenanum* and *P. denticulatum* var. *nanum* are the same.

The shell of *P. propenanum* resembles that of *Ennea nigeriensis* de Winter & de Gier, 2019 in its general shape and strongly crenellated suture. However, that species is larger (H: 5.1–6.6 mm) than *P. propenanum* and only has one palatal fold. Shells of other *Ptychotrema* (*Ennea*) species illustrated by Adam *et al.* (1994) are either more strongly ribbed

or smooth across the teleoconch whorls and/or differ in overall shape.

Remarks. The status of this species and its relationship with *P. denticulatum* var. *nanum* will remain uncertain until the type of Connolly's variety is available for study or new material is collected. The introduction of *P. propenanum* as a new species seems justified because Connolly did not mention a columellar process, which is trifid and very prominent in *P. propenanum*. Connolly (1928) speculated that var. *nanum* may merit specific status.

Etymology. From the Latin "prope", near to or close to, and "nanum", a dwarf, alluding to Connolly's variety.

Other North-east African *Ptychotrema*

Ptychotrema (*Ennea*) *denticulatum* (Morelet, 1872)

Figure 9B, C

Morelet 1872: 202, pl. 9 fig. 10; Jickeli 1874: 29; Bourguignat 1883: 76, 118, figs 89, 90 (?); Tryon 1885: 94, pl. 27 figs 12, 13; Pollonera 1888: 53; Bourguignat 1889: 127; Kobelt 1904: 139, pl. 21; Kobelt 1909: 53; Kobelt 1910: 156; Connolly 1928: 164, 178; Thiele 1933: 285, 286; Bacci 1940: 450; Bacci 1951: 100; Verdcourt 1961: 160; Zilch 1961: 111; Richardson 1988: 21; Verdcourt 1990: 345, 346, 352, pl. 33; Adam *et al.* 1994: 75; Rowson 2010: 222; Breure *et al.* 2018: 268; Brown 2023: 110.

Remarks. Morelet (1872) gave shell size as H: 7–8 mm D: 3 mm, but the specimen labelled "Typus!" in MSNG is 9.2 × 3 mm (Bogos, Eritrea (about 15.7°N 38.6°E), leg O. Beccari). A syntype (1893.2.4.109) in NHMUK, which according to Breure *et al.* (2018) is part of the Morelet collection, is 6.3 × 2.6 mm (scaled from photograph available; The Natural History Museum 2014).

Material identified as *P. denticulatum* has been reported from widely separated localities: Mount Zukwala (9000 ft, about 50 km south of Addis Ababa) and Jem Jem Forest (8000 ft, about 70 km west of Addis Ababa), both leg. Omer-Cooper Connolly (1928); north-east shore of Lake Awasa (Rift Valley about 200 km south of Addis Ababa), leg. D.S. Brown & M.V. Prosser, NHMUK (Verdcourt 1990). These localities are approximately 750–1000 km south of the type locality in Bogos, Eritrea. Bacci (1951) cited records from between Ghinda and Asmara, mountains of Habab (leg. Jickeli) and forest of Fehere Ghembre (leg. Ragazzi), although some of these may correspond to varieties of *P. denticulatum*. Given the apparently very large range of this species, it is perhaps surprising that it was not re-found during the 2015 surveys.

Ptychotrema denticulatum seems to be reasonably well characterised by its cylindrical, rather narrow, elongate shell with strong sutural crenulations, but there is clearly considerable variation in shell size (Figs 9B, C, 11). Verdcourt (1990) described the anatomy and the radula of specimens collected from the north-east shore of Lake Awasa.

Several infraspecific variants of *P. denticulatum* have been described, although it has been suggested that some may eventually be raised to specific rank (e.g. Bacci (1951) regarding var. *hildebrandti*, and Connolly (1928) in respect to var. *nanum*). Tryon (1885: 95) and Verdcourt's (1961) identification key give shell characters that separate these varieties. In view of the disparate geographical locations and the often quite subtle variation in shell form, additional material will be required before a conclusion can be drawn about the status these varieties.

Var. *nanum* Connolly, 1928

Connolly 1928: 164, 178; Bacci 1951: 100; Verdcourt 1961: 161; Richardson 1988: 21; Adam *et al.* 1994: 76; Brown 2023: 111.

Remarks. Connolly gave shell measurements as 3.1 × 1.2 mm. Additional comments on this variety are given above in the description of *P. propenanum*.

Var. *hamacenica* (Bourguignat, 1883)

Bourguignat 1883: 76, 118; Tryon 1885: 95; Bourguignat 1889: 127; Connolly 1928: 178; Thiele 1933: 286; Bacci 1951: 100; Verdcourt 1961: 161; Richardson 1988: 22; Brown 2023: 111.

Remarks. Bourguignat did not provide information on shell size. Collected at "les hauts plateaux de l'Hamacen", by M. Raffray. This location is in Eritrea (*c.* 15.5°N 38.8°E), probably very close to Bogos, the type locality for *denticulatum*. The variety is distinguished by its strongly toothed columella ("columelle fortement denticulée") and in having eight whorls instead of 10, as in the typical *P. denticulatum*.

Var. *hildebrandti* (Jickeli, 1874)

Jickeli 1874: 29-30, pl. 4 fig. 2; Bourguignat 1883: 76, 118; Tryon 1885: 95, pl. 18; Bourguignat 1889: 127; Kobelt 1904: 140, pl. 21; Kobelt 1909: 53; Kobelt 1910: 156; Thiele 1933: 286; Connolly 1928: 178; Bacci 1951: 100; Verdcourt 1961: 161; Richardson 1988: 22; Brown 2023: 111.

Remarks. H: 11 mm, D: 4 mm. Parietal lamella joining with outer lip; shell brownish; columella callously thickened and sub-biplicate.

Var. *papilliferum* (Jickeli, 1873) (= var. *quinqueplicatum* (Bourguignat, 1883))

Jickeli 1873: 108, 126; Jickeli 1874: 29, 30, pl. 4 fig. 1; Bourguignat 1883: 76, 118; Tryon 1885: 95, pl. 18; Bourguig-

nat 1889: 127; Kobelt 1904: 140, pl. 21; Kobelt 1909: 53; Kobelt 1910: 156; Connolly 1928: 178; Thiele 1933: 286; Bacci 1951: 100; Verdcourt 1961: 161; Zilch 1961: 111; Richardson 1988: 22; Brown 2023: 111.

Remarks. H: 8 mm, D: 3 mm. Abyssinia. Columella with two folds.

Ptychotrema (*Ennea*) *laeve* Thiele, 1933

Figure 9D

Thiele 1933: 288, fig. 5; Bacci 1951: 100; Verdcourt 1961: 157–161; Richardson 1988: 147; Adam *et al.* 1994: 82; Brown 2023: 117.

Remarks. H: 9 mm, D: 3 mm. Abera (Djamdjam) at 3100 m in bamboo forest, leg. O. Neumann. An elongated smooth shelled species with weak sutural denticulation.

Ptychotrema (*Ennea*) *hyalinum* Thiele, 1933

Figure 9E

Thiele 1933: 288–289, fig. 6; Bacci 1951: 100; Verdcourt 1961: 157–161; Richardson 1988: 146; Adam *et al.* 1994: 79; Brown 2023: 113.

Remarks. H: 8 mm, D: 3.4 mm. Kella Mountains, leg. O. Neumann. Shell thin, obovate, and with a weakly denticulated suture. The Kella Mountains (*c.* 07.43°N, 035.41°E) are in the Kafa area, but this species was apparently not found during the current fieldwork but see additional remarks in *P. unumiugum* sp. nov.

Ptychotrema (*Ennea*) *massauense* Thiele, 1933

Figure 9F

Thiele 1933: 289, fig. 7; Bacci 1951: 100; Verdcourt 1961: 157–161; Richardson 1988: 148; Adam *et al.* 1994: 84; Brown 2023: 120.

Remarks. H: 6.2 mm, D: 2.75 mm. Near Massaua/Massawa/Mitsiwa, Eritrea (*c.* 15.5°N 039.5°E), on the Red Sea coast, leg. Hildebrandt. Shell elongate-ovoid with a strongly thickened peristome and a projecting tooth on the outer lip.

Ptychotrema gratum Thiele, 1933

Figure 10A, B, Table 14

Thiele 1933: 288, fig. 4; Verdcourt 1961: 160; Bacci 1951: 99 (as *Ptychotrema* (*Ptychotrema*) *gratum*); Richardson 1988 (as *grata*): 146; Adam *et al.* 1995: 93 (as *P.* (*P.*) *gratum*); Brown 2023: 88.

This species was originally collected by Oscar Neumann at Abera, Djamdjam, Ethiopia at 3100 m a.s.l. Using Neumann's journal (Neumann 1902), which describes his route and includes a map, this locality is at approximately 06.3°N 038.4°E. Brown (2023) gave the type locality near Axum in northern Ethiopia, but this is almost certainly incorrect because Neumann's route did not extend that far north.

During the 2015 fieldwork, three adult specimens were found at Sites 22 (2420 m a.s.l.) and 24 (1950 m a.s.l), which are about 140 km north-east and 100 km north of the type locality respectively. Table 14 gives measurements of these shells, and also of Thiele's holotype (ZMB 109974, Fig. 9B). The following description is based on this material.

Description. The shell (Fig. 10A, B, Table 14) is very small (H: 4.10–4.50 mm D: 1.85–2.15 mm), elongate-ovoid, and consisting of 7½ whorls. The protoconch whorls are 2½ in number and smooth; the transition to the teleoconch is rather indistinct but defined by the commencement of axial ribbing. The teleoconch has regular axial ribs of variable strength among available specimens, about 17 per mm on the body whorl. The suture is impressed and weakly crenellated by the ribs. The umbilicus is open, although partly obscured by the columella, and approximately 8% of the shell diameter. The aperture is triangular and congested by seven processes. There is a large, semicircular parietal angular lamella, which is concave on the side facing the outer lip and slightly protrudes from the plane of the peristome. There are three entering columellar lamellae, with the upper one strongest and the lower weakest. The interior end of the lower columellar lamella abuts a deeply set, transverse, peg-like, palatal denticle (it is difficult to be sure whether this denticle and the lower columellar lamella are connected, but I do not think so). There is a central palatal fold situated just above, and terminating just before, the deeply set denticle. Externally, there is a wide, rather shallow palatal depression just behind the aperture, but there are no external furrows associated with the palatal fold. The palatal fold and angular lamella form an oval sinus which contains an upper palatal denticle, situated just above the end of the angular lamella, and an additional minute tubercle at the top of the sinus at the junction of the parietal and patal zones.

Remarks. The specimens collected in 2015 match Thiele's (1933) description and type specimen reasonably well,

Table 14. Shell dimensions of *Ptychotrema gratum* Thiele, 1933.

Specimen	Site (Table 1)	H	D	h	d	Whorls
Holotype, ZMB 109974	Abera, Djamdjam	4.5	1.9	—	—	7
1	24	4.45	1.90	1.45	1.00	7½
2	22	4.35	2.15	1.50	1.20	7½
3	24	4.10	1.85	1.50	1.10	6¾

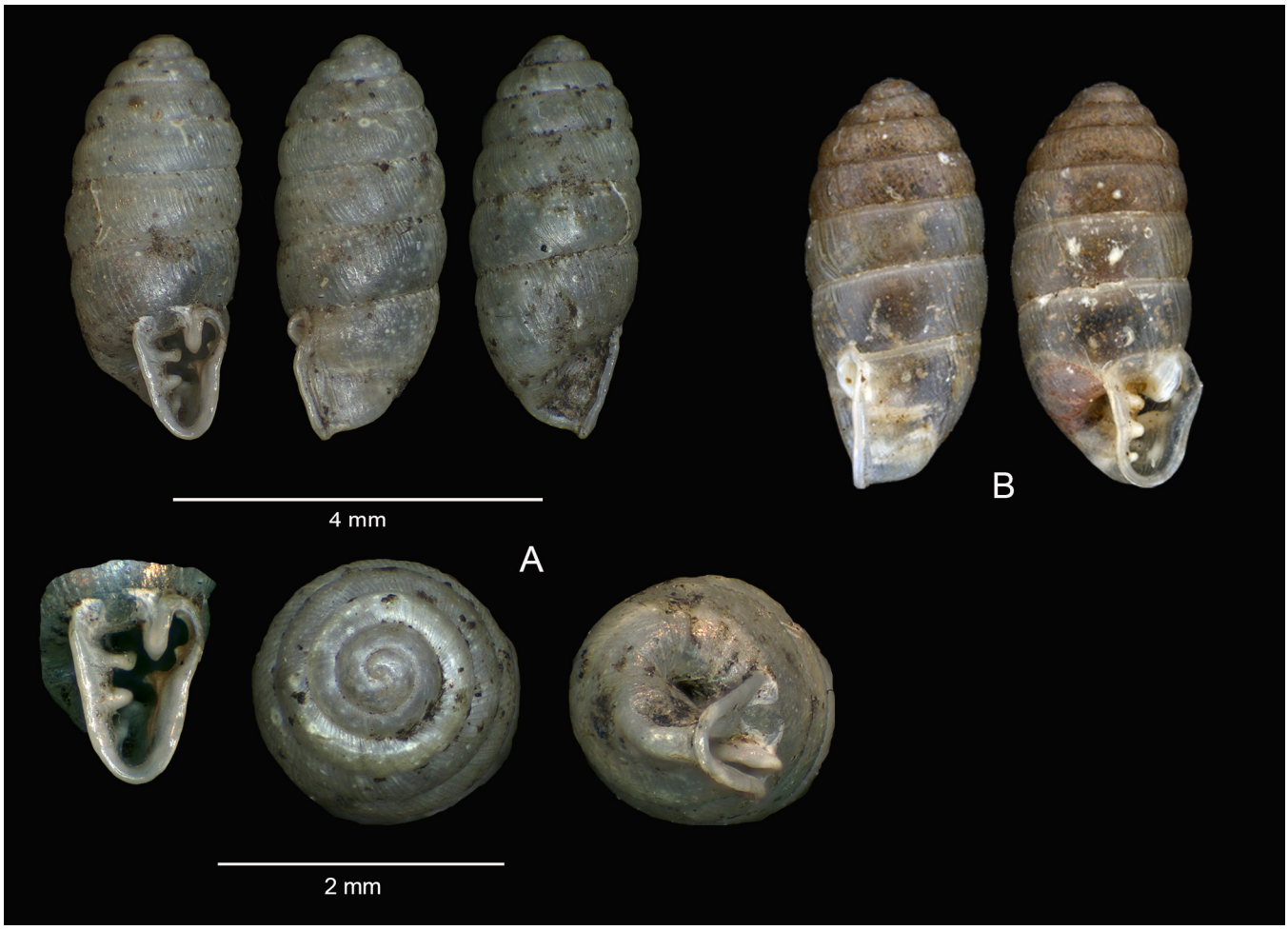


Figure 10. Ethiopian *Ptychotrema* species. **A**, **B**, *P. gratum* Thiele, 1933, shell #1, Site 22: (**B**), holotype ZMB 109974.

although there is some variation in the shape of the shell and the aperture, and in the strength of the ribbing. Compared with the type, shell #1 from Site 24 is is more strongly ribbed and narrower. The single adult shell (#2), from Site 22, is more ovoid; it has a wider aperture and its upper palatal denticle is stronger. Thiele (1933) described the dentition as comprising three columellar folds, a strong central palatal fold, a weaker one beneath it which does not reach the edge of the peristome (although this is not evident in his drawing of the shell), and a further palatal tooth opposite a strong parietal lamella. This dentition is essentially the same as in the specimens collected in 2015, although the deeply set peg-like palatal denticle present in the current material would need to be interpreted as Thiele's lower palatal fold. Thiele also did not mention the presence of a minute upper denticle within the sinus. However, overall, these differences are relatively minor, and they are not sufficient to suspect that more than one species is involved.

Conclusions. *Ptychotrema gratum* does not resemble any of the other streptaxids that have been described from northeast Africa, nor any of those that were collected during the current fieldwork. Thiele (1933) assigned this species to *Ptychotrema* (without subgenus), but the absence of palatal folds with accompanying external furrows suggests that an alternative (possibly new) genus could be more appropriate. Pilsbry (1919) erected the section *Plicigulella* to include cylindrical species with a triplicate columellar edge and well-developed basal teeth. Although the columella of *P. gratum* is furnished with three lamellae, each of these is a distinct and separate structure, which is very different from the single, 3-toothed or 3-crenate columellar structure found in *Plicigulella* species. In addition, *P. gratum* does not have any basal teeth. A.J. de Winter (pers. comm.) has noted that "*gratum* reminds me somewhat of West African '*Gulella*' species like '*G.' stolidodea* or '*G.' germaini*, especially the former, but these seem clearly too different to be closely related". Verdcourt's (1962) preliminary keys for the identification of East African *Gulella* species do not help to

identify *P. gratum* or its generic placement. Thus, based on shell morphology, *P. gratum* does not comfortably sit in any of the existing, although often artificial, streptaxid groups. Placement in the polyphyletic "*Gulella*" *sensu lato* would be an option, but transferring the problem to another genus makes no progress towards a solution, so I see little point and reluctantly leave the species in *Ptychotrema*.

Discussion

Identification. The following provisional key to the species attributed to *Ptychotrema* from Ethiopia and adjacent areas is based on adult shell characters. It utilises some of the couplets in Verdcourt's (1961) *Ptychotrema* key, especially for the separation of varieties of *P.* (*Ennea*) *denticulatum*. Connolly (1928) included two further species, *P. roberti* (Preston, 1910) and *P. raffrayi* (Bourguignat, 1883), in his Abyssinia/Eritrea list but they are not included in the key because their apertural dentition differs from that of *Ptychotrema*, and it seems clear that both would be more appropriately assigned to other genera. Thiele (1933) noted that *P. raffrayi* can hardly be considered a *Ptychotrema* because the apertural folds and external furrows are missing (the species has only a small parietal denticle). Bacci (1951) placed this species in *Gibbus* (*Gonospira*), and MolluscaBase (MolluscaBase Eds 2024b) accepts it as *Gonospira raffrayi* (Bourguignat, 1883). Referring to the classification of *roberti* in *Ptychotrema,* Verdcourt (1961: 160) commented that there "is nothing in the description to suggest the correctness of this". My examination of a single shell of *P. roberti* in the Melvill-Tomlin collection in NMW (accession number 1955.158; Abyssinia, no collector information), and online images of a syntype (Harar, Abyssinie, ex. Preston) in RBINS (2025), would support this because the palatal dentition in this species takes the form of a 3-lobed process rather than the extended folds characteristic of *Ptychotrema*. This species also lacks one or more external spiral furrows, the only external depression being immediately behind the lip and corresponding with the palatal process. Verdcourt (1961) did not suggest an alternative genus for this species, but a label associated with the RBINS co-type indicates that W. Adam considered that the species should be placed in *Gulella.* In MolluscaBase (MolluscaBase Eds 2024c), the species is currently classified in *Ptychotrema*.

1a Aperture narrowly obtriangular; three equally spaced lamellae on the columella, uppermost strongest; palatal denticles not entering deeply and not associated with external furrows ..... ***P.* (*P.*) *gratum* Thiele**

1b Aperture wider and more circular; shell with one or two palatal folds with corresponding external furrows **2**

2a One palatal fold with corresponding external furrow ..... (*Parennea*) ... **3**

2b Two external palatal furrows, usually associated with two corresponding internal folds[1] ..... (*Ennea*) ... **9**

3a Shell height <3 mm **4**

3b Shell height >3 mm **6**

4a Protoconch with fine spiral microsculpture; columella process distinctly bi-lobed **5**

4b Protoconch smooth[2]; columellar process weakly divided at most **8**

5a Umbilicus clearly open, *c.* 1/10 diameter of shell; H/D ≤ 2; palatal fold short and not wrapping around body whorl ..... ***P.* (*Pa.*) *bishanwakaense* sp. nov.**[3]

5b Umbilicus very narrow; H/D > 2; protoconch with fine spiral lines and axial riblets ..... ***P.* (*Pa.*) *keffaense* sp. nov.**

6a Shell irregularly cylindrical with one or more of the middle whorls widest **7**

6b Shell evenly cylindrical, middle whorls subequal in width ..... ***P.* (*Pa.*) *gaysayense* sp. nov.**

7a Shell with strong regular axial ribs; palatal fold strong and partly constricting body whorl ..... ***P.* (*Pa.*) *dolfi* sp. nov.**

7b Shell more or less smooth, apart from crenellate suture ..... ***P.* (*Pa.*) *somaliense* Verdcourt**

8a Shell ribbed ..... ***P.* (*Pa.*) *wondogenetense* sp. nov.**

8b Shell largely smooth apart from ribs extending from crenellate suture ..... ***P.* (*Pa.*) *tshibindanum septentrionale* Verdcourt**

9a H < 5 mm; shell strongly ribbed, biconical or cylindrical **10**

[1] The lower fold is sometimes reduced to a crease or low fold or absent (e.g. *epicratis*), but the lower external furrow is always present.

[2] *P. tshibindanum septentrionale*: Verdcourt did not mention any apical microsculpture. Alex Fedosov at SMNH (pers. comm.) has kindly examined the apex of the holotype and advised that he "could not discern any sculpture—either because it is lacking, or because the specimen seem to be slightly worn, and is also quite small".

[3] *P. bishanwakaense*: the palatal fold is very short; perhaps not *Parennea.*

9b H > 5 mm[4]; shell smooth, cylindrical or ovoid. Suture distinctly crenellate or simple **15**

10a Shell biconical, closely spaced ribs with *c.* 18–24 ribs across face body whorl..... **13**

10b Shell cylindrical, either with widely spaced ribs or suture crenellate **11**

11a Teleoconch with *c.* 11–12 ribs across face of body whorl ..... ***P.* (*E.*) *wiersbowskyi* sp. nov.**

11b Suture crenellate, remainder of shell essentially smooth **12**

12a Upper section of columella furnished with prominent trifid process; protoconch with very faint engraved spiral lines[5] ..... ***P.* (*E.*) *propenanum* sp. nov.**

12b Columellar process weaker and not trifid ..... ***P.* (*E.*) *denticulatum nanum* Connolly**

13a H ≤ 3.5 mm; lower fold in basal rather than palatal position; protoconch with faint spiral microsculpture; umbilicus open; distinct nodule at top of columella ..... ***P.* (*E.*) *harennae* sp. nov**

13b H > 4.2 mm; not with above combination of characters **14**

14a Adult aperture with two strong palatal folds, with upper fold stronger, and lower fold terminating at an area of basal thickening just inside the lip. Corresponding external furrows forming a narrow, J-shaped basal gutter. Shell rather obese (H/D: 2–2.4); peristome strongly thickened, flared, and white. Columella entire and sometimes weakly bilobed. Two parietal lamellae ..... ***P.* (*E.*) *canaliculatum* sp. nov.**

14b Adult aperture with single palatal fold. Columella thickened ..... ***P.* (*E.*) *balenense* sp. nov.**

15a Suture simple, shell ovoid or elongated ovoid **16**

15b Suture crenellate, denticulate, or serrated, sometimes weakly so[6] **17**

16a Outer-lip tooth projecting forward of palatal profile and connected to upper palatal fold, peristome thickened, 6.2 × 2.75 mm .... ***P.* (*E.*) *massauense* Thiele**

16b Lip tooth detached from palatal fold and not projecting; peristome not strongly thickened; teleoconch silky; upper whorls with very close regular weak and fine axial wrinkles, lower whorls, including body whorl, with very distinctive, regular axial reticulation of fine anastomosing incised lines ..... ***P.* (*E.*) *epicratis* sp. nov.**

17a Suture simple or very weakly serrated **18**

17b Suture strongly denticulate/crenellate **19**

18a Shell widest above the mid-point, palatal folds and external furrows weak, 8 × 3.4 mm, suture simple or very weakly crenulate ..... ***P.* (*E.*) *hyalinum* Thiele**

18b Shell elongated, about 9 × 3mm, suture finely serrated ..... ***P.* (*E.*) *laeve* Thiele**

19a Shell large, not ribbed, H ≥ 10 mm, elongated ovoid ..... ***P.* (*E.*) *aethiops* sp. nov.**

19b Shell smaller **20**

20a Shell cylindrical, (6.3–)7.1(–8.1) × (2.7–)2.9(–3.3) mm, position of lower palatal fold represented only by a low crease or ridge, columella bilobed ..... ***P.* (*E.*) *unumiugum* sp. nov.**

20b Both upper and lower palatal folds strong, columella entire or divided **21**

21a Columella smooth, no folds or teeth, only a slight fold showing in the top left corner of aperture, 4.5–9 × 3 mm ..... ***P.* (*E.*) *denticulatum* Morelet**

21b Columella with teeth or folds, sometimes not easily visible from outside **22**

22a Shell ribbed, brownish, *c.* 7.3–11 × 3.5–4 mm, columella fold callous-like, sub-biplicate; outer lip with a small tooth, upper part of outer lip joined to parietal lamella as a callus ..... ***P.* (*E.*) *denticulatum hildebrandti* Jickeli**

22b Shell smoother and with more distinct nodules on the columella **23**

23a Shell 7–8 × 2.75–3 mm, striate; columella with two distinct nodules on fold ..... ***P.* (*E.*) *denticulatum papillifera* Jickeli (= *quinqueplicata* Bourguignat)**

23b Shell with only one plication on the columella ..... ***P.* (*E.*) *denticulatum hamicenica* Bourguignat**

Figure 11 shows shell height (H) versus diameter (D) plots for *Ennea* taxa reported from north-east Africa. Notwithstanding the differences in other shell characters, this shows that many of the species segregate on shell size, and that the shells of *P.* (*E.*) *denticulatum* and varieties, and also *P.* (*E.*) *laeve*, are more elongate than most of the other species.

Biogeographical & ecological considerations. This study highlights the significant gap in knowledge regarding the Ethiopian land-snail fauna. The discovery of 13 new species of *Ptychotrema* increases the number reported from the

[4] *P. epicratis* is only just over 5 mm.

[5] Apical microsculpture unlikely to be visible on worn shells.

[6] Suture very weakly serrated in *laeve* and *hyalinum*.

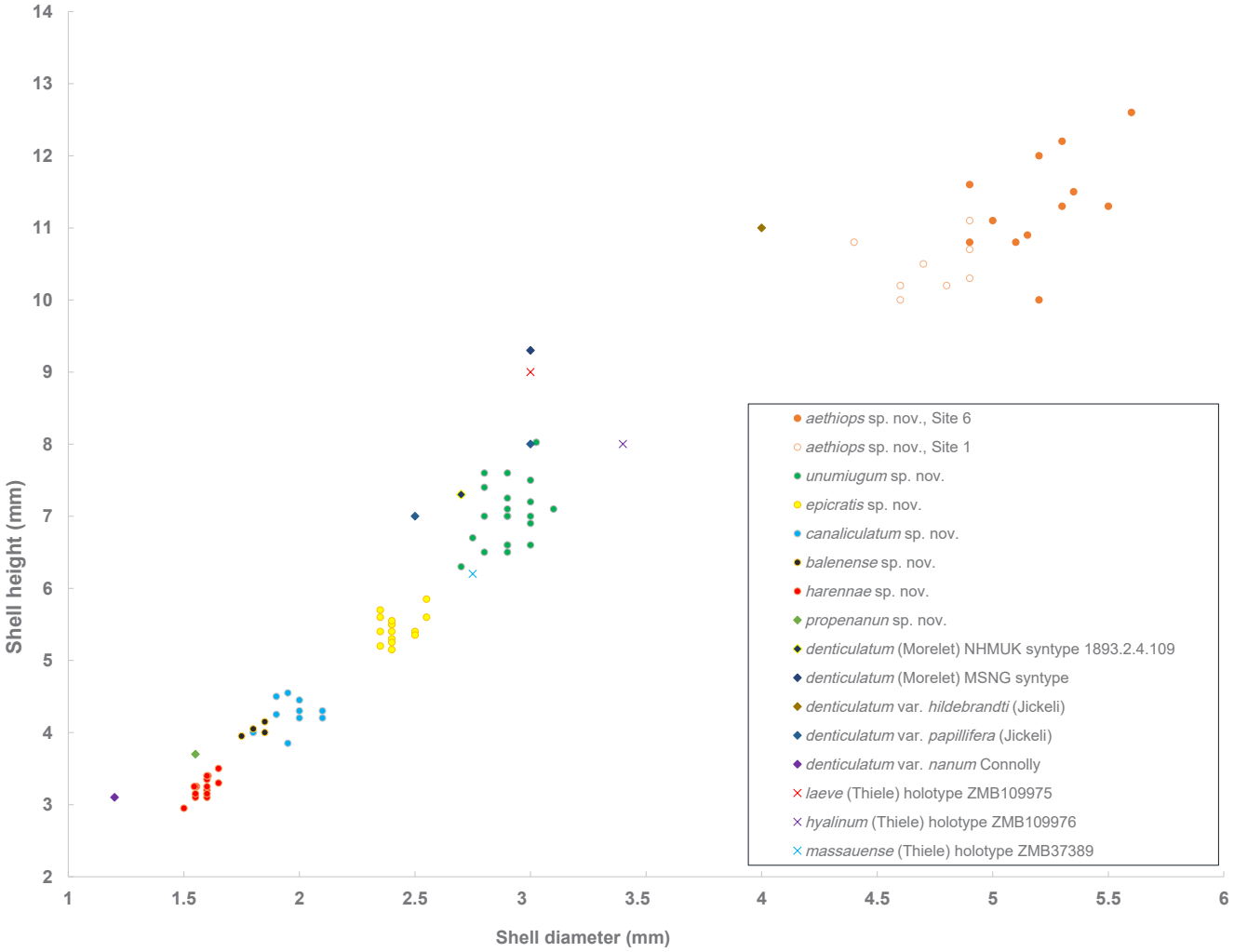


Figure 11. Shell height (H) versus shell diameter (D) for adult shells of *Ptychotrema* (*Ennea*) species from north-east Africa (note: some data points jittered for clarity).

Horn of Africa from seven to 20 (excluding subspecies/varieties of *P. denticulatum*), while the number of Streptaxidae species known from Ethiopia and Eritrea rises by approximately 50%, from about 26 to 39 species. Furthermore, additional undescribed streptaxid species were identified during these two short field expeditions (Tattersfield in prep.), emphasizing that streptaxid diversity in Ethiopia is likely to be far greater than previously understood. This finding calls into question Verdcourt's (1980: 248) conclusion that "The family Streptaxidae decreases in importance quite markedly as one moves northward from East Africa into Ethiopia and the Somali Republic and thence to tropical Arabia." While Verdcourt acknowledged that inadequate sampling could have exaggerated this pattern, he nevertheless considered it to be real.

Despite the taxonomic uncertainties and lack of comprehensive surveys, it is evident that *Parennea* and *Ennea* are strictly tropical African groups, both likely dependent on forest habitats. *Parennea* appears to prefer upland forests (van Bruggen 1989), although species from both subgenera have been documented in lowland and montane forests. In this study, all reported species were found in Afromontane forest habitats at altitudes between 1400 m and 3173 m in the Bale Mountains. Geographically, these subgenera are widespread across sub-Saharan Africa (van Bruggen 1989; Adam *et al.* 1994) but are absent in southern Africa. Recent work by de Winter & de Gier (2019) suggests that *Parennea* is also absent from West Africa, with species previously reported now being assigned to other genera. While *Ennea* does extend into West Africa (as far as Liberia, from where the type species was described, and Sierra Leone; Adam *et al.* 1994), the distributions of both subgenera otherwise follow a similar pattern, ranging from Central Africa through East Africa to Ethiopia, Somalia, and the Tanzanian coast,

and southwards to Angola (with *Parennea* also found in Zambia and Malawi) (van Bruggen 1989; Adam *et al.* 1994).

Of the 13 new species described in this paper, six were recorded from only one site, and 11 were found exclusively at sites separated by 35 km or less. Only *P.* (*E*). *unumiugum* had a wider range, with a maximum site separation of 70 km. None of the species were found on both sides of the Rift Valley, with six recorded to the west, five to the east, and one at Wondo Genet on the eastern Rift Valley wall. More extensive sampling at both local and broader geographical scales will be necessary to fully understand these distribution patterns, but they may suggest that many of these species have quite restricted geographic ranges within Ethiopia. It is perhaps surprising that Thiele's *P. hyalinum*, which was described from the Kafa area, was not found during the current studies. However, *P. hyalinum, P. aethiops*, and *P. unumiugum* have some similarities, and it is possible that further studies may reveal this as intraspecific variation, or perhaps the presence of a swarm of closely related species. Similar comments can also be made about *P.* (*E.*) *denticulatum*, which, although originally described from Eritrea, has been reported from widespread locations in Ethiopia but was not refound during the current study.

A comprehensive understanding of the wider biogeography of these subgenera remains incomplete due to insufficient surveys, but existing research in eastern Africa provides no reason to challenge van Bruggen's (1989) conclusion that the eastern Democratic Republic of the Congo supports the highest diversity of *Parennea* species. A similar analysis of *Ennea* species (Adam *et al.* 1984) points to a similar pattern (Table 15). Additional species have since been reported from Uganda (Wronski & Hausdorf 2009; Verdcourt 2006), indicating the presence of a rich fauna, although few species are found further east in Kenya and Tanzania (Table 15). This conclusion is reinforced by widespread fieldwork in Kenya and Tanzania over the past 25 years (Tattersfield, Seddon, Rowson, Lange, and Ngereza, unpublished), which has only identified one additional species provisionally assigned to *Parennea* from Tanzania. No *Ptychotrema* were recorded during intensive surveys at Laetoli in the Serengeti, Tanzania (Tattersfield *et al.* 2024), or in montane forest on isolated peaks in northern Kenya (Rowson *et al.* 2024) Moreover, despite intensive surveys (Germain 1923; Tattersfield 1996; Tattersfield *et al.* 2001; Lange and Maes 2001), neither *Parennea* nor *Ennea* has been documented in Kakamega Forest in western Kenya, which is often considered the easternmost remnant of the Guineo-Congolian forest, although also with significant Afromontane affinities. The absence of these subgenera from Kakamega Forest reinforces the idea that there is a steep decline in *Ptychotrema* diversity between the forests of west Uganda and the Albertine Rift to those in western Kenya.

Similar gradients in species richness have been reported for land snails (Wronski & Hausdorf 2008) and other biota (Hamilton 1981), with diversity decreasing from eastern Congo and western Uganda eastward. These patterns have been linked to expansion from putative forest refugia that may have persisted in eastern Congo during colder and drier periods in the Pleistocene when forest cover in wider equatorial Africa contracted (Diamond & Hamilton 1980; Hamilton 1981). The current consensus is that the southern Ethiopian highlands lost much of their forest cover around the Last Glacial Maximum (LGM, 25–18 Ka) (Fischer *et al.* 2021), with subsequent reforestation during the African Humid Period and later periods (but see Casas-Gallego *et al.* (2023) and below). No direct forest connections are thought to have existed between Ethiopia and these areas to the south and west since the LGM (Kingdon 1990), so the recognition that the Ethiopian highlands harbour a richer *Ptychotrema* fauna than previously believed (and one that is much richer than in Kenya or Tanzania) is biogeographically interesting. It may suggest that *Ptychotrema* species could have persisted in the Ethiopian highlands throughout the LGM (and earlier Pleistocene cold-dry periods), or alternatively, that recolonization from more continuously forested areas to the south and west may have contributed more significantly to shaping Ethiopia's contemporary land-snail fauna.

Table 15. Number of *Parennea* and *Ennea* species recorded from eastern African countries (data from Verdcourt 2006; Wronski & Hausdorf 2009).

Country	*Parennea*	*Ennea*
Ethiopia	6 (including 5 in this aper)	12* (including 8 in this paper)
Somalia	1	0
Kenya	3	1
Uganda	8†	6†
Tanzania	2	1
DRC	26	11‡

*Excluding varieties of *P.* (*E.*) *denticulatum.*

†Wronski & Hausdorf (2009) added seven species (three *Parennea* and four *Ennea*) to Verdcourt's (2006) Ugandan list, which perhaps suggests that Ugandan fauna is still significantly under-recorded.

‡Species listed from Zaire by Adam *et al.* (1994).

However, recent ecological niche modelling (Casas-Gallego *et al.* 2023) has challenged the consensus view and suggested that Afromontane forests in Ethiopia during the Late Glacial may have covered a significantly larger area than they do today, thus perhaps supporting the persistence hypothesis. In contrast, colonisation from the south is fraught with major obstacles for forest-dependent species, in particular in the form of the northern Kenyan deserts and low-lying floodplains around the White Nile further to the west (Kingdon 1990). The absence of *Ptychotrema* from the isolated sky islands of northern Kenya (Mounts Kulal, Marsabit, etc.; Rowson *et al.* 2024), and the very few *Ptychotrema* in Kenya more generally, provides little evidence to support the idea of significant immigration from the south.

There are fragmented highland areas in northern Uganda and South Sudan where forest may have persisted and could have provided potential, albeit tenuous, colonisation routes into western Ethiopia. Unfortunately, their malacofaunas are poorly known, although Connolly (1927) reported *Maizania elatior* (E. von Martens, 1892) from South Sudan's Didinga Mountains. *Maizania elatior* is a moderately large forest-associated operculate land snail which is mostly restricted to western areas of East Africa, also occurring in in south-western Ethiopia, across Uganda, in the Congo, and south to Angola (Verdcourt 1964; Connolly 1927). Although hardly confirmatory, this perhaps lends some support to the idea that forest patches on elevated ground in South Sudan could have acted as stepping stones between central African/Albertine Rift forests and those of south-western Ethiopia. Interestingly, *M. elatior* is absent from the northern Kenyan sky islands, which support another large *Maizania*, *M. hildebrandti* subsp. *kibonotoensis* (d'Ailly, 1910) (Rowson *et al.* 2024). These scenarios assume, of course, that the *Ptychotrema* taxa in Ethiopia are not the product of a local radiation, independent from the species concentrated in central Africa. Such a hypothesis would need to be tested using molecular data.

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